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ORIGINAL PAPER

An estimation of CO_2 fixation capacity in mangrove forest using two methods of CO_2 gas exchange and growth curve analysis

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Abstract In many coastal areas of South-East Asia, attempts have been made to revive coastal ecosystem by initiating projects that encourage planting of mangrove trees. Compared to the terrestrial trees, mangrove trees possess a higher carbon fixation capacity. It becomes a very significant option for clean development mechanism (CDM) program. However, a reliable method to estimate CO_2 fixation capacity of mangrove trees has not been established. Acknowledging the above fact, we decided to set up an estimation method for the CDM program, using gas exchange analysis to estimate mangrove productivity, we put into consideration the net CO_2 fixation of reforested *Kandelia candel* (5-, 10-, and 15-year-old stand). This was estimated by gas exchange analysis and growth curve analysis. In growth curve analysis, we drew a growth curve of a single stand using data of above- and below-ground biomass. In the gas exchange analysis, we calculated CO_2 fixation capacity by (1) measuring respiration rate of each organ of stand and calculating respiratory CO_2 emission from above- to below-ground biomass. (2) Measuring the single-leaf photosynthetic rate in response to light intensity and calculating the photosynthetic CO_2 absorption. (3) We also developed a model for the diurnal changes in temperature, and monthly averages based on one-day estimation of CO_2 absorption and emission, which we corrected by this model in order to estimate the net CO_2 fixation capacity in response to temperature. Comparing the biomass accumulation of the two methods constructed for the same forest, the above-ground biomass accumulation of 10-year-old forest (34.3 ton ha^{-1} yr^{-1}) estimated by gas exchange analysis was closely compared to those of growth curve analysis (26.6 ton ha^{-1} yr^{-1}), suggesting that the gas exchange analysis was capable of estimating mangrove productivity. The validity of the estimated CO_2 fixation capacity by the gas exchange analysis and the growth curve analysis was also discussed.

Keywords Gas exchange · Mangrove · Net CO_2 fixation · Respiration rate · Root biomass · Temperature model

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Introduction

Vast areas of mangrove forests have been destroyed by human activities over the last few decades. Mangrove trees have a very significant impact to the coastal environment, which is grossly reversed when there is over exploitation of the trees. Consequently, this results into harmful effects on the coastal flora and fauna.

The clean development mechanism (CDM) is one of the Kyoto Protocol activities. It allows developed nations to achieve part of their CO_2 reduction obligations. This is made possible by projects in developing countries that reduce CO_2 emissions and other greenhouse gases. The role of forests as a carbon sink in mitigating climate change has been underpinned at the politically binding level by the Kyoto Protocol (UNFCCC 1997), and guidelines for the inclusion of forest sector carbon sequestration in the national greenhouse gas balance have been developed (IPCC 2003). The carbon fixation capacity of mangrove forests is higher than that of the terrestrial forest (Christensen 1978; Clough et al. 1997; Clough 1998; Ong et al. 1995; Komiyama 2004). For this reason, mangroves have been considered as an important carbon sink in coastal ecosystems (Ong 1993). The higher carbon fixation capacity of mangrove trees gives a good indication for the use in CDM programs. However, although there is a call for an improved accounting methodology for post-2012 assessments (e.g., Sedjo and Marland 2003), a reliable method to estimate CO_2 fixation capacity of mangrove forests has not been established.

The CO_2 fixation capacity of mangrove trees has been estimated mainly by the allometric method and gas exchange method. The allometric method is based on a correlation between the trunk diameter at breast height (DBH, i.e., 1.3 m) and the single stand biomass (Ong et al. 1984, 1995; Ong 1993; Putz and Chan 1986; Clough and Scott 1989; Matsui 1998; Komiyama et al. 2005). This measurement is laborious and time consuming (Clough et al. 1997), taking up to 1–5 years to establish the relationship between trunk diameters and plant biomass. Thus, this method is not suitable for a broad scale survey and comparative studies involving different species in different countries and climates.

The gas exchange method is one of the alternative approaches based on an estimation of CO_2 absorption as a gross productivity of the canopy. This is obtained by measuring leaf photosynthetic rates, leaf area index (LAI), and light extinctions in the canopy (Bunt et al. 1979; Boto et al. 1984; Clough et al. 1997; Clough 1998; Ong et al. 1995). Net canopy productivity can be estimated by the difference between photosynthetic CO_2 absorption and respiratory CO_2 emission. The canopy structure responsible for canopy photosynthesis such as LAI and light extinction has been studied in the mangrove trees (Clough et al. 1997), although canopy and soil respiration has scarcely been estimated.

Ong et al. (1995) estimated the respiratory CO_2 emission of 20-year-old *Rhizophora apiculata* in Malaysia using the gas exchange method. However, they used only the above-ground biomass for CO_2 estimates. They substituted the respiration rate of single leaves for the respiration rate of all above-ground organs. The respiratory CO_2 emission, though, has never been estimated adequately for either above- and below-ground organs (Gong and Ong 1990; Clough et al. 1997). This may be due to technical difficulties in collecting complex root tissues and measuring the respiration rate of non-assimilation parts of the stand directly in situ (Clough 1998). However, an effective, direct, and convenient method in estimating CO_2 fixation is the gas exchange analysis method. The CO_2 fixation capacity of stand or canopy can be estimated as integrated CO_2 assimilation of each organ (e.g., leaf, branch, etc.) under variable meteorological conditions by measuring the gas exchange responses to environmental factors.

In this study, we measured photosynthetic CO_2 exchange rate (PCER) of individual leaves and respiratory CO_2 emission rate (RCER) of each organ to estimate the CO_2 fixation capacity at canopy level in mangrove, *Kandelia candel*. Seasonal changes and annual amount of photosynthetic CO_2 absorption and respiratory CO_2 emission were calculated in response to diurnal changes of light intensity and air temperature. In addition, we drew some growth curves of a single stand using data of above- and below-ground biomass, which was directly collected at different ages. To evaluate the feasibility of the gas exchange analysis, we have compared the annual CO_2 fixation calculated by gas exchange analysis with the biomass accumulation calculated by growth curve analysis.

Materials and methods

In this study, the word of "organ" shows each part of the stand such as leaf, sprout, branch, trunk, and root.

Study site

The study site was at the mouth of River Len (20°12′ N and 160°32′ E) flowing into Tonkin Gulf in Thanh Hoa, Vietnam. The area is characterized by subtropical climate with dry seasons (May–October) and rainy seasons (December–February). The annual mean temperature was 32.4°C at maximum and 17.8°C at minimum, the annual precipitation is 1,600 mm, and the average humidity is 85.7% (period 1997–2001).

The study was carried out in *Kandelia candel* monoculture forest of 5-, 10-, and 15-year-old stands from September 1 to 7, 2002 and from September 8 to 13, 2003. The trees in this area were planted by Red Cross Society of both Vietnam and Japan as a program of countermeasures against natural disasters. The stand density was 64.5, 89.0, and 52.0 stems/100 m^2 in 5-, 10-, and 15-year-old trees, respectively.

Estimation of a CO_2 fixation capacity with gas exchange analysis

The response of PCER to light and temperature was measured in the leaves of upper- and lower-layers in the canopy. The light extinction and the distribution of leaves in the canopy were measured to calculate CO_2 absorption capacity of the canopy. Respiratory CO_2 emission was estimated by multiplying the RCER measured using partial amount of organs and the total amount of organs in above- and below-ground portions. Monthly averages based on one whole day absorption and emission of CO_2 were corrected with the diurnal values of light intensity and air temperature. An annual CO_2 fixation capacity was estimated by integrating CO_2 balance between the absorption and emission of CO_2 in each month.

Light response of PCER

Steel towers (5–8 m in height, depending on the height of the canopy) were constructed in 10- and 15-year-old forest to measure leaf photosynthesis and investigate canopy structure.

