

# Canopy photosynthesis, canopy respiration and surplus production in a subtropical mangrove *Kandelia candel* forest, Okinawa Island, Japan

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**ABSTRACT:** The gross photosynthesis and respiration rates of leaves at different canopy depths in a *Kandelia candel* (L.) Druce stand were measured monthly over 2 yr. The maximum gross photosynthesis and dark respiration rates of the leaves existing at the top of the canopy were respectively 2 to 4 times and 2 to 7 times those of the bottom leaves throughout the year. The maximum gross photosynthesis and dark respiration rates showed positive correlations with leaf nitrogen content. Daily canopy gross photosynthesis and respiration showed apparent seasonal changes. The annual canopy gross photosynthesis, canopy respiration and surplus production were estimated as  $102.9 \pm 1.5$ ,  $44.0 \pm 2.1$  and  $58.9 \pm 0.6$  (SE) t CO<sub>2</sub> ha<sup>-1</sup> yr<sup>-1</sup>, respectively. The energy efficiency for the annual gross photosynthesis was  $2.4 \pm 0.1$  (SE) %. Optimum leaf area index (LAI) for annual surplus production was 4.54 m<sup>2</sup> m<sup>-2</sup>, which was almost the same as the actual LAI of 4.50 m<sup>2</sup> m<sup>-2</sup>. The neglect of seasonal changes in the physiological traits of leaves resulted in estimates that were 65 to 125 % of the annual surplus production. The relationship of gross primary production (GPP) to the product of LAI and warmth index (WI) was similar to those established for various types of terrestrial forests in perhumid climates.

**KEY WORDS:** *Kandelia candel* · Photosynthesis · Respiration · Surplus production · Optimum leaf area index · Sun leaf · Shade leaf · Subtropical mangrove forest

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## INTRODUCTION

Mangrove forests have been recognized as an important source of carbon sequestration (Komiya et al. 2000, Alongi et al. 2001, Fujimoto 2004). The rapid rates of primary production and slow rates of sediment carbon decomposition bring about the preservation of huge amounts of organic carbon in mangrove forests (e.g. Alongi et al. 2001). Therefore, reliable estimates of canopy photosynthesis in mangrove forests is necessary for ecological studies and forest management options.

There are only a few reports on the canopy photosynthesis of mangrove forests. Clough et al. (1997) estimated net daytime canopy photosynthesis (gross canopy photosynthesis minus canopy respiration during the daytime) in a *Rhizophora apiculata* stand in

Malaysia. Furthermore, Clough (1998) estimated net daytime canopy photosynthesis in a mixed mangrove forest in Western Australia. However, these studies did not consider seasonal variations in the physiological traits of leaves when calculating the annual canopy photosynthesis. Many reports have confirmed seasonal changes in photosynthesis and dark respiration rates of leaves for terrestrial forests (Hozumi et al. 1972, Hagihara & Hozumi 1977a,b, Nishioka et al. 1978, Kurachi et al. 1992, Katsuno-Miyaura et al. 1995). Therefore, seasonal changes in photosynthesis and dark respiration rates of leaves are probably necessary for obtaining reliable estimates of annual canopy photosynthesis and respiration in mangrove forests.

Generally, leaves show physiological changes along the vertical profile of light penetration within a canopy. Many studies confirmed that sun leaves showed

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higher maximum photosynthesis and dark respiration rates than those of shade leaves (Kira et al. 1969, Hozumi & Kirita 1970, Hagihara & Hozumi 1977b). These adaptations of physiological traits to the light environment within a canopy are due to changes in leaf nitrogen content (Hirose & Werger 1987). Mangrove species also show changes in physiological traits in accordance with changes in the light environment (Ball & Critchley 1982, Farnsworth & Ellison 1996). Therefore, vertical changes as well as seasonal changes in the physiological traits of leaves should be considered when estimating the annual canopy photosynthesis and respiration in mangrove forests.

Monsi & Saeki (1953) were the first to provide a mathematical model of canopy photosynthesis. Later studies incorporated physiological adaptations of leaves to light profiles within a canopy (Hozumi & Kirita 1970) and light absorption by leaves alone (Hagihara 1987, Kurachi et al. 1993) into the canopy photosynthesis model.

In this study, in order to evaluate the annual canopy photosynthesis and respiration of a *Kandelia candel* (L.) Druce stand under field conditions at Manko Wetland at Okinawa Island, Japan, the vertical and seasonal changes in photosynthesis and dark respiration rates of leaves were measured monthly over 2 yr. The annual canopy gross photosynthesis, canopy respiration and surplus production were estimated using the modified canopy photosynthesis model (Hagihara 1987, Kurachi et al. 1993).

## MATERIALS AND METHODS

**Study site.** All studies were carried out in a *Kandelia candel* stand at Manko Wetland (26° 11' N, 127° 40' E) between March 2002 and February 2004. The mangrove forest is young (10 to 15 yr) and mainly consists of *K. candel*. Some small colonies of *Rhizophora stylosa* Griff. and *Bruguiera gymnorhiza* (L.) Lamk. are also observed in this study site. This wetland has been recognized as an important area in the transit point or wintering area for migratory birds, and has been registered with the Ramsar Convention since 1999.

