

# Interspecific variation in photosynthesis and respiration balance of three seagrasses in relation to light availability

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**ABSTRACT:** Low light levels are a major factor determining the depth distribution of submerged macrophytes. In the Indo-Pacific tropical region, different seagrass species have specific zonation patterns from intertidal to subtidal areas along depth and light gradients. *Cymodocea serrulata* generally occurs in deeper water than *Thalassia hemprichii* and *C. rotundata*, suggesting that *C. serrulata* probably has the lowest minimum photon requirement of the 3 species. We compared photosynthesis and respiration balances of these 3 tropical seagrasses by examining photosynthesis-irradiance (P-E) curves for leaves and for the whole plant bodies. Sample collection and measurement were conducted on 2 occasions (July and February) on Ishigaki Island, southwestern Japan. Leaf photosynthetic traits were not concordant with the observed zonation pattern of the species. When respiration rates of the root and rhizome were taken into account, *T. hemprichii* had a significantly higher light compensation point (158.1  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  in July, 187.2 in February) than *C. rotundata* (47.9 in July, 41.0 in February) and *C. serrulata* (85.1 in July, 40.0 in February). The large amount of belowground respiration in *T. hemprichii* was a major cause of the variation in the compensation irradiance. This result is in concordance with the realized distribution pattern of *T. hemprichii*, which is sparse under low light conditions caused by depth or heavy siltation. Conversely, *C. serrulata* had less belowground biomass and a smaller respiration demand, enabling the species to maintain a better photosynthetic/respiration balance under lower light. *C. rotundata* had a lower saturating irradiance, a lower compensation point and a lower respiration rate than the other species. Thus, *C. rotundata* has the potential to inhabit the deepest water, although its realized distribution range is shallower than that of *C. serrulata*, suggesting that other factors limit the depth range of *C. rotundata*.

**KEY WORDS:** Biomass allocation · Depth limit · O<sub>2</sub> budget · P-E curve · Tropical seagrasses

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## INTRODUCTION

Seagrass beds in the Indo-Pacific tropical region characteristically comprise a mixed vegetation with high species diversity. Generally, depth distributions vary among species, leading to specific zonation patterns from intertidal to subtidal areas (Mukai et al. 1987, Lee Long et al. 1993, Björk et al. 1999, De Troch et al. 2001, Tanaka & Nakaoka 2004, Tanaka & Kayanne 2007). For subtidal seagrass beds, light inten-

sity is a major factor determining species' depth distributions (Duarte 1991). Interspecific variation in tolerance to light limitation is thought to be related to the ability (photosynthetic) of each species to maintain a positive whole-plant carbon balance. Photosynthetic traits of seagrasses, such as maximum photosynthetic rate, photosynthetic efficiency ( $\alpha$ ) and light compensation point may vary among species in ways similar to the patterns of sun and shade plants in terrestrial ecosystems (Larcher 2002). Even when photosynthetic

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traits do not vary, the allocation patterns of aboveground and belowground biomass may affect the O<sub>2</sub> balance of the whole plant, leading to different depth limits among species. For example, a smaller proportion of belowground biomass is thought to enable *Halophila* spp. to survive in deeper and darker sites, because of its smaller respiratory demand (Dennison 1987, Duarte 1991). To determine the whole plant minimum photon requirements, it is necessary to measure the photosynthesis and/or respiration rates of both aboveground and belowground parts. However, as Hemminga (1998) pointed out, only a few studies have measured respiration in belowground parts of seagrasses (Fourqurean & Zieman 1991, Dunton & Tomasko 1994, Dunton 1996, Herzka & Dunton 1998).

*Thalassia hemprichii*, *Cymodocea rotundata* and *C. serrulata* are dominant medium-sized seagrass species in tropical seagrass beds in Indo-Pacific coastal areas (Tanaka 2004). Leaf production and respiration of these 3 species have been studied using 3 major methods: (1) oxygen probes (Agawin et al. 1996, 2001, Vermaat et al. 1997, Abu Hena et al. 2001), (2) Diving-PAM (Hanelt et al. 1994, Björk et al. 1999, Haynes et al. 2000, Schwarz et al. 2000, Liu et al. 2005), and (3) gas-volume measurements (Pollard & Moriarty 1991, Pollard & Greenway 1993). However, there were no consistent tendencies in photosynthetic traits. To our knowledge, there have been no previous studies examining the photosynthesis–respiration balance of whole plants of these 3 species, or for any seagrass species in the Indo-Pacific tropical region. Comparisons of whole-plant O<sub>2</sub> balance may explain the differentiated depth distributions.

