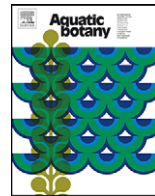




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# Forest structure of a subtropical mangrove along a river inferred from potential tree height and biomass

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### ABSTRACT

The hypothesis was tested that potential tree height and biomass in mangroves decrease downstream with the tidal gradient along the Okukubi River in Okinawa Island, Japan. The mangrove stands consisted of *Bruguiera gymnorrhiza* (L.) Lamk. and *Kandelia obovata* (S., L.) Yong (Rhizophoraceae). Four sites were selected considering the distance from the mouth of the river. Soil salinity increased downstream, while soil total nitrogen content decreased. The soil redox potential did not vary along the river. Maximum gross photosynthesis and tree height for each species decreased downstream. The potential tree height ( $H_{\max}$ ) inferred from the stem diameter ( $D_{0.1}$ )–tree height ( $H$ ) relationship ( $1/H = 1/aD_{0.1}^h + 1/H_{\max}$ ;  $a, h$ , coefficient) in each species decreased downstream. The tree density ( $\rho$ )–mean tree size ( $D_{0.1}^2 H$ ) relationships ( $D_{0.1}^2 H = K\rho^{-\alpha}$ ;  $K, \alpha$ , coefficient) determined for four sites revealed that the mean tree size at any given tree density decreased downstream, which indicates the decrease of potential biomass. Furthermore, an index for biomass ( $D_{0.1}^2 H \rho = K$ ) was homogeneous within a site regardless of tree density, i.e. the value of  $\alpha$  at each site did not differ significantly from 1.0 ( $p > 0.05$ ). The decreases in potential tree height and biomass may be partially ascribed to the stressful environments at the downstream sites characterized by high salinity ( $>2.6\%$ ) and nitrogen-poor soils ( $<0.25$  ppt) in our study area.

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## 1. Introduction

Mangrove communities show gradual changes in forest structure along tidal gradients. For instance, changes in tree height (Lugo and Snedaker, 1974) and biomass (Sherman et al., 2003) have been reported. These changes may be ascribed to stunting in plant growth in stressful environments due to high salinity and poor nutrient conditions (Cheeseman and Lovelock, 2004; Lovelock et al., 2006; Naidoo, 2006). The potential tree height and biomass would be decreased with increasing such stress factors along the tidal gradients.

We tested this hypothesis in a mangrove forest, which mainly consisted of *Bruguiera gymnorrhiza* (L.) Lamk. and *Kandelia obovata* (S., L.) Yong (Rhizophoraceae), in the estuary of the Okukubi River, Okinawa Island, Japan. These species are dominant in the mangrove forests of East Asia at high latitudes (Hosokawa et al., 1977; Lin, 1999). We evaluated the forest structure on the basis of tree censuses at different locations in the estuary. We also

quantified maximum leaf photosynthesis at these various locations in the estuary to elucidate the mechanism underlying the changes in forest structure. Maximum leaf photosynthesis of *B. gymnorrhiza* and *K. obovata* reportedly decreases gradually with increasing salinity from 0 to 500 mM NaCl (Kawamitsu et al., 1995; Kao and Tsai, 1999; Takemura et al., 2000). Furthermore, the combination of high salinity and poor nitrogen reduces leaf photosynthesis by disrupting nitrogen uptake (Kao and Tsai, 1999).

## 2. Methods

### 2.1. Field sites

This study was conducted in a mangrove forest along the Okukubi River in Okinawa Island, Japan ( $26^{\circ}27' N$ ,  $127^{\circ}56' E$ , Fig. 1). On the basis of the 1994–2003 data obtained at the Okinawa Meteorological Observatory, the mean monthly minimum and maximum temperatures were estimated to be  $16.6^{\circ} C$  (January) and  $28.7^{\circ} C$  (July), respectively. Rainfall was more than 100 mm month<sup>-1</sup> throughout the year, and the mean annual rainfall was 1978 mm year<sup>-1</sup>. The mangrove forest consisted mainly of *B. gymnorrhiza* (L.) Lamk. and *K. obovata* (S., L.) Yong. A few individuals of *Rhizophora stylosa* Griff. and *Lumnitzera racemosa* Willd. were also noted.

