



A case study for an estimation of carbon fixation capacity in the mangrove plantation of *Rhizophora apiculata* trees in Trat, Thailand



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ABSTRACT

In order to accurately evaluate the contribution of mangrove forests in reducing the effects of climate change, a precise understanding of the carbon fixation capacity of mangrove trees is needed. However, a fully reliable method to estimate carbon fixation capacity has yet to be established. In this study, net carbon fixation of a representative mangrove tree in South-East Asia, *Rhizophora apiculata*, was estimated. It was calculated with two different procedures; the gas exchange analysis and the growth curve analysis methods. The gas exchange analysis method is based on calculated carbon values of the difference between photosynthetic absorption and respiratory emission. These two parameters were calculated by using photosynthetic rates of single-leaves in response to light and temperature and respiratory rates of trunk and branch in response to temperature. These monthly values were adjusted with monthly average measurements of light intensity and temperature to improve estimation accuracy. The value of annual net carbon fixation for 3, 4, 5 and 9 year-old forests was estimated to be 2.5–30.5 Mg C ha⁻¹ yr⁻¹. The values with the temperature modification increased by 9.3–21.3%, compared to those of 2.2–25.2 Mg C ha⁻¹ yr⁻¹ without the temperature modification. However, it was found that these estimated values were significantly higher than the results produced by the growth curve analysis method, which produced 1.1–35.2 Mg C ha⁻¹ yr⁻¹. Results of this study show that further work is required to improve the estimation accuracy for both the gas exchange analysis and growth curve analysis methods. There is a particular need to take into account the respiratory carbon emissions from the plant root for the former method and determination of the maximum biomass at the mature tree phase for the latter method.

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1. Introduction

Massive losses in mangrove forest cover have occurred in South East Asia over the last few decades. In Thailand, the cover was estimated as 372×10^3 ha in 1960 but decreased to 142×10^3 ha by 1989. In 1997, the Thai Royal Forest Department (RFD) promoted a mangrove rehabilitation program (Manassrisuks et al., 2001) and the area have recovered to 244×10^3 ha in 2000 (FAO, 2004).

A critically important function of forest is to sequester and accumulate great amounts of the greenhouse gas carbon dioxide (CO₂), which is of primary significance in attempts to address the effects of global climate change. Afforestation and reforestation (AR)-clean development mechanism (CDM) is one of the prime countermeasures and the process of reducing emissions from deforestation in developing countries, incorporating conservation,

sustainable management and enhancement of forest carbon stocks (REDD plus) has been one of the most controversial issues in the climate change debate.

Mangrove trees have a higher carbon fixation capacity than terrestrial forests (Lugo and Snedaker, 1974; Mann, 1982; Chmura et al., 2003; Bouillon et al., 2008; Donato et al., 2011). The mangroves together with salt marshes and sea grasses form is referred to as the earth's 'blue carbon sinks', which capture and store between 235 and 450 trillion tons of carbon every year (Nellemann et al., 2009). Of great interest is the potential value of mangroves' in carbon mitigation programs such as REDD+.

However, when accounting for mangrove biomass, only ten equations in the five reports are approved by the United Nations Framework Convention on Climate Change (UNFCCC) (Putz and Chan, 1986; Day et al., 1987; Clough and Scott, 1989; Chave et al., 2005; Smith and Whelan, 2006). The allometric method is accordance with standard empirical relationships of tree growth such as diameter at breast height (DBH; 1.3 m from the ground), tree height and tree biomass. However, it requires laborious and

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long-term measurements in the field, and which is not sufficient for estimation accuracy. These are the most significant reasons requiring the development of new alternative assessment methods (Sedjo and Marland, 2003).

One method for estimating the net ecosystem production (NEP) is, as reported by Komiyama et al. (2008), through the eddy covariance method. However, this method is unsatisfactory, as it requires the physical deployment of expensive scientific equipment within mangrove forests, and the use of complex computational procedures (Monji et al., 2002). In addition, remote sensing provides options for continuous monitoring of mangrove over time (Diorio et al., 2007), but the present study focuses on the establishment of an accurate classification method that enables discrimination between mangrove/nonmangrove areas (Rahman et al., 2013).

As a response to the need for an alternative methodology, our previous studies have implemented the gas exchange method (Okimoto et al., 2007, 2008), in relation to *Rhizophora stylosa* in Ishigaki, Japan and *Kandelia candel* in Thanh Hoa, Vietnam. The method estimates photosynthetic carbon absorption in the canopy with a photosynthetic trait of light-response and canopy structure including leaf distribution and light penetration through the canopy. Both studies have overcome some of the weaknesses of the 'traditional' gas exchange method and then proposed an improved version as "gas exchange analysis method". According to the results, it emerges that the accuracy in measuring carbon fixation capacity can be enhanced by temperature modification, and by correcting carbon values of photosynthetic absorption and respiratory emission with a diurnal change model of temperature in each month. In addition, the "growth curve analysis method" was also proposed as an alternative procedure. The growth curve approach shows the increment in tree biomass of the planted mangrove trees, and also derives annual biomass increment values throughout the forest lifespan up to 23–28 years of age (Gong and Ong, 1995).

With the gas exchange analysis method, photosynthetic carbon absorption for natural mature trees of the *R. stylosa* was estimated to be $8.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (Okimoto et al., 2007). This value was similar to those values of $5.8\text{--}9.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for mixed mangrove species in Papua New Guinea, calculated by the traditional gas exchange method (Bunt et al., 1979). In addition, the carbon fixation capacity of $13.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for the 10 year-old *K. candel* trees in Vietnam (Okimoto et al., 2008), was similar to those of $10.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for 15 year-old *Rhizophora apiculata* trees in Thailand (Christensen, 1978) and $14.0 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for 10 year-old *R. apiculata* trees in Malaysia (Ong, 1993), both of which were calculated by the allometric method. This proximity shows the validity of our emerging methodologies and indicates the possibility that our methods could supersede the methods traditionally used to account for the carbon fixation capacity of mangrove trees.

In this study, our developing methods to estimate carbon fixation capacity were applied to the well-managed monoculture forest of *R. apiculata* in Trat, Thailand. This is one of the feasibility studies in methodological development, aiming to be valid for various mangrove species growing in South-East Asia. It is expected that data collection in this feasibility study will enhance accuracy estimation while developing the methodology. This study also proposes to estimate tree biomass not in dry weight units but both of surface area and volume by using non-destructive methods. The remaining mangrove trees and the afforested/reforested trees at the field site are strictly protected and cutting is prohibited, even for research. The non-destructive method to estimate biomass by surface area and volume calculation only is therefore highly appropriate under these local conditions.

2. Materials and methods

In this study, each component of the tree is expressed as leaf, branch, trunk and root. All these are collectively termed "organs" in this paper.

2.1. Study site

The study site was located at the mouth of River Weru in Trat province, Thailand ($12^{\circ}11'N$, $102^{\circ}34'E$). The site is about 250 km east of the capital Bangkok, close to the Cambodia border. The region has a tropical climate with annual average values of precipitation of 1942 mm; temperature, $28.4^{\circ}C$; and a relative humidity of 78%. The dry season lasts from October to May and the rainy season from June to September.