Light responses of PCER were measured in leaves on the surface of 5-year-old canopy and in upper- and lower-layer in the canopy of 10- and 15-year-old stand. This was done using a portable photosynthetic measurement system (LI-6400, Li-Cor, USA). Light intensity of photosynthetically active radiation (PAR) on leaf surfaces was automatically controlled in six steps in a descending order starting from 2,000 μmol m^{-2} s^{-1} to 0 μmol m^{-2} s^{-1}. During the measurements, leaf temperature was maintained at 30°C, vapor pressure deficit between the leaf and the air (VpdL) was 1.5 μmol m^{-2} s^{-1}, and CO_2 concentration of the reference air was 370 μmol mol^{-1}. The PCER gradually decreased after around 11–12 o'clock (Okimoto et al. unpublished). Thus, the measurements were finished before 11 o'clock.

Temperature response of PCER

Temperature responses of PCER were measured in leaves of 5-year-old stand using the LI-6400. Leaf temperature was changed from 20–35°C at 5°C intervals. In the measurements, VpdL, input CO_2, and PAR was 1.7 ± 0.3 μmol m^{-2} s^{-1}, 370 μmol mol^{-1}, and 2,000 μmol m^{-2} s^{-1}, respectively.

To obtain complementary data of PCER in response to temperature, 3-year-old stand of *K. candel* was used. This was done in Saga, Japan, where stands were grown in 8-l pots containing river sand, filled with tap water and kept in a greenhouse with heating under natural sunlight. The plants were fertilized by a 500-fold diluted solution of mixed fertilizer (No.1 and No.2 of Otsuka Hause, Otsuka Chemical Co., Ltd., Japan). Viviparous seeds of the plants were collected at Iriomote Island, Japan. Data collection in 3-year-old of *K. candel* in the greenhouse was done using the same measurement condition of LI-6400 as was done in the study site.

Canopy structure with stratified clip technique

Canopy structure was investigated by the stratified clip technique. A 1.0 × 1.73 m quadrat of the canopy was divided into 0.5 m thickness each. This was done from the top of the canopy to the forest floor. Light extinction through the canopy was calculated by a relative irradiance (%) between the light incident at the top of the canopy and the light intensity at each layer inside the canopy. The light intensity was measured using a quantum sensor (LI-190SB, Li-Cor, USA), expressed as an average value measured in each layers at five points, the center and four peripheral points 50 cm away from the center. All organs including trunk, branch, leaf, and sprouts in each layer were collected. They were divided into assimilation and non-assimilation organs, and the fresh weights were measured. Leaf areas in each layer were calculated by multiplying the leaf numbers of one layer by an average single leaf area measured in the laboratory with an automatic area meter (AAM-7, Hayashi Denkoh Co., Ltd., Japan).

Measurements of above- and below-ground biomass

All above-ground organs of a stand were cut at ground level. They were divided into five components such as leaves, branches, trunk, sprouts of leaf, and viviparous seeds. The branches were divided into three offshoot groups; first, second, and third offshoots. The first one was the primary offshoot attached to the trunk, the second one was branching from the first offshoot, and other twigs were named as third offshoot. The divided branches were separated into two parts: lignified brown (B) and non-lignified green parts (G), based on the degree of lignification and color of the branch surface. Roots were carefully collected by excavation with an engine pump (SEG-25E, KOSHIN Ltd., Japan). They were divided into main root, first lateral root, and second lateral root, following the same method described in the collection of the branches above.

The fresh weights of all organs in a single stand were measured. The volume and surface area of branch, trunk, and root were calculated by the length and diameters at the top and the bottom of each organ, based on an assumption that the organs were cone shaped. The biomass measurement was conducted on two replicates except for the roots of 15-year-old stand, and the biomass was expressed as an average value. The dry weight in the forest was estimated by multiplying the dry weight of a single stand by the stand densities.

After measurements of respiration rates, the samples were dried at 80°C for one more week, and the dry weight of the samples were measured. In addition, water content and wood density (weight per unit volume) of the samples were calculated. All leaves in the single stand were collected, and the fresh weights measured. Fifty representative leaves of the single stand were randomly selected, and an average of leaf area and dry weight in a single leaf measured.

Temperature response of RCER in each organ

Temperature response of RCER in above-ground organs was measured at a temperature range of 20–35°C at 5°C intervals. The RCER of the roots was measured at a temperature range of 15–30°C at 5°C intervals. Sample temperature was controlled by putting the samples in aluminous pan (18 cm in diameter and 18 cm in depth), which was kept inside a water bath with immersion thermo-regulator (NTT-1200, Tokyo Rikakikai Co., Japan). Air inside the pan was mixed with a propeller fan (MD825BM-12, Tokuden Co., Ltd., Japan) to maintain a constant temperature. The temperature was measured with a copper-constantan thermocouple ($\varphi = 0.32$ mm) attached to the surface of the sample and recorded with an analog recorder (EPR-3521, TOA DKK, Japan). The RCER of the sample in the aluminous pan was measured with a CO_2 analyzer (LI-800, Li-Cor, USA) for at least 5 min to obtain a stable data of linearly increasing CO_2 concentrations.

Estimation of absorption and emission of CO_2

The diurnal photosynthetic CO_2 absorption was calculated as an integration of PCER in response to light and temperature, leaf distribution, and the light extinction in the canopy. The diurnal light variation of each month was assumed to follow a sine curve, and a shape of the sine curve was determined with monthly average of the maximum light intensity and the day length (Monteith 1965):

$$Rt = R_{\max} \cdot \sin\left(\frac{t}{L} \cdot \pi\right) \quad (1)$$

where Rt (μmol m^{-2} s^{-1}) is light intensity at a given time during the day of t, t (h) is the time after sunrise,

R_{max} (μmol m^{-2} s^{-1}) is the monthly average of the maximum light intensity and L (h) is the average day length of each month. The light intensity in each layer of the canopy was calculated by multiplying relative light intensity in each layer by the calculated values of Rt. Variable PCER in single leaf were determined by assigning the light intensity at each layer to the part of I of Eq. 7 in the light response curve of Fig. 1.

Diurnal air temperature variations of each month were separated into temperatures during day and night, expressed in the following equations:

$$T_d = f(T_{max}, T_{min}, t, t_m, A) = \frac{T_{max} - T_{min}}{(t_m - A)^2 \cdot \sin\left(\frac{t_m - A}{A}\right)} \cdot (t - A)^2 \cdot \sin\left(\frac{t - A}{A} \cdot \pi\right) + T\min \quad (2)$$

where T_d is temperature (°C) at a given time during the day of t, t (h) is the time after sunrise (t_r), T_{max} is the average maximum temperature (°C) of each month at midday (t_m), T_{min} is the average minimum temperature (°C) of each month, and A is the modification day length (h). Details to obtain Eq. 2 are shown in Appendix.

Temperature at night (T_n) gradually decreases from sunset (t_s) to sunrise of the next day (t'_r). The variation of T_n was well approximated by an exponential decay function as follows:

$$T_n = f(t_n, B, C) = B \cdot t_n^{-C} \quad (3)$$

where T_n is temperature (°C) at a given time during the night of t_n, t_n (h) is the time after sunset (t_s), and B and C are coefficients. The coefficients of Eq. 3 were calculated with the simultaneous equation using the temperature data of T_{min} at sunrise (t_r) and sunset (t_s). In this study, the diurnal variation of temperature in each month was calculated based on an assumption that t_r, t_s, and t'_r was 7:00, 19:00, and 31:00 throughout the year, respectively. The gas exchange properties of this study were measured only in September. Monthly values of photosynthesis and respiration for each month were extrapolated using the gas exchange properties obtained in September.

