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ORIGINAL ARTICLE

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An alternative mechanism for shade adaptation: implication of allometric responses of three submersed macrophytes to water depth

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Abstract Allometric scaling models describing size-dependent biological relationships are important for understanding the adaptive responses of plants to environmental variation. In this study, allometric analysis was used to investigate the biomass allocation and morphology of three submerged macrophytes (*Potamogeton maackianus*, *Potamogeton malaianus* and *Vallisneria natans*) in response to water depth (1.0 and 2.5 m) in an in situ experiment. The three macrophytes exhibited different allometric strategies associated with distinct adjustments in morphology and biomass allocation in response to varying water depths. In deeper water, after accounting for the effects of plant size, *P. maackianus* and *P. malaianus* tended to enhance light harvesting by allocating more biomass to the stem, increasing shoot height and specific leaf area. *V. natans* tended to allocate more biomass to the leaf than to the basal stem (rosette), showing a higher leaf mass ratio and shoot height in deeper water. The three species decreased biomass allocation to roots as water depth increased. The main effect of water depth treatments was reduced light availability, which induced plastic shoot or leaf elongation. This shows that macrophytes have evolved responses to light limitation similar to those of terrestrial plants.

Keywords Allometry · Biomass allocation · Submersed macrophyte · Water depth

Introduction

Variability in plant morphology and biomass allocation is central to plant adaptation to different environments (Tilman 1988; Grime 2001). According to the optimal partitioning theory, plants that increase biomass allocation to leaf or stem tissues in shade environments will decrease biomass allocation to other tissues (e.g., roots and seeds) (Bloom et al. 1985), experiencing morphological changes in order to alleviate the stress caused by resource limitation (Westoby et al. 2002; Poorter et al. 2012). Environmentally induced changes in biomass allocation and morphology are often dependent largely on plant growth and development (Coleman et al. 1994; Niklas 1994; Niklas and Enquist 2002; Weiner 2004). Allometry—defined as the quantitative relationship between plant size and phenotypic traits—is powerful in summarizing plant development over time and is thus more informative than biomass ratio (Jasienski and Bazzaz 1999; Poorter et al. 2012). Further, the intrinsic plasticity (true plasticity) in phenotypic traits, generally considered as an adaptive response to environment stress, can be identified through allometric analysis (Niklas 2004; Weiner 2004). Many studies have revealed allometric relationships between plant size and phenotypic traits of terrestrial plants in responses to environmental variation (Huber and Stuefer 1997; Müller et al. 2000; Bonser and Aarssen 2003; Lusk et al. 2008; Renton and Poorter 2011). However, few reports have applied allometric analysis to investigate the phenotypic plasticity of submersed macrophytes under resource limitation (but see Strand and Weisner 2001).

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Submersed macrophytes inhabit in aquatic littoral zone that is affected by frequent water level fluctuation (Spence 1982; Wantzen et al. 2008; Thomaz et al. 2006). Increased water depth reduces the amount of available light penetrating the leaf surface of submersed macrophytes (Spence et al. 1973; Canfield et al. 1985; Wersal et al. 2006). Submersed macrophytes are highly plastic in morphology and biomass allocation in response to varying water depths, with adaptations including changes in the stem length, leaf length, branching pattern, specific leaf area, root:shoot biomass ratio and growth rate (Spence et al. 1973; Barko and Smart 1981; Maberly 1993; Ni 2001; Strand and Weisner 2001; Richards et al. 2011). However, which traits are more responsive to varying water depths is dependent largely on the plant growth form (Chambers 1987; Chambers and Kalff 1987). Erect species, such as *Myriophyllum spicatum* (Strand and Weisner 2001) and *Potamogeton obtusifoius* (Maberly 1993), tend to increase biomass allocation to shoot, grow taller and thus form dense canopies for enhancing light interception in deeper water; in contrast, rosette species, such as *Vallisneria americana* Michx (Owens et al. 2008), increase biomass allocation to leaf, leaf length or area under low light stress. Although macrophytes generally occupy distinct ranges along water depths, differences in morphological adjustments and biomass allocations in response to increasing water depths among distinctly contrasting growth forms of submersed macrophytes have not been studied sufficiently (Chambers and Kalff 1985; Middelboe and Markager 1997). As the reasons accounting for differences in adapting to light deficiency between macrophyte species with contrast growth forms and between macrophytes and terrestrial shade plants still remain unclear, it is thus valuable to examine the adaptive mechanisms of different submersed macrophytes to different water depths.

