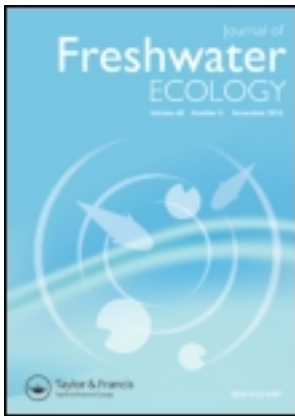


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## Editor's choice article

# Relationships between relative growth rate and its components across 11 submersed macrophytes

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The relationships between relative growth rate and its components across 11 submersed macrophytes were examined in a short-term experimental study. Plants were grown in identical conditions in pots that were submersed in tanks. The average values for relative growth rate ranged from 17.4 to 94.5 mg g<sup>-1</sup> d<sup>-1</sup>. The net assimilation rate, based on the increase in plant dry weight per unit leaf area in a fixed time, varied fivefold among species and showed a strong, positive correlation with relative growth rate. The leaf area ratio, leaf mass ratio, and specific leaf area were not significantly correlated with the relative growth rate, although these parameters were important in the adaptive responses of macrophytes to environmental stress. These results suggest that the physiological components (net assimilation rate) would be the main determinant of relative growth rate in submersed macrophytes, which highlights the importance of net assimilation rate in explaining differences in macrophyte species performance in freshwater habitat.

**Keywords:** relative growth rate; net assimilation rate; leaf area ratio; leaf mass ratio; specific leaf area; submersed macrophytes

## Introduction

Plant species vary greatly in their relative growth rate (RGR, rate of dry mass production per unit total dry mass and time) even when comparing them under similar environmental conditions (Grime and Hunt 1975). Variation of RGR among plant species could be attributed to morphological differences in the leaf area ratio (LAR, the ratio of leaf area to total dry mass) and physiological variations in the net photosynthetic assimilation rate (NAR, rate of dry mass production per unit leaf area and time; Hunt 1982; Poorter 1989). LAR can be further divided into two components, the leaf mass ratio (LMR, fraction of total biomass allocated to the leaves) and the specific leaf area (SLA, the ratio of leaf area to leaf dry mass) (Evans 1972). In general, plant species enhance performance (e.g., potential RGR) by adjusting morphological and physiological traits in response to a varying environment. These adjustments might confer a competitive advantage to fast growing

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species under benign conditions or, conversely, limit their potential growth in adverse environments (Poorter and Remkes 1990). Therefore, it is important to evaluate the mechanisms accounting for the interspecific variation in RGR and to understand the ecological advantage of a plant's growth potential.

Many studies have examined the relationships between RGR and its components in terrestrial plants and the key determinant of RGR does not seem to be consistent. Some studies emphasize the importance of morphological components like SLA (Poorter 1989; Poorter and Remkes 1990; Garnier 1992; Lambers and Poorter 1992; Cornelissen et al. 1998), while others focus on the physiological components like NAR (Veneklaas and Poorter 1998; McKenna and Shipley 1999; Meziane and Shipley 1999). Poorter and Van der Werf (1998) and Shipley (2002, 2006) concluded that the determinant of variation in RGR was dependent on light availability in the plant habitat, with LAR or SLA being the main factor explaining variation in RGR at low light, and NAR being the dominant factor at high light. Although submersed macrophytes generally enhance performance (e.g., potential RGR) through their high degree of plasticity in morphology and physiology in response to a varying environment (Barko and Smart 1981; Maberly 1993; Strand and Weisner 2001), the factors that determine the interspecific variation in RGR have not been identified (Nielsen and Sand-Jensen 1991). Thus, examining the relationships between growth parameters and RGR in submersed macrophytes will be valuable.