Estimation of biomass accumulation by growth curve analysis

A growth curve of the stand biomass was calculated by dry weights of some stands at different ages and the given maximum dry weight of stand, using following formula:

$$Y = \frac{D}{1 + E \cdot \exp^{-F \cdot s}} \quad (4)$$

where Y is the stand biomass (kg DW/stand) at the age of s, s is the stand age (yr), D is the maximum stand biomass, E is an integration constant, and F is the growth coefficient showing the maximum value of annual biomass accumulation. The value of E can be calculated by both D and an initial value of Y_0 with a following equation:

$$E = \frac{D - Y_0}{Y_0} \quad (5)$$

The derivative value of the growth curve ($\Delta Y/\Delta T$) was calculated by the following formula, and an

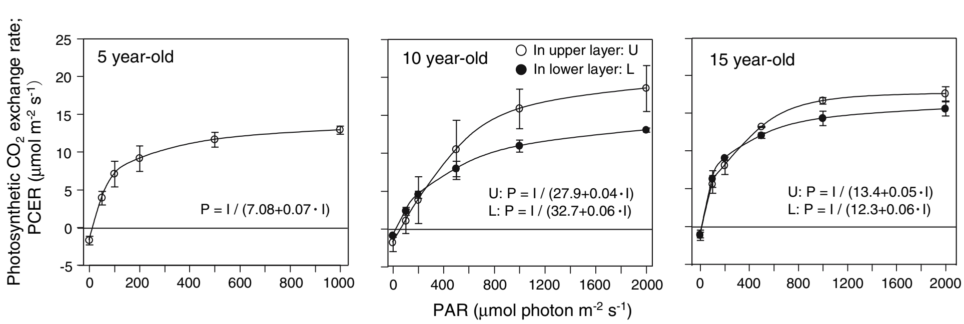

Fig. 1 Light response of photosynthetic CO_2 exchange rate (PCER) measured at leaf temperature of 30°C in the leaves of *Kandelia candel* in 5-, 10-, and 15-year-old stand. In the leaves of 10- and 15-year-old stand, light responses were measured in the leaves in upper (U) and lower-layer (L) of the canopy. PAR in *Y*-axis shows photosynthetically active radiation

annual CO_2 fixation along the stand growth was estimated with this value:

$$\frac{\Delta Y}{\Delta T} = \frac{D \cdot E \cdot F \cdot \exp^{-F \cdot s}}{(1 + E \cdot F \cdot \exp^{-F \cdot s})^2} \quad (6)$$

The maximum stand biomass was assumed to be following three steps; the first one was 33 kg per stem observed in 15-year-old stand biomass. This was because the height of 15-year-old stand (7.12 m) was higher than the prevalent maximum height of *K. candel* stand, showing 7 m (Tomlinson 1986). The second one was 46 kg per stem, which was calculated by dividing the forest biomass of 15-year-old *Rhizophopra apiculata* (100 ton C ha^{-1}; Ong 1993) by the stand density of 15-year-old *K. candel* (52 stems/100 m^2). The third one was 39 kg per stem, which was the average of two maximum stand biomasses as shown above.

Results

Photosynthetic traits of individual leaves

Light response of PCER

Light responses of PCER at 30°C of leaf temperature were shown in Fig. 1. Maximum PCER (P_{max}) at three different stand ages was saturated at over PAR of 1,000 μmol m^{-2} s^{-1}. The highest P_{max} was observed in the upper leaves of 10-year-old stand. The P_{max} value of upper leaves belonging to 5-, 10-, and 15-year-old stand was 17.5, 18.6, and 12.9 μmol m^{-2} s^{-1}, respectively. The photosynthetic capacity of upper leaves was 30% higher than those of lower leaves. The PCER at below 200 μmol m^{-2} s^{-1} was not different between the leaves.

The light responses of PCER were expressed as a following modified rectangular hyperbola:

$$P = \frac{I}{\alpha + \beta \cdot I} \quad (7)$$

where P is PCER of individual leaves at light intensity of I (μmol m^{-2} s^{-1}) and α and β are coefficients to determine the convexity of the hyperbola.

Temperature response of PCER

Temperature responses of PCER in 3-year-old stand (the greenhouse) and in 5-year-old stand (the study site) were shown in Fig. 2. In the greenhouse stand, the PCER was 9.21 μmol m^{-2} s^{-1} and 9.32 μmol m^{-2} s^{-1} at 20.3°C and 35.6°C of leaf temperatures, respectively. Those values were 60% of P_{max}. A quadratic curve was fit for the temperature responses of the greenhouse stand (Fig. 2):

$$P = -0.07x^2 + 3.79x - 37.1 \quad (8)$$

where P is PCER of individual leaves at leaf temperature of x (°C).

While in the research site stand, P_{max} was 16.6 μmol m^{-2} s^{-1} at 26.1°C of leaf temperature. The temperature responses of PCER from 25°C to 33°C of leaf temperature were similar between the plants grown in the different places. In order to use the quadratic curve of the greenhouse stand for the temperature modification in the field, Eq. 8 was moved in parallel by the difference of the PCER at 30°C of leaf temperature.

Canopy structure and light profile in the canopy

The productive structures in the three different forest of *K. candel* were shown in Fig. 3. Leaf area index (LAI) of 5-, 10-, and 15-year-old canopy was 4.2, 6.8, and 3.0, respectively. The majority of leaf in each canopy was distributed in the middle or lower layer of the 5- and 10-year-old canopy, and in the top layer

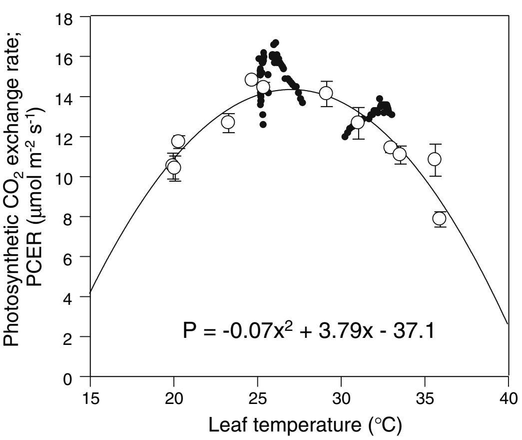

Fig. 2 Temperature response of photosynthetic CO_2 exchange rate (PCER) measured in the leaves of *Kandelia candel*, in both 3-year-old stand in greenhouse (○) and 5-year-old stand in situ condition in Thanh Hoa, Vietnam (•). A quadratic curve in the graph was a regression of temperature response of PCER

of the 15-year-old canopy. Light extinction coefficient (K) was obtained by relating cumulative leaf area and logarithms of relative light intensities of each layer. K in the 5-, 10-, and 15-year-old canopy was 0.23, 0.22, and 0.25, respectively (Fig. 3).

Temperature responses of RCER in each organ

Temperature responses of RCER in above-ground organ and root were shown in Figs. 4 and 5, respectively. The highest RCER was observed in sprouts of leaf, 18.2 μmol kg^{-1} s^{-1}, which were 1.7 times higher than those of leaves. Average RCER in each organ was the lowest in branches, which was about 35% of those in leaves. The RCER of green branches was 3–4 times higher than that of the brown branches. The RCER in roots was similar to that of the above-ground organs (Fig. 5). The RCER of the first lateral roots was slightly higher than that of the second lateral roots.

The temperature response of RCER was well regressed with an exponential equation:

$$Y = H \cdot \exp^{J \cdot X} \quad (9)$$

where Y is the RCER (μmolCO_2 kg^{-1} s^{-1}), X is the sample temperature (°C), and H and J are coefficients (Table 1).

Above- and below-ground biomass

The biomass of each organ in a single stand at different ages was expressed as dry weight (Fig. 6), surface area, and volume (data not shown). The total dry weight of the 5-, 10-, and 15-year-old single stands was 4.48, 11.5, and 31.3 kg DW, respectively. Their total dry weight per unit hectare was 28.9, 102, and 163 ton DW, respectively.