*Kandelia candel* has a wide distribution from Western and Eastern India and Myanmar, through the South China Sea region, to the Ryukyu Islands and Southern Japan (Spalding et al. 1997). Recently, *K. candel* in the regions of China and Japan has been classified as a new species, *K. obovata* (Sheue et al. 2003).

On the basis of the data from 1992 to 2001 obtained from Okinawa Astronomical Observatory, the warmth index (i.e. cumulative temperature of monthly mean temperatures >5°C over a year; Kira 1977) was esti-

mated to be 218.2°C month, thereby indicating that this region belongs to the subtropical zone. Mean monthly minimum temperature (16.8°C) and mean monthly maximum temperature (28.8°C) occurred in February and July, respectively, and mean annual temperature was 23.2°C. Rainfall was over 100 mm mo<sup>-1</sup> throughout the year and mean annual rainfall was 2086 mm yr<sup>-1</sup>.

Considering the maximum tree height of 3.00 m, a sample plot of 4 × 4 m was established in a mono-specific *Kandelia candel* stand whose canopy was completely closed. Table 1 provides a general description of the sample plot. The leaf area index (LAI) of 4.50 m<sup>2</sup> m<sup>-2</sup> was obtained in a previous study (Khan et al. 2004), which was carried out in a nearby stand using the stratified clipping method (Monsi & Saeki 1953). The light transmissivity of leaves was measured for 10 samples with a quantum sensor (LI-190SB, LICOR). Mean soil salinity on a dry weight basis of soil taken from the surface to a depth of 100 cm was 7.0 ± 0.4 (SE) ppt using a salt meter (ES-421, Atago).

**Gross photosynthesis and dark respiration rates of leaves.** Three leaves were randomly selected from each specified height, located at intervals of 20 cm that extended from the top of the canopy downward. The relative photosynthetic photon flux density (PPFD) of each height was measured monthly at 100 points with a pair of quantum sensors (LI-190SB, LI-COR). The net photosynthesis rate and dark respiration rate under 360 ppm CO<sub>2</sub> were measured monthly *in situ* using a portable photosynthesis system (LI-6400, LI-COR). The PPFD inside the chamber was regulated at 8 levels: 1600, 800, 400, 200, 100, 50, 25 and 0 μmol photon m<sup>-2</sup> s<sup>-1</sup>. The block temperature was regulated at the mean monthly temperature of Naha city over the past 10 yr. The gross photosynthesis rate was defined as the sum of net photosynthesis rate and dark respiration rate. Leaf nitrogen content at the specified height was also analyzed in August 2002 using a CNH-coder (JM 10, J-Science).

Table 1. *Kandelia candel*. General description of the plot. DBH: diameter at breast height; LAI: leaf area index; PPFD: photosynthetic photon flux density

Stand characteristics	
Stand age (yr)	10 to 15
Tree density (m <sup>-2</sup> )	3.75
Tree height (m)	2.91 ± 0.02 (SE)
Maximum tree height (m)	3.00
DBH (cm)	2.9 ± 0.1 (SE)
Maximum DBH (cm)	3.9
LAI (m <sup>2</sup> m <sup>-2</sup> )	4.50
PPFD transmissivity of leaves (×10 <sup>-3</sup> )	8.05 ± 0.48 (SE)
Soil salinity (ppt)	7.04 ± 0.43 (SE)

**Diurnal change in PPFD and daily total solar radiation.** The PPFD incident on the canopy was measured at intervals of 5 min with a quantum sensor (LI-190SB, LI-COR) connected to a data logger (LI-1400, LI-COR) throughout the research period. The daily total solar radiation was also measured with a radiometric sensor (LI-190SA, LI-COR) throughout the research period.

**Statistical analysis.** All regression analyses were conducted using a nonlinear least-squares method (KaleidaGraph v3.51, Synergy Software). Differences in the seasonal trends of canopy gross photosynthesis and respiration between the first and the second year were tested by Spearman's rank correlation coefficient  $r_s$ .

## MODELS

**PPFD attenuation within the canopy.** The attenuation process of PPFD through the canopy was expressed by Beer-Lambert's law (Yim et al. 1969, Kurachi et al. 1986):

$$I_R = e^{-(K_F F + K_C C)} \quad (1)$$

where  $I_R$  is the relative PPFD at a given canopy depth,  $F$  and  $C$  are, respectively, the cumulative leaf area density and the cumulative wood silhouette area density until the canopy depth,  $K_F$  is the light extinction coefficient for leaves, and  $K_C$  is the light extinction coefficient for woody organs. On the assumption that  $C$  is proportional to  $F$ , Eq. (1) is equated to the equation proposed by Monsi & Saeki (1953):

$$I_R = e^{-KF} \quad (2)$$

where  $K$  is the apparent light extinction coefficient (Yim et al. 1969). Relative PPFD  $I_{Rc}$  after leaf clipping, i.e.  $F = 0$  in Eq. (1), can be written as follows:

$$I_{Rc} = e^{-K_C C} \quad (3)$$

Considering Eqs. (1) & (3), the following equation can be derived (Yim et al. 1969):

$$\frac{I_R}{I_{Rc}} = e^{-K_F F} \quad (4)$$

In a previous study (Khan et al. 2004), values of  $K$  and  $K_F$  were estimated on the basis of the arithmetic mean of relative PPFD from Eqs. (2) & (4), respectively. However, Ogawa (1980) pointed out that the geometric mean of relative PPFD provides better accuracy of estimates than the arithmetic mean, because the relative PPFD at a given canopy depth shows a logarithmic normal distribution rather than a normal distribution. Based on the geometric mean of relative PPFD, values of  $K$  and  $K_F$  were estimated from Eqs. (2) & (4) as 0.61

and  $0.53 \text{ m}^2 \text{ m}^{-2}$ , respectively. These values were employed for evaluating canopy photosynthesis and respiration in this study.

