Journal of
Plant Ecology

VOLUME 4, NUMBER 4,
PAGES 283–291

DECEMBER 2011

doi: 10.1093/jpe/rtq038

Advanced Access published
on 15 February 2011

available online at
www.jpe.oxfordjournals.org

Effects of water depth on clonal characteristics and biomass allocation of *Halophila ovalis* (Hydrocharitaceae)

Na-Na Xu[1], *Xin Tong*[1], *Po-Kueug Eric Tsang*[2], *Hong Deng*[1] *and Xiao-Yong Chen*[1,*]

[1] *Department of Environmental Sciences, Shanghai Key Laboratory for Ecological Processes and Restoration in Urban Area, East China Normal University, Shanghai 200062, China*
[2] *Department of Science and Environmental Studies, Hong Kong Institute of Education, Hong Kong, China*
*Correspondence address. Department of Environmental Sciences, East China Normal University, Shanghai 200062, China. Tel: 86-21-6223-3303; Fax: 86-21-6223-3303; E-mail: xychen@des.ecnu.edu.cn

Abstract

Aims

Halophila ovalis is a dioecious seagrass with a wide geographical and water depth range. The objective of this study was to understand its plasticity in clonal characteristics and biomass and also its allocation between above- and belowground in seagrass beds at different water depths.

Methods

Four monospecific *H. ovalis* beds, Shabei, Xialongwei, Beimu and Yingluo, which have different water depths at maximum tide level (MTL) but otherwise similar environmental conditions, were studied. We measured main clonal characteristics, i.e. horizontal internodal length, branching angle, shoot height, leaf length and width, and rhizome diameter. Above- and belowground biomasses of *H. ovalis* were also estimated using a harvest method.

Important Findings

We found no significant differences in coverage, leaf pair density or number of stem nodes per square meter between the four study sites. However, horizontal internodal length, leaf length, width, rhizome diameter and shoot height all increased significantly with the increases in water depth from 2- to 9-m MTL and decreased when the water depths were greater than 9-m MTL. No significant difference in above- or belowground biomass between the seagrass beds was found. However, the ratio of above- to belowground biomass was significantly higher in the shallowest site compared to the other three seagrass beds, indicating that more biomass was stored belowground in deeper water. The results demonstrated plastic responses in clonal characteristics and biomass allocation in *H. ovalis* across the water depth gradient.

Keywords: *Halophila ovalis* • water depth gradient • rhizome • shoot • biomass allocation • seagrass

Received: 13 September 2010 Revised: 22 November 2010
Accepted: 6 December 2010

INTRODUCTION

Seagrasses are productive and fundamental component of coastal ecosystems with important ecological and economic functions (Boström *et al.* 2006; Duffy 2006; Shi *et al.* 2010; Short *et al.* 2007). Recent studies indicated that global seagrasses are declining at an increasing rate as a consequence of human activities, such as pollution, coastal development and climate change (Orth *et al.* 2006; Waycott *et al.* 2005, 2009). The distribution and abundance of seagrasses are also affected by other factors, such as temperature, sediment stability, nutrient availability, salinity and water quality (Cabaço *et al.* 2008; de Boer 2007; Holmer and Laursen 2002; Kilminster *et al.* 2006; Kuo and Lin 2010; Ibarra-Obando *et al.* 2004; Torquemada *et al.* 2005; Udy and Dennison 1997).

Water depth is an integrative index that may reflect the effects of light intensity, water pressure and stability of environmental factors. Deeper water, in general, means lower light intensity, higher pressure, and lower fluctuations in temperature, salinity, nutrients and disturbance. Given the