The objective of this study was to quantify the whole-plant minimum photon requirements by comparing photosynthetic characteristics among the 3 seagrass species in order to determine whether light could be a factor causing the interspecific differences in depth distribution. Firstly, we measured photosynthesis and respiration for each part of the shoot. Secondly, we measured the aboveground and belowground biomass allocation of each species. Thirdly, we calculated and compared the whole-plant O<sub>2</sub> balances of the 3 species along a light gradient.

## MATERIALS AND METHODS

**Environmental measurement.** This study was conducted at Shiraho on Ishigaki Island in the Ryukyu Islands group, southwestern Japan (24° 21' N, 124° 15' E; see Tanaka & Nakaoka 2004 for more detailed information on the study site). Sampling and experiments were performed on 2 occasions (July 2001 and February 2002). A data logger-type underwater

quantum cosine sensor (MPQ-1, Sanyo-Sokki) and thermometer (MWQ-3, Sanyo-Sokki) were installed at canopy height (100 cm below mean sea level) during 2 periods: from 29 June to 21 July 2001 and 1 February to 25 February 2002. Photon doses (photon irradiance × time) were calculated based on data taken by the data logger-type sensor. The light attenuation coefficient ( $K_d \text{ m}^{-1} \pm \text{SE}$ ) was  $0.60 \pm 0.04$  in this study site (Tanaka & Nakaoka 2006). Therefore, at sampling depth (100 cm below mean sea level), light intensity was about half of that at the surface.

**Photosynthesis–respiration measurements.** Three dominant seagrass species, *Thalassia hemprichii*, *Cymodocea rotundata* and *C. serrulata* were collected at the same depth (about 100 cm below mean sea level). Shoots with the belowground parts were kept in outdoor containers with circulating seawater. Photosynthesis and respiration measurements were performed within 48 h of sampling. Immediately preceding the start of the experiment, leaf segments were cut at 2 to 9 cm from the bases of the second youngest leaves of shoots. Photosynthesis and respiration were measured using a differential gas-volumeter (Productmeter, see Yokohama et al. 1986, Abe et al. 2001) in a dark room. Measurements of O<sub>2</sub> evolution of leaves were conducted between dawn and sunset. Water temperatures in the gas-volumeter were almost the same as those at the sampling site (within 1.4°C). A halogen lamp (150 W) was used as a light source. Photosynthetically active radiation (PAR) was measured using a submersible photon irradiance sensor (192SA, Li-Cor). The O<sub>2</sub> evolution of each leaf was measured successively at 8 levels of photon flux, viz. approximately 0, 30, 45, 60, 90, 150, 300 and 600  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ . After measurement of O<sub>2</sub> evolution, leaves were dried at 105°C for more than 24 h, and their dry weights were measured. Respiration rates of roots and horizontal rhizomes were measured in darkness. Photosynthesis-irradiance (P-E) curves were fitted to the data using the equation of Chalker (1981):

$$P_{\text{net}} = P_{\text{max}} \times \tanh(E/E_k) + R_d$$

where  $P_{\text{max}}$  is the maximum photosynthetic rate,  $E_k$  is the saturating irradiance (a constant determined by the initial slope and  $P_{\text{max}}$ ),  $R_d$  is the dark respiration rate, and  $E$  is photon irradiance. The light compensation point ( $E_c$ ) was determined as light intensity at which the net photosynthetic rate ( $P_{\text{net}}$ ) = zero. The photosynthetic efficiency ( $\alpha$ ) was calculated as the initial linear slope of the photosynthetic response to light.

**Estimation of whole-plant O<sub>2</sub> balance.** To estimate the relationship between O<sub>2</sub> balance and light intensity at the whole plant level, the allocation of aboveground and belowground biomass was measured for each species. Samples for biomass allocation were col-