**Diurnal course of PPFD incident on the canopy.** The diurnal course of PPFD  $I_0$  incident on the canopy in a month was expressed in the form (Kuroiwa 1966):

$$I_0 = I_{0M} \sin^2\left(\frac{\pi}{d} t\right) \quad (5)$$

where  $I_{0M}$  is the maximum PPFD and  $d$  is the day length of the month. An example of the diurnal course of  $I_0$  is shown in Fig. 1.

**Canopy photosynthesis.** The  $p$ - $I$  curve was expressed by the hyperbolic equation (Tamiya 1951, Ledermann & Tett 1981):

$$p = p_{\max} \left[ \frac{I}{I_k + I} \right] \quad (6)$$

where  $p$  is gross photosynthesis rate and  $I$  is PPFD on a leaf surface, and  $p_{\max}$  and  $I_k$  are the maximum gross photosynthesis rate and half saturation constant, respectively. Eq. (6) is rewritten in the form:

$$p = \frac{I_k \phi I}{I_k + I} \quad (7)$$

where  $\phi$  is the quantum yield in the lower range of  $I$ .

The dependencies of  $I_k$  and  $\phi$  on  $I_R$  were expressed as follows (Hozumi & Kirita 1970):

$$\frac{1}{I_k} = \frac{A}{I_R} + B \quad (8)$$

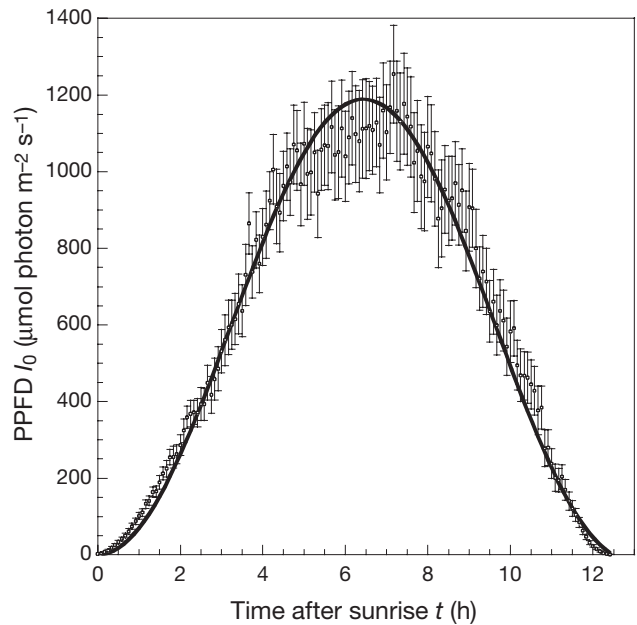


Fig. 1. *Kandelia candel*. Diurnal course of photosynthetic photon flux density (PPFD)  $I_0$  incident on the canopy (January 2004); curve given by Eq. (5) ( $R^2 = 0.98$ ). Error bars: SE

$$\phi = \frac{C}{I_R} + D \tag{9}$$

where  $A$ ,  $B$ ,  $C$  and  $D$  are coefficients specific to months.

By assuming Eqs. (1) & (2), PPFD  $I$  on a leaf surface at a given canopy depth is given by the following equation (Hagihara 1987, Kurachi et al. 1989):

$$I = \frac{K_F I_0}{1 - m} e^{-KF} \tag{10}$$

Here,  $m$  is the PPFD transmissivity of leaves (Saeki 1960).

Taking into account Eqs. (2), (5) & (7–10), the daily canopy gross photosynthesis  $P$  can be estimated by the following equation (Hagihara 1987, Kurachi et al. 1993), the conditions of which are  $A \neq 0$  and  $B \neq 0$ :

$$P = \int_0^F \int_0^d p(F, t) dt dF \tag{11}$$

$$= \frac{d}{KA} \left[ KCF + \frac{2(AD - BC)}{B} \ln \frac{1 + M}{1 + N} + \frac{C}{L} \ln \frac{(M + L)(N - L)}{(M - L)(N + L)} \right]$$

$$\begin{cases} L = \left[ 1 + \frac{K_F I_{0M} A}{1 - m} \right]^{1/2} \\ M = \left[ 1 + \frac{K_F I_{0M} (A + B)}{1 - m} \right]^{1/2} \\ N = \left[ 1 + \frac{K_F I_{0M} (A + B e^{-KF})}{1 - m} \right]^{1/2} \end{cases}$$