Most of the parts in above-ground stand were composed of lignified brown trunk and first branches. Dry weight of leaves belonging to 10- and 15-year-old stand were almost the same. They were 2.3 times higher than those of the 5-year-old stand. Root biomass was mainly composed of the main roots. The ratio of dry weights of the main roots was about 43, 36, and 58%, respectively. Their T/R ratios (the ratio of total weight of above-ground biomass to dry weight of the root) were 1.45, 3.85, and 2.54, respectively. These T/R ratios were similar with those of the mangrove forest of *Xylocarpus granatum* in Thai, showing 0.95–2.14 (Pongparn et al. 2002).

Estimation of CO_2 absorption

Photosynthetic CO_2 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 Eqs. 1–3, 7, and 8. Seasonal changes of CO_2 absorption corrected for the monthly variation of light and temperature were shown in Fig. 7. Monthly values of the CO_2 absorption tended to decrease in May–August. A slight decrease of the CO_2 absorption was noted in February because it is a shorter month. Monthly values of CO_2 absorption in September of

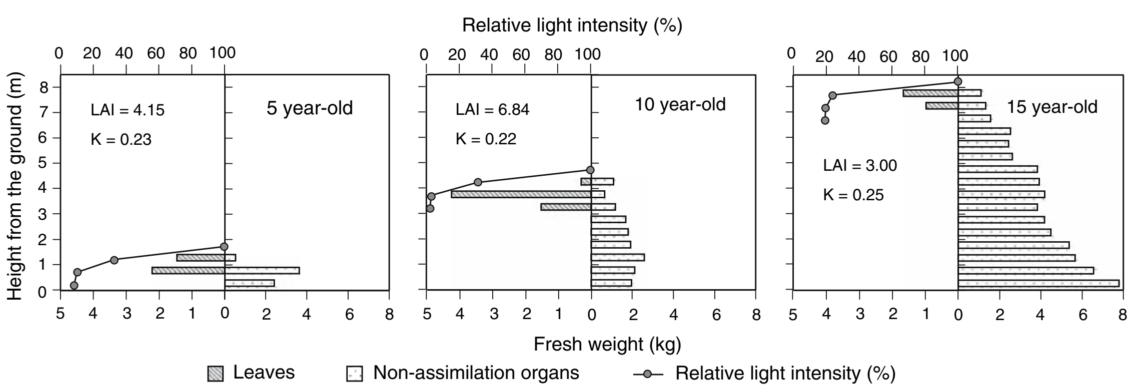

Fig. 3 Canopy structure and light profile in 5-, 10-, and 15-year-old canopy of *Kandelia candel* measured with stratified clip method. LAI and K in the graph show leaf area index and a light extinction coefficient, respectively

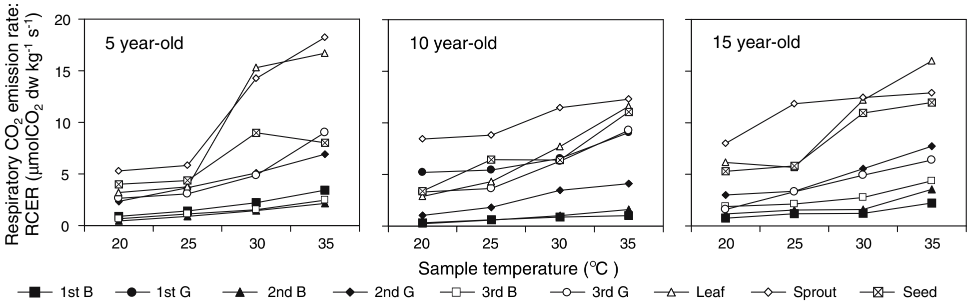

Fig. 4 Temperature response of respiratory CO_2 emission rate (RCER) of each organ in above-ground in three kinds of stand age. The values of respiration rate in the graph were calculated per unit of dry weight of each organ. The branches were divided into three offshoot groups; the first, second, and the third offshoots. "B = brown surface of the branch; G = green surface of the branch"

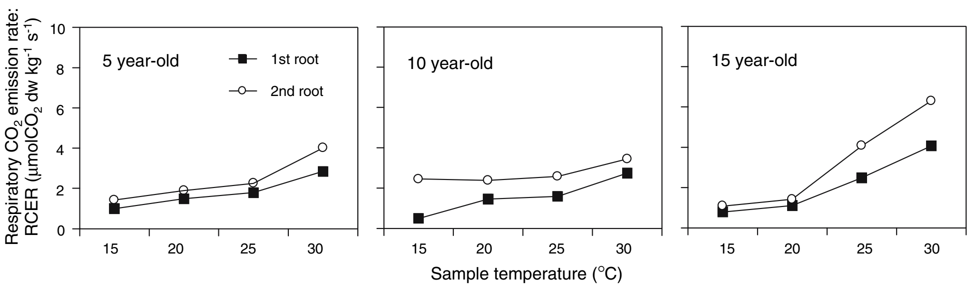

Fig. 5 Temperature response of respiratory CO_2 emission rate (RCER) of roots in three kinds of stand age. The values of RCER here were calculated in the unit of dry weight of roots

Table 1 Parameters of an exponential regression formula ($Y = H \cdot \exp^{J \cdot X}$), which was consistent with temperature response of RCER (respiratory CO_2 emission rate) of each organ in three kinds of stand age

	1st B	1st G	2nd B	2nd G	3rd B	3rd G	Leaf	Sprout	V.S.	1st root	2nd root
5-year-old											
H	0.15	–	0.07	0.57	0.13	0.47	0.23	0.75	1.28	0.38	0.49
J	0.09	–	0.10	0.07	0.08	0.08	0.13	0.09	0.06	0.07	0.07
R^2	1.00*	–	0.99*	0.98*	0.99*	0.94	0.86	0.90	0.77	0.97**	0.95**
10-year-old											
H	0.07	2.28	0.02	0.15	–	0.68	0.43	4.65	0.89	0.13	1.61
J	0.08	0.04	0.14	0.10	–	0.07	0.09	0.03	0.07	0.10	0.02
R^2	0.90	0.89	0.95**	0.95**	–	0.94	0.99*	0.92	0.90	0.90	0.77
15-year-old											
H	0.24	–	0.29	0.73	0.57	0.29	1.25	4.90	1.46	0.13	0.15
J	0.06	–	0.07	0.07	0.06	0.09	0.07	0.03	0.06	0.11	0.13
R^2	0.88	–	0.82	0.95**	0.93	0.95**	0.84	0.75	0.89	0.97**	0.94

The branches were divided into three offshoot groups; the first, second, and the third offshoots. ''B = brown surface of the branch; G = green surface of the branch''

R^2 is a coefficient of determination

*Significant at 2% level; **significant at 5% level

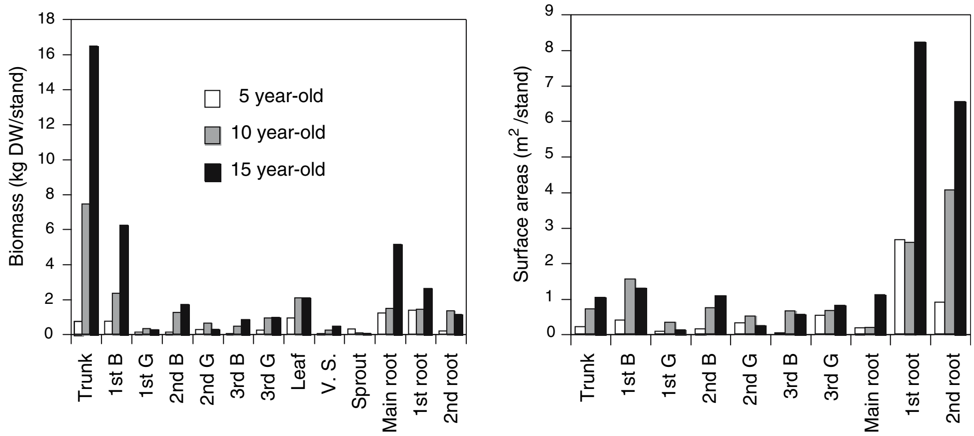

Fig. 6 Biomass of each organ in one stand of *Kandelia candel* in three kinds of stand age. The dry weight was calculated by multiplying fresh weight by water content. In *Y*-axis, B shows brown part of the branch, G shows green parts of the branch, and V.S. shows viviparous seed

