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Comparative carbon dioxide efflux rates from respiration of coarse woody debris among three mangrove species in Thailand

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ABSTRACT

Coarse woody debris (CWD) is an important component in forest ecosystems. A knowledge of CWD respiration, in addition to its storage, is necessary to clarify the carbon dynamics in a forest ecosystem. However, data on CWD respiration in mangrove forests is still scarce. We measured the carbon dioxide (CO₂) efflux rates from the CWD respiration of three mangrove species (Avicennia alba, Rhizophora spp. and Xylocarpus granatum) using gas chromatography (GC) and soda-lime (SL) methods. The results revealed that the CO₂ efflux rates obtained by the SL method were not significantly different to those obtained by the GC method for all three species. Therefore, the CO₂ efflux rate from CWD respiration of the three mangrove species was measured by the SL method without calibration. The CO₂ efflux rate of A. alba CWD was significantly higher than the other two species, whereas the CO₂ efflux rates of Rhizophora spp. and X. granatum were not different. The differences in the CO₂ efflux among the species was likely to be due to their different wood densities and water contents, and the interaction of these terms. Although, the CO₂ efflux rate from CWD respiration showed a relatively low value in comparison to that from soil respiration, the CO₂ efflux rates from CWD respiration should still be measured for clarifying the carbon dynamics in a mangrove ecosystem, especially those with a high CWD mass.

Key words: carbon dynamics, method comparison, CWD respiration, dead wood, mangrove

INTRODUCTION

Coarse woody debris (CWD) is the large dead wood material, and includes fallen branches, fallen trees, stumps and standing dead trees (Jia-bing et al. 2005, Enrong et al. 2006). It plays an important role in the long-term carbon storage in forest ecosystems because of its large size and slow-decomposition rate (Harmon et al. 1986, Brais et al. 2005, Olajuyigbe et al. 2012). Mangrove forests, generally located on coastal and river edges, have been reported to have a high CWD storage that range from 23.2–56.5 Mg ha⁻¹, and this is partially because they are affected by severe storms, which will potentially increase in occurrence with climate changes (Krauss et al. 2005, Kauffman and Cole 2010).

In order to clarify the carbon dynamics, the carbon budget of CWD should be balanced between the supply and decomposition rates. A low rate of fallen wood decomposition in tropical mangrove forests has been reported by Robertson and Daniel (1989). The partitioning of the carbon dioxide (CO₂) efflux of below-canopy components in a subtropical mangrove forest at Florida (Troxler et al. 2015) gave an estimated CWD respiration of 33 % of the soil respiration level, and revealed a relatively high contribution of CO₂ efflux from CWD respiration. However, the CO₂ efflux from CWD respiration has not been reported for a tropical mangrove forest in Southeast Asia, yet they cover the largest area and account for some 33.5 % of the total mangrove forest area in the world (Tuck et al. 2012).

Measurement of the CO₂ efflux rate from respiration is usually evaluated using gas chromatography (GC), soda-lime (SL) and dynamic infrared gas analysis (IRGA) methods. For the GC method, the gas sample is directly collected from a respiration chamber and injected into a GC instrument to measure the CO₂ concentration (Makken et al. 1999, Progar et al. 2000, Mackensen
and Bauhus 2003, Barker 2008). However, in a direct comparison, the CO₂ efflux from soil respiration measured by the GC method gave a closer value to the actual CO₂ efflux, as measured by an open dynamic system with IRGA, than that obtained by the SL method (Knoepp and Vose 2002).

Although the IRGA method provides a high accuracy and is less time-consuming to measure the CO₂ concentration (Pongarcic et al. 1997), it may be not suitable for measurement of the CO₂ efflux from CWD samples of a large size. Moreover, the instruments required for the IRGA and GC methods are costly. However, the GC method is more suitable than the IRGA one because the chamber is easily modified. In contrast to the GC and IRGA methods, the SL method is cheaper and is practical for use in field conditions. As a result, the comparative rate of CO₂ effluxes has been reported between the SL and GC methods (Raich et al. 1990) and between the SL and IRGA methods (Janssens and Ceulemans 1998, Herrmann and Bauhus 2008), and established that when the CO₂ efflux rate is measured by the SL method, a calibration to the GC or IRGA method is required to correct the overestimation of the SL method.