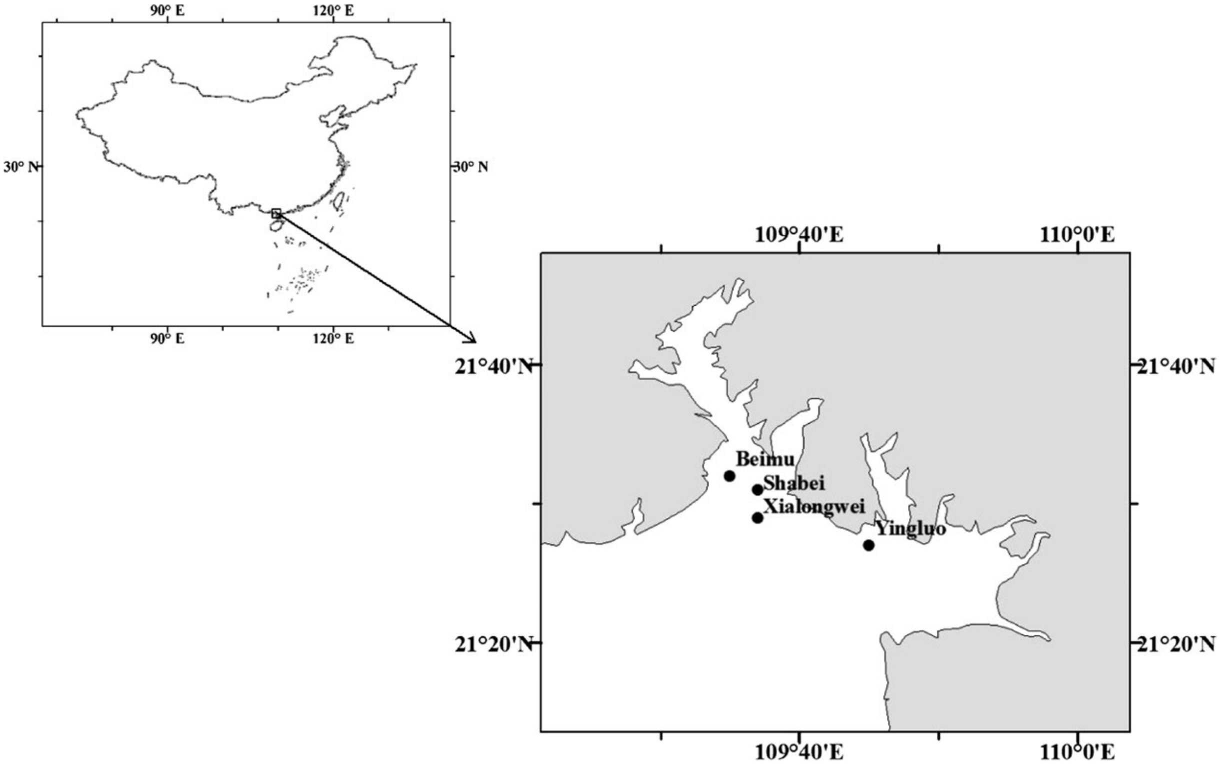

Figure 1: locations of the four *Halophila ovalis* seagrass beds sampled in the present study.

differences in these environmental factors, zonation of seagrasses can be observed along water depth gradients (Short *et al.* 2007). For the same species, differences in morphology, physiology or coverage may also be observed along water depth gradients. For example, in deeper water, *H. stipulacea* grew longer leaves and longer internodes, and photosynthetic electron transport rates were relatively slow (Schwarz and Hellblom 2002). The shoots of *Posidonia oceania* became shorter, but the leaves grew wider (Via *et al.* 1998). In eelgrass, average cover showed a bell-shaped pattern with water depth (Krause-Jensen *et al.* 2003).

Halophila ovalis is a small, leafy and fast growing seagrass species (Marbà and Duarte 1998). This species occurs in the tropical Indo-West Pacific and extends to some areas beyond the tropics (Den Hartog and Kuo 2006). *Halophila ovalis* has a strong ability to grow clonally, which plays a critical role in its adaption to various environments. Populations of *H. ovalis* can rapidly recover after extensive grazing through horizontal rhizome elongation (Nakaoka and Aioi 1999). This species is capable of living in a range of salinities, sediment types and temperatures (Benjamin *et al.* 1999; Hillman *et al.* 1995). It can also survive in a broad range of water depths from shallow intertidal environments to very deep water (up to 60 m) (Kuo *et al.* 2001). Some studies have investigated the primary production of *H. ovalis* at different water depths, mixed results were observed across water depths (Erftemeijer and Stapel 1999; Hillman *et al.* 1995; Huong *et al.* 2003). There is little information about the plasticity in clonal characteristics and biomass allocation on this species. Furthermore, global warming has resulted in rising sea level across the globe (Clark and Huybers 2009). It is both timely and important to understand the growth strategies of seagrasses for their survival in deeper water.

China has a long coastline ranging from the tropics to temperate, and both tropical and temperate seagrass species have been reported (Shi *et al.* 2010). However, there is very limited information on seagrasses in China (Huang *et al.* 2006; Shi *et al.* 2010). In this study, we surveyed the largest *H. ovalis* seagrass beds in Guangxi of China with the following aims: (i) to identify the plasticity in clonal characteristics along a water depth gradient, and (ii) to estimate biomass and its allocation between above- and belowground in seagrass beds at different water depths.