**Canopy respiration.** The decreasing tendency of the dark respiration rate,  $r$ , of leaves with  $I_R$  was described by the empirical equation:

$$r = gI_R + h \tag{12}$$

where  $g$  and  $h$  are coefficients specific to months. Taking account of Eqs. (2) & (12), daily canopy respiration  $R$  was estimated by the following equation (Hagihara & Hozumi 1977b):

$$R = \int_0^F \int_0^d r(F, t) dt dF = 24 \left[ hF + \frac{g}{K} (1 - e^{-KF}) \right] \tag{13}$$

**Nitrogen-related maximum gross photosynthesis and dark respiration rates.** The relationships of maximum gross photosynthesis rate  $p_{max}$  and dark respiration rate  $r$  to leaf nitrogen content  $N$  were expressed by the following equations, respectively:

$$p_{max} = \alpha_p (N - N_{min})^{\beta_p} \tag{14}$$

$$r = \alpha_r (N - N_{min})^{\beta_r} \tag{15}$$

where  $N_{min}$  is the minimum leaf nitrogen content, and  $\alpha_p$ ,  $\beta_p$ ,  $\alpha_r$  and  $\beta_r$  are the coefficients.

## RESULTS

### Canopy photosynthesis

Fig. 2 shows the  $p$ - $I$  curves of leaves taken from different canopy depths. Maximum gross photosynthesis rate,  $p_{max}$ , of the top leaves was ca.  $19 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in summer and  $10 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in winter. The  $p_{max}$  of top leaves was 2 to 4 times that of bottom leaves throughout the year.

Fig. 3 shows a sharp decrease of half saturation constant  $I_k$  and slight increase of quantum yield  $\phi$  with decreasing relative PPFD  $I_R$ , respectively, according to Eqs. (8) & (9). The values of  $A$ ,  $B$ ,  $C$  and  $D$  in Eqs. (8) & (9) were not negative, even though the value of  $C$  was

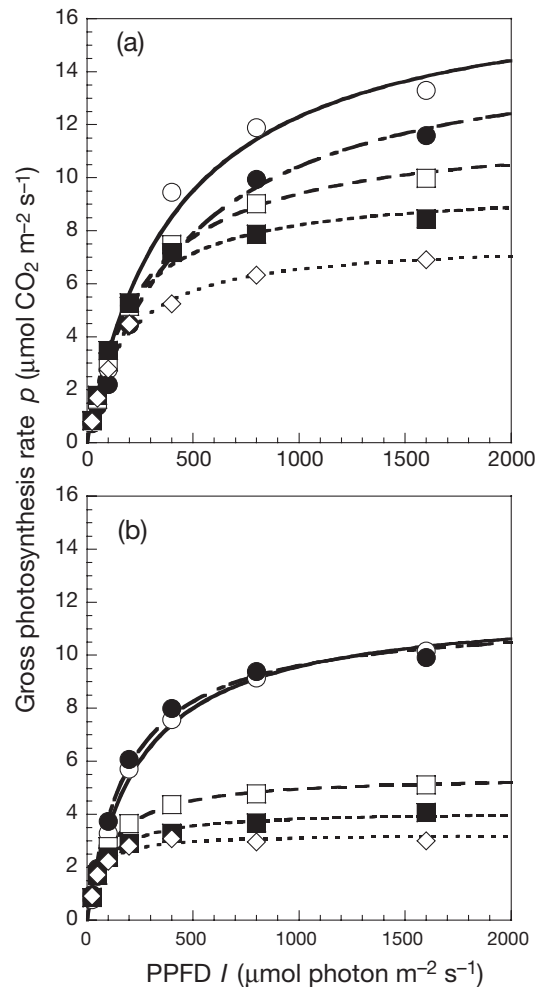


Fig. 2. *Kandelia candel*.  $p$ - $I$  curves of leaves at different canopy depths in (a) summer (August 2002) ( $R^2 = 0.99, 1.00, 1.00, 0.99$  and  $0.99$  from the top downwards), and (b) winter (January 2004) ( $R^2 = 0.99, 0.99, 0.99, 0.99$  and  $0.97$  from the top downwards). Data fitted to Eq. (7).  $\circ$ , top;  $\bullet$ , 20 cm;  $\square$ , 40 cm;  $\blacksquare$ , 60 cm;  $\diamond$ , 80 cm. Each point is mean of 3 leaves

sometimes 0; i.e. quantum yield of photosynthesis for leaves is constant irrespective of the light environment where leaves existed. The same trends expressed by Eqs. (8) & (9) were reported for a warm-temperate evergreen oak forest (Hozumi et al. 1972, Nishioka et al. 1978), a *Chamaecyparis obtusa* plantation (Hagihara & Hozumi 1977a), and a *Larix leptolepis* plantation (Kurachi et al. 1992). The value of PPFD transmissivity of leaves  $m$  was  $8.05 \times 10^{-3}$  (Table 1), which was quite low compared to the value of 0.022 reported by Hozumi et al. (1972) in the warm-temperate evergreen oak forest.