In this study, we measured the rate of CO₂ efflux from the CWD respiration of three major mangrove tree species in Thailand (Avicennia alba Blume, Rhizophora spp. (mainly R. apiculata Blume and R. mucronata Poir.) and Xylocarpus granatum Koenig). Avicennia alba is a common species that is distributed on new mudflats, while X. granatum is distributed in the ecotone between the mangrove and terrestrial forests (Smith 1992, Hogarth 2007). Rhizophora trees are commonly found in most areas of natural mangrove forest and are always used for mangrove re plantation in Thailand (Department of Marine and Coastal Resources 2009). The aims of the study were (1) to compare the CO₂ efflux rate from CWD respiration between the SL and GC methods of these mangrove trees and (2) to compare the CO₂ efflux rates from CWD respiration with the soil respiration rates. We also discussed the rates of CO₂ efflux related to the causative factors of wood density and water content.

**MATERIALS AND METHODS**

**CWD sampling**

The CWD samples (including downed wood and standing dead trees) were collected from a permanent plot in secondary mangrove forest along the Trat River in Trat Province, eastern Thailand (12°12’N, 102°33’E). The annual precipitation and average air temperature in 2015 was 3,918 mm and 26.8 ± 1.8°C, respectively (Department of Meteorology, Thailand). This forest showed three clear vegetation zones from the river to inland part based on the dominant tree species of the Avicennia, Rhizophora and Xylocarpus zones, respectively. Umnouysin et al. (2017) reported that the tree density (tree diameter at breast height ≥ 4.5 cm) of the Avicennia, Rhizophora and Xylocarpus zones was 882, 1718 and 3505 stems ha⁻¹, respectively. The average diameter at breast height was 13.6, 13.3 and 9.5 cm for the Avicennia, Rhizophora and Xylocarpus zones, respectively, with an aboveground biomass of living- tree in the Avicennia, Rhizophora and Xylocarpus zones were 78.4, 128.9 and 111.1 t C ha⁻¹, respectively. The Avicennia zone, which was located on the river edge, was submerged by the daily tide for longer than the Rhizophora and Xylocarpus zones, respectively (Pourngparn et al. 2009). The zonal distribution of aboveground CWD in this forest has been previously reported to be 0.78, 2.35 and 2.95 t C ha⁻¹ for the Avicennia, Rhizophora and Xylocarpus zones, respectively, (Umnouysin et al. 2017).

Accordingly, we randomly collected the CWD samples, including various sizes and CWD wood characters (wood intact, slightly decayed wood and mostly decayed wood) from the three dominant species (24 samples/species) of A. alba, Rhizophora spp. and X. granatum. The average diameter of CWD in the study plot was 9.4 ± 0.9 cm for the three species, and we collected CWD samples of A. alba, Rhizophora spp. and X. granatum within the size range of 4.5–16.7, 4.5–17.5 and 4.5–17.6 cm in diameter, respectively. The CWD samples were cut into approximately 20-cm length pieces, so as to be able to fit into the chamber (Width 20.5 cm × Length 27.0 cm × Height 19.5 cm) made from polycarbonate. The cut CWD samples were carefully washed in tap water to remove the soil. The diameter at both ends and length of the sample were measured to calculate the volume assuming a cylindrical shape. The CWD samples were individually kept in a plastic bag to prevent the loss of their moisture, and were brought to the laboratory. The fresh weight of the sample was obtained before each measurement of the CWD respiration, and after the final CWD respiration measurement the sample was oven-dried at 80°C until at a constant weight to calculate the wood density and water content. The wood density of each sample was calculated from the ratio of its dry weight to fresh volume. The water content of CWD was evaluated as the ratio of the difference between the fresh and dry weight to the dry weight.
**Measurement of the CO\textsubscript{2} efflux from the CWD respiration**

Because the diameter of CWD samples was distributed over a wide range (4.5–17.6 cm), the samples were divided into two size categories of a small (<10 cm) and a large (>10 cm) diameter. The decay class of the respective species was separated into the three wood density categories of: fresh, moderate (40–70 % of fresh wood density) and advanced (<40 % of fresh wood density). Then, we measured the CO\textsubscript{2} efflux rate from the CWD respiration by the GC and SL methods, as outlined in turn below.