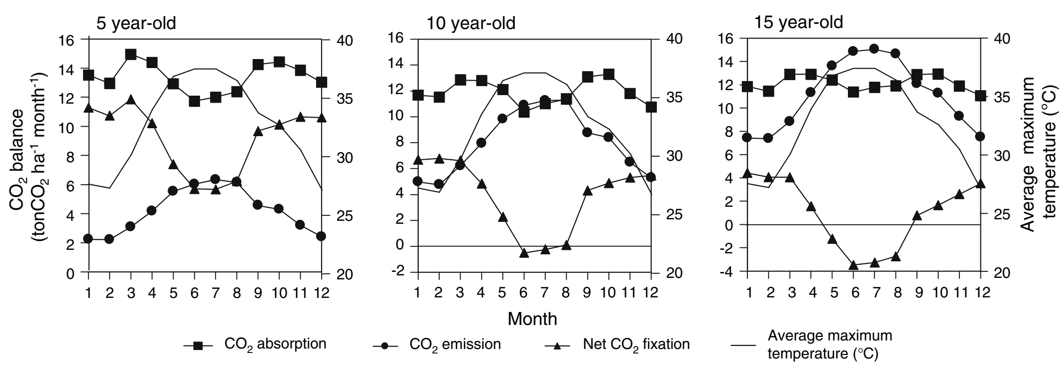

Fig. 7 Monthly variations of the amount of above-ground CO_2 balance in the canopy of *Kandelia candel* in three kinds of stand age in Thanh Hoa, Vietnam

5-, 10-, and 15-year-old canopy were 14.2, 13.1, and 12.9 tCO_2 ha^{-1} month^{-1}, respectively (Table 2).

Estimation of CO_2 emission

Diurnal change of RCER was determined by the temperature at a given time of the day (Eqs. 2 and 3) and the regression curve of the temperature response of RCER in each organ (Eq. 9, Table 1). The RCER per unit of dry weight was used to estimate CO_2 emission of each organ. However, for the calculation of CO_2 emission from the trunk and the main root, the RCER per unit of surface area was used. This was measured in the brown part of the first branch. Because Yoda (1971) has shown that physiological activity of large-diameter tissues was limited only to the epidermis and cambium layers. The respiration rate of the large-diameter tissue was proportional to its surface area. The CO_2 emission from the leaves was estimated by the RCER per unit leaf area during the night. To correct the root RCER in response to variable temperatures, mean monthly value of sea-water temperature was used. This was obtained near the research site. The mean monthly value of the temperature was 23.3°C at maximum in July and 16.0°C at minimum in February (Dao 2002). Seasonal changes of CO_2 emission were shown in Fig. 7. Monthly CO_2 emission tended to be higher in June, July, and August but lower in January and February. The monthly values of CO_2 emission in September of 5-, 10-, and 15-year-old forest were 4.56, 8.77, and

Table 2 Monthly values of absorption, emission, and net fixation of CO_2 estimated with the gas exchange method, in the forest of *Kandelia candel* in three kinds of forest age in Thanh Hoa, Vietnam

Month	Absorption	Respiration								Net Fixation	
		Branch	Trunk	Leaf	Sprout	V.S.	Total in above-ground	Root	Total in whole stand	In above-ground	In whole stand
5-year-old forest											
1	13.5	1.00	0.15	0.27	0.50	0.31	2.24	1.37	3.61	11.3	9.91
2	12.9	0.99	0.15	0.27	0.49	0.31	2.21	1.19	3.41	10.7	9.54
3	14.9	1.35	0.21	0.43	0.69	0.40	3.09	1.61	4.70	11.9	10.2
4	14.4	1.83	0.30	0.59	0.96	0.50	4.17	1.76	5.93	10.2	8.45
5	12.9	2.42	0.40	0.78	1.30	0.62	5.52	1.90	7.43	7.39	5.49
6	11.7	2.58	0.43	0.97	1.40	0.65	6.02	1.94	7.97	5.70	3.75
7	12.0	2.70	0.45	1.05	1.47	0.67	6.34	2.31	8.64	5.66	3.36
8	12.4	2.54	0.42	1.17	1.37	0.64	6.15	2.25	8.40	6.23	3.97
9	14.2	1.94	0.32	0.75	1.03	0.53	4.56	2.11	6.68	9.68	7.57
10	14.4	1.80	0.29	0.76	0.94	0.50	4.30	1.89	6.19	10.1	8.24
11	13.8	1.39	0.22	0.47	0.71	0.41	3.20	1.49	4.69	10.6	9.16
12	13.0	1.07	0.17	0.29	0.54	0.34	2.41	1.47	3.88	10.6	9.14
Total	160	21.6	3.51	7.81	11.4	5.89	50.2	21.3	71.5	110	88.8
10-year-old forest											
1	11.7	2.51	0.23	1.49	0.33	0.43	4.99	2.43	7.42	6.68	4.25
2	11.5	2.48	0.23	1.36	0.30	0.38	4.75	2.15	6.90	6.79	4.64
3	12.8	2.97	0.28	2.10	0.36	0.51	6.22	2.68	8.90	6.63	3.95
4	12.8	3.97	0.39	2.56	0.39	0.66	7.96	2.80	10.8	4.84	2.04
5	12.1	4.96	0.49	3.10	0.44	0.84	9.84	2.98	12.8	2.27	–0.72
6	10.4	5.42	0.54	3.60	0.45	0.88	10.9	2.99	13.9	–0.51	–3.50
7	11.0	5.49	0.55	3.84	0.46	0.92	11.3	3.40	14.7	–0.24	–3.65
8	11.4	5.18	0.51	4.26	0.45	0.88	11.3	3.35	14.6	0.10	–3.25
9	13.1	4.19	0.41	3.07	0.40	0.69	8.77	3.17	11.9	4.32	1.15
10	13.3	3.81	0.37	3.17	0.40	0.65	8.40	2.97	11.4	4.89	1.92
11	11.8	3.12	0.30	2.20	0.35	0.52	6.50	2.52	9.02	5.31	2.79
12	10.8	2.45	0.22	1.88	0.33	0.42	5.30	2.53	7.83	5.46	2.93
Total	143	46.6	4.51	32.6	4.66	7.79	96.2	34.0	130	46.5	12.6
15-year-old forest											
1	11.8	3.97	1.48	1.17	0.13	0.68	7.43	4.17	11.6	4.42	0.25
2	11.4	3.94	1.47	1.17	0.13	0.68	7.38	3.99	11.4	4.07	0.08
3	12.9	4.72	1.72	1.47	0.14	0.79	8.84	5.05	13.9	4.05	–1.00
4	12.9	6.26	2.19	1.70	0.16	1.01	11.3	5.85	17.2	1.58	–4.27
5	12.4	7.75	2.63	1.86	0.17	1.21	13.6	6.19	19.8	–1.23	–7.41
6	11.4	8.43	2.83	2.11	0.18	1.30	14.9	6.61	21.5	–3.48	–10.1
7	11.8	8.53	2.86	2.16	0.18	1.32	15.0	7.84	22.9	–3.27	–11.1
8	11.9	8.09	2.74	2.38	0.18	1.26	14.6	7.62	22.3	–2.74	–10.4
9	12.9	6.62	2.30	1.94	0.16	1.06	12.1	7.34	19.4	0.78	–6.55
10	12.9	6.04	2.13	1.97	0.16	0.98	11.3	6.13	17.4	1.66	–4.47

Table 2 continued

Month	Absorption	Respiration								Net Fixation	
		Branch	Trunk	Leaf	Sprout	V.S.	Total in above-ground	Root	Total in whole stand	In above-ground	In whole stand
11	11.9	4.96	1.79	1.56	0.14	0.83	9.28	4.78	14.1	2.61	–2.17
12	11.1	3.88	1.45	1.38	0.13	0.67	7.52	4.52	12.0	3.54	–0.98
Total	145	73.2	25.6	20.9	1.87	11.8	133	70.1	203	12.0	–58.1

Units of values are all in tCO_2 ha^{-1} $month^{-1}$. ''Whole = a total value in both above- and below-ground and V.S. = viviparous seed''

12.1 tCO_2 ha^{-1} $month^{-1}$ in above-ground, and 2.11, 3.17, and 7.34 tCO_2 ha^{-1} $month^{-1}$ in below-ground, respectively (Table 2).