Fig. 4 illustrates the seasonal change in daily canopy gross photosynthesis  $P$  calculated from Eq. (11). The  $P$  attained a maximum between June and July and a minimum between November and January. The sea-

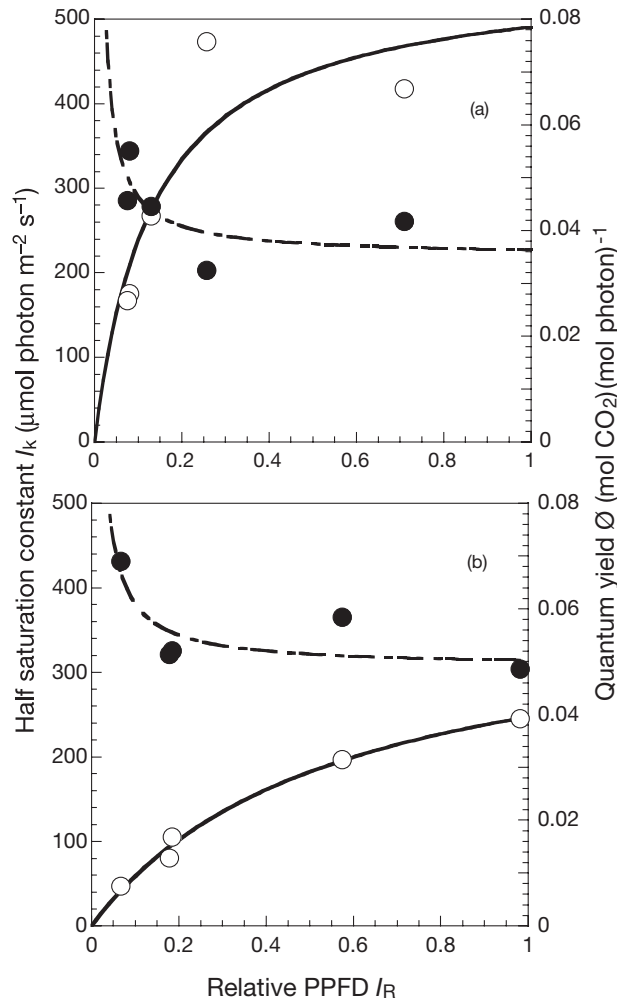


Fig. 3. *Kandelia candel*. Relationships of half saturation constant  $I_k$  and quantum yield  $\phi$  in Eq. (7) to relative PPFD  $I_R$ . (a) August 2002 ( $R^2 = 0.79$  for  $I_k$  and 0.51 for  $\phi$ ), (b) January 2004 ( $R^2 = 0.97$  for  $I_k$  and 0.65 for  $\phi$ ). Curves based on Eqs. (8) & (9), respectively.  $\circ$ ,  $I_k$ ;  $\bullet$ ,  $\phi$

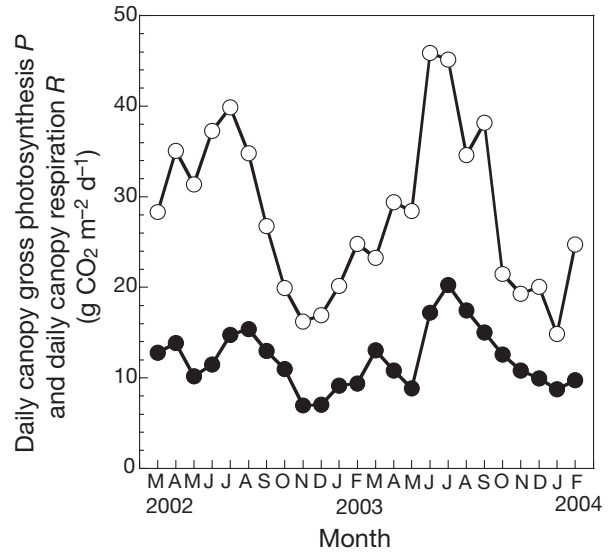


Fig. 4. *Kandelia candel*. Seasonal changes in daily canopy gross photosynthesis  $P$  and daily canopy respiration  $R$ .  $P$  and  $R$  calculated from Eqs. (11) & (13), respectively.  $\circ$ ,  $P$ ;  $\bullet$ ,  $R$

sonal trend of  $P$  was the same between the 2 years ( $r_s = 0.72$ ,  $p < 0.01$ ).

The annual canopy gross photosynthesis was estimated as  $101 \text{ t CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$  in the first year and  $105 \text{ t CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$  in the second year. By assuming that the radiation energy of 3.19 MJ is used for the conversion of 6 moles of  $\text{CO}_2$  into 1 mole of  $\text{C}_6\text{H}_{10}\text{O}_5$  (Lieth 1968), the energy efficiency for the annual canopy gross photosynthesis was calculated to be 2.5% in the first year and 2.2% in the second year. The present results for energy efficiency were within the range of 2.1 to 3.2% summarized by Kira (1976) for various types of terrestrial forest.

### Canopy respiration

As illustrated in Fig. 5, dark respiration rate ( $r$ ) of the top leaves was ca.  $1.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in summer and  $1.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in winter. The value of  $r$  decreased continuously with decreasing relative PPFD  $I_R$ , according to Eq. (12). The same trend expressed by Eq. (12) was reported for a *Chamaecyparis obtusa* plantation (Hagihara & Hozumi 1991), a *Larix leptolepis* plantation (Kurachi et al. 1992), and a *Cryptomeria japonica* plantation (Katsuno-Miyaura et al. 1995). The  $r$  value for top leaves was 2 to 7 times that of bottom leaves throughout the year.