**GC method**

In the laboratory, an individual CWD sample was placed into a closed chamber made of polycarbonate and sealed with silicone at the top cover, which was drilled (1 cm in diameter) for gas sampling and input with a rubber stopper for a vial to protect against air leaks. The CWD sample was incubated in the closed chamber in a temperature controlled room (25 ± 3°C) for 24 h. Three replications per CWD sample were performed. Before each replicate determination of the CO\textsubscript{2} emission from the CWD sample, the moisture level of the CWD sample was first maintained by spraying with 50 mL of distilled water, and then reweighed. After 24 h of incubation, the internal gas was mixed using a 10-mL syringe with a needle (the gas was withdrawn and put back to the chamber for five cycles) prior to removal of 1 mL of mixed gas in the syringe for analysis. The gas sample was injected into a GC equipped with a thermal conductivity detector (GC-RIA, Shimadzu, Kyoto, Japan) for determination of the CO\textsubscript{2} concentration (Makky et al. 2014). Three blank chambers (no CWD sample) were set up at the same time. To obtain the optimum weight of SL granules (a mixture of NaOH and Ca(OH)\textsubscript{2} performed by varying the weight of used SL granules (15, 20 and 25 g) in the measurement of the CO\textsubscript{2} efflux from the CWD of A. alba. The SL granules on a 5-cm diameter petri dish were weighed, oven-dried at 105°C for 24 h and then reweighed. The petri dish was sealed with paraffin and kept in a desiccator. For the CO\textsubscript{2} measurement, the dried SL was spray-wetted with 5 mL of distilled water, so as to activate the reaction between SL and CO\textsubscript{2}, and placed in the same chamber as that used in the GC method with the CWD sample and incubated for 24 h in a temperature controlled room (25 ± 3°C). The petri-dish with the SL granules was then removed, oven-dried (105°C) for 24 h and weighed. Three replications were performed for each sample. Before measurement of each replicate, the CWD sample was remoistened and weighed as described in the GC method above. Three blank chambers were set up at the same time.

The CO\textsubscript{2} efflux rate, as a measurement of CWD respiration, was calculated on the basis of CWD sample dry weight (g CO\textsubscript{2} kg\textsuperscript{-1} d\textsuperscript{-1}) from the difference of the weight gain of the SL granules between CWD sample and average of the blank, and a correction factor of 1.69 (Grogan 1998), as shown in equation (Ohtsuka et al. 2014);

\[
\text{CO}_2\text{ efflux (g CO}_2\text{ kg}^{-1}\text{ d}^{-1}) = \frac{\text{sample weight gain} - \text{mean blank weight} \times (1 - \text{V}_{\text{CWD}}/\text{V}_{\text{chamber}}) \times 1.69 \times 24}{\text{CWD weight (kg)} \times \text{duration of exposure (h)}}
\]

where the sample weight gain is the difference between the dry weight of SL granules before and after measurement of the CO\textsubscript{2} efflux from the CWD sample (g), the mean blank weight is the difference between the dry weight of SL granules before and after measurement of the CO\textsubscript{2} efflux from the blank chamber (g), \(V_{\text{CWD}}\) is the CWD volume (m\textsuperscript{3}) and \(V_{\text{chamber}}\) is the volume of the chamber (m\textsuperscript{3}). The duration of exposure of the present study was 24 h.

We found that the CO\textsubscript{2} efflux measured using 20 g of SL granules was higher than that using 15 g of SL granules, but was not significantly different from that with 25 g of SL granules (data not shown). So, the optimum weight of SL granules was selected as 20 g and was used for the subsequent measurements of the CO\textsubscript{2} efflux rate from the CWD samples.