Submersed macrophytes typically inhabit low light environments and exhibit highly variable morphological and physiological traits as an acclimation to a varying light regime (Barko and Smart 1981; Bowes and Salvucci 1989; Ni 2001). In contrast to the light limitation of terrestrial photosynthesis in air, the extremely low diffusion rate of CO<sub>2</sub> in water is a major factor affecting net photosynthesis of submersed macrophytes. Thus, the inherent difference in RGR for submersed macrophytes should be determined more by the plant's ability to assimilate carbon rather than capture light. Therefore, the component accounting for most of the variation in RGR among submersed macrophytes is speculated to differ from those observed in terrestrial plants.

Many plant characters contribute to a plant's RGR, including biomass allocation, germination time and life history (Poorter and Remkes 1990). In the present study, we limit the analyses to relationships between RGR and its components across 11 co-occurring submersed macrophytes and discuss the mechanisms that result in interspecific variation in RGR. The plants are quite different in leaf morphology and growth form. In their laboratory study on 14 macrophytes, Nielsen and Sand-Jensen (1991) demonstrated that the RGR variability is more closely related to physiological traits (e.g., carbon affinity) than morphological traits (e.g., the surface/volume ratio). Therefore, we also test the hypothesis that the physiological trait NAR would be the determinant of RGR across the species.

## Methods

### *Experimental design*

Eleven submersed macrophytes, *Potamogeton crispus*, *P. lucens*, *P. acutifolius*, *P. maackianus*, *P. perfoliatus*, *P. pectinatus*, *P. malaianus*, *Myriophyllum spicatum*, *Ceratophyllum demersum*, *Hydrilla verticillata*, and *Vallisneria natans*, that

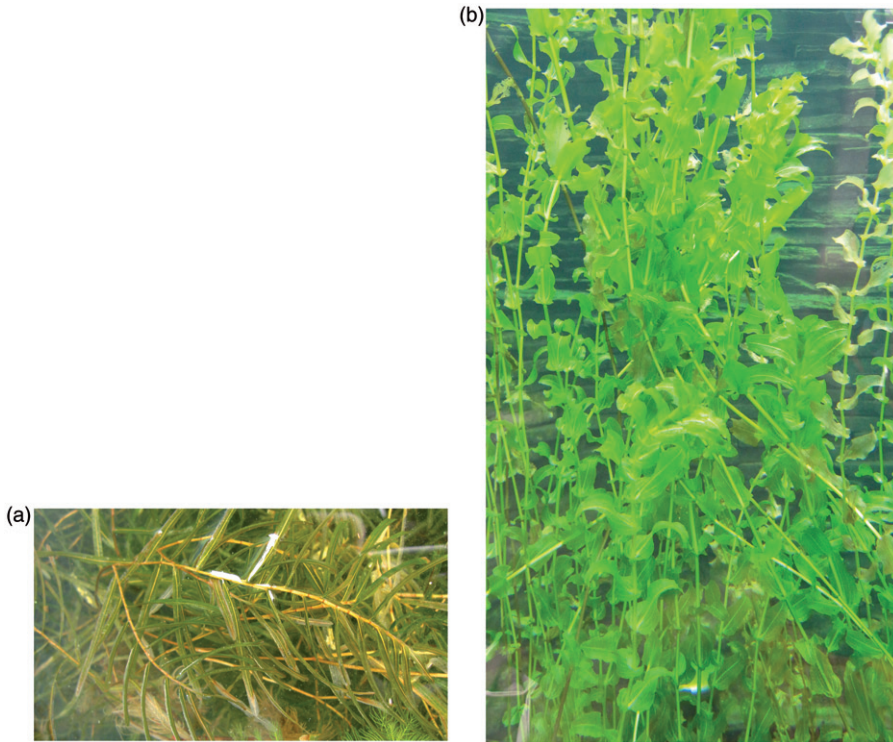


Figure 1. Photos of (a) *P. maackianus* and (b) *P. perfoliatus*. Photo credit: Hu Fui.

co-occurred in Erhai Lake (N 25°52', E 100°06') and sprouted during spring, were grown from locally field-gathered shoots/seedlings in identical conditions. The plants are canopy-formers with regard to growth forms, except for *V. natans* which forms a rosette. The plants of *Potamogeton* have alternate, oblong or linear entire leaves (Figure 1). *M. spicatum* and *C. demersum* have finely dissected and whorled leaves. *V. natans* has tape-like leaves arising from a basal stem.