MATERIALS AND METHODS

Study site

The study was conducted in Hepu Dugong National Nature Reserve, Guangxi (N21°18′–21°30′, E109°34′–109°47′) (Fig. 1), which has the second largest seagrass bed in China (Huang *et al.* 2006; Shi *et al.* 2010). The dominate tidal wave in this study area is diurnal tide, and the annual minimum and maximum tidal level of 2008 were 0.64 and 6.69 m, respectively, with the tidal datum of −3.59 m (China Ocean Information

Table 1: Major environmental factors and clonal characteristics of *Halophila ovalis* beds in Hepu Dugong National Nature Reserve, Guangxi of China

Site	GC	WD (m)	WS (‰)	TN (mg kg^{-1})	OM (g kg^{-1})	WT (°C)	C (%)	LD (m^{-2})	SD (m^{-2})	RD (mm)	LL (mm)	LW (mm)	LDW (mg)	SH (mm)
Shabei	21°31′N, 109°37′E	13.2 ± 0.1	7.77	316 ± 162	3.69 ± 0.81	22.0	48 ± 8	525.8 ± 87.2 (9)	1979.1 ± 406.2 (9)	1.14 ± 0.02^{b} (90)	24.3 ± 0.4^{b} (90)	12.4 ± 0.2^{b} (90)	8.2 ± 0.4^{a} (90)	52.3 ± 1.0^{b} (90)
Xialongwei	21°29′N, 109°37′E	8.7 ± 0.2	8.47	518 ± 96	2.82 ± 0.84	24.1	49 ± 8	381.7 ± 15.2 (6)	997.3 ± 82.6 (6)	1.41 ± 0.04^{a} (60)	24.5 ± 0.6^{b} (60)	13.2 ± 0.3^{b} (60)	8.1 ± 0.5^{ab} (60)	53.7 ± 1.3^{ab} (60)
Beimu	21°32′N, 109°35′E	7.7 ± 0.4	7.77	673 ± 265	4.19 ± 0.19	24.9	44 ± 8	704.3 ± 150.2 (8)	902.5 ± 189.5 (8)	1.40 ± 0.03^{a} (80)	26.5±0.5^{a} (80)	14.2 ± 0.3^{a} (80)	7.7 ± 0.4^{ab} (80)	57.1 ± 1.2^{a} (80)
Yingluo	21°27′N, 109°45′E	2.0 ± 0.5	—	581 ± 113	7.43 ± 1.07	22.7	25 ± 6	832.0 ± 69.1 (5)	1446.4 ± 116.1 (5)	0.84 ± 0.02^{c} (50)	19.3 ± 0.6^{c} (50)	11.0 ± 0.3^{c} (50)	6.1 ± 0.6^{b} (50)	34.8 ± 1.3^{c} (50)
Average	—	—	—	—		—	43 ± 4	660.6 ± 58.7 (28)	1366.0 ± 163.9 (28)	1.22 ± 0.02 (280)	24.1 ± 0.3 (280)	12.8 ± 0.2 (280)	7.7 ± 0.2 (280)	50.9 ± 0.7 (280)

GC = geographic coordinate; WD = water depth at MTL; WS = salinity; TN = total nitrogen; OM = organic matter content; WT = water temperature; C = coverage; LD = leaf pair density; SD = stem nodes density; RD = diameter; LL= leaf length; LW = leaf width; LDW = leaf dry weight; SH = shoot height. Same superscript letters indicate no significant difference. Values in parenthesis are the number of measurements.

Center 2007). The annual average air and water temperature was 22.9 and 23.49°C, respectively, with the annual average lowest water temperature being 15.65°C in January (Huang and Huang 2007). In 2002, the area of seagrass beds was estimated as 540 hm^2 (Huang *et al.* 2006; Shi *et al.* 2010), but was reduced to 250 hm^2 in December 2008 (Q Qin, personal communications). Most of the seagrass beds were monospecific and dominated by *H. ovalis*. However, *Zostera japonica*, *Halophila beccarii*, and *Halodule uninervis* were also found in this region (Huang *et al.* 2006; Fan *et al.* 2007). Four monospecific *H. ovalis* beds, which were different in water depth at maximum tide level (MTL), were studied (Table 1). The sediments were composed of medium to fine sands (Huang *et al.* 2006) and had similar nutrient contents, salinity and temperature (Table 1).