**SL method**

The CO\textsubscript{2} efflux rate from CWD respiration of the same samples as those measured using the GC method was measured by the SL method as previously reported (Barker 2008), using SL granules (a mixture of NaOH and Ca(OH)\textsubscript{2}) with a granule size of 2–5 mm (Indicator Grade, Merck KGaA, Germany). To obtain the optimum weight of SL granules for use in each assay, a preliminary test was performed by varying the weight of used SL granules (15, 20 and 25 g) in the measurement of the CO\textsubscript{2} efflux from the CWD of A. alba. The SL granules on a 5-cm diameter petri dish were weighed, oven-dried at 105°C for 24 h and then reweighed. The petri dish was sealed with paraffin and kept in a desiccator. For the CO\textsubscript{2} measurement, the dried SL was spray-wetted with 5 mL of distilled water, so as to activate the reaction between SL and CO\textsubscript{2}, and placed in the same chamber as that used in the GC method with the CWD sample and incubated for 24 h in a temperature controlled room (25 ± 3°C). The petri-dish with the SL granules was then removed, oven-dried (105°C) for 24 h and weighed. Three replications were performed for each sample. Before measurement of each replicate, the CWD sample was remoistened and weighed as described in the GC method above. Three blank chambers were set up at the same time.

The CO\textsubscript{2} efflux rate, as a measurement of CWD respiration, was calculated on the basis of CWD sample dry weight (g CO\textsubscript{2} kg\textsuperscript{-1} d\textsuperscript{-1}) from the difference of the weight gain of the SL granules between CWD sample and average of the blank, and a correction factor of 1.69 (Grogan 1998), as shown in equation (Ohtsuka et al. 2014);

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\]

where the sample weight gain is the difference between the dry weight of SL granules before and after measurement of the CO\textsubscript{2} efflux from the CWD sample (g), the mean blank weight is the difference between the dry weight of SL granules before and after measurement of the CO\textsubscript{2} efflux from the blank chamber (g), \(V_{\text{CWD}}\) is the CWD volume (m\textsuperscript{3}) and \(V_{\text{chamber}}\) is the volume of the chamber (m\textsuperscript{3}). The duration of exposure of the present study was 24 h.

We found that the CO\textsubscript{2} efflux measured using 20 g of SL granules was higher than that using 15 g of SL granules, but was not significantly different from that with 25 g of SL granules (data not shown). So, the optimum weight of SL granules was selected as 20 g and was used for the subsequent measurements of the CO\textsubscript{2} efflux rate from the CWD samples.

**Data analysis**

The CO\textsubscript{2} efflux rates are presented as the mean ± one standard deviation (SD). Statistically significant differences among species were analyzed by one-way analysis of variance (ANOVA), followed by Duncan’s multiple range tests (DMRT). Linear mixed effected model (lme4) analysis were fixed to clarify the effect of wood density, diameter
and water content on the CO₂ efflux among species. Akaike's information criterion (AIC) was used to identify the model of best fit. All models were ranked by their AIC values. The best model was selected from the model with the lowest AIC value, and used to explain factors controlling the CO₂ efflux of CWD. To compare the CO₂ efflux rates measured by GC and SL methods, a regression analysis between the CO₂ efflux rate measured by the GC and SL methods was performed. All statistical analyses were performed using the R version 3.3.2 (R development Core Team 2016) and library lme4 version 1.1–12 software.

RESULTS AND DISCUSSION

Comparison of the GC and SL measurement methods

The average rates of CO₂ efflux ranged from 0.114–3.067 and 0.154–3.145 g CO₂ kg⁻¹ d⁻¹ for the GC and SL methods, respectively (Table 1). The average rate of CO₂ efflux from CWD respiration measured by the SL method was slightly higher than that by the GC method for all samples except for the moderate density small diameter CWD of A. alba. The ratio of the CO₂ efflux rate between the GC to SL methods was 0.95, 0.89 and 0.84 for the CWD respiration of A. alba, Rhizophora spp. and X. granatum, respectively. They were not significantly different among species (one-way ANOVA, \( P = 0.175 \)). According to Fig. 1, it showed a lower ratio (<1.0) at low rates of CO₂ flux, and a ratio close to 1.0 at higher CO₂ efflux rates in all species. Thus, the accuracy of the CO₂ efflux measurement by the SL method depended on the CO₂ flux in the chamber, which resulted in the CO₂ diffusion. In accord, Nay et al. (1994) demonstrated that the CO₂ efflux rate from soil respiration was overestimated by the SL method at low flux rates (at 2.9 and 5.8 g CO₂ m⁻² d⁻¹) and attributed this to the high CO₂ gradient between the substrate and headspace in the chamber that increased the CO₂ diffusion and induced the localized high CO₂ concentration to absorb onto the SL granules. In contrast, at high flux rates of soil respiration (18.5 g CO₂ m⁻² d⁻¹), the SL method underestimated the CO₂ efflux because the low CO₂ gradient between the substrate and headspace in the chamber decreased CO₂ diffusion which resulted in a