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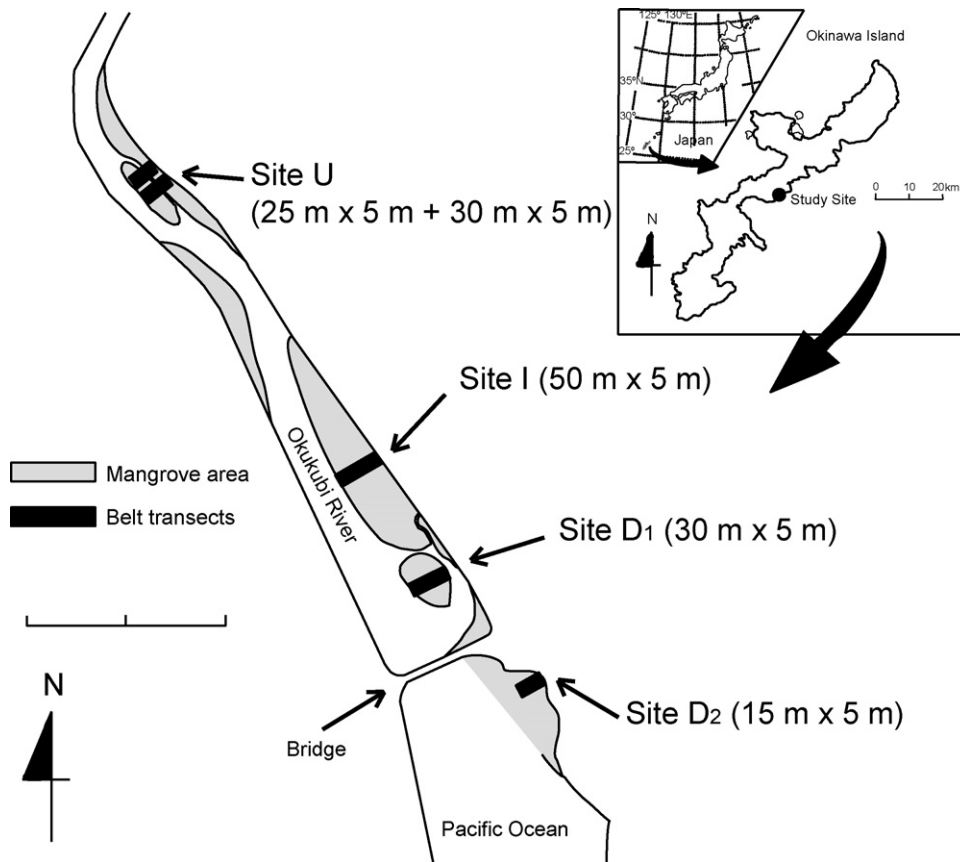


Fig. 1. Map of the study area.

Four sites were selected considering the distance from the mouth of the river (Fig. 1). Site U consisted of two belt transects located close to each other. Sites I, D<sub>1</sub>, and D<sub>2</sub> consisted of a single belt transect each. Each 5 m-wide belt transect traversed the mangrove forest perpendicularly to the river and was divided into 5 × 5-m subplots. The total lengths of the belt transects were 55 m (Site U), 50 m (Site I), 30 m (Site D<sub>1</sub>), and 15 m (Site D<sub>2</sub>).

## 2.2. Tree census

All individual trees within the belt transects were counted and measured for height ( $H$ , m) and stem diameter at  $H/10$  ( $D_{0.1}$ , cm) in November 2004. We used the stem diameter at  $H/10$ , rather than at breast height (DBH), as the measure of stem diameter. This was necessary because the height of short trees under the stressful conditions in mangroves often never reach breast height (1.3 m above the ground); therefore, the DBH of these stunted trees cannot be measured (Hogarth, 1999; Ross et al., 2001; Coronado-Molina et al., 2004). Thus, using  $H/10$  allows us to measure the stem diameters of such short trees (Ogawa and Kira, 1977; Gaihara et al., 1993; Khan et al., 2005; Suwa et al., 2008).

To measure soil salinity (%), soil pore water was extracted from three points in each subplot using a plastic tube connected to a 500-mL cylinder, taking care to avoid mixing the pore water and surface water (McKee et al., 1988). However, this method could not be applied in some plots where the soil consisted mainly of sand. In such cases we dug holes to collect the soil pore water. Salinity of the collected pore water was immediately measured in the field with a salinometer (ES-421, Atago, Japan). The soil redox potential (mV) was simultaneously measured at a depth of 10–20 cm in each subplot using an electrode oxidation–reduction potential meter (RM 20P, TOA, Japan). Three soil cores were sampled from the

topsoil in each subplot (0–10 cm deep) to measure total nitrogen content (ppt). The soil samples were dried to a constant mass at 80 °C and powdered before measuring total nitrogen content with a CHN-coder (JM 10, J-Science Lab, Japan).