Measures of clonal characteristics

Halophila ovalis was investigated in four seagrass beds, i.e. Shabei, Xialongwei, Beimu and Yingluo Bay (Fig. 1). In the study area, *H. ovalis* was found in the tidal flat of the intertidal zone and the clay-like and arenaceous parts of subtidal zones (Shi *et al.* 2010). Our study was conducted during low tide in December 2008. Five to 9 quadrats of 50 × 50 cm were randomly established with an interval of >100 m between quadrats. Each quadrat was positioned using a GPS receiver (eTrexC, GARMIN, Taiwan) and the water salinity and temperature were recorded using PCS Testr 35 (Thermo Fisher Scientific, China).

In view of the fact that water depth changes with the tides, the water depth (WD) of each quadrat was calibrated at the MTL using the following equation: $\mathrm{WD} = \mathrm{MTL} - \mathrm{TL} - \mathrm{AH}$, where TL and AH were altitudes of tidal datum and the plot, respectively. In each quadrat, all above- and belowground parts of *H. ovalis* were collected after coverage was measured. Samples were transported to the laboratory located at the management station of Hepu Dugong National Natural Reserve. Specimens were identified and washed carefully with fresh water. The numbers of leaf pairs and stem nodes from each quadrat were then counted.

Intact fragments were selected to characterize clonal traits: horizontal internodal length, branching angle, shoot height, leaf length, width, and rhizome diameter. The distances between consecutive nodes were measured using a millimeter graduated scale, so were the shoot height, including petiole and leaf. The branching angle was estimated using a protractor between conjoint stems. For a single leaf, the longest and widest measured values were taken as length and width. The diameter of the horizontal rhizome was measured using a micro Vernier caliper.

Estimation of biomass

After the measurements were completed, leaves, rhizomes and roots were sorted, oven-dried at 60°C for 48 h and weighed. Aboveground biomass of leaf materials were measured and

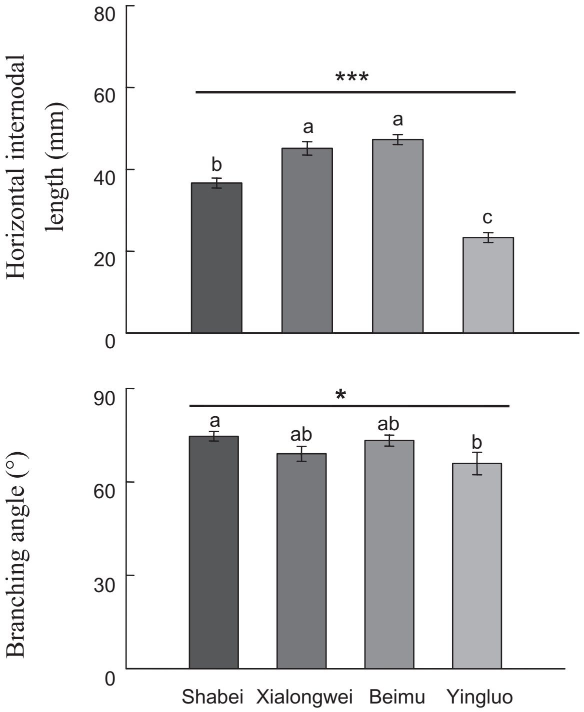

Figure 2: horizontal internodal length and branching angle of *Halophila ovalis*. Error bars are SEM. Asterisks indicate significant differences among four seagrass beds (*$P < 0.05$, ***$P < 0.001$), and the same letters above the vertical bars indicate no significant difference.

belowground biomass was calculated as the sum of rhizome and root materials.

Statistical analysis

Statistical analysis was performed using SPSS for Windows (SPSS, Chicago, XII). For all variables, the effect of water depth was analyzed by one-way analysis of variance, followed by Bonferroni *post hoc* test. In all cases, the significance level was set at 5%. Additionally, one element regression analysis was performed to determine the relationships between clonal characteristics and water depth.

RESULTS

The mean coverage of *H. ovalis* was 43 ± 4% (mean ± SE), without significant differences among the four seagrass beds. The average shoot density was 600.6 ± 58.7 leaf pairs per square meter, with no significant difference among the four beds ($P = 0.056$). The average number of stem nodes per square meter of the four beds was 1366.0 ± 163.9 and differed significantly among the four beds ($P = 0.037$) (Table 1).

