INTRODUCTION

Forest trees are most important in relation to global climatic change, because they play a prominent role in the global carbon balance (Jarvis 1989). The biomass of a forest ecosystem is large compared with other plant ecosystems, and carbon accumulates in vast amounts in woody components. Net production alone cannot be a stable measure of the potential primary productivity of forest stands, but the best measure of forest productivity should be the gross production (net production plus respiration loss) (Kira 1991). Although there have been hundreds of estimates of whole-stand net primary production around the world, the estimates of whole-stand respiration, or even total aboveground respiration, are still fairly rare (Sprugel et al. 1995).

Respiration is a major factor in individual tree, tree stand or ecosystem energy budgets, and estimated to consume anywhere from 30 to 70% of the total carbon fixed (Hagihara & Hozumi 1991, Ryan 1991, Sprugel & Benecke 1991). A large fraction of all carbohydrates that trees assimilate each day is expended as respiration to the atmosphere during the same period (Lambers et al. 2008). Hence, tree respiration is a key component of the global CO₂ budget and plays a crucial role in a wide range of ecological phenomena, from the performance of individual trees to global atmospheric CO₂ concentrations (Atkin et al. 2005b). Estimating respiration rate is of fundamental importance because it is linked to the rates of many other biological activities (Glazier 2005). The measurement of respiration loss is therefore indispensable in view of the dry mat-
ter economy of forest stands and the global CO₂ budget.

Respiration can be defined as the oxidation of food substrates in living cells, bringing about the release of energy. The energy released is stored as chemical energy in the substrate molecules. Products of respiration include energy and metabolic intermediates that provide carbon skeletons for cell constituents. Both products are required for growth and maintenance of tissues, absorption of mineral nutrients and translocation of organic and inorganic materials (Pallardy 2008). According to Kramer & Kozlowski (1979), the factors affecting respiration are age and physiological condition of tissues, available substrate, hydration, soil moisture, soil and air temperatures, composition of the atmosphere, injuries and mechanical stimuli, and chemicals. The metabolic rate of individual organisms can vary in response to many intrinsic and extrinsic factors, especially an organism’s activity level and the ambient temperature (Glazier 2005). One of the major factors affecting respiratory processes in plants is air temperature. Respiration is expected to be largely under temperature control via kinetic effects on respiratory enzymes (Brown et al. 2004, Atkin et al. 2005a). Indeed, it is typically correlated with natural (daily or seasonal) temperature fluctuations and responsive to short-term temperature manipulations over time scales of minutes or hours (Hagihara & Hozumi 1991, Larcher 2003, Bruhn et al. 2008).

Among different forest types, mangroves have a significant effect on the coastal environment. The carbon fixation capacity of mangrove forests is higher than that of terrestrial forests (Christensen 1978, Clough 1998). For this reason, mangroves are considered an important carbon sink in coastal ecosystems (Ong 1998). Respiration can be defined as the oxidation of food substrates in living cells, bringing about the release of energy. The energy released is stored as chemical energy in the substrate molecules. Products of respiration include energy and metabolic intermediates that provide carbon skeletons for cell constituents. Both products are required for growth and maintenance of tissues, absorption of mineral nutrients and translocation of organic and inorganic materials (Pallardy 2008).

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MATERIALS AND METHODS

Study site. This study was carried out at Manko Wetland in the southern part of Okinawa Island, Japan (26° 11’ N, 127° 40’ E). This wetland has been registered under the Ramsar Convention as an important stopover point and wintering area for migratory birds. On the basis of data from 1997 to 2006 (Okinawa Astronomical Observatory), the warmth index was 220.4 ± 0.1°C month (mean ± SE), which is within the range of 180 to 240°C month of the subtropical region defined by Kira (1991). The mean annual temperature was 23.4 ± 0.1°C; the mean monthly minimum temperature of 17.1 ± 0.3°C and the mean monthly maximum temperature of 28.8 ± 0.2°C occurred in January and July, respectively. The mean monthly rainfall was over 100 mm throughout the year and the mean annual rainfall was 2227 ± 163 mm.

Sample trees for respiration. Stand age, tree density, mean tree height and mean stem diameter measured at a height of 10% of the tree height were 12 yr, 4.50 m–2, 4.31 m and 5.83 cm, respectively, based on a tree census of a 20 × 20 m Kandelia obovata stand carried out in May 2007. Six K. obovata sample trees representing the tree size class distribution were selected for the measurement of nighttime aboveground respiration from the stand, whose canopy is completely closed (Analuddin et al. 2009). The general features of the sample trees are shown in Table 1. Monthly measurements of the sample
trees were made at a tree height, \( H \), and stem diameter, \( D_{0.1H} \), measured at a height of \( H/10 \).