Daily canopy respiration ( $R$ ) calculated from Eq. (13) attained a maximum between July and August and a minimum between November and January (Fig. 4). Furthermore, a depression in both  $R$  and  $P$  was ob-

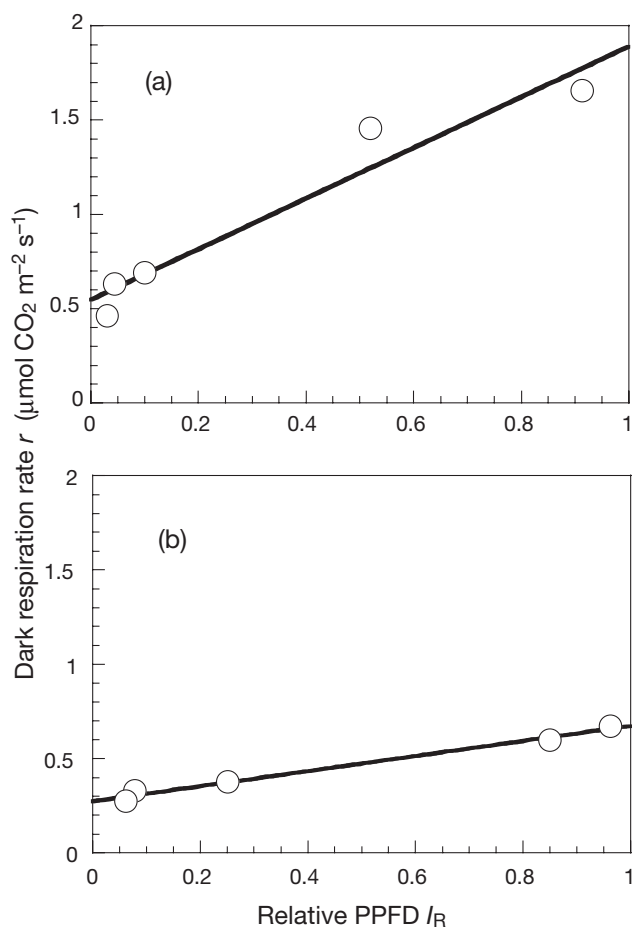


Fig. 5. *Kandelia candel*. Decreasing tendencies of dark respiration rate  $r$  with decreasing relative PPFD  $I_R$  in (a) summer (June 2003) ( $R^2 = 0.94$ ), and (b) winter (December 2002) ( $R^2 = 0.99$ ). Data fitted to Eq. (12). Each point is mean of 3 leaves

served during the May rainy season. The value of  $R$  showed the same seasonal trend between the 2 years ( $r_s = 0.86$ ,  $p < 0.01$ ).

The annual canopy respiration was estimated as 41 t  $\text{CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$  in the first year and 47 t  $\text{CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$  in the second year. As a result, annual surplus production (annual canopy gross photosynthesis minus annual canopy respiration) was 60 t  $\text{CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$  in the first year and 58 t  $\text{CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$  in the second year.

## DISCUSSION

### Vertical changes in canopy photosynthesis and respiration

The  $p$ - $I$  curve and  $r$  varied within the canopy (Figs. 2 & 5). These physiological traits of leaves are strongly influenced by the light environment (Hozumi & Kirita 1970, Hagihara & Hozumi 1977b). The present study

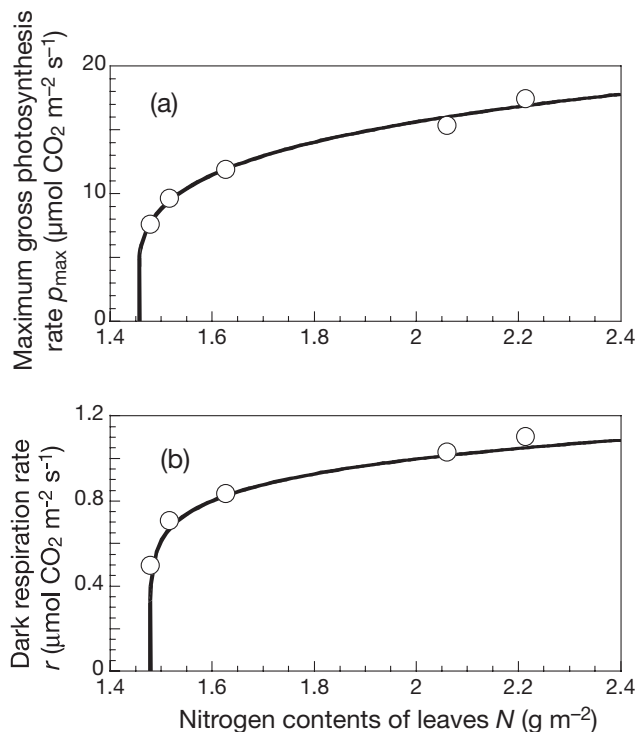


Fig. 6. *Kandelia candel*. Relationships of (a) maximum gross photosynthesis rate  $p_{\text{max}}$  ( $R^2 = 0.99$ ), and (b) dark respiration rate  $r$  ( $R^2 = 1.00$ ) to leaf nitrogen content  $N$  (August 2002). Curves based on Eqs. (14) & (15), respectively

confirmed the dependencies of these physiological traits on the light environment within the canopy (Figs. 3 & 5). Such acclimation of leaves to the light environment was also reported for other mangrove species (Ball & Critchley 1982, Farnsworth & Ellison 1996).