Rhizome diameter ranged from 0.50 to 2.16 mm. Rhizome diameter at the shallowest site, Yingluo (0.84 ± 0.02 mm), was significantly smaller than those at the other three sites ($P < 0.001$), while the rhizome diameter of the deepest site, Shabei (1.14 ± 0.02 mm), was significantly smaller than those of moderate water depths ($P < 0.001$) (Table 1). Horizontal internodal length showed the same trend as the rhizome diameter. Xialongwei and Beimu seagrass beds had significantly longer horizontal internodal length than those in Shabei and Yingluo seagrass beds (Fig. 2). In addition, the branching angle differed significantly between sites ($P = 0.028$) (Fig. 2); branching angle at Yingluo was significantly smaller than that at the deepest seagrass bed Shabei ($P = 0.049$).

The traits of leaves and shoots varied among the four seagrass beds. Both the length and width of leaves were significantly different ($P < 0.001$). Significant differences were detected in the size of leaves among seagrass beds, except that between Shabei and Xialongwei. In the Yingluo seagrass bed, leaves of *H. ovalis* were the smallest with average length and width of 19.3 ± 0.3 and 11.0 ± 0.3 mm, respectively. The dry weight of a single leaf differed significantly between sites ($P = 0.017$) (Table 1). Shoot length observed in the four sites was significantly different, and the smallest shoot length occurred in the shallowest seagrass bed Yingluo (Table 1). These results indicated that the traits did not change linearly with water depth. Regression analysis indicated that a quadratic equation can be used to describe the relationships between clonal characteristics and water depth. All characteristics had maximum values at a water depth of ~9 m (Fig. 3).

The total biomass of *H. ovalis* ranged from 17.38 ± 4.71 to 37.62 ± 8.83 g DW·m^{-2} in the four seagrass beds. There was no significant difference in above- or belowground biomass per square meter among the four seagrass beds ($P = 0.361$). However, allocation of biomass varied significantly ($P = 0.035$). In the Yingluo seagrass bed, aboveground biomass was 1.58-fold greater than found in belowground biomass, while in the other seagrass beds, aboveground biomass was less than or almost equaled to belowground biomass (Fig. 4).

DISCUSSION

All seagrass species grow through horizontal rhizome elongation, which plays an important role in the survival and persistence of seagrass beds (Marbà and Duarte 1998; Miao *et al.* 2009). Rhizome diameter and the size of leaves of *H. ovalis* reported here were similar to those found in previous reports (Vermaat *et al.* 1995). However, horizontal internodal length was longer than previously reported on the same species (Table 2). The obvious morphological variation in the genus *Halophila* reflects the plasticity of clonal growth, as a response to the variations in environmental factors.

Water depth is an important environmental factor shaping clonal characteristics of *H. ovalis*. This may be accomplished by affecting light availability because there is a strong negative correlation between seagrass colonization depth and light extinction coefficient (Duarte *et al.* 2007; Nielsen and Pedersen 2000). It was demonstrated that the rate of electron transport and efficiency of photosynthesis declined with increasing