**Respiration measurement.** The respiration was non-destructively measured monthly throughout a year (from May 2007 to April 2008) with a modified enclosed standing tree method (cf. Ninomiya & Hozumi 1983a, Yokota et al. 1994). The aerial parts of each sample tree were enclosed in a cylindrical chamber made of 0.1 to 0.2 mm thick polyvinyl chloride film. To avoid air leakage, potter’s clay was applied to the base of the stem before tying the skirt of the chamber firmly to the stem base. A fan was installed to circulate the air inside the chamber to maintain a uniform CO2 concentration. CO2 increment and the temperature inside the chamber were measured using an infrared gas analyser (Carbon Dioxide Probe GMP343) installed inside the chamber. CO2 concentration was measured at 5 s intervals during a 10 to 30 min period. The monthly respiration measurement was completed within 1 night.

Respiration rate \( r_0 \) per tree (µmol CO2 s\(^{-1}\) tree\(^{-1}\)) was calculated following the formula:

\[
r_0 = V \cdot \frac{273.2 \cdot \theta}{273.2 + \theta} \cdot \frac{P}{1013} \cdot \frac{1}{22.4} \cdot \Delta C
\]  

where \( V \) is the chamber volume (l) per tree, \( \theta \) is the air temperature inside the chamber (°C), \( P \) is the air pressure (hPa) and \( \Delta C \) is the CO2 increment rate (ppm CO2 s\(^{-1}\)). The upper part of the chamber was cylindric and the lower part was shaped like a cone.

The \( r_0 \) was adjusted to the respiration rate \( r \) at a monthly mean temperature considering the \( Q_{10} \) value as 2 (Lambers et al. 2008), which is the rate of change in the respiration rate with a 10°C rise in temperature. Hence, \( r \) was calculated following the formula:

\[
r = r_0 \cdot Q_{10}^{\frac{r - \theta}{10}}
\]  

where \( t \) is the mean temperature (°C) of the month when the respiration was measured.

**Measurement of mass.** At the end of the study year, 13 sample trees (including 6 trees whose respiration were measured) representing different size classes available in the whole Manko Wetland were harvested to measure the individual aboveground mass \( m \) (kg [dry weight [dw]]) per tree. A data set of 12 trees used in a previous paper (Khan et al. 2005) was added. As a result, data from 25 trees were used for the establishment of the allometric relationship. After the sample trees were felled, their \( H \) (m) and \( D_{0.1H} \) (cm) were measured, and then the leaves and branches were separated from the stem. The fresh weight was measured for the stem, branches and leaves. Samples of the stem, branches and leaves were taken for estimating the ratio of dry/fresh mass. All samples were dried in a ventilated oven at 85°C for 72 h, desiccated at room temperature and then weighed. As shown in Fig. 1, the resultant allometric relationship was given as:

\[
m = 0.0341(D_{0.1H}^2H)^{1.03}
\]

### RESULTS

**Size-dependence of respiration**

Examples of the dependence of the respiration rate \( r \) (µmol CO2 s\(^{-1}\) ) per tree on individual tree mass \( m \) [kg [dw]] are shown in Fig. 2. The dependence was successfully described with a power-functional relationship throughout a year (0.50 \( \leq R^2(m,r) \leq 0.88 \)). The relationship is written as follows:

\[
r = fm^h
\]

where \( f \) is the multiplying coefficient and \( h \) is the scaling exponent specific to months. The value of \( h \) for each month is shown in Table 2. The highest value of \( h \), 1.085, was found in January and the lowest value, 0.723, was found in July.

**Temperature-dependence of the exponent \( h \)**

A significance probability of the value of \( h \) was examined for the null hypothesis \( h = 1.0 \) (Ninomiya &
Hozumi 1981, Reich et al. 2006), 3/4 (West et al. 1999) and 2/3 (Ninomiya & Hozumi 1983a,b, Hagihara et al. 1989), as compiled in Table 2. No values were significantly different from 1.0, 3/4 or 2/3 at a significance level of 0.01. However, there was a clear trend that in the cool dormant season (when temperatures are below the mean annual temperature of ca. 24°C) \( h \) was closer to 1.0 than to 3/4 and 2/3; whereas in the warm growing season (when temperatures are above ca. 24°C) \( h \) was closer to 3/4 than to 1.0 and 2/3 except for October. These results support the dominance of the 3/4 power scaling in the warm growing season and the isometric scaling in the cool dormant season. In addition, June was the transition period from the cool dormant season to the warm growing season, whereas October was the transition period from the warm growing season to the cool dormant season, because in these 2 months the significance probabilities for the null hypotheses \( h = 1.0 \) and \( h = 3/4 \) were almost similar.