Table 1. CO₂ efflux rate from mangrove CWD, as estimated by the GC and SL methods, for each diameter and decay class of CWD from A. alba, Rhizophora spp. and X. granatum.

| Species          | Diameter class | Decay class | Wood density (g cm⁻³) | Water content (%) | CO₂ efflux by GC (g CO₂ kg⁻¹ d⁻¹) | CO₂ efflux by SL (g CO₂ kg⁻¹ d⁻¹) |
|------------------|----------------|-------------|-----------------------|-------------------|----------------------------------|----------------------------------|
| A. alba          | Small          | Fresh       | 0.518 ± 0.008         | 119.9 ± 15.2      | 0.214 ± 0.040                     | 0.235 ± 0.023                     |
|                  |                | Moderate    | 0.394 ± 0.050         | 135.2 ± 41.7      | 1.117 ± 0.124                     | 1.112 ± 0.104                     |
|                  |                | Advanced    | 0.231 ± 0.056         | 214.9 ± 88.3      | 3.067 ± 0.047                     | 3.145 ± 0.082                     |
|                  | Large          | Fresh       | 0.506 ± 0.003         | 91.75 ± 7.48      | 0.195 ± 0.006                     | 0.254 ± 0.020                     |
|                  |                | Moderate    | 0.423 ± 0.016         | 129.3 ± 27.0      | 1.088 ± 0.065                     | 1.113 ± 0.059                     |
|                  |                | Advanced    | 0.314 ± 0.003         | 165.6 ± 33.0      | 3.017 ± 0.127                     | 3.126 ± 0.149                     |
| Rhizophora spp.  | Small          | Fresh       | 0.681 ± 0.015         | 80.22 ± 0.80      | 0.116 ± 0.001                     | 0.154 ± 0.002                     |
|                  |                | Moderate    | 0.532 ± 0.041         | 76.86 ± 13.6      | 0.208 ± 0.007                     | 0.224 ± 0.005                     |
|                  |                | Advanced    | 0.369 ± 0.018         | 126.0 ± 23.3      | 0.468 ± 0.019                     | 0.469 ± 0.012                     |
|                  | Large          | Fresh       | 0.727 ± 0.015         | 63.22 ± 4.17      | 0.114 ± 0.007                     | 0.155 ± 0.002                     |
|                  |                | Moderate    | 0.596 ± 0.016         | 57.18 ± 4.28      | 0.208 ± 0.024                     | 0.232 ± 0.012                     |
|                  |                | Advanced    | 0.426 ± 0.055         | 92.91 ± 13.5      | 0.478 ± 0.003                     | 0.469 ± 0.009                     |
| X. granatum      | Small          | Fresh       | 0.512 ± 0.007         | 73.57 ± 5.09      | 0.123 ± 0.002                     | 0.165 ± 0.002                     |
|                  |                | Moderate    | 0.426 ± 0.018         | 85.05 ± 21.9      | 0.212 ± 0.036                     | 0.244 ± 0.011                     |
|                  |                | Advanced    | 0.265 ± 0.076         | 141.4 ± 71.1      | 0.292 ± 0.013                     | 0.329 ± 0.009                     |
|                  | Large          | Fresh       | 0.565 ± 0.018         | 76.09 ± 4.50      | 0.127 ± 0.004                     | 0.166 ± 0.003                     |
|                  |                | Moderate    | 0.417 ± 0.019         | 103.0 ± 12.1      | 0.213 ± 0.009                     | 0.243 ± 0.010                     |
|                  |                | Advanced    | 0.343 ± 0.011         | 80.66 ± 27.4      | 0.265 ± 0.037                     | 0.320 ± 0.017                     |

Data are shown as the mean ± 1SD, derived from four samples.