In the present study, an allometric analysis was used to examine the morphology (i.e., plant size, specific leaf area and shoot height) and biomass allocation of three submerged macrophytes, *Potamogeton maackianus* (Potamogetonaceae), *Potamogeton malaianus* (Potamogetonaceae) and *Vallisneria natans* (Hydrocharitaceae) in response to different water depths in a lake located in Yunnan Province, China. The three species differ in leaf morphology and growth form (Sun 1995). The two *Potamogeton* species are erect growth form with leaves locating on the upper stem. In spring, *P. maackianus* recruits mainly through the above ground stem, and *P. malaianus* sprouts from the below ground stolon. *V. natans* is a perennial rosette with strap-like leaves locating on the basal stem. We tested three hypotheses: (1) the *Potamogeton* species would allocate more biomass to the stems and thus elongate to alleviate low light stress, with greater stem biomass and shoot height for a given plant size in deeper water; (2) the rosette species would allocate more biomass to the leaves and exhibit higher shoot height to achieve a given plant size in deeper water; (3) the three macrophytes would decrease biomass allocation to roots, as indicated by the lower root mass for a given plant size in deeper water.

Materials and methods

Study site

The experiment was carried out in Erhai Lake (25°52′N, 100°06′E) in the Yunnan Province, China. The lake is characterized by a surface area of 250 km^2, with a maximum depth of 21 m, and an average water depth of 11 m. The in situ experiment was conducted on a floating platform (25 m × 20 m) constructed with steel and anchored at a bay in the Lake, where the average water depth was about 8 m during the experimental period. The experimental system was protected by a surrounding net (mesh size 2.5 cm) to avoid herbivorous fishes.

The in situ experiment started on 27 July 2010, and was lasted for 52 days. During the experimental period, the water characteristics (i.e., Secchi depth, temperature and nutrients) were measured at each depth at noon every 5 days. Photosynthetic active irradiation (PAR) was measured by a Li-COR UWQ-4341 sensor and a Li-1800 data logger (Li-Cor, Lincoln, NE). The average PAR was 214 ± 98 and 29 ± 11 μmol m^{-2} s^{-1} at water depths of 1.0 and 2.5 m, respectively; the Secchi depth was 1.3–1.5 m; and the water temperature was 15–18 °C. The concentrations of NO_3, NH_4 and PO_4 in water column at the experimental site were 0.42 ± 0.05, 0.02 ± 0.006 and 0.008 ± 0.002 mg L^{-1}, respectively, and did not differ between water depths.

Experimental designs and procedure

Shoots of the *Potamogeton* species and seedlings of *V. natans* used for the experiment were collected from Erhai Lake. The shoots/seedlings were similar in size and healthy in appearance. For *P. maackianus*, the apical shoot was 35 cm in length, ten intact leaf blades and without flower; for *P. malaianus*, the apical shoot length was 30 cm in length, three intact leaf blades and without flower; and for *V. natans* intact seedlings were 20–30 cm long with seven leaves. The shoots/seedlings were planted evenly in plastic pots (diameter 43 cm, height 36 cm) containing 25 cm sediment collected from the Lake, with 20 shoots pot^{-1} for *P. maackianus* and five shoots pot^{-1} for *V. natans* and *P. malaianus*. The shoot/seedling density used in our study was similar to those of the plants' natural population in this lake. All the plants were cultured in situ at 80 cm water depth for 5-days acclimation, and then were grown at water depths of 1.0 and 2.5 m, respectively, by hanging the pots from the floating platform to the two water depths; 12 pots were used for each species at each water depth, and there were a total of 72 pots.