Our investigation was carried on single tree specimens of 3, 4, 5 and 9 year-old *R. apiculata* during March 9–13, 2001 and November 20–25, 2003. This mangrove species is very widespread in South-East Asia. The trees are thinned by the RFD during the management. The current tree intervals are 1.0, 1.5, 2.0 and 4.0 m for 3, 4, 5 and 9 year-old plantations and the tree density was 100, 44.4, 25.0 and $6.3 \times 10^2 \text{ trees ha}^{-1}$, respectively. Heights of the representative single trees were 1.0, 1.7, 3.7 and 9.6 m, respectively. With the official authorization of the RFD, the 4 year-old single above-ground tree was cut and measurements taken on its properties of photosynthesis and respiration.

2.2. An estimation of net carbon fixation capacity by using analysis methods of gas exchange and growth curve

The net carbon fixation capacity in 3, 4, 5 and 9 year-old *R. apiculata* forests in Trat was estimated by the both methods of gas exchange and growth curve analysis and the details are described in Okimoto et al. (2008). In the gas exchange analysis method, a response of PCER (Photosynthetic CO_2 Exchange Rate) to light and temperature was measured in leaves of the upper- and lower-layers of the canopy. Light extinction and distribution of the leaves in the canopy were measured to calculate carbon absorption capacity of the canopy. Respiratory carbon emission was estimated by multiplying the RCER (Respiratory CO_2 Exchange Rate) measured in a partial number of organs by the total amount of each organ in above-ground tree. Monthly averages based on whole day absorption and emission of carbon was corrected with the diurnal values of light intensity and air temperature. An annual carbon fixation capacity was estimated by integrating carbon balance between the absorption and emission of carbon in each month.

In the growth curve analysis method, single tree biomass of 3, 4, 5 and 9 year-old *R. apiculata* trees was measured in the units of both surface area and volume by using non-destructive method. A growth curve was calculated by plotting the volumes at different tree ages and the given maximum dry weight of tree, based on the formulation described in Okimoto et al. (2008).

2.3. Light response of PCER

Steel towers (4–10 m in height, depending on the canopy height) were constructed in 5 and 9 year-old forests to measure leaf photosynthesis and investigate the canopy structure. Light responses of PCER in full-expanded leaves of 4, 5 and 9 year-old trees were measured by using a portable photosynthetic measurement system (LI-6400, Li-Cor). The leaves used for the measurement were located in the upper canopy for the 4 year-old tree. For the 5 and 9 year-old trees, leaves used for measurement were located in the vertical three layers of the canopy, i.e. the top, mid-

dle and lower layers. The light intensity of photosynthetically active radiation (PAR) on leaf surfaces was automatically controlled in six steps in a descending order starting from 2000 to $0 \mu\text{mol m}^{-2} \text{s}^{-1}$. During measurement, the leaf temperature was maintained at 25°C , vapor pressure deficit between the leaf and the air (VpdL) was $1.7 \pm 0.3 \text{ kPa}$ and CO_2 concentration of the reference air was $370 \mu\text{mol mol}^{-1}$. At least three separate measurements were taken for each sample and then averaged to obtain a final value.

2.4. Temperature response of PCER

The temperature responses of PCER in the leaves of 4 and 9 year-old trees, located in the upper canopy, were measured using the LI-6400 instrument. Leaf temperature was changed from 20 to 37°C on a random basis. In the measurements, VpdL, input CO_2 and PAR was $1.7 \pm 0.3 \text{ kPa}$, $370 \mu\text{mol mol}^{-1}$ and $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively.

2.5. Canopy structure with stratified clip technique

The canopy structure of 5 and 9 year-old forests was investigated using the stratified clip technique, in which a $1.0 \times 1.73 \text{ m}^2$ quadrat of the canopy was divided into a 0.5 m thickness from the canopy top to the forest floor. Light extinction through the canopy was calculated by the percent relative irradiance between the light incident at the canopy top and the light intensity at each layer inside the canopy. The light intensity was measured using a quantum sensor (LI-190SB, Li-Cor) and the leaf area index (LAI) was estimated, following procedures outlined in an earlier report (Okimoto et al., 2008).

2.6. Measurements of above- and below-ground biomass

The biomass of branch and trunk in 3, 4, 5 and 9 year-old trees was measured in the units of surface area and volume. The branch was divided into four offshoot groups; first, second, third and fourth offshoots by using the same method of the previous study (Okimoto et al., 2008). Roots in the 4 year-old tree were carefully collected by excavation with an engine pump (SEG-25E, Koshin Ltd.). They were divided into four offshoot groups; main root, first lateral root, second lateral root and third lateral root. The main root was separated into four part; upper-, upper-middle, middle-lower and lower-part of the root with gradual increase in depth, while the lateral roots were separated into two parts; brown (B) and white (W), based on the color of the root surface. These biomass samples were used for the RCER measurement. After extracting these, the samples were dried at 115°C for more than a week. The dry weight, water content and wood density (weight per unit volume) were estimated. The biomass in hectares was calculated by multiplying the single tree biomass in dry weight by tree density.

2.7. Temperature response of RCER in each organ

Before the measurement, the samples were kept in a refrigerator at 8.0°C for one night to avoid measuring any excess CO_2 release. The temperature response of RCER in trunk, branch and root was measured in the temperature range of $15\text{--}35^\circ\text{C}$ at 5°C interval. The samples were treated similarly to the previous study (Okimoto et al., 2008) using an aluminum pan (18 cm in diameter and 18 cm in depth) with a propeller fan (MD825BM-12, Tokuden Co., Ltd.) attached inside for mixing the air to maintain a constant temperature. The RCER of the sample in the aluminum pan was measured with a CO_2 analyzer (LI-800, Li-Cor) for at least 5 min to obtain a stable data of linearly increasing CO_2 concentrations.

2.8. Estimation and temperature modification of absorption, emission and net carbon fixation

Photosynthetic carbon absorption in the whole canopy was calculated as an integration of PCER in each layer. The PCER at a given time during the day was corrected for the light intensity and temperature calculated by the equations described in Okimoto et al. (2008).

Temperature modification in the gas exchange analysis method followed the methods described in Okimoto et al. (2008). The average diurnal temperature value of each month in the study site was calculated by using the temperature data of the study site, Trat (2000–2001; Thailand Meteorological Department). The values of PCER and RCER varying in each time of the day and month were calculated by substituting the diurnal temperature variation into the regression formulas obtained from the temperature responses of PCER and RCER. Those corrected carbon balances derive the net carbon fixation with the temperature modification. By comparing both values with and without the temperature variation, the effect of temperature modification in calculating net carbon fixation could be determined. In the event of no temperature modification, the PCER and RCER were measured at an annual average temperature of 27.3°C in the study site.

2.9. Annual biomass accumulation estimated by growth curve analysis

In drawing a growth curve of single tree biomass, it is necessary to have actual tree biomass in different growth stages and the maximum tree biomass in the mature period. The data of the tree biomass, starting with a very low initial value (i.e. the biomass of a propagule), determines the shape of the growth curve. A derivative value of the growth curve was calculated and an annual biomass increment was calculated. It was impossible to cut trees down and measure the actual physical biomass in units of dry weight, because the site is designated a strict mangrove reserve by the Thai government. Tree biomass was instead estimated using a non-destructive method, by measuring the diameters of the top and bottom part of each organ, as reported previously by Okimoto et al. (2008). The volume of the entire tree was calculated by successively accumulating the volumes of each above-ground organ. A growth curve was drawn using the above-ground volumes of the 3, 4, 5 and 9 year-old trees.