As shown in Fig. 6, decreases in maximum gross photosynthesis rate  $p_{\text{max}}$  ( $=I_k\phi$ ) and  $r$  occurred with a concomitant decrease in leaf nitrogen content  $N$  according to Eqs. (14) & (15), respectively. Many previous studies reported the positive correlation between  $p_{\text{max}}$  and  $N$  (DeJong & Doyle 1985, Hirose & Werger 1987, Schieving et al. 1992, Anten et al. 1995, Hikosaka 2004). This is because  $p_{\text{max}}$  is limited by the primary carboxylating enzyme RuBP carboxylase/oxygenase, which constitutes a major part of  $N$  (Björkman 1981). The positive correlation between  $r$  and  $N$  was also reported in previous studies (Hirose & Werger 1987, Schieving et al. 1992, Anten et al. 1995). This is because  $r$  is regulated by substrates supply (Lambers 1985), which indicates the dependence of  $r$  on  $N$ . Furthermore, leaves with the highest photosynthetic capacity (highest  $N$ ) require the highest respiration cost to maintain themselves (Mooney & Gulmon 1982).

In consideration of these physiological adaptations of leaves to the light environment within a canopy, the relationship of annual canopy photosynthetic production to LAI was examined from the viewpoint of the opti-

mization of annual surplus production. Fig. 7 illustrates that the annual canopy gross photosynthesis increased rapidly and then increased gradually, while the annual canopy respiration increased continuously with increasing LAI. As a result, the annual surplus production showed a maximum value at an optimum LAI of  $4.54 \text{ m}^2 \text{ m}^{-2}$ , which was almost the same as the actual LAI in the stand of  $4.50 \text{ m}^2 \text{ m}^{-2}$  (Table 1). This correspondence indicated that the *Kandelia candel* stand maximizes annual surplus production through physiological adaptations of leaves to the light environment.

Monsi & Saeki (1953) were the first to apply optimization theory to leaf area distribution in a canopy. They determined that canopy photosynthesis is maximized if the LAI of the canopy is such that leaves in the lowest part of the canopy receive an amount of light that is equal to their light compensation point. The analyses described above assume that light availability is the primary limiting resource that constrains photosynthetic performance. However, many factors may limit photosynthetic productivity, one of the most important of these being nitrogen availability. Even under highly illuminated conditions, a stand may have an actual LAI that is well below the optimum LAI, particularly where soil resources are poor (Anten 2005). However, the stand in the present study showed that the actual LAI was nearly equal to optimum LAI. This is because the site would be favorable for growth of *Kandelia candel* trees. In actual fact, *K. candel* expanded its habitat area in the Manko Wetland from 4 ha in 1977 to 50 ha in 2001 (Nakasuga 2002).

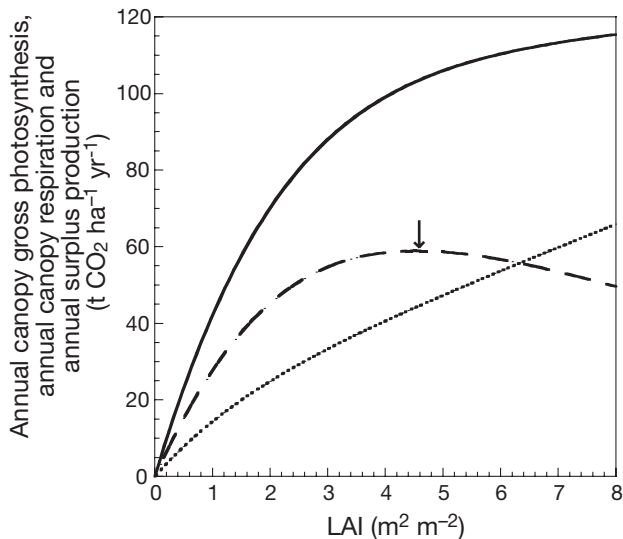


Fig. 7. *Kandelia candel*. Relationships of annual canopy gross photosynthesis (solid line; Eq. 11), annual canopy respiration (dotted line; Eq. 13), and annual surplus production (broken line) to leaf area index (LAI). Arrow indicates actual LAI ( $4.50 \text{ m}^2 \text{ m}^{-2}$ ; Table 1)

### Seasonal changes in canopy photosynthesis and respiration

In the present result, the apparent seasonal changes in physiological traits of leaves were observed. Maximum gross photosynthesis rate ( $p_{\text{max}}$ ) of the top leaves in summer (27 to 29°C) was ca. 1.4 times that in winter (17 to 19°C) (Fig. 2). The value of  $r$  for the top leaves in summer was also ca. twice as much as in winter (Fig. 5). These seasonal changes can affect the estimation of annual canopy photosynthetic production. The annual canopy gross photosynthesis, canopy respiration and surplus production were tentatively calculated by adopting the physiological traits of leaves specific to each month during the whole year. As a result, the estimates ranged from 80 to 117% of the mean annual canopy gross photosynthesis of  $103 \text{ t CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$ , 58 to 168% of the mean annual canopy respiration of  $44 \text{ t CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$ , and 65 to 125% of the mean annual surplus production of  $59 \text{ t CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$ . Therefore, consideration of the seasonal changes in the physiological traits of leaves would be necessary for evaluating reliable estimates of the annual canopy photosynthetic production in subtropical mangrove forests.