To perform morphological and biomass measurements, four pots of each species were collected at 15, 30 and 45 days after the start of the experiment, and five individual plants (randomly for *P. maackianus*) of each species at each harvest were selected for those measurements. This sampling schedule was aimed to obtain plants of different size in each depth, and evaluate the effects of plant size on the phenotypic traits. For each intact individual plant, the shoot height (cm) and leaf area (cm^2) were measured immediately after harvesting. Shoot height was measured as the distance from the base to the top of shoots (main stem or leaf). For leaf area measurement, leaves (ten intact leaflets) were photographed using a digital camera with a graph paper as background and the leaf area was estimated using software Photoshop CS (Adobe, http://www.adobe.com/). Specific leaf area (leaf area per unit of leaf mass) was calculated and expressed as $m^2\ kg^{-1}$. We calculated biomass of leaf, stems and roots by weighing leaf, stem and roots after drying at 80 °C for 48 h. The leaf area for each individual was calculated by multiplying the specific leaf by the leaf mass. Total biomass of an individual plant (plant size) was the sum of leaf, stem and root mass.

Statistical analyses

All the selected plants were nested within pots for statistical analysis, with pots as the random factor. Analysis of variance of all variables showed no significant differences (all $P > 0.05$) between the four pots at each depth on each date, so we used measurements for each individual plant (rather than each pot) as the independent units for the following analysis. Two-way ANOVA was used to evaluate effects of water depth and time on the total biomass of each species. One-way ANCOVA was used to evaluate the effects of water depth (factor) on the relationships between root, stem and leaf mass, specific leaf area and shoot height (response variables), and the total biomass of species (covariate). All data of the response variables were Ln-transformed to meet assumptions of normality and homogeneity.

Standardized major axis (SMA) slope-fitting techniques were used for the allometric analyses (Sokal and Rohlf 1995). Allometric relationships between traits are generally understood as exponential relationships described by the equation $y = \beta x^{\alpha}$, or more commonly $\mathrm{Ln}\ (y) = \mathrm{Ln}\ (\beta) + \alpha\ \mathrm{Ln}\ (x)$ (Sokal and Rohlf 1995), where x (total biomass or leaf mass) and y (response variables) are the two traits, α is the scaling coefficient (slope) and β is a regression constant (intercept) (Warton et al. 2006). In this study, allometric relationships between total biomass and response variables were tested for each species and depth, using a likelihood ratio method (Warton and Weber 2002). When there were parallel slopes between water depths (test for homogeneity, $P > 0.05$), differences in intercept were tested by t test as demonstrated by Warton et al. (2006). Noting that the change in y with respect to difference in plant size x (i.e., $\Delta y/\Delta x$) equals $\alpha\beta x^{\alpha-1}$, the magnitude of y will be independent of intra- or interspecific differences in x when $\alpha = 1.0$; it will increase disproportionately with increasing x when $\alpha > 1.0$; and it will fail to keep pace with intra- or interspecific increases in x when $\alpha < 1$.

Results

Water depth significantly affected total biomass of the three macrophytes (Table 1; Fig. 1). These species showed great differences in growth rate at each depth. At the end of the experiment, biomass of *P. maackianus*, *P. malaianus* and *V. natans* increased by 11.9, 15.5 and 8.3-fold at water depths of 1.0 m, and by 6.6, 6.4 and 4.8-fold at water depth of 2.5 m, respectively.

Leaf mass of *P. malaianus* and *V. natans* was affected significantly by water depth (Table 2). The three species showed significant changes in leaf mass with the covariate (total biomass), and there were no significant interactions between water depth and total biomass (Table 2). Allometric relationships (slope) between leaf mass and total biomass of each species were not affected significantly by water depth, as indicated by the homogeneity of the slopes between depths ($P > 0.05$). At 2.5 m depth, *P. maackianus* and *P. malaianus* allocated less biomass to the leaves (Fig. 2, t test: $P < 0.001$), and *V. natans* allocated more biomass to the leaves (Fig. 2, t test: $P < 0.001$). Leaf mass ratio decreased with increased plant size (total biomass) for the two *Potamogeton* species ($\alpha < 1$, $P < 0.001$), and increased for *V. natans* ($\alpha > 1$, $P < 0.001$).

The specific leaf area of *P. malaianus* and *V. natans* also varied with water depth, and that of *V. natans* was dependent strongly on total biomass (Table 2). Significant interaction between water depth and total biomass was observed only in *P. maackianus* (Table 2). Allometric relationships between leaf area and leaf mass of each species were not affected significantly by water depth ($P > 0.05$) and showed specific responses to water depth. *P. maackianus* and *P. malaianus* showed higher leaf area for a given leaf mass at 2.5 m depth (Fig. 3, t test: $P < 0.01$), and *V. natans* did not change its specific leaf area with water depth (Fig. 3, t test: $P > 0.05$).