Given the absence of literature on mangrove tree biomass estimation by volume, the maximum biomass was assumed based on the biggest tree biomass among the four trees in this study, the 9 year-old $10.3 \times 10^{-2} \text{ m}^3/\text{tree}$. We assumed that the maximum biomass was arbitrarily assumed to be about 1.5, 2.0 and 2.5 times larger than that of 9 year-old tree, i.e. 15 , 20 and $25 \times 10^{-2} \text{ m}^3/\text{tree}$, respectively, which is in the first attempt at drawing a growth curve in volume biomass. It is reported that mangroves reach their climax in 23–28 years (Gong and Ong, 1995), thus the growth curves were drawn assuming that the tree biomass reaches its maximum at 25 years.

3. Results

3.1. Light response of PCER

The light responses of PCER in the leaves of 4, 5 and 9 year-old tree are shown in Fig. 1. The maximum value of PCER (P_{max}) was 10.9, 12.4 and $13.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$, respectively. The light responses of PCER were well fitted to modified rectangular hyperbola (Baily, 1935):

$$P = I/(\alpha + \beta \cdot I) \quad (1)$$

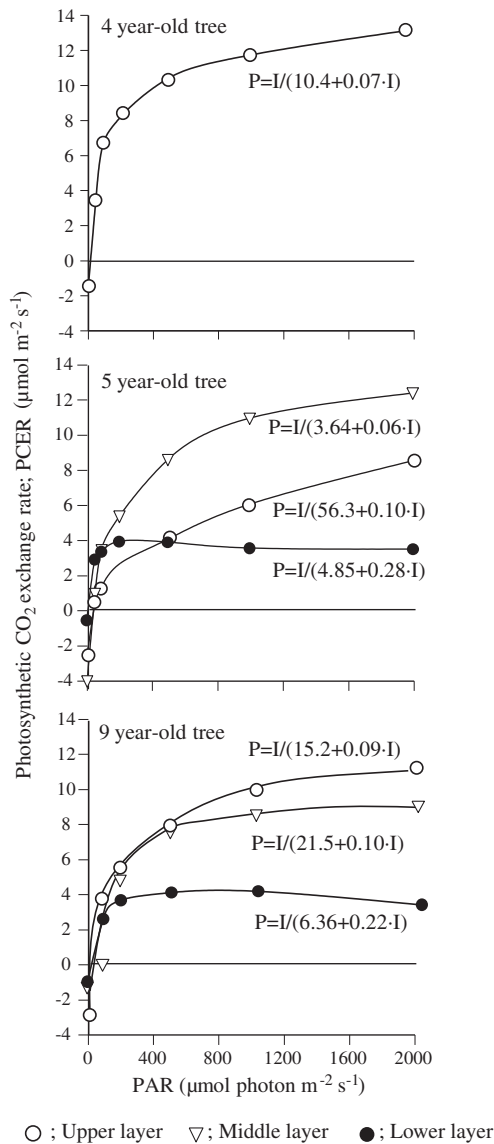


Fig. 1. Light response of photosynthetic CO_2 exchange rate (PCER) measured in the leaves located in the upper canopy of 4 year-old and in three layers of the canopy of 5 and 9 year-old *Rhizophora apiculata* grown in Trat, Thailand. They were measured at 25 °C leaf temperature. PAR in Y-axis shows photosynthetically active radiation.

where P ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) is PCER of individual leaves at light intensity of I ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$) and α and β are coefficients to determine the convexity of the hyperbola.

3.2. Temperature response of PCER

The temperature responses of PCER in the leaves of 4 and 9 year-old tree are shown in Fig. 2. The P_{max} value acquired from 4 year-old tree was $13.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 33 °C leaf temperature and that from the 9 year-old tree was $13.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 26 °C leaf temperature. Although both of these are similar, the leaf temperature obtained for the P_{max} value is quite different. The temperature responses fit a quadratic curve as follows (Fig. 2):

$$4 \text{ year-old tree : } P = -0.086x^2 + 5.37x - 70.6 \quad (2)$$

$$9 \text{ year-olds tree : } P = -0.033x^2 + 1.89x - 13.6 \quad (3)$$

where P ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) is PCER of individual leaves at leaf temperature of x (°C). Although the temperature responses in the leaves

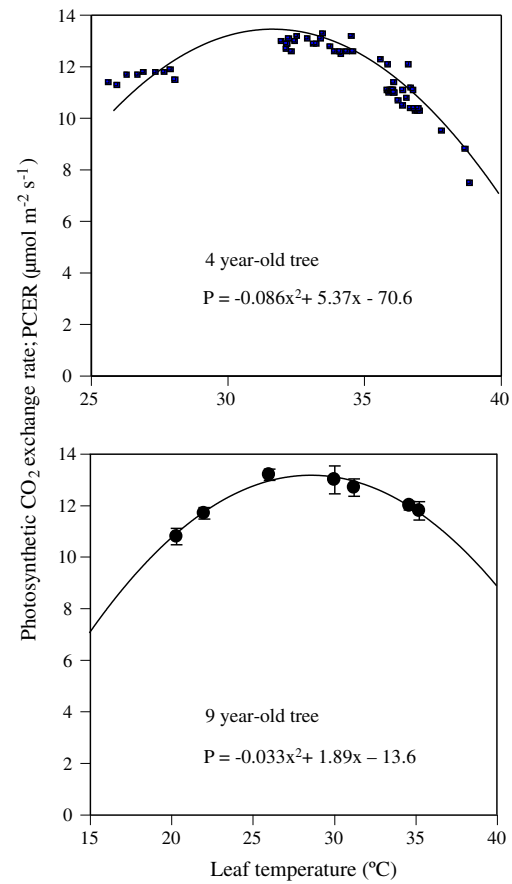


Fig. 2. Temperature response of photosynthetic CO_2 exchange rate (PCER) measured in the leaves of 4 and 9 year-old *Rhizophora apiculata* tree in Trat, Thailand. A quadratic curve in the graph was a regression of temperature response of PCER. They were measured at $1000 \text{ mmol m}^{-2} \text{ s}^{-1}$ of PAR. Vertical bars in the graph for 9 year-old tree show standard deviation ($n = 5$).

of the 3 and 5 year-old tree were not measured, they were assumed to be similar to that obtained for 4 year-old tree.

3.3. Canopy structure and light profile in the canopy

The productive structure in a 5 and 9 year-old forest and light profile inside the forests is shown in Fig. 3. The leaf area index (LAI) of the 3, 4, 5 and 9 year-old forest was 0.46, 2.13, 3.15 and 4.75, respectively. The light extinction coefficient (K), obtained by relating the cumulative leaf area and logarithms of the relative light intensities of each layer. The K value in the 5 and 9 year-old forest was 0.34 and 0.30, respectively. In the 3 and 4 year-old forest, light extinction inside the forest could be disregarded because all single trees in the study site were independent and without the competition of neighboring trees for growth.