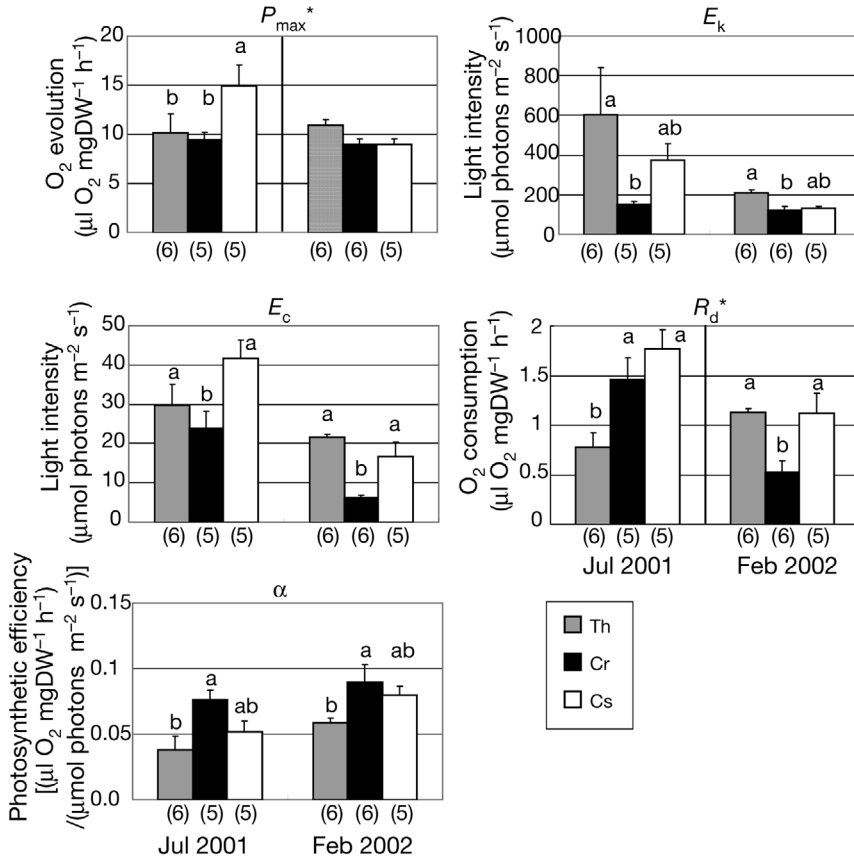


Fig. 1. *Thalassia hemprichii* (Th), *Cymodocea rotundata* (Cr), *Cymodocea serrulata* (Cs). Comparison of photosynthetic traits of leaf among species and seasons. Means + SE. Maximum photosynthetic rate ( $P_{max}$ ), saturating photon irradiance ( $E_k$ ), compensation point ( $E_c$ ), respiration rate ( $R_d$ ) and initial slope ( $\alpha$ ). Numbers in parentheses show sample sizes. Asterisk and dividing line between seasons for  $P_{max}$  and  $R_d$  indicate the existence of significant interactions in 2-way ANOVA. Different letters denote pairs of treatments for which significant variation was detected by post-hoc comparisons (Tukey's)

lected using a stainless corer (diameter 20 cm, height 50 cm) in July 2001 and February 2002. Three cores were collected for each species. The samples were washed gently in fresh water and separated into 6 parts: leaf, live sheath, dead sheath, vertical rhizome, horizontal rhizome, and root. After drying at 105°C for more than 24 h, the weight of each part was measured.

Whole-plant  $\text{O}_2$  balances were calculated for each core sample (3 replicates) by multiplying the biomass of each part by the average production and respiration rates per part at each light level. Because respiration rates of vertical rhizomes and live sheaths were not measured, we used data for horizontal rhizomes and leaves, respectively. Dead sheaths were eliminated from the calculations. The P-E curve for the whole plant was fitted, and  $P_{max}$ ,  $E_k$ ,  $E_c$ ,  $R_d$  and  $\alpha$  were determined as described above.

**Statistical analyses.** Interspecific and seasonal variation in  $P_{max}$ ,  $E_k$ ,  $E_c$ ,  $R_d$  and  $\alpha$  of leaf parts and of the

whole plant were tested using 2-way analysis of variance (ANOVA). The respiration of belowground parts (rhizome and root) was also tested using 2-way ANOVA. Prior to ANOVA, heterogeneity of variance was tested using Cochran's C test. When the variances were heterogeneous, data were log-transformed. When significant variation was detected by ANOVA, post-hoc comparisons were performed using Tukey's test. When significant interactions were detected in 2-way ANOVA, 1-way ANOVA and multiple comparisons of means were conducted separately for each season by Tukey's test using mean square of residuals of original 2-way ANOVAs (Day & Quinn 1989, Quinn & Keough 2002).

## RESULTS

### Light and temperature

The photon dose (photon irradiance  $\times$  time) was relatively high in July ( $16.6 \pm 4.3 \text{ mol m}^{-2} \text{ d}^{-1} \pm \text{SD}$ ) and low in February ( $14.3 \pm 6.5 \text{ mol m}^{-2} \text{ d}^{-1}$ ), although seasonal variation was not apparent. Water temperature was high in July ( $30.6 \pm 1.2^\circ\text{C}$ ) and low in February ( $20.0 \pm 1.7^\circ\text{C}$ ).