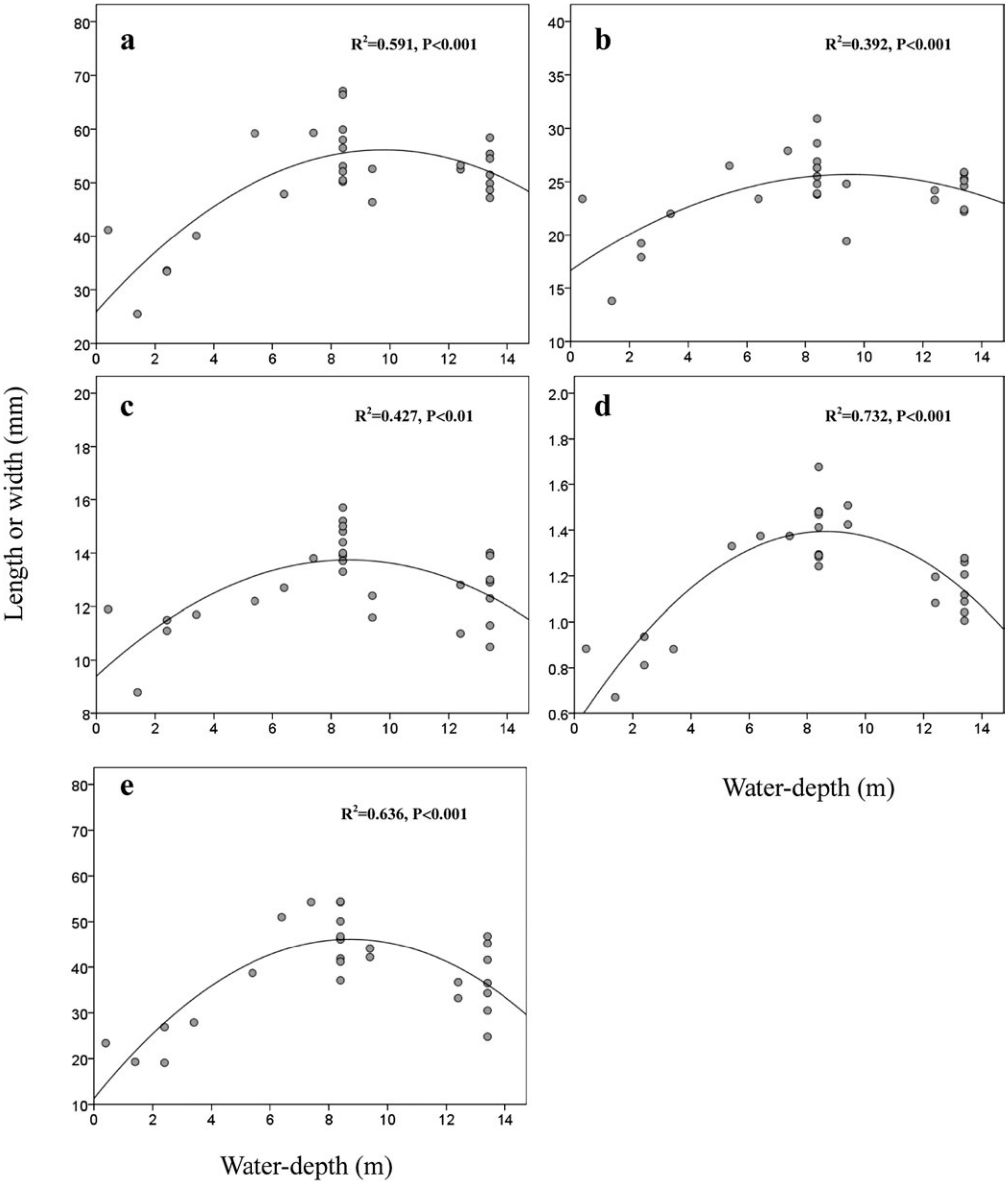

Figure 3: relationships between water depth and clonal characteristics of *Halophila ovalis*. Each point represents the average values for each quadrat. The vertical axis indicates (a) shoot height, (b) leaf length, (c) leaf width, (d) rhizome diameter and (e) horizontal internodal length, respectively.

depth in the congeneric *H. stipulacea* growing along a depth gradient from 7 to 30 m in the Gulf of Aqaba (Schwarz and Hellblom 2002). With increasing water depth, light is generally reduced for submerged seagrasses, and this has negative effects on seagrass growth, leading to morphological changes (Erftemeijer and Stapel 1999; Longstaff *et al.* 1999; Ralph *et al.* 2007). *Halophila stipulacea* grew longer leaves and internodes with increasing water depth (Schwarz and Hellblom 2002). However, a study showed that *Zostera caulescens* has the longest shoot at moderate water depth (Sultana and Komatsu 2002). Our study indicated that clonal characteristics did not change linearly with water depth. Shoots, leaves and horizontal rhizomes of *H. ovalis* became larger with increasing water depth ranging from 2- to ~9-m MTL and then became smaller at water depths below 9-m MTL (Fig. 3). This result indicated that 9-m MTL seemed to be the optimum water depth for the growth of *H. ovalis* in the study region. Growing in shallow water, *H. ovalis* may suffer from disturbances due to periodical tides and exposure to excessive light, which may have negative effects on growth. In deep water, the light levels are too low and the growth is limited.