Table 1 Two-way ANOVAs of the effects of water depth (1.0 and 2.5 m) and time (15, 30 and 45 days) on total biomass of each species. All data were LN-transformed ($n = 20$)

Variable	*df*	Total biomass (g DW)		
		Potamogeton maackianus	*Potamogeton malaianus*	*Vallisneria natans*
Water depth (*W*)	1	125.51***	55.33***	56.68***
Time (*T*)	2	178.35***	103.03***	233.48***
W × *T*	2	4.28*	7.33***	9.81***

* $P < 0.05$; *** $P < 0.001$

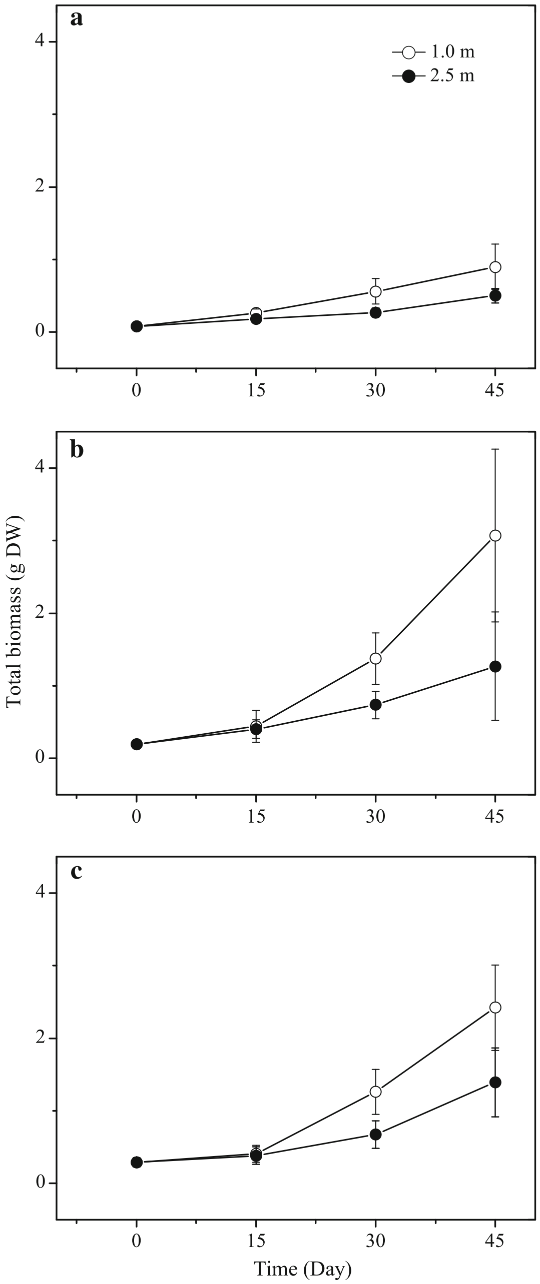

Fig. 1 Variations in total biomass of individual plant with water depth (*open circles* 1.0 m; *filled circles* 2.5 m) and time for three submerged macrophytes. Values are mean ± SD ($n = 20$). **a** *Potamogeton maackianus*; **b** *Potamogeton malainus*; **c** *Vallisneria natans*

Specific leaf area increased with increased plant size for *P. malaianus* and *V. natans* ($\alpha > 1$, $P < 0.001$), and was kept invariable for *P. malaianus* ($\alpha = 1$, $P < 0.001$).

Stem mass was affected by water depth for *P. malaianus*, and dependent strongly on total biomass for the two *Potamogeton* species (Table 2). A significant interaction between water depth and total biomass was found only in *V. natans* (Table 2). Allometric relationships between stem mass and total biomass differed significantly between water depths for *V. natans* ($P < 0.05$), but did not differ between water depths for the two *Potamogeton* species ($P > 0.05$). At 2.5 m depth, *P. maackianus* and *P. malaianus* allocated more biomass to the stems (Fig. 2, *t* test: $P < 0.001$), while *V. natans* exhibited lower stem mass for a given total biomass (Fig. 2). The stem mass ratio increased with increased plant size (total biomass) for *P. maackianus* ($\alpha > 1$, $P < 0.001$), was kept invariable for *P. malaianus* ($\alpha = 1$, $P < 0.001$), and decreased for *V. natans* ($\alpha < 1$, $P < 0.001$).