### Photosynthetic traits of leaves

P-E curves of leaves varied among species and seasons (Fig. 1). For the maximum photosynthetic rate ( $P_{max}$ ,  $\mu\text{l O}_2 \text{ mgDW}^{-1} \text{ hour}^{-1}$ ), the species  $\times$  season interaction was significant (Table 1). Post-hoc comparisons revealed that in July,  $P_{max}$  of *Cymodocea serrulata* was significantly higher than those of *Thalassia hemprichii* and *C. rotundata* (1-way ANOVA,  $F_{2,27} = 5.1$ ,  $p = 0.01$ ). Post-hoc comparisons revealed that in February, amongspecies variation in  $P_{max}$  was not significant (1-way ANOVA,  $F_{2,27} = 0.8$ ,  $p = 0.45$ ).

Saturating photon irradiance ( $E_k$ ,  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) was significantly lower in February than in July. Post-hoc comparison showed that *Cymodocea rotundata* had a significantly lower  $E_k$  than *Thalassia hemprichii* (Fig. 1, Table 1).

The light compensation point ( $E_c$ ,  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) was significantly lower in February than in July. Post-hoc comparison revealed that *Cymodocea rotun-*

data had a significantly lower  $E_c$  than the other 2 species (Fig. 1, Table 1).

A significant species  $\times$  season interaction was found for leaf dark respiration ( $R_d$ ,  $\mu\text{l O}_2 \text{ mgDW}^{-1} \text{ h}^{-1}$ ; Table 1). Post-hoc comparisons revealed that in July,  $R_d$  of *Thalassia hemprichii* was significantly lower than those of *Cymodocea rotundata* and *C. serrulata* (1-way

Table 1. *Thalassia hemprichii*, *Cymodocea rotundata*, *C. serrulata*. Two-way ANOVA for photosynthetic traits of leaves: maximum photosynthetic rate ( $P_{\max}$ ), saturating irradiance ( $E_k$ ), compensation point ( $E_c$ ), respiration rate ( $R_d$ ) and initial slope ( $\alpha$ ). The data for  $E_k$  were log-transformed to reduce heterogeneity of variances

	df	MS	F	p
<b><math>P_{\max}</math></b>				
Species	2	20.4	2.3	0.12
Season	1	24.0	2.7	0.11
Species $\times$ Season	2	33.5	3.7	0.04
Error	27	9.0		
<b><math>E_k</math></b>				
Species	2	1.7	4.7	0.02
Seasons	1	2.8	7.5	0.01
Species $\times$ Season	2	0.3	0.8	0.46
Error	27	0.4		
<b><math>E_c</math></b>				
Species	2	673.8	8.9	<0.01
Seasons	1	2223.3	29.5	<0.01
Species $\times$ Season	2	193.6	2.6	0.10
Error	27	75.4		
<b><math>R_d</math></b>				
Species	2	0.9	6.2	<0.01
Seasons	1	1.2	8.7	<0.01
Species $\times$ Season	2	1.3	9.6	<0.01
Error	27	0.1		
<b><math>\alpha</math></b>				
Species	2	$3.5 \times 10^{-3}$	7.0	<0.01
Seasons	1	$3.5 \times 10^{-3}$	7.1	0.01
Species $\times$ Season	2	$1.3 \times 10^{-4}$	0.3	0.77
Error	27	$5.0 \times 10^{-4}$		

ANOVA,  $F_{2,27} = 10.4$ ,  $p < 0.01$ ; Fig. 1). Post-hoc comparisons revealed that in February,  $R_d$  of *C. rotundata* was significantly lower than those of *T. hemprichii* and *C. serrulata* (1-way ANOVA,  $F_{2,27} = 5.1$ ,  $p = 0.01$ ; Fig. 1).

The photosynthetic efficiency [ $\alpha$ , ( $\mu\text{l O}_2 \text{ mgDW}^{-1} \text{ h}^{-1})/(\mu\text{mol photons m}^{-2} \text{ s}^{-1})$ ] was significantly higher in February than in July. Post-hoc comparison showed that *Cymodocea rotundata* had a significantly higher  $\alpha$  than *Thalassia hemprichii* (Fig. 1, Table 1).

### Respiration of belowground parts

The consumption of  $\text{O}_2$  per unit mass ( $R_d$ ,  $\mu\text{l O}_2 \text{ mgDW}^{-1} \text{ h}^{-1}$ ) was greater in roots than in rhizomes for