The experiment was performed outdoors in spring 2011 (from 26 April to 13 May) in an open space located near Erhai Lake in the Yunnan Province, China. Seedlings of *V. natans* and apical shoots of the other plants were collected from Erhai Lake. Twenty-four shoots/seedlings of each species, similar in size (approximately 10 cm in length) and healthy in appearance, were selected and separately planted in plastic pots (6 cm diameter  $\times$  7.5 cm in height) containing 5 cm sediment. The sediment used in this study was well mixed after being collected from Erhai Lake. Two hundred and sixty-four pots together with the shoots/seedlings were incubated in 44 large tanks (length 27 cm  $\times$  width 20 cm  $\times$  height 30 cm, six pots per tank), consisting of four tanks of triplicate plants for each of the 11 macrophyte species.

Water depth in these tanks was maintained at 28 cm. All the plants were cultured in tanks for 5 days of acclimation and then re-located in a randomized arrangement in these 44 tanks (Milne et al. 2007). Plants experienced the same environmental conditions and the experimental system was covered with one layer of shade net for controlling the light environment. Because most of these species grow so fast, the

plants would quickly fill the tanks; therefore, the experiment only lasted for 20 days to minimize the influences of self-shading and competition within species.

During the study period, photosynthetically active radiation (PAR) 5 cm below the water surface was approximately  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$  at noon and the water temperature was approximately  $15/20^\circ\text{C}$  at night/day and the daily water temperature ranged from  $16.3^\circ\text{C}$  to  $23.8^\circ\text{C}$ . Tap water (pH=8.2–8.8) that contained a moderate concentration of dissolved inorganic carbon (DIC) at 2.52–2.85 mM (measured by Gran-titration; Stumm and Morgan, 1970) was supplied during the experiment, and was replaced completely every 6 days. The water was aerated with atmospheric air and circulated by a submersible pump to avoid thick boundary layers surrounding the plant surfaces. Filamentous algae attaching to the plant leaves were gently cleaned weekly by brushing the foliage. The average ( $n=44$ ) concentration of  $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$ , and  $\text{PO}_4\text{-P}$  in the water column was 0.39, 0.02, and  $0.005 \text{ mg L}^{-1}$ , respectively, with no significant changes during the study period. The average ( $n=44$ ) concentration TN, TP, and organic material in sediment was  $2.12 \text{ mg g}^{-1}$ ,  $0.68 \text{ mg g}^{-1}$ , and 2.56%, respectively.

### Growth analysis

For the biomass and morphological measurements of the plants ( $n=12$ ), three pots of each species per tank were collected at each sampling on the 5th and the 20th day. Biomass in dry weight (g DW) of the stem and the leaf was determined after drying at  $80^\circ\text{C}$  for 48 h. Leaf area ( $\text{cm}^2$ ) was scanned immediately after the harvesting with a scanner (600 dpi) connected to a computer and estimated using the software Image-Pro Plus 6.0 (Media Cybernetics Co., USA). Total leaf area of a single leaf was calculated by multiplying the scanned leaf area by two for the species with apparently flat leaves and by  $\Pi$  for *P. pectinatus*, *M. spicatum*, and *C. demersum* with cylindrical leaves (Nielsen and Sand-Jensen 1991). Mean values and standard error of RGR ( $\text{mg g}^{-1} \text{d}^{-1}$ ), NAR ( $\text{g m}^{-2} \text{d}^{-1}$ ), LAR ( $\text{m}^2 \text{kg}^{-1}$ ), LMR ( $\text{g g}^{-1}$ ), and SLA ( $\text{m}^2 \text{kg}^{-1}$ ) were estimated according to Hunt et al. (2002).