Estimation of net CO_2 fixation

Monthly changes of the amount of CO_2 absorption, CO_2 emission, and net CO_2 fixation were shown in Fig. 7. Monthly values of net CO_2 fixation in September of 5-, 10-, and 15-year-old forest was 9.68, 4.32, and 0.78 tCO_2 ha^{-1} $month^{-1}$ (2.64, 1.18, and 0.21 tC ha^{-1} $month^{-1}$) in above-ground, and 7.57, 1.15, and –6.55 tCO_2 ha^{-1} $month^{-1}$ in the whole stand, respectively (Table 2). The monthly values of net CO_2 fixation of 10- and 15-year-old forest were in part negative values.

Estimation of CO_2 fixation capacity by the growth curve analysis

Dry weight accumulations as a function of time in the growth curve analysis were shown in Fig. 8. All the growth curves corresponded well to the dry weights of the single stands measured at different three ages. Annual growth rates of the total stand biomass of 5-, 10-, and 15-year-old stand calculated by derivative values of the growth curve were 1.00, 3.82, and 4.39 kg DW $stand^{-1}$ yr^{-1}, in which the maximum

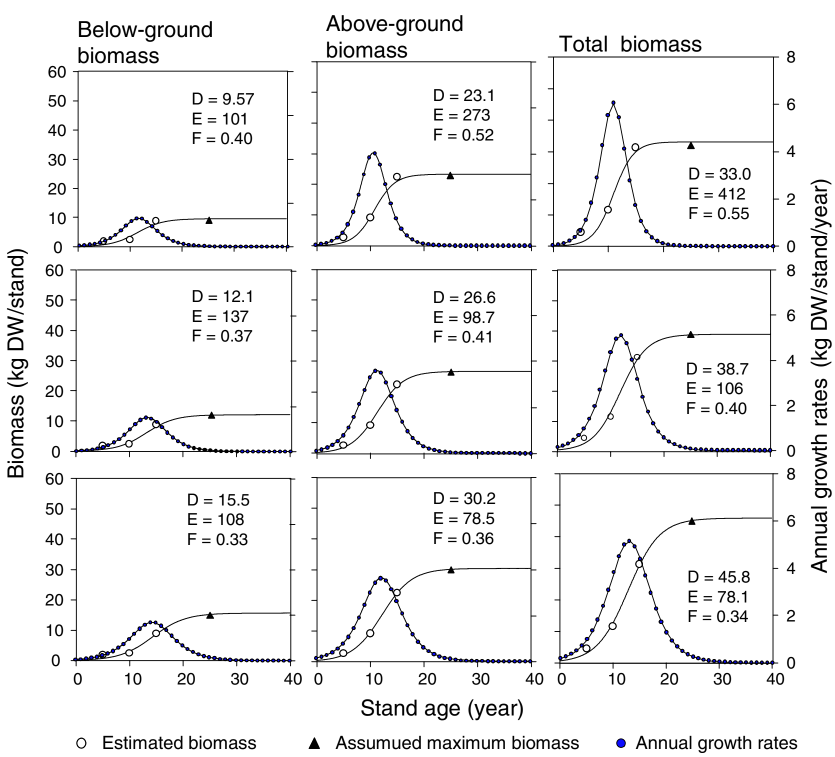

Fig. 8 Growth curves made with both estimated stand biomass, above- and below-ground biomass and total stand biomass in three kinds of stand age in Thanh Hoa, Vietnam. Maximum stand biomass was assumed in three levels, details referred in ''Materials and methods''. Values of D, E, and F show the parameters of growth curve equation of $Y = D/(1 + E \cdot \exp^{-F \cdot s})$, where D is an assumed maximum stand biomass, $E = (D - Y_0)/Y_0$ where Y_0 is an initial value of stand biomass, s is a stand age, and F is a growth coefficient

Table 3 Comparison of both CH_2O productivity obtained in gas exchange analysis and annual biomass accumulation in growth curve analysis (ton ha^{-1} yr^{-1} in the forest, kg $stand^{-1}$ yr^{-1} in one stand)

Stand age	Gas exchange analysis				Growth curve analysis				
	Forest		Stand		Forest			Stand	
	Above-ground	Total	Above-ground	Total	Above-ground	Root	Whole	Above-ground	Whole
5	75.1	60.6	11.6	9.39	4.96	1.48	6.45	0.77	1.00
10	31.7	8.56	3.57	0.96	26.6	8.42	34.0	2.99	3.82
15	8.18	–39.6	1.57	–7.62	13.6	8.63	22.8	2.62	4.39

In table, ''Whole'' shows the summed value of above- and below-ground biomass

value of the total stand biomass was postulated at 45.8 kg DW $stand^{-1}$ (Fig. 8). The net CO_2 fixation capacity of 5-, 10-, and 15-year-old canopy estimated by growth curve analysis was 6.45, 34.0, and 22.8 ton ha^{-1} yr^{-1} (Table 3), and was calculated by multiplying the annual growth rates of single stand by the stand density (64.5, 89.0, and 52.0 stems/100 m^2), respectively. The derivative values described in Eq. 6 can be substituted for the actual biomass accumulations of the stand in each growth stages. Hence, the growth curve estimations could be used as a reference value of net CO_2 fixation capacity of this study.

Discussion

In this study, net CO_2 fixation capacity of *K. candel* monoculture forest was evaluated by the gas exchange analysis and the growth curve analysis.

Validity of the gas exchange analysis

Annual values of net CO_2 fixation in 5-, 10-, and 15-year-old forest were extrapolated using the gas exchange properties measured in September. They were estimated as 104, 50.2, and 5.33 tCO_2 ha^{-1} yr^{-1} in above-ground and 83.1, 16.3, –64.8 tCO_2 ha^{-1} yr^{-1} in the whole stand, respectively (Table 2).

The gas exchange analysis in this study was sufficient to conduct an adequate estimation of mangrove productivity, compared to the results of gas exchange studies reported previously (Bunt et al. 1979; Boto et al. 1984; Clough et al. 1997; Clough 1998; Ong et al. 1995). Annual values of carbon accumulation of 12.7 tC ha^{-1} yr^{-1} in above-ground 10-year-old forest (Table 2) was consistent with those of 10-year-old *R. apiculata* forest in Malaysia estimated by the allometric method (14.0 tC ha^{-1} yr^{-1}) (Ong 1993). In addition, annual values of dry matter accumulation of 31.7 ton ha^{-1} yr^{-1} in above-ground biomass of 10-year-old forest (Table 3) was also approximated to those of 15-year-old *R. apiculata* forest in Thailand, and estimated by the allometric method (27 ton ha^{-1} yr^{-1}) (Christensen 1978). These results suggested that this gas exchange analysis would be useful for estimating of mangrove productivity.