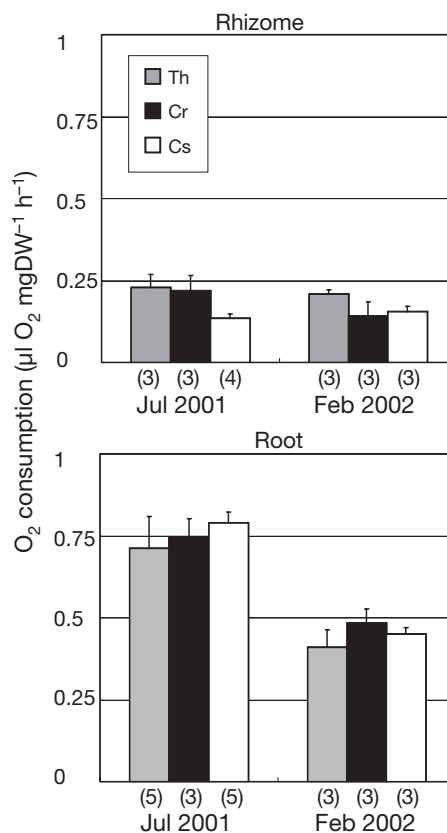


Fig. 2. *Thalassia hemprichii* (Th), *Cymodocea rotundata* (Cr), *Cymodocea serrulata* (Cs). Interspecific and seasonal variation in respiration of rhizome and root. Means + SE. Numbers in parentheses are sample sizes

all species and seasons (Fig. 2). There were no significant differences in rhizome  $R_d$  among species or seasons (Table 2). Root  $R_d$  was significantly greater in July than in February. Among-species variation in root  $R_d$  was not significant (Table 2).

Table 2. *Thalassia hemprichii*, *Cymodocea rotundata*, *C. serrulata*. Two-way ANOVA for respiration rate of rhizome and root. Data for roots were log-transformed to reduce heterogeneity of variances

	df	MS	F	p
<b>Rhizome</b>				
Species	2	$8.9 \times 10^{-3}$	3.1	0.08
Season	1	$2.5 \times 10^{-3}$	0.8	0.37
Season $\times$ Species	2	$3.6 \times 10^{-3}$	1.2	0.32
Error	13	$2.9 \times 10^{-3}$		
<b>Root</b>				
Species	2	$3.0 \times 10^{-2}$	0.9	0.41
Season	1	1.4	43.7	<0.01
Season $\times$ Species	2	$6.7 \times 10^{-3}$	0.2	0.81
Error	16	$3.2 \times 10^{-2}$		

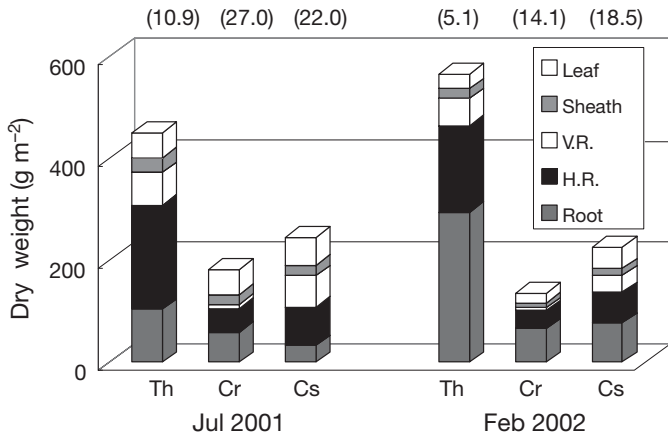


Fig. 3. *Thalassia hemprichii* (Th), *Cymodocea rotundata* (Cr), *Cymodocea serrulata* (Cs). Comparison of mean biomass allocations among species and seasons.  $n = 3$  cores, V.R. = vertical rhizome, H.R. = horizontal rhizome. Numbers in parentheses are the ratios of leaf biomass to whole-plant biomass (%)

### Biomass allocation

*Thalassia hemprichii* had the largest total biomass per area, followed by *Cymodocea serrulata* and *C. rotundata* in that order (Fig. 3). The proportion of total biomass contributed by leaves was smallest for *T. hemprichii* in both July and February (Fig. 3). The relative leaf biomass decreased in February for all species.

### Whole-plant O<sub>2</sub> balance

The relationship between light intensity and whole-plant photosynthesis-respiration balance varied among species and seasons (Fig. 4). The maximum photosynthetic rates ( $P_{max}$ ,  $\mu\text{l O}_2 \text{ mgDW}^{-1} \text{ h}^{-1}$ ) were significantly reduced in February compared to those in July. Post-hoc comparisons revealed that *Cymodocea rotundata* had a significantly lower  $P_{max}$  than *C. serrulata* (Fig. 4, Table 3).

Saturating irradiance ( $E_k$ ,  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) showed a significant species  $\times$  season interaction (Table 3). Post-hoc comparisons revealed that in July,  $E_k$  of *Cymodocea serrulata* was highest, followed by *Thalassia hemprichii* and then *C. rotundata*

(1-way ANOVA,  $F_{2,12} = 4.32 \times 10^6$ ,  $p < 0.01$ ). Post-hoc comparisons revealed that in February,  $E_k$  of *T. hemprichii* was highest, followed by *C. serrulata* and then *C. rotundata* (1-way ANOVA,  $F_{2,12} = 1.03 \times 10^6$ ,  $p < 0.01$ ).