## 2.3. Photosynthetic measurement

Photosynthetic photon flux density (PPFD)–net photosynthesis curves were determined for *B. gymnorrhiza* and *K. obovata* in May 2006 with a portable photosynthesis system (LI-6400, LI-COR, USA). Seven sun leaves per species were chosen at each site. The PPFD ( $I$ ) inside the chamber was regulated at eight levels (1600, 800, 400, 200, 100, 50, 25, and 0  $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ ) using an LED light source (6400-02B, LI-COR, USA). Leaf temperature was controlled within the range of 25–27 °C, considering the ambient air temperature during the measurement period. CO<sub>2</sub> concentration was regulated at 370 ppm.

## 2.4. Models

To quantify the potential tree height for each species at each site, the stem diameter ( $D_{0.1}$ )–tree height ( $H$ ) relationship was examined with the generalized allometric function (Ogawa and Kira, 1977)

$$\frac{1}{H} = \frac{1}{aD_{0.1}^h} + \frac{1}{H_{\max}} \quad (1)$$

where  $a$  and  $h$  are the coefficients, and  $H_{\max}$  is the potential tree height. In a previous paper (Suwa et al., 2008), the value of  $h$ , i.e. the ratio of the relative growth rate of  $H$  to that of  $D_{0.1}$  in small trees, could be assumed to be one. In the present study, the value of  $h$

**Table 1**

Stand characteristics at each site. Values in parentheses indicate standard error. Different lowercase letters indicate significant differences among species within a site (Bonferroni post-hoc test,  $p < 0.05$ ); different uppercase letters indicate significant differences among sites within species (Bonferroni post-hoc test,  $p < 0.05$ ).

	Site U	Site I	Site D <sub>1</sub>	Site D <sub>2</sub>
Study area (m <sup>2</sup> )	275	250	150	75
Distance from the mouth of river (m)	807 and 793	448	317	179
Total number of individuals	213	503	328	54
Pore water salinity (%)	1.80 (0.09) <sup>A</sup>	1.81 (0.08) <sup>A</sup>	2.58 (0.02) <sup>B</sup>	2.63 (0.11) <sup>B</sup>
Soil redox potential (mv)	-3.55 (51.27) <sup>A</sup>	18.80 (44.31) <sup>A</sup>	59.83 (38.44) <sup>A</sup>	49.67 (84.92) <sup>A</sup>
Soil total nitrogen (ppt)	0.76 (0.06) <sup>A</sup>	0.67 (0.04) <sup>A</sup>	0.26 (0.02) <sup>B</sup>	0.25 (0.02) <sup>B</sup>
Canopy openness (%)	96.4 (0.33) <sup>A</sup>	85.9 (0.88) <sup>A</sup>	22.9 (5.14) <sup>B</sup>	28.2 (5.33) <sup>B</sup>
Tree density (25 m <sup>-2</sup> )				
<i>B. gymnorrhiza</i>	17.73 (2.30) <sup>a,A</sup>	42.20 (8.90) <sup>a,B</sup>	26.67 (3.98) <sup>a,A,B</sup>	9.67 (4.98) <sup>a,A</sup>
<i>K. obovata</i>	1.64 (0.70) <sup>b,A</sup>	8.10 (4.55) <sup>b,A,B</sup>	28.00 (11.66) <sup>a,B</sup>	8.33 (3.93) <sup>a,A,B</sup>
Tree height (m)				
<i>B. gymnorrhiza</i>	6.12 (0.12) <sup>a,A</sup>	3.99 (0.07) <sup>a,B</sup>	1.91 (0.07) <sup>a,C</sup>	1.67 (0.19) <sup>a,C</sup>
<i>K. obovata</i>	6.69 (0.17) <sup>a,A</sup>	3.19 (0.23) <sup>b,B</sup>	0.98 (0.04) <sup>b,C</sup>	0.98 (0.08) <sup>a,A</sup>
Stem diameter (cm)				
<i>B. gymnorrhiza</i>	8.52 (0.35) <sup>a,A</sup>	4.93 (0.11) <sup>a,B</sup>	5.71 (0.45) <sup>a,B</sup>	5.64 (0.86) <sup>a,B</sup>
<i>K. obovata</i>	11.8 (0.66) <sup>b,A</sup>	4.95 (0.36) <sup>a,B</sup>	2.70 (0.09) <sup>b,C</sup>	5.61 (0.64) <sup>a,B</sup>

could not be assumed to be one, because the value of  $h$  changed largely among sites in each species.