3.4. Above- and below-ground biomass

The biomass of each organ in a single tree of 3, 4, 5 and 9 year-old was calculated by its surface area and volume (Fig. 4). Total surface area in a single tree of 3, 4, 5 and 9 year-old was 0.1, 0.6, 2.0 and 19.8 m^2 . While, the total volume of each tree was 0.1, 0.1, 0.6 and $10.3 \times 10^{-2} \text{ m}^3$. In the biomass as estimated by surface area, a ratio of the branch to the total single trees of 3, 4, 5 and 9 year-old was 51.4%, 76.1%, 73.4% and 71.4%, respectively, which was similar at trees of different ages. The ratio in volumes was dif-

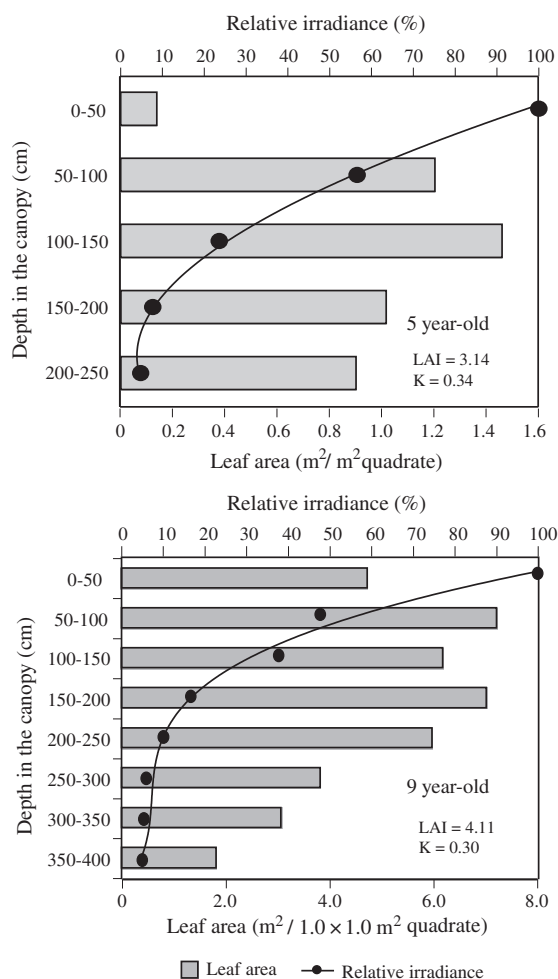


Fig. 3. Leaf distribution and light profile in 5 and 9 year-old *Rhizophora apiculata* forest in Trat, Thailand. LAI and K in the graph show leaf area index and a light extinction coefficient, respectively.

ferent, calculated as 21.0, 50.3, 39.2 and 30.3% in the 3, 4, 5 and 9 year-old trees, respectively.

To calculate the dry weight of tree biomass at different ages, the wood density obtained from samples of the 4 year-old tree (0.510 and 0.488 g cm⁻³ for trunk and branch, respectively, Table 1) was multiplied by the calculated value of tree biomass in volume. The calculated tree biomass of 3, 4, 5 and 9 year-old was 0.1, 0.3, 1.2 and 20.1 kg C trunk⁻¹, respectively. The above-ground tree biomass in hectares was 1.0, 1.3, 3.0 and 12.6 Mg C ha⁻¹, respectively.

The root biomass of the 4 year-old tree shown in Fig. 5 indicates 5.8 m² in surface area and 1.9 × 10⁻² m³ in volume. Both of these figures are 10 times higher than those of the above-ground biomass. The root biomass of the 4 year-old tree in dry weight was measured as 2.5 kg C trunk⁻¹, calculated using the wood density of root (0.329 g cm⁻³, Table 1). T/R ratio (the ratio of total weight of above-ground biomass to dry weight of the root) was 0.114.

3.5. Temperature response of RCER in each organ

Temperature responses of RCER measured in trunk and branch of 4 year-old tree are shown in Fig. 6. The RCER values measured in the temperature range of 15–35 °C were 5.8–18.6 μmol CO₂ m⁻² s⁻¹ for trunk and 1.1–17.9 μmol CO₂ m⁻² s⁻¹ for branch, respectively. The RCER values observed in the trunk and the brown part

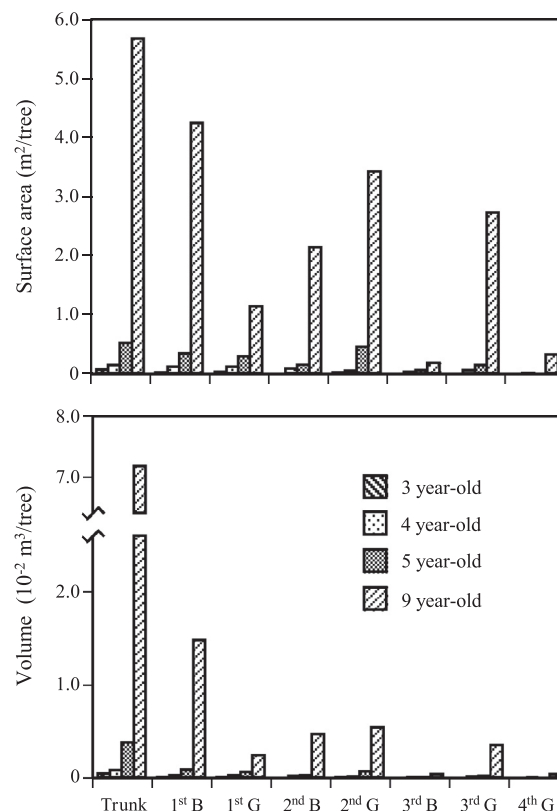


Fig. 4. Surface area and volume of trunk and each offshoot of branch in 3, 4, 5 and 9 year-old trees of *Rhizophora apiculata* in Trat, Thailand. Branches were divided into four offshoot groups; first, second, third, and fourth offshoots. “B” and “G” in the graph mean surface color of each part, i.e. lignified brown (B) and non-lignified green (G), respectively.

Table 1

Properties of quantitative characteristics of the representative part of 4 year-old *Rhizophora apiculata* tree in Trat, Thailand.

	Surface area (cm ²)	Volume (cm ³)	Fresh weight (gFW)	Dry weight (gDW)	Wood density (g cm ⁻³)
<i>Trunk</i>					
B	350	172	219	105	0.610
G	334	88	104	36	0.409
<i>Branch</i>					
1st B	329	142	197	95	0.669
1st G	287	67	88	30	0.448
2nd B	395	84	95	42	0.500
2nd G	681	106	142	41	0.387
3rd B	248	37	49	21	0.568
3rd G	484	54	93	28	0.519
4th B	140	18	20	7.8	0.433
4th G	436	46	66	19	0.413
5th B	111	12	19	5.4	0.450
<i>Main root</i>					
Upper	132	116	147	68	0.586
Upper-middle	214	293	389	171	0.584
Middle-lower	171	187	179	74	0.396
Lower	138	127	112	37	0.291
<i>Lateral root</i>					
1st B	681	423	377	119	0.281
2nd B	572	156	128	30	0.192
2nd W	1615	1190	216	27	0.023
3rd W large	170	18	17	1.9	0.106
3rd W small	167	18	51	9.1	0.506

of first branch are slightly higher. The temperature response of RCER is well regressed with an exponential equation and each parameter of the equation shown in Table 2.