* Diameter class: CWD were divided into the two categories of small (<10 cm) and large (>10 cm) diameters.

* Decay class: CWD were categorized with respect to their density as: Fresh, Moderate (40–70 % of fresh wood density) and Advanced (<40 % of fresh wood density).
decreasing CO₂ absorption by the SL granules. Moreover, the CO₂ efflux by the SL method may be underestimated at a high CO₂ flux because of the decreasing CO₂ absorption as the amount of remaining unreacted SL granules decreased. Kirita and Hozumi (1966) reported that the absorption rate of CO₂ by a KOH solution decreased with a decrease in the remained amount of unreacted KOH. Nevertheless, the absorption manner between liquid (KOH solution) and SL granular (our study) may be slightly different.

When regression analysis was performed to verify the accuracy of the CO₂ efflux measurement by the SL method in comparison to the GC method (Fig. 1), it was found that the slope was not significantly different from the 1:1 line ($P = 0.185$) with a high correlation coefficient ($r = 0.999$). This indicated that the CO₂ efflux rates obtained by the SL and GC methods were not significantly different, and so the CO₂ efflux rate from CWD respiration of these three mangrove species could be estimated by the SL method without a calibration.

**Comparison the CO₂ efflux rate among species**

Regardless of the method of measurement, the average CO₂ efflux rates of *A. alba* CWD ranged widely from 0.225 to 3.106 g CO₂ kg⁻¹ d⁻¹, while those of *Rhizophora* spp. and *X. granatum* CWD were lower and distributed in a more narrow range (0.135–0.473 and 0.144–0.311 g CO₂ kg⁻¹ d⁻¹, respectively; Table 1). For each respective species, the CO₂ efflux rate differed among the different decay classes. The advanced decay class in each species showed the highest CO₂ efflux rate at 3.089, 0.471 and 0.302 g CO₂ kg⁻¹ d⁻¹ for *A. alba*, *Rhizophora* spp. and *X. granatum* CWD, respectively (Table 1). The CO₂ efflux from the CWD respiration of *A. alba* was significantly higher than *Rhizophora* spp. and *X. granatum* CWD (one-way ANOVA, $P<0.0001$), but the CO₂ efflux rates from the respiration of *Rhizophora* spp. and *X. granatum* CWD were not significantly different (Table 2). The average CO₂ efflux rate of the two methods for each species was plotted along the change in CWD wood density (Fig. 2). It showed that the average CO₂ efflux rate of the three species (0.225, 0.177 and 0.146 g CO₂ kg⁻¹ d⁻¹, respectively for *A. alba*, *Rhizophora* spp. and *X. granatum* CWD) were the same at wood densities over 0.500 g cm⁻³ (one-way ANOVA, $P = 0.191$). But the average CO₂ efflux rate of the three species were significantly different at wood densities of <

![Fig. 1. Regression of the CO₂ efflux rate determined by the GC and SL methods for *A. alba* ( ), *Rhizophora* spp. ( ) and *X. granatum* ( ). The solid and broken lines represent the 1 : 1 and the regression lines, respectively.](image_url)

**Table 2. Average diameter, wood density, water content and the average (from both GC and SL estimates) CO₂ efflux rate from mangrove CWD of each species.**

| Species         | Average diameter (cm) | CWD wood density (g cm⁻³) | Water content (%) | CO₂ efflux rate (g CO₂ kg⁻¹ d⁻¹) | Fresh wood of living tree |
|-----------------|-----------------------|---------------------------|-------------------|----------------------------------|---------------------------|
|                 |                       |                           |                   |                                  |                           |
| *A. alba*       | 9.55 ± 3.51ᵃ         | 0.395 ± 0.096ᵇ           | 140.1 ± 50.4ᵇ     | 1.382 ± 1.063ᵇ                   | 0.534 ± 0.021ᵇ           | 237.7 ± 32.4ᵇ             |
| *Rhizophora* spp.| 9.22 ± 3.48ᵃ         | 0.553 ± 0.120ᵇ           | 78.81 ± 24.1ᵇ     | 0.261 ± 0.129ᵇ                   | 0.742 ± 0.040ᵇ           | 144.8 ± 6.87ᵇ             |
| *X. granatum*   | 8.97 ± 3.59ᵃ         | 0.419 ± 0.093ᵇ           | 93.48 ± 33.1ᵇ     | 0.226 ± 0.061ᵇ                   | 0.548 ± 0.006ᵇ           | 158.8 ± 31.6ᵇ             |
| *P*-value       | 0.848                 | <0.0001                   | <0.0001           | <0.0001                          | <0.0001                   |