The tree density ( $\rho$ , ha<sup>-1</sup>)–mean tree size ( $D_{0.1}^2 H$ ) relationship was expressed in the power equation

$$D_{0.1}^2 H = K \rho^{-\alpha} \quad (2)$$

where  $K$  and  $\alpha$  are the coefficients. Eq. (2) can be transformed to a linear equation after taking logarithms as follows

$$\ln D_{0.1}^2 H = \ln K - \alpha \ln \rho \quad (3)$$

The PPFD ( $I$ )–net photosynthesis ( $p_n$ ,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) curve was expressed in the Michaelis–Menten equation

$$p_n = \frac{p_{g_{\max}} \phi I}{p_{g_{\max}} + \phi I} - r_d \quad (4)$$

where  $p_{g_{\max}}$  is the maximum gross photosynthesis rate;  $\phi$  is the quantum yield in the lower range of  $I$ ;  $r_d$  is the dark respiration rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ).

### 2.5. Statistics

We used one-way analysis of variance (ANOVA) to examine differences in mean values among sites using statistical software (SPSS ver. 14.0J, SPSS Japan Inc., Japan). Two-way (2 species  $\times$  4 sites) ANOVA was used to examine differences in mean values among sites and species. When ANOVA detected a significant main effect or interaction between site and species, we performed a Bonferroni post-hoc test to examine pair-wise differences among sites or species.

To examine differences in the stem diameter ( $D_{0.1}$ )–tree height ( $H$ ) relationships in Eq. (1) among sites within a species, one-way ANOVA was carried out on the basis of the residual sum of squares (RSS) when the pooled data were regressed and the sum of RSS when data for each site were regressed separately (Aiba and Kohyama, 1997). If ANOVA detected a significant main effect, we performed a Bonferroni post-hoc test to examine pair-wise differences in potential tree height ( $H_{\max} = H|_{D_{0.1} \rightarrow \infty}$ ) in Eq. (1) among sites.

To test whether the tree density ( $\rho$ )–mean tree size ( $D_{0.1}^2 H$ ) relationships expressed in Eq. (3) were equal among sites, we used analysis of covariance (ANCOVA) using statistical software (SPSS ver. 14.0J, SPSS Japan Inc., Japan). If the slope did not differ significantly among sites, we tested for a significant difference among the intercepts on the assumption that the slope was the

same. When the ANCOVA detected a significant main effect of site on the response variable, we performed a Bonferroni post-hoc test to examine pair-wise differences among sites. We performed non-linear regression analyses based on Eq. (1) or (4) using Kaleida Graph (Synergy Software, USA).

### 3. Results

Soil salinity and soil total nitrogen content varied significantly among sites (soil salinity,  $F_{(3, 86)} = 14.6$ ,  $p < 0.01$ ; soil total nitrogen content,  $F_{(3, 86)} = 13.7$ ,  $p < 0.01$ , Table 1). Soil salinity increased downstream while soil total nitrogen content decreased. Differences in soil redox potential among sites were not significant ( $F_{(3, 26)} = 0.470$ ,  $p > 0.05$ ).