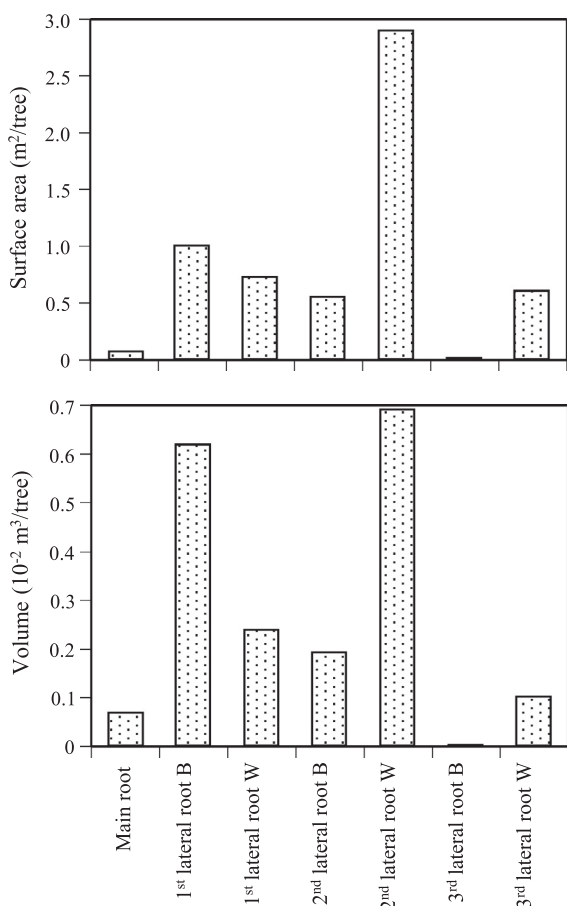


Fig. 5. Surface area and volume of root in 4 year-old *Rhizophora apiculata* tree in Trat, Thailand. Lateral roots were divided into 1st to 3rd lateral roots, and they were also divided into the brown part (B) and the white part (W).

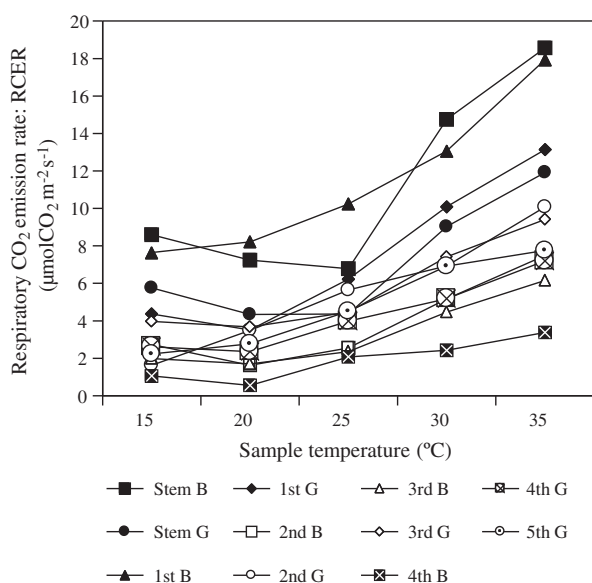


Fig. 6. Temperature response of respiratory CO₂ emission rate (RCER) of each organ in 4 year-old *Rhizophora apiculata* tree in Trat, Thailand. The values of RCER were calculated in surface area of each organ.

The temperature responses of RCER value measured in the root of the 4 year-old tree are shown in Fig. 7. The RCER values were 4.8–26.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the main root, 3.4–14.1 μmol

$\text{CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the first lateral root and 1.0–6.3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the second and third lateral roots, respectively. Among the root samples, the RCER values were the highest for the main root. They increased dramatically at a temperature of 35 °C. The RCER values in the temperature ranges of 15–30 °C were 1.0–6.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, similar to those obtained for the trunk and the branch or slightly smaller.

3.6. Diurnal temperature model

The calculated temperature values were well fitted to the observed temperature values in each month (Fig. 8). In the diurnal temperature variation in Trat, the modified coefficient was 4–8 h throughout the year. These temperature values derived from the modified diurnal temperature model were used for temperature modification of the monthly values of photosynthetic absorption and respiratory emission of carbon.

3.7. Estimation of carbon absorption

Seasonal changes of carbon absorption corrected for the monthly variation of light (without temperature modification) and that corrected for light and temperature (with temperature modification) are shown in Fig. 9a and b, respectively. Monthly values of the carbon absorption and the seasonal variations are both similar in the two kinds of calculation. Annual values of the carbon absorption in 3, 4, 5 and 9 year-olds forests corrected without the temperature modification were 4.1, 19.2, 25.8 and 42.5 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$, respectively. Meanwhile, the annual values corrected with the temperature modification were 4.4, 20.4, 27.8 and 48.0 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$, respectively (Table 3). As a result, the annual values of carbon absorption increased 6.3–12.8% due to the temperature modification.

3.8. Estimation of carbon emission

Monthly values of carbon emission corrected for light but without temperature and that corrected for the both of the light and temperature are shown in Fig. 9a and b. The monthly values look almost completely unchanged with the temperature modification. Annual values of the carbon emission in 3, 4, 5 and 9 year-old forests corrected without the temperature modification were 1.9, 5.7, 7.6 and 17.4 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$, respectively (Table 3). Meanwhile, those corrected with the temperature modification were 1.9, 5.6, 7.5 and 17.4 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$, respectively (Table 3). Both the annual values of carbon emission were quite similar, despite correction with and without temperature modification.

The monthly value of carbon emission from the root of 4 year-old tree was calculated using the average value of root respiration of 5.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. It is the RCER value at an annual temperature average of 27.3 °C at the study site, which is calculated from an exponential equation regressing the temperature responses of the RCER (Table 2). This RCER value was multiplied by the whole tree biomass of the 4 year-old tree calculated in surface area (5.8 m^2) to calculate carbon emission from the whole root of the tree. Annual value of carbon emission from the root was 83.7 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$, calculated by multiplying the single tree value by the wood density of 4 year-old tree (66.7 trunks/100 m^2).

3.9. Estimation of net carbon fixation

The seasonal variation of net carbon fixation both with and without the temperature modification are shown in Fig. 9a and b. The annual values of the net carbon fixation in 3, 4, 5 and 9 year-old forests were 2.2, 13.5, 18.2 and 25.2 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ without the temperature modification, while 2.5, 14.8, 20.2 and 30.5 Mg

Table 2
Parameters of regression equation ($Y = A \cdot 10^{B \cdot X}$) that shows the relationship between temperature (X) and respiratory CO₂ emission rate (RCER, Y) measured in each organ of 4 year-old *Rhizophora apiculata* tree in Trat, Thailand. The values of Y were calculated in the unit of surface area (mmol CO₂ m⁻² s⁻¹).

	Trunk B	Trunk G	1st B	1st G	2nd B	2nd G	3rd B	3rd G	4th B	4th G	5th G
A	1.49	0.86	3.67	1.16	0.20	0.54	0.27	0.93	0.05	0.60	0.79
B	0.03	0.03	0.02	0.03	0.05	0.04	0.04	0.08	0.97*	0.03	0.03
R ²	0.85	0.89	0.96*	0.81	0.99*	0.95	0.98*	0.03	0.82	0.98*	0.97*
	Main root				Lateral root						
	Upper	Upper-middle	Middle-lower	Lower	1st B	2nd B	2nd W	3rd W large	3rd W small		
A	1.46	1.93	1.28	0.96	0.45	0.54	0.27	0.08	0.26		
B	0.03	0.03	0.04	0.03	0.04	0.03	0.03	0.04	0.04		
R ²	0.95	0.90	0.88	0.95	0.93	0.93	0.93	0.97*	1.00*		

* Significant at 5% level.