As a small seagrass with a height <5 cm, *Halophila* beds generally have lower standing biomass, but higher productivity compared to large seagrasses. The mean above- and

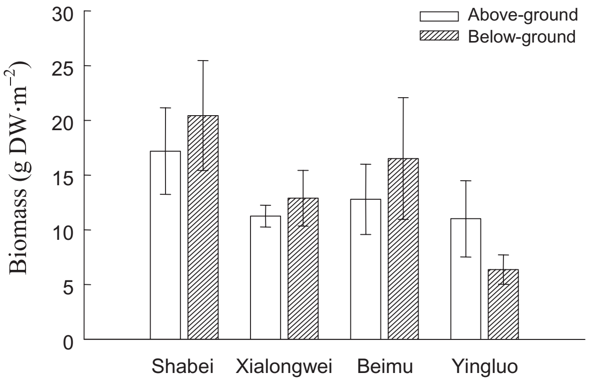

Figure 4: the average above- and belowground biomass (g DW·m^{-2}) of *Halophila ovalis* in studied sites. The blank and the shaded columns represent above- and belowground biomass, respectively. The error bars are standard errors.

belowground biomasses of 30 seagrass species were 224 and 237 g·m^{-2}, respectively (Duarte and Chiscano 1999). Among these species, aboveground biomasses of *Halophila*, ranging from 2.3 to 104 g m^{-2}, were lowest, while *Amphibolis antarctica* had the highest aboveground biomass (1 005 g m^{-2}) (Duarte and Chiscano 1999). *Halophila ovalis* biomass in the present study ranged from 17.38 to 37.62 g m^{-2}. These values were higher than *H. ovalis* biomass reported in the Northern hemisphere (Table 2, Duarte and Chiscano 1999), but lower than *H. ovalis* biomass in Western Australia (Hillman *et al.* 1995).

Other environmental factors and animal grazing may also affect depth range and biomass of seagrasses (Abal and Dennison 1996; Hammerstrom *et al.* 2006). For example, Paynter *et al.* (2000) found that *Thalassia testudinum* biomass was correlated with sediment nature, while Smith *et al.* (2008) found that in *Heterozostera nigricaulis* seagrass beds, the shoreward edge always had lower seagrass biomass. Peak biomass values in *Halophila ovalis* (Hillman *et al.* 1995) and *Z. caulescens* (Sultana and Komatsu 2002) were found at the moderate depths. In west Florida shelf, *H. decipiens* biomass was lowest at the offshore/deeper station (Hammerstrom *et al.* 2006). These values, however, were considerably lower than those reported in deeper sites at St Croix, US Virgin Island (Josselyn *et al.* 1986). These mixed findings might be explained by differences in environmental factors. We found no significant difference in total biomass among the four study sites (Fig. 4), which was most likely due to insignificant difference in sediment types and nutrients.

Although biomass did not vary greatly among the studied sites, a significant difference was found in the allocation of biomass. The ratio of above-/belowground biomass at the shallow site, Yingluo, was significantly higher than those found at the deeper sites. These ratios were also higher than those observed at Langkai Island where the water depth was 14–16 m (Erftemeijer and Stapel 1999). With increasing water depth, seagrasses grow extensive rhizomes and store more carbohydrates, leading to lower above-/belowground biomass ratios (Carlson and Acker 1985; Elkalay *et al.* 2003). Such a tendency is likely the result of its response to reduced light intensity. In experiments of light deprivation for *H. ovalis*, the ratio of above- to belowground biomass appeared to decline with light reduction (Longstaff *et al.* 1999). Also, a larger quantity of stored carbohydrate was found in the belowground biomass of *Zostera noltii* under low light intensity (Peralta *et al.* 2002). These observations suggest that seagrasses could adjust their biomass allocation with the changes in light density. When light intensity was low, more biomass was allocated to belowground when the energy generated through photosynthesis was lower than the energy consumed by respiration. This behavior is quite different from that of land plants, where a higher shoot/root + rhizome ratio for plants grown at low light, but may be mediated by nutrients (He *et al.* 2007).

CONCLUSIONS

Our results show that the variations in clonal characteristics and biomass allocation in *H. ovalis* were closely related to water depth. Larger-size leaves and taller but sparser shoots were found at water depths from 2- to 9-m MTL, but below 9 m, these characteristics were found to subside. In deep water, more biomass was allocated to belowground parts. The strong phenotypic plasticity in clonal characteristics and biomass may play an important role in maintaining the abundance of seagrasses in view of the environmental effects caused by global issues such as climate change and recovery from ecological disturbances, such as grazing or harvesting of shellfish. At present, *H. ovalis* seagrass beds do not seem to be suffering significantly from the negative impacts of sea level rise in the area under study. Nevertheless, further studies and monitoring are needed to gain more understanding of the changes in seagrass beds in this region, especially under the existing and predicted future impacts of human activities.