Clough et al. (1997) estimated an annual canopy gross photosynthesis of  $229 \text{ t CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$  in a *Rhizophora apiculata* stand in Malaysia. This value is very much higher than the result presented in this study. On the other hand, Clough (1998) estimated the net daytime canopy photosynthesis in a mixed mangrove forest in Western Australia to be  $107 \text{ t CO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$ , which was about 50% lower than that of Clough et al. (1997). Clough (1998) ascribed this discrepancy to differences in LAI and net photosynthesis rate of leaves between the 2 stands. However, estimates of both Clough et al. (1997) and Clough (1998) should be carefully compared with the result from the present study. Clough et al. (1997) did not consider the seasonal change in sunlight when calculating the annual canopy photosynthetic production, whereas Clough (1998) did. Moreover, these reports did not consider seasonal changes in the physiological traits of leaves when estimating the annual canopy photosynthetic production.

### Comparison of GPP between the present mangrove forest and terrestrial forests

Fig. 8 shows the hyperbolic relationship reported by Kira (1991) between annual gross primary production GPP and the product of LAI and warmth index (WI) in various types of terrestrial forest in the Western Pacific under perhumid climates. Assuming a dry matter/ $\text{CO}_2$

conversion factor of 0.614, we calculated the GPP as  $63.2 \pm 0.9$  (SE) t dry matter  $\text{ha}^{-1} \text{yr}^{-1}$ . The present data fell near the regression curve determined by Kira (1991). The GPP in the *Kandelia candel* stand is also likely to depend on LAI and WI just like it does in terrestrial forests in the Western Pacific under perhumid climates.

## CONCLUSIONS

Firstly, the present study evaluated vertical changes in physiological traits of leaves (Figs. 3 & 5), and from there estimated canopy photosynthetic production using empirical equations (Eqs. 8, 9 & 12) that expressed the relationships of physiological traits to the light environment within the canopy. The vertical profiles of the physiological traits were explained by the allocation of nitrogen content (Fig. 6). Furthermore, it was concluded that the annual surplus production was maximized through the adaptations of physiological traits to the light environment within the canopy (Fig. 7).

Secondly, we observed the apparent seasonal change in canopy photosynthetic production (Fig. 4). As a result, it was emphasized that seasonal changes in physiological traits should be considered for reliable

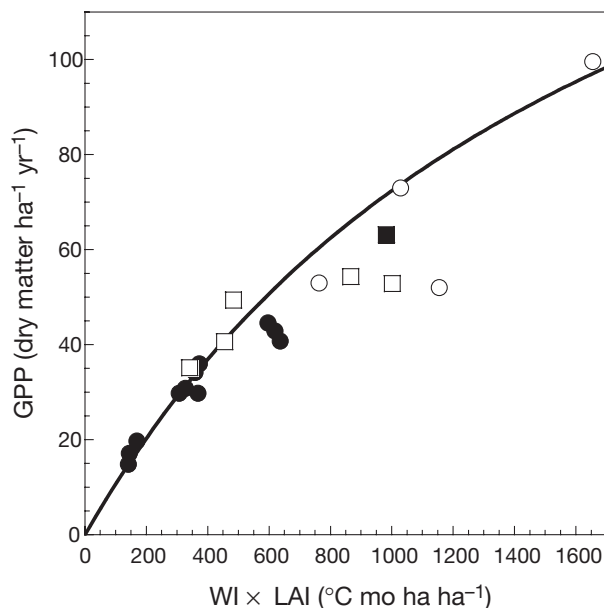


Fig. 8. Hyperbolic relationship between gross primary production (GPP) and the product of LAI and warmth index (WI) for various types of forest in the Western Pacific under perhumid climates (Kira 1991). O, evergreen broadleaf forest; ●, deciduous broadleaf forest; □, evergreen conifer forest; ■, *Kandelia candel* mangrove forest from present study

estimation of annual canopy photosynthetic production.

Finally, annual GPP was compared with various types of terrestrial forest in the Western Pacific under perhumid climates, taking into account WI and LAI (Fig. 8). The comparison indicated that GPP in the *Kandelia candel* stand is also likely to depend on LAI and WI, just as it does in terrestrial forests in the Western Pacific under perhumid climates.

**Acknowledgements.** We are grateful to our colleagues Dr. L. Alhamd, Messrs S. M. Feroz, P. Wane, K. Analuddin and K. Nakamura, and Ms. K. Matsubara for their participation in field work. We are also grateful to Prof. M. Tsuchiya for his helpful suggestions. This study was partially supported by a Grant-in-Aid for Scientific Research (Nos. 16201009 and 16651009) from the Ministry of Education, Culture, Sports, Science and Technology, Japan, and the 21st Century COE program of the University of the Ryukyus.

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Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

Submitted: August 11, 2005; Accepted: January 23, 2006  
Proofs received from author(s): August 5, 2006