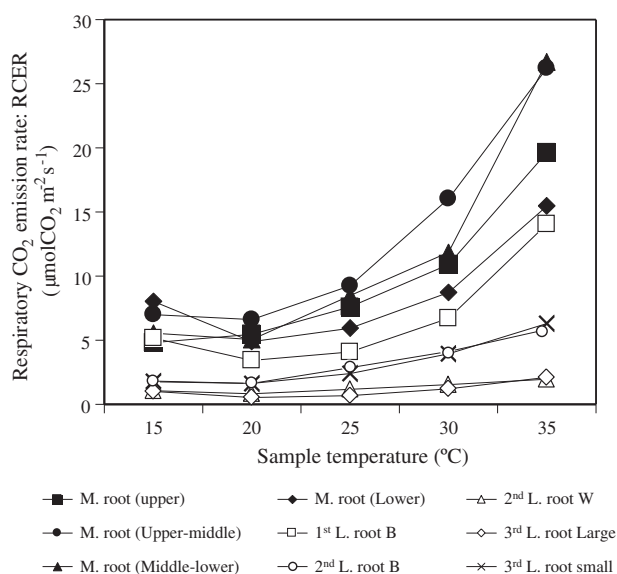


Fig. 7. Temperature response of respiratory CO₂ emission rate (RCER) of root in 4 year-old *Rhizophora apiculata* in Trat, Thailand. The values of RCER were calculated in surface area of each organ. "B" and "W" in the figure show the brown and white part of the lateral root, respectively.

C ha⁻¹ yr⁻¹ with the temperature modification, respectively (Table 3). The annual value of net carbon fixation increased from 9.3% to 21.3% due to the temperature modification.

3.10. Estimation of net carbon fixation by growth curve analysis

The accumulations of volume in the single tree as a function of time in the growth curve analysis method are shown in Fig. 10. The three kinds of growth curves with different values of the maximum tree biomass corresponded well to the single tree volumes obtained from the four different ages. As indicated in the growth curves, it can be predicated that single tree biomass attains its peak at around 13 years of age. Meanwhile, the annual increments of tree biomass in volume reach their maximum value at 8 or 9 year-old, which were $5.3\text{--}9.4 \times 10^{-2} \text{ m}^3 \text{ trunk}^{-1} \text{ yr}^{-1}$. In the growth curve with the maximum tree biomass of $20 \times 10^{-2} \text{ m}^3/\text{trunk}$, annual increments of the tree volume in 3, 4, 5 and 9 year-old tree was $0.1, 0.2, 0.6$ and $5.8 \times 10^{-2} \text{ m}^3 \text{ trunk}^{-1} \text{ yr}^{-1}$, respectively, which was calculated from derivative values of the growth curve. These values in volume can be converted into dry weight values by multiplying the calculated values by the wood density obtained from the samples of 4 year-old tree (0.486 g cm^{-3} , Table 1). The calculated values of annual carbon accumulation in above-ground portion of 3, 4, 5 and 9 year-old forests were 1.3, 2.7, 6.0 and $28.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, respectively (Table 4). Also from the growth curves with the

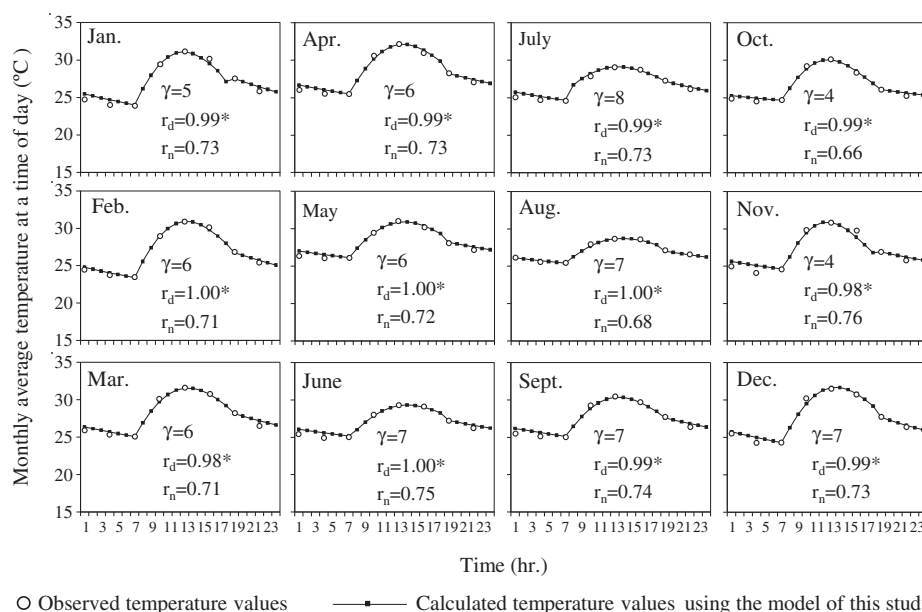


Fig. 8. Comparison of the diurnal variation of temperature in each month between the observed data in Trat, Thailand and that calculated by the model of this study. Temperature variations during the day and night were divided and the details of equations are described in Okimoto et al. (2008). * show significant correlation at 0.1% level.

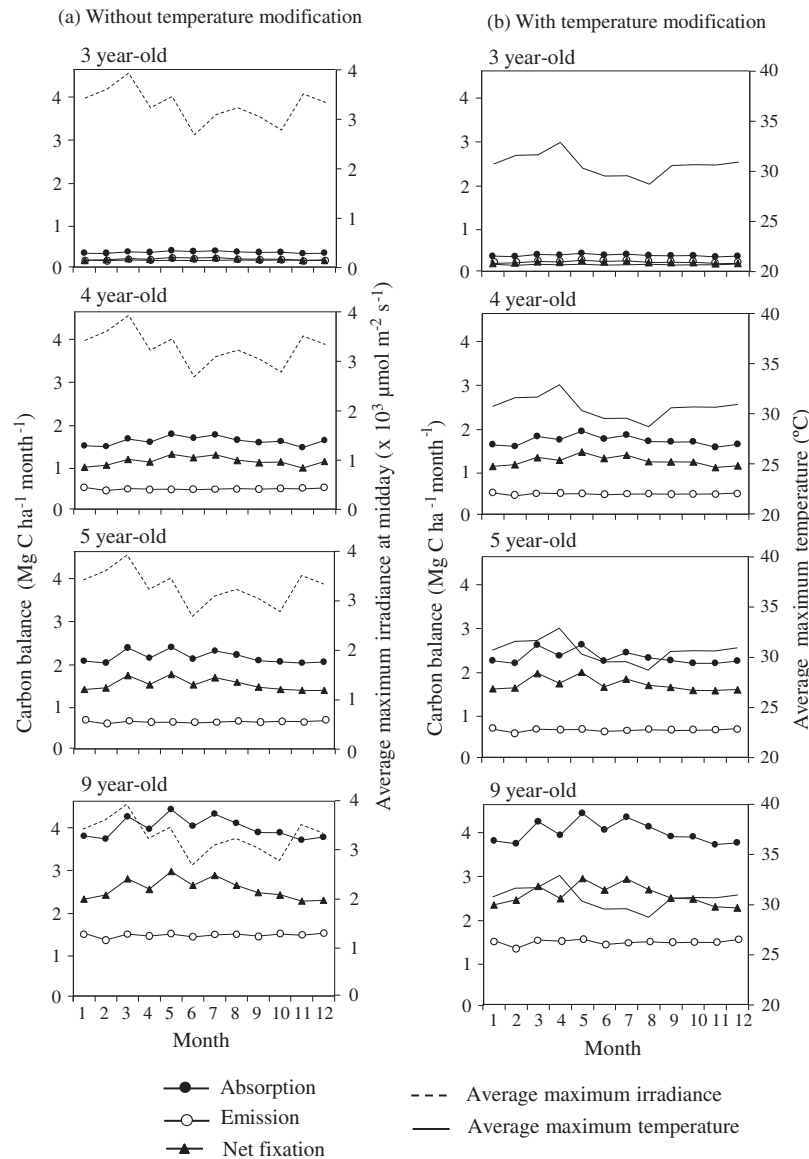


Fig. 9. Monthly variation in the amount of above-ground carbon balance in four tree ages of *Rhizophora apiculata* canopy in Trat, Thailand. These estimations were calculated.