FUNDING

The National High-tech Research and Development Program of the Ministry of Science and Technology of China (2007AA09Z432); ''211 Project'' of East China Normal University.

ACKNOWLEDGEMENTS

The authors wish to acknowledge the officers and crew of the Management Station of Hepu Dugong National Natural Reserves for their professional assistance during the field surveys. In particular, we would like to thank Chun-Miao Lai, Yun Ning, Qiu-Rong Qin, Hong-Ke Zhang, Juan Liu, Jun-Guo Zhang, Ke-Wei Wu and Jing Du for help during samples collection and measurement, and we thank Fei-Ge Zhu and Min-Yan Cui for preparing maps of study sites. We thank Binhe Gu and two anonymous reviewers for helpful comments on the earlier version of the manuscript. We thank William Geoffrey Douglas for grammatical revision.

Conflict of interest statement. None declared.

Table 2: Clonal characteristics and ratio of above/below ground biomass (R) of *Halophila* species

Species	Location	WD (m)	LD (m^{-2})	RD (mm)	IL (mm)	LL (mm)	LW (mm)	BA (°)	LDW (mg)	TB (g m^{-2})	R	Source
Halophila ovalis	Guangxi, China	2–13	381.7–832.0	0.84–1.41	23.3–47.3	19.3–26.5	11.0–14.2	65.9–74.7	6.1–8.2	17.38–37.62	0.94–1.58	The present study
H. ovalis	Cape Bilinao, Philippine	3	16	1.09	17.0	15.4	8.5	72.0	3.5	0.2	1.0	Vermaat *et al.* (1995)
H. ovalis	W. Australia	2	—	—	—	—	—	—	7.3–14.2	Up to 120	—	Hillman *et al.* (1995)
H. ovalis	Indonesia	12–16	1 099	—	—	—	—	—	—	10.93	0.72	Erftemeijer and Stapel (1999)
H. ovalis	Masirah Island	<0.5–3	—	—	—	—	—	—	—	0.5–11.4	—	Jupp *et al.* (1996)
H. ovalis	North Kenya	Up to 3	—	—	—	13–27	4–10	—	—	—	—	McMahon and Waycott (2009)
Halophila capricorni	Coral sea	20	—	0.9–1.5	—	15–30	5–9	—	—	—	—	Larkum (1995)
Halophila decipiens	Okinawa Island, Japan	15–18	—	0.8–1	15–25	Up to 20	4–6	—	—	—	—	Kuo *et al.* (1995)
H. decipiens	US virgin Island	15–27	1 099–4 600	—	—	—	—	—	—	5–12	1.06	Josselyn *et al.* (1986)
H. decipiens	US virgin Island	14–32	4 120	—	—	—	—	—	—	9.15	—	Erftemeijer and Stapel (1999)
H. decipiens	Hawaiian	1–40	—	0.57–0.7	2.8–29.8	12.9–18.5	3.8–6.3	—	—	—	—	McDermid *et al.* (2002)
H. decipiens	Costa Baja, CA	4–6	2 964–4 016	—	—	14.5–18.6	4.6–5.8	—	—	5.2–8.5	—	Santamaría-Gallegos *et al.* (2006)
H. decipiens	North Kenya	Up to 3	—	—	—	13–30	4–10	—	—	—	—	McMahon and Waycott (2009)
Halophila stipulacea	Aqaba, Jordan	10	403							—	0.4	Erftemeijer and Stapel (1999)
H. stipulacea	Vulcano Island, Oliver-Tindari, the western Mediterrarean	2–25	—	—	1.24–2.91	4.96–8.43	0.65–1.01	—	—	—	—	Procaccini *et al.* (1999)
H. stipulacea	Florida	10–20	118–1 990							0.02–2.64		Hammerstrom *et al.* (2006)
H. stipulacea	Gulf of Aqaba, the Red Sea	7–30	—	—	6.8–11.2	29.9–44.3	—	—	—	—	1.56–2.50	Schwarz and Hellblom (2002)
H. stipulacea	Dominica, West Indies	2–18	—	1–2	7–50	22–57	5–9	—	—	—	—	Willette and Ambrose (2009)
Halophila sulawesii	Indonesia	15	—	0.3–0.8	Up to 50	10—25	—	—	—	—	—	Kuo (2007)

WD = water depth; LD = leaf pair density; RD = mean rhizome diameter; IL = horizontal internodal length; LL = leaf length; LW = leaf width; BA = branching angle; LDW = leaf dry weight; TB = total biomass.

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