Shoot height of *V. natans* was affected significantly by water depth and total biomass (Table 2). A significant interaction between water depth and the total biomass was observed in the two *Potamogeton* species (Table 2). Allometric relationships between shoot height and total biomass differed significantly between water depths for the two *Potamogeton* species ($P < 0.05$), but did not differ between water depths for *V. natans* ($P > 0.05$). At 2.5 m depth, however, the three species showed higher shoot height for a given total biomass (Fig. 3, *t* test: $P < 0.01$). Shoot height per unit total biomass decreased with increased plant size for the three species ($\alpha < 1$, $P < 0.001$), and shoot height increased more rapidly at 2.5 m depth where the allometric slopes were steeper than that in 1.0 m depth.

Root mass in *P. malaianus* was correlated strongly with total biomass (Table 2). A significant interaction between water depth and total biomass was found in *P. maackianus* and *V. natans* (Table 2). Allometric relationships between root mass and total biomass of each species were not influenced significantly by water depth ($P > 0.05$) and exhibited similar responses to water depth. At 2.5 m depth, the three species tended to allocate less biomass to the roots (Fig. 2, *t* test: all $P < 0.01$). Root mass ratio increased with increased plant size (total biomass) for the three species ($\alpha > 1$, $P < 0.001$).

Discussion

In the present study, the two erect submersed macrophytes, *P. maackianus* and *P. malaianus*, allocated more biomass to the stem and increased their shoot height in deeper water, as indicated by the greater stem mass and shoot height for a given plant size. This result was in agreement with the first hypothesis. The light availability for plants leaves in 2.5 m water depth was reduced by 71 % (214 μM)—far below the photosynthetic light saturation point (500–600 μM) for submersed macrophytes (Bowes and Salvucci 1989). As an additional adaption to the low light stress, both species also showed higher leaf area for a given leaf size and thus greater specific leaf area, which can enhance light use efficiency greatly (Spence et al. 1973). Similar to our results, in a mesocosm experiment, *P. maackianus* allocated more biomass to the stem and less to the root and leaf in response to water level adjustment (Yang et al. 2004). Other submersed macrophytes, *Potamogeton obtusifo-*

Table 2 One-way ANCOVAs of the effect of water depth (1.0 and 2.5 m), using total biomass as a covariate, on response variables of each species

	LM (g)	SLA (m^2 kg^{-1})	SM (g)	SH (cm)	RM (g)
P. maackianus					
Water depth (*W*)	0.11 ns	26.81***	8.7**	391.78***	39.04***
Total biomass (*B*)	490.76***	33.77***	2,424.71***	307.14***	341.56***
W × *B*	3.04 ns	19.25***	1.74 ns	109.81***	11.63**
P. malaianus					
Water depth (*W*)	10.91**	19.99***	0.04 ns	191.64***	0.65 ns
Total biomass (*B*)	1,446.01***	0.27 ns	2,812.09***	286.73***	466.10***
W × *B*	0.98 ns	0.07 ns	2.31 ns	28.27***	2.12 ns
V. natans					
Water depth (*W*)	54.09***	53.55***	195.54***	185.35***	33.43***
Total biomass (*B*)	5,615.25***	122.32***	100.83***	250.73***	1,168.81***
W × *B*	1.46 ns	2.35 ns	28.22***	1.19 ns	7.1**

F values are shown ($n = 60$)

LM Leaf mass, *SLA* specific leaf area, *SM* stem mass, *SH* shoot height, *RM* root mass