Table 3

Estimates of annual carbon balance in $\text{Mg C ha}^{-1} \text{yr}^{-1}$ in above-ground *Rhizophora apiculata* forest in four kinds of tree ages in Trat, Thailand. They were estimated without and with temperature modification; the former is corrected only for monthly variations of the light intensity, and the latter is corrected for those of the light intensity and temperature, respectively.

Stand ages (yr)	Absorption ($\text{Mg C ha}^{-1} \text{yr}^{-1}$)	Emission ($\text{Mg C ha}^{-1} \text{yr}^{-1}$)	Net fixation ($\text{Mg C ha}^{-1} \text{yr}^{-1}$)
<i>Calculated values without temperature modification</i>			
3	4.1	1.9	2.2
4	19.2	5.7	13.5
5	25.8	7.6	18.2
9	42.5	17.4	25.2
<i>Calculated values with temperature modification</i>			
3	4.4	1.9	2.5
4	20.4	5.6	14.8
5	27.8	7.5	20.2
9	48.0	17.4	30.5

maximum tree biomass of 15 and $25 \times 10^{-2} \text{ m}^3/\text{trunk}$, the annual values of carbon accumulation were $1.1\text{--}21.2 \text{ Mg C ha}^{-1} \text{yr}^{-1}$ and $1.5\text{--}35.2 \text{ Mg C ha}^{-1} \text{yr}^{-1}$, respectively (Table 4).

3.11. Comparison of the calculated values of net carbon fixation derived from the two analysis methods

Derived values of growth can be substituted for actual biomass accumulations of the tree at each growth stage. In this study the growth curve estimates were used as a reference value of net carbon fixation capacity. Annual values of net carbon fixation calculated by the gas exchange analysis method were compared to those of dry matter accumulation calculated with growth curve analysis method (Table 4). The values of 9 year-old tree were approximately similar between the two methods, although the values of 3, 4 and 5 year-old trees were different by a factor of between 2 and 7 times (Table 4). The differences in the 9 year-old forest were 7.2% and 13.4% when the maximum tree biomass was assumed at 20 and $25 \times 10^{-2} \text{ m}^3$, respectively (Table 4).

4. Discussion

In this study, net carbon fixation capacity of *R. apiculata* monoculture forest was evaluated by both the gas exchange and growth curve analysis methods.

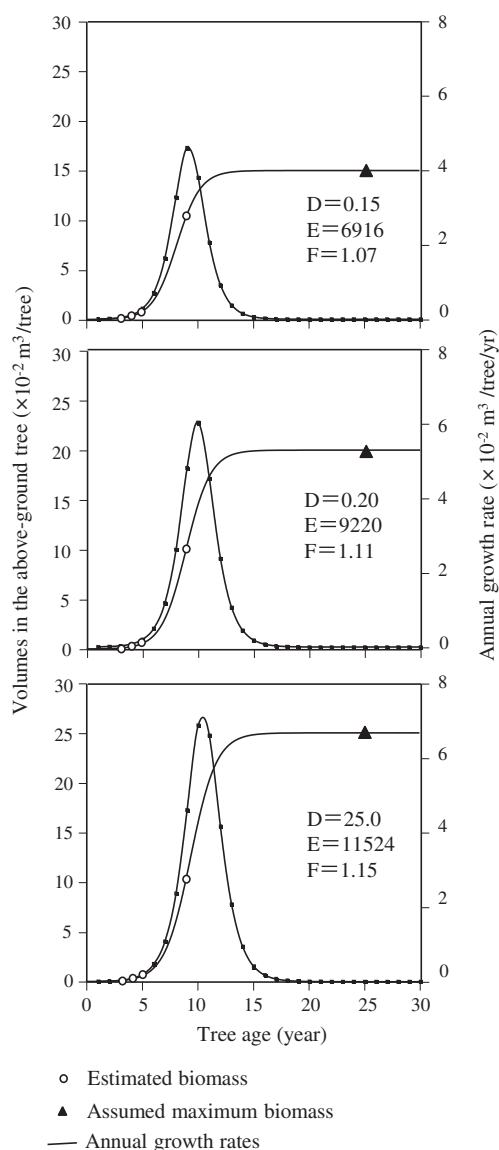


Fig. 10. Growth curves made using the estimated data of above-ground biomass in four kinds of tree ages in Trat, Thailand. Maximum tree biomass was assumed in three levels, details referred in Section 2. Values of D , E and F show the parameters of growth curve equation of $Y = D / (1 + E \cdot \exp^{-Ft})$, where D is an assumed maximum tree biomass, $E = (D - Y_0) / Y_0$ where Y_0 is an initial value of tree biomass, t is a tree age, and F is a growth coefficient.

Annual values of carbon absorption in 5 and 9 year-old forest were compared to the reported values of $56 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for *R. apiculata* forest in Malaysia (Clough et al., 1997) and $29 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for the mixed mangrove species forest in Australia (Clough, 1998), which were calculated by the traditional gas exchange method (Table 3). These results show that the gas exchange analysis method used in our study is an alternative to the traditional method, which can provide an adequate estimation of mangrove productivity.

The data on photosynthetic properties in the leaves of 4 and 9 year-old trees were obtained in November 2003 and March 2001, respectively, when both seasons had temperatures over 30°C . As a result, the P_{max} values of 4 and 9 year-old trees were similar, but the leaf temperatures obtained the P_{max} were different at 33 and 26°C , respectively (Fig. 2). Those optimum temperatures did not correspond with the maximum temperature of each research period in November and March that is similar as shown

Table 4

Comparisons of the annual carbon increment ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$) in the forests of *Rhizophora apiculata* in Trat, Thailand. They were estimated by gas exchange method and growth curve analysis method.

Stand age (yr)	Gas exchange estimations ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$)	Growth curve estimations		
		Assumed maximum stand biomass ($\times 10^2 \text{ m}^3 \text{ tree}^{-1}$)		
		15	20	25
3	2.5	1.1	1.3	1.5
4	14.8	2.2	2.7	3.1
5	20.2	4.8	6.0	7.3
9	30.5	21.2	28.5	35.2

in Fig. 8. Concerning the seasonal variation of photosynthetic properties, Moore et al. (1972, 1973) reported that optimum temperature ranges and P_{max} value observed in the leaves of *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa* in the south of Florida, shows a tendency for the values to be higher in winter than in summer. The difference we found in our data might be caused by local characteristics of the mangroves, influenced by meteorological factors including cumulative light intensity and temperatures. From this observation, it appeared that the seasonal data of PCER should be accumulated to account for net carbon fixation capacity with the gas exchange analysis method.