Ong et al. (1995) have also shown that net productivity of above-ground 20-year-old *R. apiculata* in Malaysia estimated by the allometric method was compared with those estimated by the gas exchange method using the mean value for a whole day's net photosynthesis measurement (6 μmol m^{-2} s^{-1}) and leaf respiration (1.5 μmol m^{-2} s^{-1}). They did not estimate the RCER of non-leaf tissues and below-ground biomass. They assumed that RCER of the non-leaf tissues was the same as for leaves. We estimated the respiratory CO_2 emission to develop the estimation of the net CO_2 fixation by the gas exchange analysis.

In this study, the net CO_2 fixation capacity with the gas exchange analysis was estimated by the difference between CO_2 absorption and CO_2 emission. Many studies on the productivity of mangrove forests indicated that reliable measurements of respiration by woody tissues and below-ground roots are critically needed (Gong and Ong 1990; Ong et al. 1995; Clough et al. 1997; Clough 1998). Although the gas exchange method reported previously was corrected only for light intensity (Bunt et al. 1979; Boto et al. 1984; Clough et al. 1997; Clough 1998; Ong et al. 1995), in addition to the correction by light intensity, we have used the temperature correction of PCER of individual leaves (Fig. 2) and RCER of each organ (Figs. 4 and 5).

We realize that the gas exchange properties of this study were obtained in a short period (September), which may be not representative data to estimate annual budgeting of the CO_2 balances. Moore et al. (1973) reported that mangrove leaves of *Avicennia*, *Rhizophora*, and *Laguncularia* showed a shift to higher optimum temperatures for photosynthesis. Also, respiratory properties in each part of the stand may need to be considered in this point. Seasonal variations of the gas exchange properties could be the next topic, which will improve the accuracy of annual budgeting with the gas exchange method of this study.

Validity of the growth curve analysis

The growth curve analysis was as effective in estimating mangrove productivity as the allometric method. The growth curve analysis showed the annual biomass accumulations of *K. candel* forest ranged from 6.45 to 34.0 ton ha^{-1} yr^{-1} (Table 3). This result was similar to those of over 5-year-old mangrove trees of mixed species such as *Rhizophora stylosa*, *R. apiculata*, and *Ceriops australis* in Australia (5.9 ton ha^{-1} yr^{-1}) (Clough 1998) and 11- to 14-year-old *R. apiculata* forest in Thailand (27 ton ha^{-1} yr^{-1}) (Christensen 1978), both of which were estimated by the allometric method. These results suggested that the growth curve analysis could be an alternative method to the allometric method to estimate net CO_2 fixation capacity of mangrove forest. Furthermore, the growth curve analysis showed that the biomass of *K. candel* stand attains the maximum at around 25 years after forestation (Fig. 8).

A growth curve derived from the gas exchange analysis

Based on the validity of the values of the two models constructed for the same forest, the above-ground biomass accumulation of 10-year-old stand estimated by gas exchange analysis (31.7 ton ha^{-1} yr^{-1}) was closely compared to those of growth curve analysis calculated by direct measurements of stand biomass (26.6 ton ha^{-1} yr^{-1}) (Table 3). This result suggested that the gas exchange analysis was an effective estimation of mangrove productivity. In addition, these values were also approximated to the maximum biomass accumulation at 12-year-old (32.2 ton ha^{-1} yr^{-1}) estimated by the growth curve in which the maximum biomass of the above-ground stand was postulated at 30.2 kg DW $stand^{-1}$ (Fig. 8). The growth curve is determined by the maximum biomass and the growth coefficient, which corresponds to the maximum biomass accumulation rate (Eq. 4). In establishing the growth curve, the maximum biomass can be substituted for a reference value, but it is difficult to obtain a reasonable value of the growth coefficient. As described above, our results showed that the above-ground biomass accumulation estimated by the gas exchange analysis (31.7 ton ha^{-1} yr^{-1}) fitted closely to the maximum biomass accumulation estimated by the growth curve analysis (32.2 ton ha^{-1} yr^{-1}). This finding suggested that the gas exchange analysis was effective in estimating the growth coefficient of the growth curve. Moreover, the gas exchange analysis can estimate the biomass accumulation in accordance with meteorological factors such as temperature and radiation at the study site. Although there are some insufficiencies in the gas exchange analysis of this study as described later, it is possible to suggest that the gas exchange analysis can establish the growth curve to predict the biomass accumulation in a new plantation area by estimating the growth coefficient of the growth curve.

Factors causing the discrepancy of CO_2 fixation estimations

Some discrepancies of the biomass accumulation estimations in whole plants were noted (Table 3). The value estimated by gas exchange analysis of 5-year-old trees was larger, while those of 10- and 15-year-old trees were smaller, compared to the values estimated by growth curve analysis. On the discrepancy for the value of 5-year-old trees (Table 3), litter fall could be one of the reasons. The values of gas exchange analysis contained the litter fall as a part of the photosynthetic productions, while the values of growth curve analysis did not contain the litter fall because it was calculated based on the amounts of living organs of the stand. It was noted that about 8% of the total amount of photosynthetic CO_2 absorption was litter fall (Clough et al. 1997), which was equivalent to 2–6 tC ha^{-1} yr^{-1} (Ong 1993). Also noted were differences in the estimated biomass of 5-year-old trees, which were larger than the amount of litter fall (Table 3), indicating there could be other reasons for this discordance.

Another reason for the deviation in the values of 5-year-old trees could be an overestimation of the photosynthetic CO_2 absorption. This discordance is prominent, if root biomass of a single stand was completely collected and the effect of exudation of organic compounds (Clough 1998) ignored in the values of the growth curve analysis. In this study, the CO_2 absorption was calculated using the value of PCER in the light response curve (Fig. 1). Cheeseman (1994) has reported that PCER under the artificial light condition on *Bruguiera parviflora* leaves were 35 ± 25% higher than the values obtained under natural sunlight. In addition, leaf areas in the trees could have been overestimated by quadrate sampling (Fig. 3), nevertheless the 5-year-old trees have some canopy gaps between the stands that grow scattered at certain intervals (64.5 stems/ 100 m^2).

On the discrepancy for the values of 15-year-old forest (Table 3), overestimation of CO_2 emission could be one reason, because the amount of CO_2 absorption in this study (Table 2) was similar to those reported elsewhere on mangrove forests of other species (Clough et al. 1997). The overestimation was also suggested by the ratio of emission (E) to absorption (A) of CO_2 (E/A). It has been reported that the E/A is 25–50% in terrestrial forest species (Landberg 1986) and 80–90% in other mangrove forests (Ong 1993). The E/A in this study tended to be higher than these values. In 15-year-old stand, the E/A was 96% for above-ground and 145% for above- and below-ground (Fig. 7, Table 2). The respiratory CO_2 emission was calculated by measuring RCER of each organ with temperature modification. Therefore, the overestimation could have arisen mainly from the temperature modification that corrected the RCER of each organ for variable temperature.

The value of temperature derived from its diurnal variation model (Fig. 9) might also contribute to the overestimation of CO_2 emission. The CO_2 emission

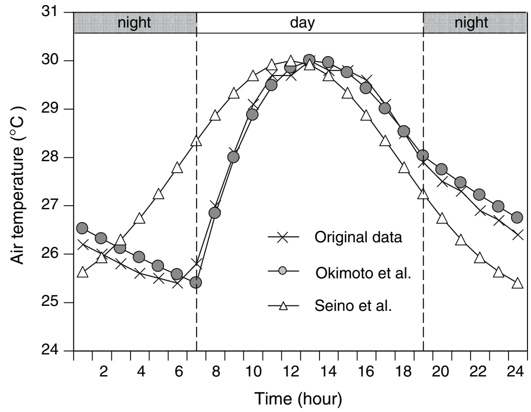

Fig. 9 Comparison of diurnal change in air temperature between original data and calculated values both of this study and Seino et al. (1981). Details are shown in Appendix. Data of temperature was calculated based on September in Nam Dinh, near to the study site of Thanh Hoa, Vietnam

from all organs, such as leaves on top of the canopy and trunks inside the canopy, was calculated using the diurnal variations of temperature based on this model. Ong et al. (1995) reported that the temperature at the top of the canopy was about 10°C higher than those at ground level, suggesting that the temperature used in this study might be substantially higher than the actual temperatures in the canopy. Temperature influences emission and absorption of CO_2, its influence on CO_2 emission was more than on CO_2 absorption. For example, the RCER of branches at 35°C was three times higher than those at 20°C (Fig. 5), whereas the PCER of leaves at above 30°C was only 20% lower than those at 26.1°C (Fig. 2). Thus, temperatures inside the canopy and of diurnal variation should be used to improve the accuracy to estimate net CO_2 fixation adequately. The development of temperature modification will make the gas exchange analysis the most effective method to estimate net CO_2 fixation capacity of mangrove forests.