There was a significant species  $\times$  season interaction for light compensation point ( $E_c$ ,  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ , Table 3). Post-hoc comparisons revealed that in July,  $E_c$  of *Thalassia hemprichii* was higher than those of *Cymodocea serrulata* and *C. rotundata* (1-way ANOVA,  $F_{2,12} = 19.7$ ,  $p < 0.01$ , Fig. 4). Post-hoc comparisons revealed that in February,  $E_c$  of *T. hemprichii* was  $>4$  times higher than those of the other 2 species (1-way ANOVA,  $F_{2,12} = 45.1$ ,  $p < 0.01$ , Fig. 4).

There was no significant difference in dark respiration ( $R_d$ ,  $\mu\text{l O}_2 \text{ mgDW}^{-1} \text{ h}^{-1}$ ) between seasons (Table 3).  $R_d$  of *Thalassia hemprichii* was significantly greater than that of *Cymodocea rotundata*.

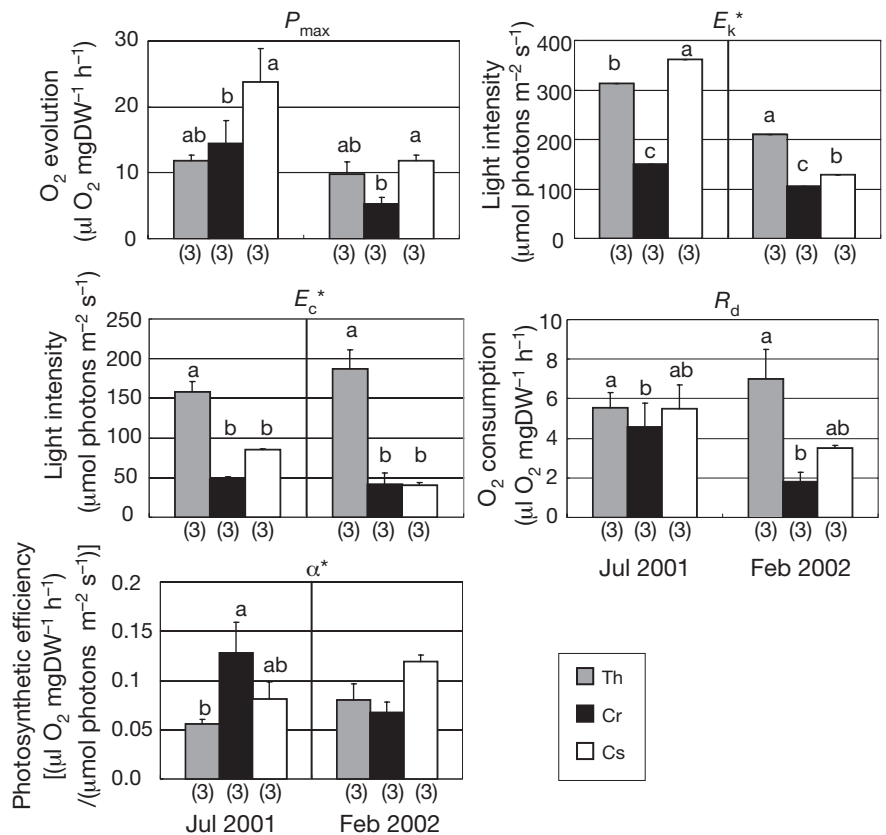


Fig. 4. *Thalassia hemprichii* (Th), *Cymodocea rotundata* (Cr), *Cymodocea serrulata* (Cs). Comparison of photosynthetic traits at whole-plant level among species and seasons. Means + SE. Maximum photosynthetic rate ( $P_{max}$ ), saturating irradiance ( $E_k$ ), compensation point ( $E_c$ ), respiration rate ( $R_d$ ) and initial slope ( $\alpha$ ). Numbers in parentheses show sample sizes. Asterisk and dividing line of seasons for  $E_k$ ,  $E_c$  and  $\alpha$  indicate existence of significant interactions in 2-way ANOVA. Different letters denote pairs of treatments for which significant variation was detected by post-hoc comparisons (Tukey's)