Data are shown as the mean ± 1SD, derived from 24 samples. Average wood density and water content of fresh wood (mean ± 1SD) from living tree reported by Umnouysin et al. (2017). Different letters within a column indicate a significant difference among species at $P<0.05$, ns refers to non-significant values, as determined by one-way ANOVA, followed by DMRT.
0.500 g cm\(^{-3}\) (one-way ANOVA, \(P = 0.024\)). The average CO\(_2\) efflux rate of \(A.\ alba\) (2.098 g CO\(_2\) kg\(^{-1}\) d\(^{-1}\)) was dramatically higher than the other two species at wood densities of < 0.500 g cm\(^{-3}\) (Fig. 2; Table 1). Being lower than \(A.\ alba\), the average CO\(_2\) efflux rates of \(Rhizophora\) spp. (0.471 g CO\(_2\) kg\(^{-1}\) d\(^{-1}\)) and \(X.\ granatum\) (0.265 g CO\(_2\) kg\(^{-1}\) d\(^{-1}\)) were almost same as each other at each wood density. This indicated that the different CO\(_2\) efflux rate among species occurred at the low range of wood density, which was supported by the statistical analysis showing that the wood density of CWD was the main factor affecting the CO\(_2\) efflux rates among these three species (Table 3). However, we found significant interactions (\(P < 0.05\)) between the wood density and water content and between the wood diameter and water content (Table 3). That the AIC value of the former interaction was lower than those of the latter two interactions suggested that differences in the CO\(_2\) efflux rates among species largely depended on the interaction of these two parameters of CWD.

However, the AIC of water content was lower than that of wood density (Table 3). It indicated that the effect of increasing initial rate of CWD water content on the CO\(_2\) efflux was larger than that of wood density reduction. Although the water content in the fresh CWD was lower than that in the living trees (Fig. 3) because newly dead trees likely lose moisture from the cells after death (Markstrom et al. 1977), the water content of CWD tended to increase with a decreasing wood density. The decomposition process of CWD by microorganisms is considered to reduce the wood density, and consequently increases the water content. Furthermore, the CWD in mangrove forest was usually inundated by the daily tide resulting in an increased their water contents.

\(Rhizophora\) spp. had a high wood density when alive, and a low water content until the wood density declined to an approximate value of 0.500 g cm\(^{-3}\) (Fig. 3). Then, the water content of \(Rhizophora\) spp. CWD increased with a decreasing wood density. As for \(X.\ granatum\) CWD, it had a relatively low density as a fresh wood and its water content increased with decreasing wood density. It was noticeable that both the living tree and CWD of \(A.\ alba\) had the lowest wood density with the highest water content among the three species (Fig. 3). The low wood density of \(A.\ alba\) was consistent with the low wood density of pioneer species with a fast-growing rate in the mangrove forests reported by Komiyama et al. (2005). The high water content of \(A.\ alba\) CWD was due to the low wood density and long inundation period in the \(Avicennia\) forest that was located on the river edge. This may promote wood softening of \(A.\ alba\), and thus \(A.\ alba\) was the most perishable among the

![Fig. 2. Relationship between wood density and average rate of CO\(_2\) efflux of CWD](image)

Table 3. Effect of wood density, diameter and water content of CWD on the CO\(_2\) efflux among the three species (\(n = 144\)), as analyzed using a linear mixed effects model.

| Parameter                        | \(P\)-value | AIC   |
|----------------------------------|-------------|-------|
| Wood density                     | <0.0001     | 163.86|
| Diameter                         | 0.964       | 182.80|
| Water content                    | <0.0001     | 134.53|
| Wood density x diameter          | 0.217       | 169.86|
| Wood density x water content     | 0.040       | 130.93|
| Diameter x water content         | 0.043       | 132.12|
| Wood density x diameter x water content | 0.095     | 126.23|

AIC: Akaike’s information criterion
three species.