To apply mangrove productivity for a CDM project that achieve reductions of greenhouse CO_2, reliable and convenient methods are essential for an adequate estimation of the net CO_2 fixation capacity of mangrove forests. The gas exchange analysis could be effective and convenient to gather data in a short time, and be applicable in forests growing different environmental conditions in various regions. Further studies on estimation of respiratory CO_2 emission and below-ground biomass of the stand in the managed mangrove plantations will increase the accuracy of gas exchange and growth curve analysis.

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Appendix

Approximation to diurnal temperature variation

A model for predicting diurnal variations of air temperature using the maximum and minimum temperatures has been developed. In this model, a truncated sine curve was used to predict temperature variations during the day and an exponential function was used to predict temperature variations during the night. Mathematical descriptions of the model were shown in ''Materials and methods'' as Eqs. 2 and 3. The model was compared with a modified sine curve model using a cubic sine function (Seino et al. 1981). The diurnal variations of the temperature calculated by the model of this study were more approximated with the real values of temperature (Fig. 9).

Approximation model of temperature variation in daytime

Temperature variation during the day from sunrise to sunset showed asymmetric curve with respect to T_{max} at midday (Fig. 9). It was assumed that the temperature variation during the day could be approximated with the following equation, which inverted an asymmetric sine curve of $Y = x^2 \cdot \sin x$ (Fig. 10a) with respect to the Y-axis (Fig. 10b):

$$Y = -x^2 \cdot \sin x (-\pi < x < 0) \tag{10}$$

If the temperature variation during the day (T_d) from sunrise (t_r) to sunset (t_s) was approximated with the truncated sine curve of Eq. 10, the condition of these variables were as follows:

$$t_r \leqq t \leqq t_s \tag{11}$$

$$T_{\min} \leqq T_d \leqq T_{\max} \tag{12}$$

where $T_{\min}$ is the minimum temperature and $T_{\max}$ is the maximum temperature of each month.

To express the temperature variation during the day by Eq. 10, the truncated sine curve was moved to the X axis by the length of π to fit the sunrise time (t_r) with the origin (Fig. 10c):

$$T_d = -(t - \pi)^2 \cdot \sin\left(\frac{t-\pi}{\pi} \cdot \pi\right) \tag{13}$$

To express the temperature at t_s by Eq. 13, the length of the truncated curve (π) was accorded with A, which was sum of the day length (L) and an arbitrary time (γ) (Fig. 10d).

$$T_d = -(t - A)^2 \cdot \sin\left(\frac{t-A}{A} \cdot \pi\right) \quad A = L + \gamma \tag{14}$$

In addition, to correspond an amplitude of Eq. 14 to that of the temperature variation during the day, the modification rate of δ was multiplied (Fig. 10e). It was calculated by dividing a daily difference of the temperature ($T_{\max} - T_{\min}$) from the value of temperature at midday (t_m).

$$\delta = \frac{T_{\max} - T_{\min}}{-(t_m - A)^2 \cdot \sin\left(\frac{t_m - A}{A} \cdot \pi\right)} \tag{15}$$

To correspond the modification amplitude of the truncated curve to the temperature variation during the day, the truncated curve of $Y = -x^2 \cdot \sin x$ was moved to the Y-axis by $T_{\min}$ (Fig. 10f).

$$T_d = \frac{T_{\max} - T_{\min}}{(t_m - A)^2 \cdot \sin\left(\frac{t_m - A}{A} \cdot \pi\right)} \cdot (t - A)^2 \cdot \sin\left(\frac{t-A}{A} \cdot \pi\right) + T_{\min} \tag{16}$$

Following these procedures on t and T_d, the truncated sine wave based on Eq. 10, satisfying the both condition of 11 and 12 was defined. The temperature variation during the day was approximated with Eq. 16, which equals to Eq. 2 as shown in ''Materials and methods''.

Examining on the variable A with the meteorological data of September (about 12 h of day length) at Nam Dinh (Nguyen et al. 2004) where is close to the study site, the most appropriate value of A was 18.

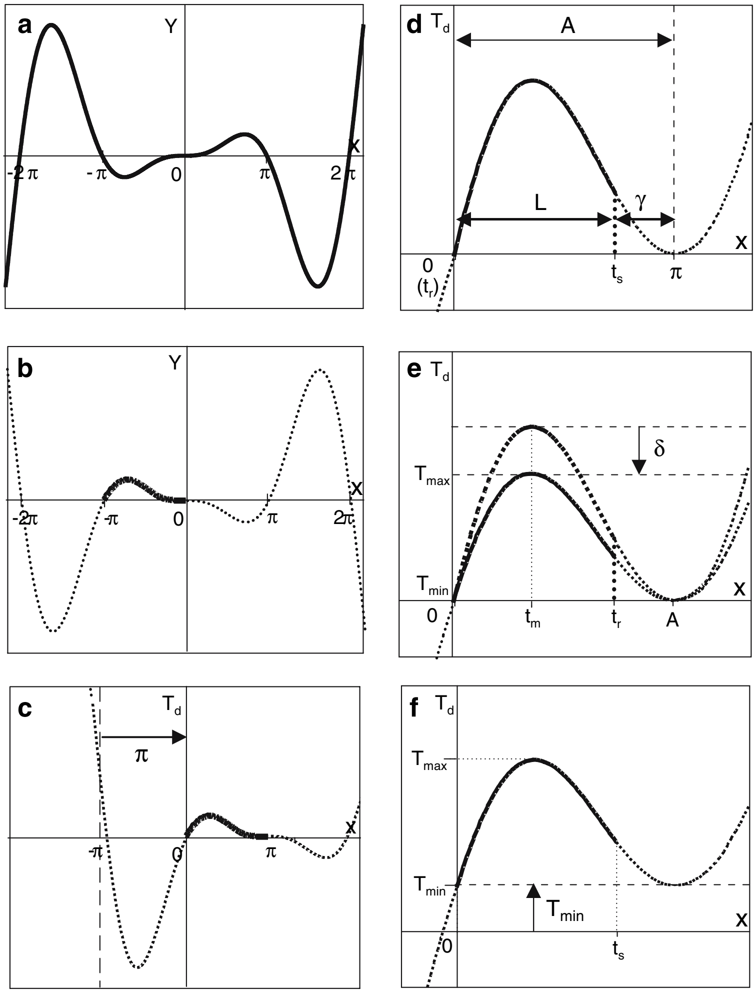

Fig. 10 Procedures to approximate the temperature variation during the day. *L*, day length of each month (h); *x*, time in daytime (h); x_r, time at sunrise (h); x_s, time at sunset (h); x_m, midday time at T_{max} (h); T_d, temperature in daytime (°C); T_{max}, maximum temperature of each month (°C); T_{min}, minimum temperature of each month (°C); *γ*, modified coefficient; *A*, modified day-length ($A = L + \gamma$); *δ*, modification rate of the amplitude of the curve

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