The effect of temperature modification for *R. apiculata* in Trat was different from the effect of temperature modification for *R. stylosa* in Ishigaki, Japan, reported by Okimoto et al. (2007). The annual values of carbon absorption increased 6.3–12.8% by temperature modification (Table 2), while, those of carbon emission (with the temperature modification) were not changed at all, even though the monthly values of carbon emission were increased and decreased with the temperature modification. This was caused by self-compensation in the monthly values of carbon emissions throughout the year. Meanwhile, the effect for *R. stylosa* in Ishigaki was that the carbon absorption values decreased 15.6%, but those of the carbon emission decreased 48%. The strong effect of temperature modification in Ishigaki was partly due to a larger seasonal temperature variation than in Trat. It is considered that lower latitude in Trat brings the smaller seasonal variation in temperature and it is less vulnerable to the temperature modification, despite that annual averages of temperature in Trat and Ishigaki were similar at 27.3 and 25.1°C , respectively. This finding suggests that the gas exchange properties of mangrove trees show regional characteristics, as mentioned above. The calculated values of carbon emissions in this study was based on the RCER data obtained only from 4 year-old tree. That is based on the value in surface area, which more closely matches to that in volume. By collecting more RCER data of each organ and tree age and those seasonal variations, the accuracy of calculated carbon emissions and net carbon fixation capacity in the gas change analysis method could be improved. In addition, it was found that the RCER values in surface area lead to more closely matching values of the carbon emission compared to those calculated with volume, because respiratory activity of the woody organ is dynamic mostly in the cambium layer just beneath the epidermis layer.

Our previous studies (Okimoto et al., 2007, 2008) had resulted in $3.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for the mature *R. stylosa* tree in Okinawa, Japan ($24^\circ 30' \text{N}$) and 30.0 , 12.7 and $3.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for the *K. candel* monoculture of 5, 10 and 15 year-old tree in Thanh Hoa, Vietnam ($20^\circ 12' \text{N}$), respectively. The results of this study ($12^\circ 11' \text{N}$) were almost larger than our previous results (Table 3). The values of PCER and RCER were similar among the different species (Figs. 1, 2 and 6), thus the difference of net CO_2 fixation

was rather resulted in LAI and light penetration (Fig. 3), culm-foliage ratio (Fig. 4) and temperature in each site (Fig. 8).

The annual values of biomass increment calculated by the growth curve analysis method were similar to those of $7.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for 10 year-old *R. apiculata* forest in Malaysia (Ong et al., 1984) and $5.6\text{--}13.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for 6–14 year-old *Rhizophora candelaria* forest in Thailand (Aksornkoae, 1976), which were calculated by the traditional allometric method (Table 4). This result suggests that the growth curve analysis method was as effective in estimating mangrove productivity as the allometric method.

The annual values of biomass increment derived from the growth curve analysis method are unsatisfactory because they were based on some assumption such as the calculated values of the dry matter by using woody density obtained from the measurement samples of RCER (Table 1) and the predicted values of maximum tree biomass in volume (Fig. 10). Incidentally, the wood density observed in this study (0.486 g cm^{-3} , Table 1) was similar to the reported value of $0.486\text{--}0.980 \text{ g cm}^{-3}$ (Clough, 1992). If the upper limit of these wood densities (0.980 g cm^{-3}) was applied, annual value of the dry weight accumulation should be doubled. However, our proposed growth curve analysis method could be useful to evaluate net carbon fixation capacity in where it is not allowed to cut the tree in the preserved monocultures.

Regarding the values of net carbon fixation estimated by both methods, only relatively small differences of 7.2% and 13.4% for the values of 9 year-old forest were observed (Table 4). As described in Fig. 10, a growth curve is determined by the following three factors: the maximum tree biomass (D), an integration constant (E) calculated by an initial value of (Y_0) and D , and the growth coefficient (F). In fact, the F value marks the largest slope of the growth curve at its flexion point. It was observed to occur at around the age of 8 years in this study, which is roughly the period at which values of net carbon fixation estimated by the both methods were approximated in the range of 15% at 9 year-old forest age (Fig. 10, Table 4). If the F value could be alternatively predicted from the estimated values of the gas exchange analysis method, it would be no longer necessary to measure each tree biomass at different forest ages to draw a growth curve. This is a potential aspect of the gas exchange analysis method that is yet to be developed.

The values calculated by the gas exchange analysis method in 3, 4 and 5 year-old forests are about 2–7 times higher than those calculated by the growth curve analysis method (Table 4). One of the most likely reasons is that the values of the gas exchange analysis method do not incorporate carbon amounts of litter falls and exudations from roots (Clough, 1998). However, litter fall is reported to be about 8% of the total amount of photosynthetic carbon absorption (Clough et al., 1997) and $2\text{--}6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ (Ong, 1993). The differences in the annual values of biomass accumulation were larger than the amount of litter falls (Table 3). It shows that the gas exchange analysis method tend to overestimate during the younger growth stages. The other reason speculated is a lack of appropriate estimation of carbon emission from the below-ground root. As indicated with the T/R ratio of 0.114, which is smaller than those of any worldwide mangroves (Komiya, 2008), the 4 year-old tree has a large amount of the root biomass. In its juvenile stages, the trees prop-roots may not yet have developed but only the below-ground root to support the tree. The below-ground biomass is an important component in mangroves because it comprises a relatively higher proportion of the ecosystem compared to terrestrial forests (Komiya et al., 2008). In our future study, data collection of the below-ground biomass will be enhanced to improve the estimation accuracy of the gas exchange analysis method.

It is considered that the differences between the calculated values estimated by both methods should be the main factor in future

attempts to improve accuracy of the gas exchange analysis method. Although this study was focused on the above-ground biomass of the forests, the above-ground net carbon fixation values of the gas exchange analysis method deservingly decrease by adding the root carbon emission. It is clear that the respiratory carbon emissions from the below-ground root should be included. A trial estimation of the root respiratory carbon emission in this study ($83.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) was apparently overestimated, while the photosynthetic carbon absorption was $19.2\text{--}20.4 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. In order to overcome the issue, our study has attempted to take full account of the values of root RECR and response to low oxygen concentrations (Okimoto, 2008), accurately simulating the anaerobic soil conditions found in the mangrove forest. The results show that the root RCER diminished along the O_2 concentration decrease, in fact the RCER value at 12% O_2 was half of that at 21% O_2 . Improvement of the O_2 correction of the root RCER and the carbon emission is of key importance developing and improving the accuracy of the gas exchange analysis method.

An adequate and reliable estimate of the net carbon fixation capacity is an essential factor when evaluating the productivity of mangrove forests and their contribution in ameliorating the effects of climate change. Accuracy is the criterion against which the success of an image processing method should be judged: no matter how innovative or sophisticated the classification procedure, the value of any map is severely compromised if it is accuracy is insufficient to fulfill project objectives (Green et al., 1998). Meanwhile, the eddy covariance method has emerged as an important tool for evaluating fluxes of CO_2 in the terrestrial forest (Baldocchi, 2003), the peat swamp forests (Hirano et al., 2012) and the mangrove forest (Barr et al., 2012). The gas exchange analysis method, as used in this study, is effective, convenient, and also applicable to the most of mangrove species and also other types of monoculture forests in the SE Asia regions. Further studies on the estimation of respiratory carbon emission and below-ground biomass of the tree in managed mangrove plantations can be expected to improve the accuracy of both the gas exchange and growth curve methods.

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