Table 3. *Thalassia hemprichii*, *Cymodocea rotundata*, *C. serrulata*. Two-way ANOVA for whole plant photosynthesis and respiration balance: maximum photosynthetic rate ( $P_{\max}$ ), saturating irradiance ( $E_k$ ), compensation point ( $E_c$ ), respiration rate ( $R_d$ ) and initial slope ( $\alpha$ )

	df	MS	F	p
<b><math>P_{\max}</math></b>				
Species	2	110.6	5.1	0.03
Season	1	266.7	12.2	<0.01
Species × Season	2	40.0	1.8	0.20
Error	12	21.9		
<b><math>E_k</math></b>				
Species	2	$3.2 \times 10^4$	$3.71 \times 10^6$	<0.01
Season	1	$7.3 \times 10^4$	$8.42 \times 10^6$	<0.01
Species × Season	2	$1.4 \times 10^4$	$1.64 \times 10^6$	<0.01
Error	12	$8.6 \times 10^{-3}$		
<b><math>E_c</math></b>				
Species	2	$2.9 \times 10^4$	60.5	<0.01
Season	1	$2.6 \times 10^2$	0.5	0.47
Species × Season	2	$2.1 \times 10^3$	4.3	0.04
Error	12	$4.8 \times 10^2$		
<b><math>R_d</math></b>				
Species	2	14.2	4.6	0.03
Season	1	5.4	1.7	0.21
Species × Season	2	7.6	2.5	0.13
Error	12	3.1		
<b><math>\alpha</math></b>				
Species	2	$1.9 \times 10^{-3}$	2.2	0.15
Season	1	$3.4 \times 10^{-6}$	$3.9 \times 10^{-3}$	0.95
Species × Season	2	$4.3 \times 10^{-3}$	5.0	0.03
Error	12	$8.6 \times 10^{-4}$		

The photosynthetic efficiency [ $\alpha$ , ( $\mu\text{l O}_2 \text{ mgDW}^{-1} \text{ h}^{-1}$ )/( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ )] showed a significant species × season interaction (Table 3). In July,  $\alpha$  of *Cymodocea rotundata* was highest, followed by *C. serrulata* and then *Thalassia hemprichii* (1-way ANOVA,  $F_{2,12} = 4.7$ ,  $p = 0.03$ , Fig. 4). In February, among-species variation in  $\alpha$  was not significant (1-way ANOVA,  $F_{2,12} = 2.5$ ,  $p = 0.12$ , Fig. 4).

## DISCUSSION

The photosynthesis–respiration balance in *Thalassia hemprichii* shifted significantly towards respiration in low light conditions, as shown by the significantly higher light compensation point of this species for both seasons compared to those of the other 2 species (when root and rhizome respiration were taken into account). This difference among species was not observed when we compared the  $\text{O}_2$  budgets per leaf. Thus the inter-specific variations cannot be ascribed fully to differences in leaf characteristics. The high light compensation point of *T. hemprichii* is due to its large belowground biomass, which has high respiratory

demand. The present study demonstrates that whole-plant evaluations are essential in identifying differences in  $\text{O}_2$  budgets among seagrass species.

These results are in accordance with the actual distribution pattern of *Thalassia hemprichii*, which is not dominant in deeper, darker locations (Table 4). The species is also sparse in sites with high silt and clay content in the sediment, where light penetration is reduced (Bach et al. 1998, Terrados et al. 1998). In contrast, *T. hemprichii* is dominant in shallow waters where light conditions are more suitable (Duarte et al. 2000, Tanaka & Kayanne 2007). A possible explanation for its dominance may relate to its large belowground biomass. The ratio of leaf biomass to whole-plant biomass of *T. hemprichii* was lowest among the 3 species in both July (10.9%) and February (5.1%). The observed ratio for the Ishigaki Island population falls within the typical ranges of this species and the congeneric *T. testudinum*, e.g. between 5.7 and 10.8% for *T. hemprichii* in Papua New Guinea (Brouns 1985), and between 5 and 13% for *T. testudinum* in Texas, USA (Herzka & Dunton 1998). *T. hemprichii* is a good competitor for nutrients, because its roots can reach deeper into the substratum to acquire nutrients that other species can not access (Duarte et al. 1998). This trade-off between the  $\text{O}_2$  budget and nutrient acquisition of the large belowground biomass may determine species occurrence and abundance across environmental gradients such as depth.

In previous studies, the long vertical rhizome of *Cymodocea serrulata* was considered to be advantageous for light acquisition, and for preventing the plant from being buried by sediment, because it enables the canopy to reach higher into the water column (Vermaat et al. 1997, Duarte et al. 1997, Bach et al. 1998, Terrados et al. 1998). Here, we showed that the small belowground biomass of *C. serrulata* had a small respiratory demand, which enables the species to survive in environments with low light intensity (as shown by lower light compensation point compared to that of *Thalassia hemprichii*). These morphological traits (i.e. reduced belowground biomass and long vertical rhizomes) may both contribute to the dominance of *C. serrulata* in deep habitats.