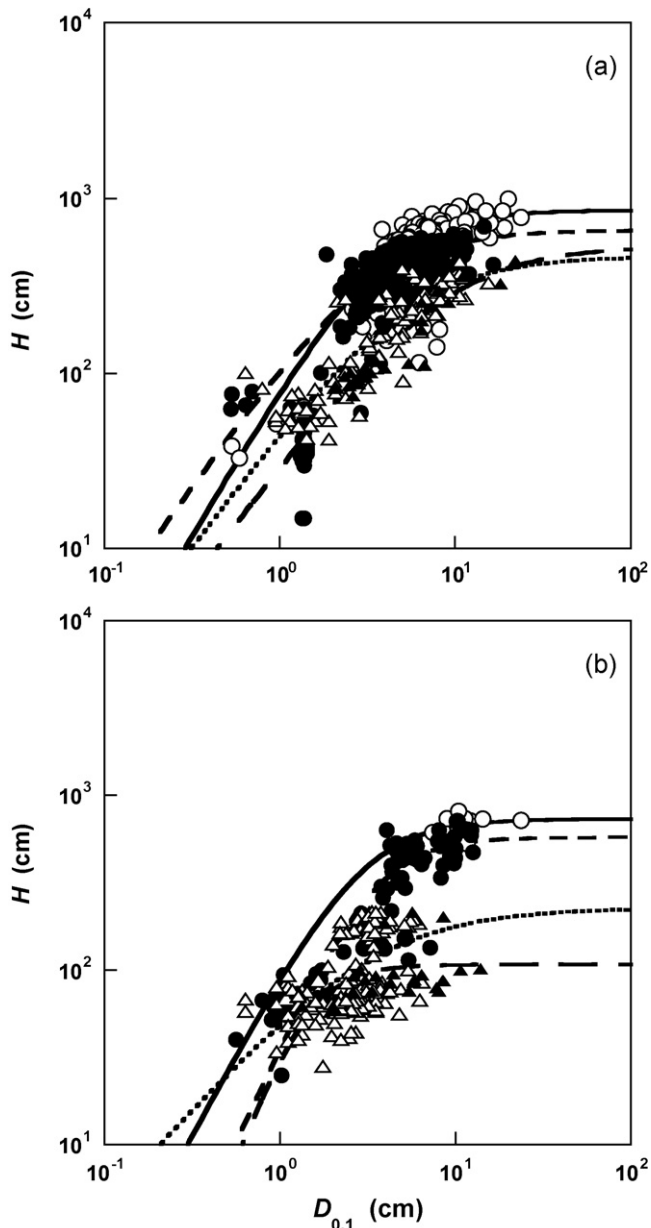
We counted a total of 1048 individuals (Table 1). Tree density varied among sites ( $F_{(3, 1040)} = 4.89$ ,  $p < 0.01$ ) and species ( $F_{(1, 1040)} = 6.58$ ,  $p < 0.05$ ). The tree density for each species did not show any clear trends along the river. The tree density was higher for *B. gymnorrhiza* than for *K. obovata* at the upstream sites (Site U and Site I), but did not differ between the two species at the downstream sites (Site D<sub>1</sub> and Site D<sub>2</sub>).

As shown in Table 1, tree height ( $H$ ) and stem diameter at a height of  $H/10$  ( $D_{0.1}$ ) varied among sites ( $H$ ,  $F_{(3, 1040)} = 25.4$ ,  $p < 0.01$ ;  $D_{0.1}$ ,  $F_{(3, 1040)} = 64.3$ ,  $p < 0.01$ ); while the difference was not significant between species ( $H$ ,  $F_{(1, 1040)} = 3.81$ ,  $p > 0.05$ ;  $D_{0.1}$ ,  $F_{(1, 1040)} = 0.940$ ,  $p > 0.05$ ). However, significant interactions existed between sites and species for tree height and stem diameter ( $H$ ,  $F_{(3, 1040)} = 4.63$ ,  $p < 0.01$ ;  $D_{0.1}$ ,  $F_{(3, 1040)} = 17.7$ ,  $p < 0.01$ ).

Tree height decreased gradually downstream for each species. Tree height was greater for *B. gymnorrhiza* than for *K. obovata*, with the exception of Site U. For each species, the stem diameter was greater at Site U than at the other sites. *Kandelia obovata* had a greater stem diameter than *B. gymnorrhiza* at Site U, but *B. gymnorrhiza* exhibited a greater  $D_{0.1}$  than *K. obovata* at Site D<sub>1</sub>. These differences were significant.

The  $D_{0.1}$ – $H$  relationships varied among sites in each species (Fig. 2a, *B. gymnorrhiza*,  $F_{(9, 742)} = 15.3$ ,  $p < 0.01$ ; Fig. 2b, *K. obovata*,  $F_{(9, 280)} = 56.6$ ,  $p < 0.01$ ). The potential tree height ( $H_{\max}$ ) in Eq. (1) decreased downstream in each species, and the differences between sites within a species were significant except between Sites D<sub>1</sub> and D<sub>2</sub> (Bonferroni post-hoc test,  $p < 0.05$ ), i.e. the tree shape for each species changed along the environmental gradient.