The average CO₂ efflux rate from the CWD respiration were 1.382, 0.261 and 0.226 g CO₂ kg⁻¹ d⁻¹ for *A. alba*, *Rhizophora* and *X. granatum* CWD, respectively, (Table 2). When we multiplied these rates by the CWD mass stock of this forest, as reported by Umnouysin et al. (2017), of 0.78, 2.35 and 2.95 t C ha⁻¹ for the *Avicennia*, *Rhizophora* and *Xylocarpus* zones, respectively, the annual CWD respiration was calculated as 0.2 t C ha⁻¹ y⁻¹. Currently, only one study (Troxler et al. 2015) has reported an annual CWD respiration for a mangrove forest, being 1.6 t C ha⁻¹ y⁻¹ for mangrove trees of *R. mangle*, *A. germinans* and *Laguncularia racemosa* with an average diameter of 10 cm in a subtropical mangrove forest in Florida. The reason for the marked (eight-fold lower) difference in the CWD respiration between our study and that of Troxler et al. (2015) is unclear because no information on the CWD quality and quantity was mentioned in their study.

**Comparison of mangrove forest CWD and soil respiration**

In a mangrove forest, the soil and CWD respiration are components of heterotrophic respiration. The soil in mangrove forests is usually submerged, where the respiration of belowground roots is mostly released through the lenticels on the surface of aboveground roots (Poungparn et al. 2009). In the same tropical mangrove forest in Thailand as that used in this study, Poungparn et al. (2009) reported an average soil respiration during a low tide to be 2.3 t C ha⁻¹ y⁻¹. For this rate of the soil respiration, the CO₂ efflux from the CWD respiration in this study (0.2 t C ha⁻¹ y⁻¹) accounted for 9% of the soil respiration. Troxler et al. (2015) partitioned the CO₂ efflux among below-canopy components (surface water, soil, leaf litter, CWD, prop roots, soil plus leaf litter and soil plus pneumatophore) in a subtropical mangrove forest at Florida coastal Everglade, where the CO₂ efflux from CWD respiration (1.6 t C ha⁻¹ y⁻¹) was three-fold lower (or 33% of) than that from the soil respiration (4.8 t C ha⁻¹ y⁻¹). Although the CO₂ efflux from the CWD respiration was lower than that from soil respiration in both the subtropical and tropical mangrove forests, the CO₂ efflux of the CWD respiration also depends on the tree mortality to provide a CWD source into the forest. Because the mangrove forests located on a coastal area are sensitive to high storm intensities, the tree mortality will be high. Kauffman and Cole (2010) reported that the tree mortality in a Micronesian mangrove forest, which was affected by typhoon, was indeed high and ranged from 6–32%. Therefore, the CWD respiration will be unlikely to be negligible in mangrove forests that are severely disturbed by storms.

**CONCLUSION**

The CO₂ efflux from CWD respiration measured by the SL method was consistent with that by the GC method.
in the range of the CO$_2$ flux and chamber size in this study, although the difference between the GC and SL methods depends on the magnitude of CO$_2$ flux. The strong relationship between the CO$_2$ efflux estimates obtained by the GC and SL methods confirmed that the CO$_2$ efflux rate from CWD respiration of three mangrove species could be estimated using the SL method, which was cheaper and more practical than the GC method for measurement in mangrove forests. The CO$_2$ efflux rate from the CWD of A. alba was significantly higher than those from Rhizophora spp. and X. granatum, which was because of the interaction between wood density and water content, which occurred from variation in the wood density and inundation regimes among the vegetation zones. Avicennia alba CWD had the highest rate of CO$_2$ efflux, followed by those of Rhizophora spp. and X. granatum, respectively. Although the CO$_2$ efflux rate from CWD respiration was lower than in the soil respiration in both a tropical (this study) and a subtropical (Troxler et al. 2015) mangrove forest, estimation of the CO$_2$ efflux rate from CWD respiration is highly recommended for mangrove forests where a large amount of CWD may occur, for example due to increasing storm intensities. This will provide information for clarifying the carbon dynamics in mangrove ecosystems that are susceptible to climate change.

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