* $P < 0.05$; ** $P < 0.01$;*** $P < 0.001$, *ns* no significant difference

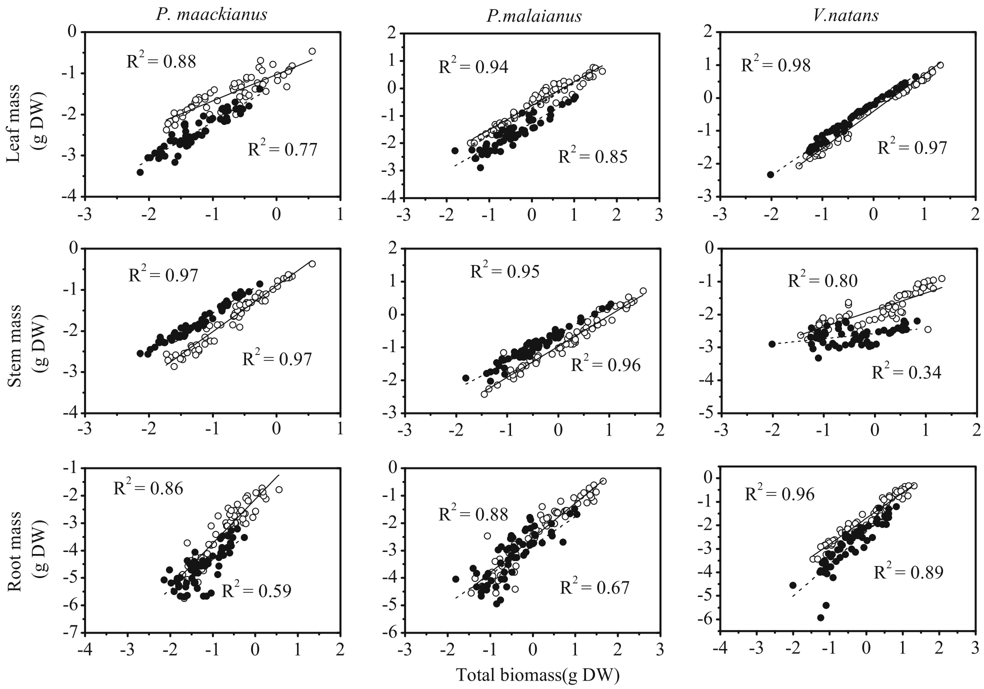

Fig. 2 Effect of water depth (*open circles* 1.0 m; *filled circles* 2.5 m) on the allometric relationships between total biomass and root mass, stem mass and leaf mass, respectively, for three submersed macrophytes species (*P. maackianus*, *P. malaianus* and *V. natans*). All data were LN-transformed ($n = 60$)

lius, *Potamogeton praelongus* and *Myriophyllum spicatum* growing in deep water also showed lower leaf dry mass and increased shoot height (Spence and Chrystal 1970; Chambers 1987; Strand and Weisner 2001). As light availability attenuates sharply in deep water, the elongation of shoots can alleviate the low light stress efficiently given that the leaves of most plants are located at the top of the shoots (Chambers 1987). Therefore, the erect submersed macrophytes elongate shoots toward the water surface, as most herbaceous terrestrial plants with erect stems extend their stems in response to shading (Bonser and Geber 2005; Valladares and Niinemets 2008; Niinemets 2010). This is, in fact, one of the best investigated responses allowing plants to adapt to shaded conditions (Valladares and Niinemets 2008). This response is ubiquitous, largely independent of the type of shading, and the presence of vertical light gradients usually just increases the response (Franklin 2008; Valladares and Niinemets 2008). Thus, macrophytes do not differ from terrestrial plants with respect to stem elongation. There may be, however, a difference with respect to the costs associated with shade-induced elongation processes. While erect plants need to invest in the maintenance of biomechanical stability for the