The relationship between tree density ( $\rho$ ) and mean tree size ( $D_{0.1}^2 H$ ) was examined for each site (Fig. 3).  $D_{0.1}^2 H$  can be considered

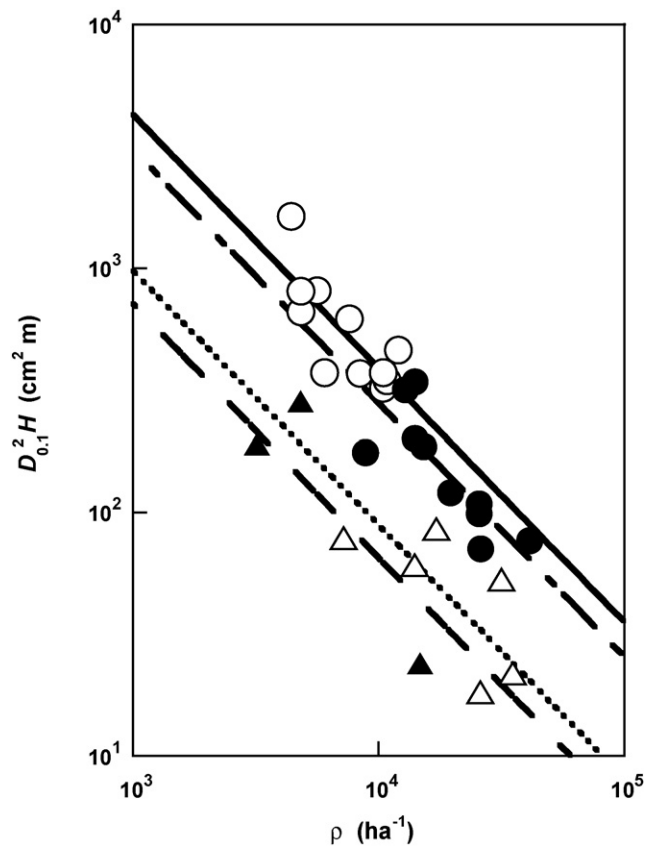


**Fig. 2.**  $D_{0.1}$ - $H$  relationships for (a) *Bruguiera gymnorrhiza* and (b) *Kandelia obovata* at each site. Open circles and solid line, Site U; closed circles and short-dashed line, Site I; open triangles and dotted line, Site D<sub>1</sub>; closed triangles and long-dashed line, Site D<sub>2</sub>. Each curve is based on Eq. (1), where  $R^2 = 0.50, 0.71, 0.74,$  and  $0.81$  for *B. gymnorrhiza* in Site U, I, D<sub>1</sub>, and D<sub>2</sub>, respectively, and  $R^2 = 0.11, 0.75, 0.23,$  and  $0.36$  for *K. obovata* in Site U, I, D<sub>1</sub>, and D<sub>2</sub>, respectively.

as an index for tree mass (Khan et al., 2005). The coefficient  $\alpha$  in Eq. (3) did not differ among sites ( $F_{(3, 22)} = 0.910, p > 0.05$ ), and the common  $\alpha$  was estimated to be  $1.04 \pm 0.16$  (SE). Significant effects of tree density and site on mean tree size were detected ( $\rho, F_{(1, 26)} = 40.8, p < 0.01$ ; site,  $F_{(2, 26)} = 26.3, p < 0.01$ ). The y-intercept ( $\ln K$ ) in Eq. (3) was estimated to be  $15.55 \pm 0.09$  (SE),  $15.22 \pm 0.11,$   $14.07 \pm 0.21,$  and  $13.76 \pm 0.38$  for Sites U, I, D<sub>1</sub>, and D<sub>2</sub>, respectively. A Bonferroni post-hoc test with a significance level set at 0.05 showed that the intercept was significantly lower at the downstream sites (D<sub>1</sub> and D<sub>2</sub>) than at the upstream sites (U and I).

In addition, the common  $\alpha$ , estimated as  $1.04 \pm 0.16$  (SE), did not differ from 1.0 ( $t_{(28)} = 0.246, p > 0.05$ ). Therefore, Eq. (3) can be rewritten as follows

$$D_{0.1}^2 H \rho = K \quad (5)$$



**Fig. 3.** Relationships of mean tree size ( $D_{0.1}^2 H$ ) to tree density ( $\rho$ ) at different sites. The meanings of symbols and lines are the same as Fig. 2. Each line is based on Eq. (3), where  $R^2 = 0.55, 0.37, 0.13,$  and  $0.47$  for Site U, I, D<sub>1</sub>, and D<sub>2</sub>, respectively.