The seasonal trend of monthly mean temperature \( t \) and the scaling exponent \( h \) of Eq. (4) is shown in Fig. 3. The exponent value increased rapidly from summer (July), reached a maximum value in winter (January) and decreased abruptly from winter to summer. In contrast, the temperature tended to decrease from July (29.6°C) to February (16.1°C), and then increased from February to July. This indicates a reverse trend between 2 variables. The exponent \( h \) significantly

Table 2. Scaling exponent of the power equation and its significance probability for the null hypotheses. Temperature is the mean temperature of the month when respiration was measured. The multiplying coefficient \( f \) and scaling exponent \( h \) of Eq. (4) are shown as mean ± SE. Numbers in bold: highest significance probability for the null hypotheses

<table>
<thead>
<tr>
<th>Month</th>
<th>Temperature (°C)</th>
<th>( \ln f \pm SE )</th>
<th>( h \pm SE )</th>
<th>Probability for null hypothesis of ( h )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.0</td>
</tr>
<tr>
<td>May 2007</td>
<td>23.8</td>
<td>-3.047 ± 0.144</td>
<td>0.910 ± 0.097</td>
<td>0.407</td>
</tr>
<tr>
<td>June 2007</td>
<td>26.7</td>
<td>-3.056 ± 0.162</td>
<td>0.874 ± 0.109</td>
<td>0.313</td>
</tr>
<tr>
<td>July 2007</td>
<td>29.6</td>
<td>-3.344 ± 0.215</td>
<td>0.723 ± 0.144</td>
<td>0.127</td>
</tr>
<tr>
<td>Aug 2007</td>
<td>28.8</td>
<td>-3.349 ± 0.174</td>
<td>0.799 ± 0.117</td>
<td>0.162</td>
</tr>
<tr>
<td>Sep 2007</td>
<td>28.2</td>
<td>-3.330 ± 0.273</td>
<td>0.781 ± 0.180</td>
<td>0.292</td>
</tr>
<tr>
<td>Oct 2007</td>
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<td>-3.561 ± 0.272</td>
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<td>0.541</td>
</tr>
<tr>
<td>Nov 2007</td>
<td>22.2</td>
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<td>0.959 ± 0.159</td>
<td>0.811</td>
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<tr>
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<td>-4.021 ± 0.225</td>
<td>1.016 ± 0.156</td>
<td>0.925</td>
</tr>
<tr>
<td>Jan 2008</td>
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<td>-4.049 ± 0.162</td>
<td>1.085 ± 0.112</td>
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<tr>
<td>Feb 2008</td>
<td>16.1</td>
<td>-4.155 ± 0.186</td>
<td>1.040 ± 0.128</td>
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<tr>
<td>Mar 2008</td>
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<td>1.025 ± 0.097</td>
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<tr>
<td>Apr 2008</td>
<td>21.4</td>
<td>-4.137 ± 0.175</td>
<td>0.983 ± 0.120</td>
<td>0.895</td>
</tr>
</tbody>
</table>
Hoque et al.: Seasonal variation in mangrove respiration
decreased with increasing temperature $t$: $r(t,h) = 0.96$, $p < 0.01$. On the other hand, the coefficient $f$ significantly increased with increasing $t$: $r(t,\ln f) = 0.86$, $p < 0.01$.

As shown in Fig. 4, the respiration rate of each individual tree was examined for the monthly mean temperature. In every individual, the respiration increased with increasing temperature. For each individual, the respiration $r$ was successfully formulated with an exponential function of the temperature $t$:

$$ r = r_0 e^{kt} $$

where $r_0$ and $k$ are coefficients. The $k$-value is an indicator of the sensitivity of respiration to temperature or seasonality. Higher $k$-values indicate higher respiration with increasing temperature. The $k$-value ranged from 0.034 to 0.149°C$^{-1}$, and its logarithmic value significantly decreased with an increase of the logarithmic value of tree mass: $r(\ln m, \ln k) = 0.81$, $p < 0.01$ (Fig. 5).

**DISCUSSION**

**Size-dependence of metabolism**

Von Bertalanffy (1957) stated 3 forms of size-dependence of metabolism: the metabolic rate is (1) proportional to surface area $m^{2/3}$, (2) proportional to mass $m$ and (3) proportional to one intermediate between surface area and mass. All 3 patterns have been observed in trees. On the one hand, Ninomiya & Hozumi (1983a,b) found in a stand of 24 yr old Chamaecyparis obtusa (Seib. et Zucc.) Endl. during a self-thinning stage that the annual respiration of individual trees is nearly proportional to their surface area in large-sized trees, with the exception of smaller trees that were not undergoing self-thinning at the time. The self-thinning results from respiration surpassing photosynthesis, i.e. bankruptcy (Yokota & Hagiwara 1996). On the other hand, Ninomiya & Hozumi (1981), Ogawa et al. (1985) and Yokota et al. (1994) all found that the annual respiration of individual trees is proportional to their mass in young conifer stands (<10 yr old). In a broad summary of studies covering many species, Reich et al. (2006) also showed that whole-plant respiration rate scales are approximately proportional to total mass.