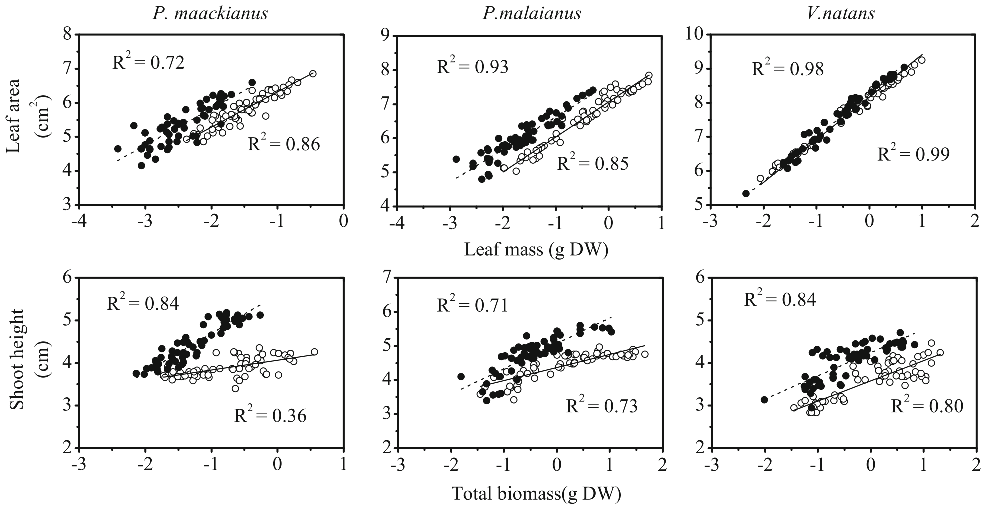

Fig. 3 Effect of water depth (*open circles* 1.0 m; *filled circles* 2.5 m) on the allometric relationships between leaf mass and leaf area (*upper row*), and between total biomass and shoot height (*lower row*), respectively, for three submersed macrophytes species (*P. maackianus*, *P. malaianus* and *V. natans*). All data were LN-transformed ($n = 60$)

elongated stems (Bonser and Geber 2005; Weijschede et al. 2006), these costs may be lower for aquatic plants as the stems may be supported by the water column. In aquatic environments, however, hydrodynamic forces caused by water movement can be many times the drag forces produced by wind on land (Puijalon et al. 2011). It is thus speculated that aquatic plants must invest more resources to resist mechanical forces than terrestrial species. Generally, the magnitude of mechanical forces encountered by plants exposed to moving fluids (air or water) depends not only on fluid velocity but also on plant morphology and size (Puijalon et al. 2011). To minimize the negative impacts of elongated stems in deep water, the three macrophytes tended to decrease plant size and concentrate branches and leaves on the water surface, which may greatly reduce the force encountered over a given area.

In deeper water, the rosette submersed macrophyte, *V. natans*, allocated more biomass to leaves and had a higher shoot height to achieve a given plant size, which was consistent with the second hypothesis. These results were in accordance with the results from other in situ experiments (Chambers and Kalff 1987; Titus and Stephens 1983). *V. natans* has strap-like leaves on a stunted basal stem that is unable to elongate effectively under low light stress. Therefore, the increased leaf mass and leaf length of *V. natans* may have the same effect as investing in stem elongation in *Potamogetons*: both result in a shift of leaf area into higher illuminated areas within the water column (Chambers and Kalff 1987; Valladares and Niinemets 2008; Duursma et al. 2012).

In deeper water, the three macrophytes tended to allocate less biomass to the roots, with lower root mass at a given plant size, which supported the third hypothesis. This result is consistent with the root responses to low light stress of aquatic (Chambers and Kalff 1987; Strand and Weisner 2001) and terrestrial (McConnaughay and Coleman 1999; Niinemets 2010; Poorter et al. 2012) plants. In this study, the decreased root mass ratio in deep water was attributed largely to increased biomass allocation to aboveground tissues (e.g., stem and leaf), because resources allocated to one organ are therefore not available to other organs (Bloom et al. 1985; Poorter et al. 2012). Furthermore, submersed macrophytes can take up nutrients not only by roots but also by leaves (Madsen and Cedergreen 2002), which may compensate for the reduced nutrient uptake associated with decreased root mass ratio.

Remarkably, the changes in biomass allocation and morphology for the three macrophytes were dependent strongly on plant size, with increasingly larger investments in support tissues (i.e., stem for the *P. maackianus* and leaf for *V. natans*) expected for larger plants. Although plants grown in deeper water were smaller, they showed higher shoots when plants are compared at a common size, due largely to the greater shoot height per unit total biomass. Similarly, deep-water-grown plants had a lower root mass ratio mostly because of their smaller size. Thus, the three macrophytes respond to deep water not only by reducing the growth rate but also by actively reprogramming the allometric trajectory.

In conclusion, as indicated by the significant effects of water depth on the allometric relationships between plant size and phenotypic traits, the present study showed that the two *Potamogeton* species increased biomass allocation to the stems, shoot height and specific leaf area to alleviate low light stress; in contrast, *V. natans* increased biomass allocation to the leaves and leaf length in deeper water. Therefore, the main effect of the water depth treatments was reduced light availability, which induced plastic shoot or leaf elongation. Our results imply that, due to the sharply vertical attenuation of underwater light intensity, macrophytes might have evolved responses to light limitation similar to those of terrestrial plants.

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