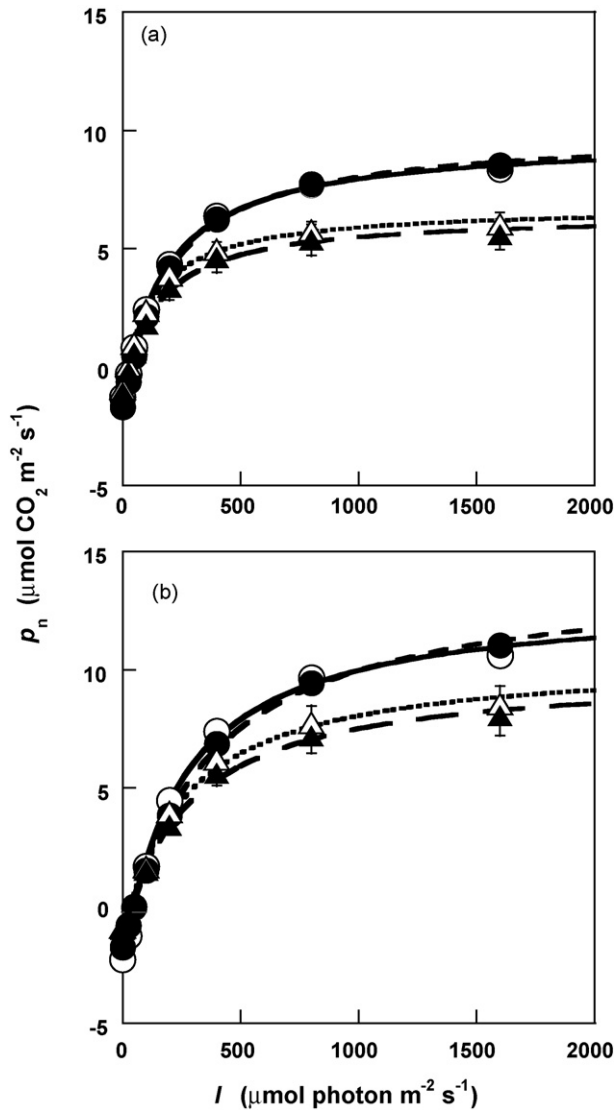
where  $D_{0.1}^2 H \rho$  ( $\text{cm}^2 \text{m ha}^{-1}$ ) is an index for biomass corresponding to  $K$ . By assuming Eq. (5), the indices for biomass ( $D_{0.1}^2 H \rho$  or  $K$ ) at Sites U, I, D<sub>1</sub> and D<sub>2</sub> were estimated to be  $4.13 \times 10^6 \pm 4.12 \times 10^5$  (SE)  $\text{cm}^2 \text{m ha}^{-1}$ ,  $2.88 \times 10^6 \pm 3.06 \times 10^5 \text{cm}^2 \text{m ha}^{-1}$ ,  $9.66 \times 10^5 \pm 2.00 \times 10^5 \text{cm}^2 \text{m ha}^{-1}$ , and  $7.76 \times 10^5 \pm 3.03 \times 10^5 \text{cm}^2 \text{m ha}^{-1}$ , respectively. The estimated index for biomass differed among the sites ( $F_{(3, 26)} = 15.6, p < 0.01$ ), and the pair-wise difference between sites was significant between the upstream sites (U and I) and the downstream sites (D<sub>1</sub> and D<sub>2</sub>; Bonferroni post-hoc test,  $p < 0.05$ ). This indicates that biomass differed among sites, but was homogeneous within a site regardless of  $\rho$ .

Equation (4) described the PPFd ( $I$ )-net photosynthesis ( $p_n$ ) relationships well as shown in Fig. 4, where the average values of seven leaves are plotted. The value of  $R^2$  in the PPFd-net photosynthesis curve for a leaf was over 0.99 in 56 leaves (7 leaves  $\times$  4 sites  $\times$  2 species). Maximum gross photosynthesis ( $p_{g\text{max}}$ ) varied among the sites ( $F_{(3, 48)} = 15.9, p < 0.01$ ) and species (Fig. 5,  $F_{(1, 48)} = 54.4, p < 0.01$ ). The maximum gross photosynthesis ( $p_{g\text{max}}$ ) decreased downstream and was greater for *K. obovata* than for *B. gymnorrhiza* at each site.

#### 4. Discussion

As shown in Table 1, the upstream sites (U and I) were mostly occupied by *B. gymnorrhiza*, while *K. obovata* and *B. gymnorrhiza* were equally abundant downstream (Sites D<sub>1</sub> and D<sub>2</sub>). In general, the two species often coexist, but *B. gymnorrhiza* tends to dominate upstream, whereas *K. obovata* dominates downstream (Duke et al., 1998; Lin, 1999; Enoki et al., 2009). Therefore, the distribution pattern in the present study can be considered typical.