In the present study, *Cymodocea rotundata* had a lower saturating irradiance, lower light compensation point, and lower respiration rate than other species when compared on a whole-plant basis. This suggests that *C. rotundata* has the potential to grow at greater depths than the other species. However, the realized distribution range of *C. rotundata* is shallower than that of *C. serrulata* (Table 4). This discrepancy suggests that factors other than photosynthetic ability and whole-plant  $\text{O}_2$  balance under low light conditions limit the occurrence of *C. rotundata* in deep water.

Table 4. *Thalassia hemprichii* (Th), *Cymodocea rotundata* (Cr), *C. serrulata* (Cs). Comparison of lower depth limit (LDL) and mean or dominant depth of occurrence (MDDO)

Location	LDL/MDDO			Source
	Th	Cr	Cs	
Australia: between Cape York and Hervey Bay	3.2 m/1.7 m <sup>a</sup>	3.6 m/1.4 m	18.0 m/4.6 m	Lee Long et al. (1993)
The Phillipines: Silaqui Island	3.0 m/0.0 m <sup>b</sup>	1.0 m/0.5 m	3.0 m/1.0 m	Bach et al. (1998)
Tanzania: Zanzibar	Shallow	Shallow	Deep	Björk et al. (1999)
Japan: Ishigaki Island	2.2 m/1.1 m <sup>a</sup>	2.6 m/1.1 m	3.0 m/2.4 m	Tanaka & Kayanne (2007)

<sup>a</sup>From mean sea level, <sup>b</sup>from mean low tide

Recently, it has been shown that self-shading strongly affects the production of the seagrasses (Enríquez et al. 2002, Enríquez & Pantoja-Reyes 2005). Monsi & Saeki (2005) compared productive structures of broad-leaf and grass type terrestrial plant communities. The broad leaf plants spread leaves horizontally, while grasses extend them vertically. Consequently, the grass type community has an advantage in community productivity, because a reduction in self shading increases the interception of solar radiation. Although *Cymodocea rotundata* and *C. serrulata* are congeners, the direction of leaf extension seems different between them. *C. rotundata* extends leaves rather more vertically than *C. serrulata*. Hence, the morphology of *C. rotundata* may be advantageous for prevention of self-shading. On the other hand, this characteristic seems inefficient for photon capture under low light conditions.

When weights per unit area (mg cm<sup>-2</sup>) of leaf samples were calculated, post-hoc comparisons revealed that of *Cymodocea serrulata* was significantly smaller than those of the other species both in July (1-way ANOVA,  $F_{2,13} = 30.9$ ,  $p < 0.001$ ) and in February (1-way ANOVA,  $F_{2,14} = 25.6$ ,  $p < 0.001$ ). Specific leaf weight (g m<sup>-2</sup>) of *Zostera asiatica* in northeastern Japan was smaller in a deeper site (3 m deep) than in a shallow site (1.5 m) (Watanabe et al. 2000). The small specific leaf weight of *C. serrulata* may be advantageous for survival under low-light circumstances. In this study, the illumination was projected perpendicularly toward the leaf pieces and there was no apparent difference in photosynthetic traits between *C. rotundata* and *C. serrulata*. However, the morphological traits may affect their photosynthetic efficiency *in situ* and consequently zonal distribution.

In conclusion, the present study of whole-plant photosynthesis and respiration balance in 3 medium-sized seagrass species demonstrated that the depth limit of *Thalassia hemprichii* can be explained by its poor photosynthesis versus respiration balance under low light conditions (due to its larger amount of non-photosynthetic biomass). On the other hand, *Cymodocea serrulata* can survive dark conditions because of the smaller

respiratory demands of its belowground parts. However, the photosynthesis and respiration balance of *C. rotundata* did not explain its absence in deep water. In future studies, experimental approaches such as transplantation would be useful to examine the observed discrepancy between the realized distributional depth ranges of these seagrasses and those predicted from the measurements of biomass allocation and photosynthetic traits.

**Acknowledgements.** We thank M. Taira, H. Shimabukuro and Y. Umezawa for assistance with the field research. T. Hayashibara and other staff at the Ishigaki Tropical Station of the Seikai National Fisheries Research Institute provided laboratory equipment. H. Hata helped with the photosynthesis analysis. K. Yamada supported us with statistical discussions. H. Kayanne, I. Koike, H. Mukai and T. Miyajima provided invaluable support. We also thank K. L. Heck Jr and 3 anonymous reviewers for their constructive comments. This research was supported by a Sasakawa Scientific Research Grant (The Japan Science Society).

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*Editorial responsibility: Kenneth Heck (Contributing Editor), Dauphin Island, Alabama, USA*

*Submitted: July 5, 2006; Accepted: May 31, 2007  
Proofs received from author(s): November 6, 2007*