Hagiwara & Hozumi (1991) suggested that in a young stand the annual respiration per tree may be directly proportional to its mass, because the heartwood is still active in young trees. However, in a mature stand the annual respiration per tree is proportional to its surface area, because active cells concentrate near the sapwood. In our experiment, the monthly exponent ranged from 0.723 to 1.085 (Table 2); this range is in agreement with the third statement of von Bertalanffy (1957).

**Seasonal dependence of respiration scaling**

In the warm summer (growing season), $h$ was closer to $3/4$ than to $1.0$ or $2/3$ (Table 2) except in October. Since Kandelia obovata in southern Japan is at the northernmost limit of its distribution (Spalding et al. 1997), the warm summer is favourable for K. obovata. As a result, the assumption of Brown et al. (2004) holds for the mangrove species in the higher temperature range, i.e. respiration is constrained by resource delivery through internal branching networks in the mangrove. Under optimal growth conditions when the re-
source supply matches the demand, respiration rate scales to the 3/4 power of biomass (Banavar et al. 2002).

In the cool winter (dormant season), $h$ was closer to 1.0 than to 3/4 or 2/3 (Table 2). The whole respiration is the combination of growth respiration proportional to absolute growth rate and maintenance respiration proportional to mass (Hesketh et al. 1971). Since the absolute growth rate is almost zero for the mangrove species during the winter season, the growth respiration is negligible. This means that the respiration mainly consists of maintenance respiration alone, so that the respiration might be proportional to $m$, rather than $m^{3/4}$. Under resource limiting conditions, organisms must allocate an increasing proportion of their internal resources and total biomass towards resource acquisition. An increase in the ability to harvest resources with body size might lead to an increase in the scaling exponent of individual based respiration rate (Finkel et al. 2004).

The relationship between the ratio of mean summer respiration $r_{sum}$ (June to September) to mean winter respiration $r_{win}$ (October to May) and tree mass $m$ is shown in Fig. 6. The $r_{sum}$ was higher than $r_{win}$ in the whole range of $m$. The ratio $r_{sum}/r_{win}$ decreased in inverse proportion to increasing mass $m$ and then gradually approached a minimum asymptote of 1.24. Respiration is more sensitive to seasonal temperature in the small-sized trees, i.e. suppressed trees, than in the large-sized trees (Fig. 5). As a result, a relative decrease in respiration from the warm summer to the cool winter is larger in the small-sized trees than in the large-sized trees.

CONCLUSIONS

The respiration of *Kandelia obovata* increased with increasing size. The size-dependence (Fig. 2) was expressed with a power-function of Eq. (4) throughout a year (Table 2). The monthly exponent was higher in the cool winter (dormant season), whereas it was lower in the warm summer (growing season). The present study site, where the mean annual temperature is $23.4 \pm 0.1^\circ C$, is closer to the northernmost distribution limit of *K. obovata*, so that seasonal temperature may affect such dependence. Another explanation of this dependence is that in winter the main component of respiration is maintenance respiration, which is proportional to mass $m$, so that the amount of respiration is proportional to the mass of respiring tissue. However, during summer, woody tissues are growing, and woody tissue growth occurs at the surfaces, so that woody tissue growth respiration may be proportional to the surface area; i.e. to $m^{2/3}$. Since maintenance respiration of both leaves and stems continues through the summer, total respiration (maintenance plus growth) scales somewhere between mass and surface area. However, the present experiment indicates that the separation of maintenance and growth respiration is necessary to better understand the dependence of respiration on size and temperature.

Acknowledgements. We are grateful to our colleagues, Drs. S. M. Feroz and K. Analuddin, Messrs. Y. Mori and D. Takagi, and Ms. N. Ferdousee for their cooperation and active participation in the field work. This study was financed in part by a Grant-in-Aid for Scientific Research (No. 20510011) from the Ministry of Education, Culture, Sports, Science and Technology, Japan, and by the 21st Century COE program of University of the Ryukyus.

LITERATURE CITED


Yokota T, Ogawa K, Hagihara A (1994) Dependence of the aboveground respiration of hinoki cypress (Chamaecyparis obtusa) on tree size. Tree Physiol 14:467–479

Editorial responsibility: Hans Heinrich Janssen, Oldendorf/Luhe, Germany

Submitted: August 10, 2009; Accepted: January 20, 2010
Proofs received from author(s): March 30, 2010