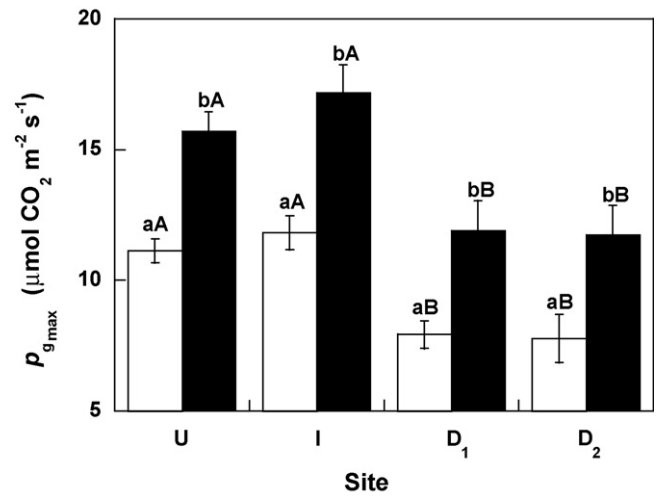




**Fig. 4.** Photosynthetic photon flux density ( $I$ )–net photosynthesis ( $p_n$ ) curves for (a) *Bruguiera gymnorrhiza* and (b) *Kandelia obovata* at each site. The meanings of symbols and lines are the same as Fig. 2. Each point is the mean of seven leaves. Error bars indicate standard error. Each curve is based on Eq. (4), where  $R^2 = 1.00$ , 1.00, 0.99, and 0.99 for *B. gymnorrhiza* in Site U, I, D<sub>1</sub>, and D<sub>2</sub>, respectively, and  $R^2 = 1.00$ , 1.00, 0.99, and 1.00 for *K. obovata* in Site U, I, D<sub>1</sub>, and D<sub>2</sub>, respectively.

The downstream sites had a high salinity and nitrogen-poor soils compared to the upstream sites (Table 1), suggesting more stressful conditions at the downstream sites. We observed that the maximum photosynthesis ( $p_{g,max}$ ) decreased downstream for both species (Fig. 5), which confirms such suggested stresses.

For both species tree height decreased downstream (Table 1). This decreasing tendency was also reported for another mangrove forest in Japan (Enoki et al., 2009). The decrease in tree height can be explained by the decreasing potential tree height downstream (Fig. 2), i.e. the tree height at the downstream sites would never reach that observed at the upstream sites. The slope ( $\alpha$ ) in Eq. (3) (Fig. 3) did not differ among sites, and the y-intercept ( $\ln K$ ) was lower downstream (Sites D<sub>1</sub> and D<sub>2</sub>) than upstream (Sites U and I). The absolute segregation in the tree density relationships between the upstream and downstream sites reflects differences in the potential mean tree mass at a given tree density, i.e. the mean tree size can be considered as an index for mean tree mass (Khan et al., 2005). Furthermore, the index for stand biomass ( $D_{0.1}^2 H \rho$ ) was homogeneous within a site regardless of tree density, because  $\alpha$  in



**Fig. 5.** Maximum gross photosynthesis rate ( $p_{g,max}$ ) based on Eq. (4) for each species and site. Error bars indicate standard error. Open and closed columns represent *Bruguiera gymnorrhiza* and *Kandelia obovata*, respectively. Different lowercase letters indicate significant differences among species within a site (Bonferroni post-hoc test,  $p < 0.05$ ); different uppercase letters indicate significant differences among sites within a species (Bonferroni post-hoc test,  $p < 0.05$ ).

Eq. (2) did not differ significantly from 1.0. This implies that a tree stand maintains a homogeneous biomass specific to a given site.

Although the decreases in tree height and biomass do not necessarily imply stunted plant growth (Suwa et al., 2008), mangroves frequently exhibit decreased tree height according to tidal gradients along with parallel stunting of plant growth accompanied by decreased leaf photosynthetic capability (Cheeseman and Lovelock, 2004; Lovelock et al., 2006; Naidoo, 2006). Indeed, we found that maximum photosynthesis decreased downstream. In conclusion, our data suggest reduced photosynthesis as well as potential tree height and biomass with increased salinity and decreased soil nitrogen, in both species.

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