### Statistics

Regression analyses were performed to test correlation strength between RGR and its components, using adjusted  $R^2$  to correct for the degrees of freedom. The relationship among growth parameters was analyzed by Pearson correlation analysis since all data sets were normally distributed. In order to compare the relative contribution of each growth component, we calculated a growth response coefficient (GRC) according to Poorter and Van der Werf (1998) as the slopes estimated from linear regressions where  $\ln(\text{LAR})$ ,  $\ln(\text{NAR})$ ,  $\ln(\text{LMR})$ , and  $\ln(\text{SLA})$  were the dependent variables and  $\ln(\text{RGR})$  was the independent variable. The GRC indicates how a proportional difference in a growth parameter scales with the observed difference in RGR. For example, a  $\text{GRC}_{\text{NAR}}$  value of 1 indicates that a given difference in RGR is accompanied by a proportional difference in NAR; a  $\text{GRC}_{\text{NAR}}$  of 0 indicates that a difference in RGR is not accompanied by any systematic difference in NAR.

Sample size in all analyses was 8–12 for each species at each harvest, as the rest of the plants appeared to be necrotic or dead. Because the belowground tissues

Table 1. Species means  $\pm$  SE ( $n=8-12$ ) of relative growth rate (RGR), net assimilation rate (NAR), specific leaf area (SLA) and leaf mass ratio (LMR) in this experiment for plants on day 15, with PAR at 10 cm below the water surface being  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$  at noon and water temperature approximately  $15/20^\circ\text{C}$  at night/day.

Species	RGR ( $\text{mg g}^{-1} \text{d}^{-1}$ )	NAR ( $\text{g m}^{-2} \text{d}^{-1}$ )	LAR ( $\text{m}^2 \text{kg}^{-1}$ )	LMR ( $\text{g g}^{-1}$ )	SLA ( $\text{m}^2 \text{kg}^{-1}$ )
<i>P. crispus</i>	$94.5 \pm 48.2$	$1.13 \pm 0.47$	$95.4 \pm 12.7$	$0.69 \pm 0.07$	$139.3 \pm 16.3$
<i>M. spicatum</i>	$70.0 \pm 17.8$	$0.88 \pm 0.22$	$78.3 \pm 12.3$	$0.56 \pm 0.08$	$136.9 \pm 19.2$
<i>C. demersum</i>	$48.3 \pm 14.4$	$0.52 \pm 0.14$	$93.6 \pm 11.9$	$0.70 \pm 0.07$	$134.7 \pm 19.8$
<i>P. lucens</i>	$39.5 \pm 15.2$	$0.56 \pm 0.18$	$69.2 \pm 8.0$	$0.58 \pm 0.07$	$119.9 \pm 12.1$
<i>P. acutifloius</i>	$37.7 \pm 13.5$	$0.40 \pm 0.13$	$93.5 \pm 13.6$	$0.53 \pm 0.06$	$176.9 \pm 14.6$
<i>H. verticillata</i>	$35.8 \pm 17.1$	$0.44 \pm 0.08$	$192.5 \pm 71.2$	$0.58 \pm 0.10$	$347.5 \pm 175.6$
<i>V. natans</i>	$26.4 \pm 16.6$	$0.55 \pm 0.33$	$47.5 \pm 7.1$	$0.59 \pm 0.08$	$79.9 \pm 5.8$
<i>P. maackianus</i>	$26.1 \pm 10.1$	$0.38 \pm 0.14$	$70.7 \pm 9.4$	$0.48 \pm 0.05$	$147.7 \pm 13.1$
<i>P. perfoliatus</i>	$25.7 \pm 13.3$	$0.27 \pm 0.13$	$98.5 \pm 11.7$	$0.56 \pm 0.06$	$178.1 \pm 17.5$
<i>P. pectinatus</i>	$19.4 \pm 9.8$	$0.30 \pm 0.13$	$72.3 \pm 6.4$	$0.83 \pm 0.06$	$87.4 \pm 6.2$
<i>P. malaianus</i>	$17.4 \pm 6.5$	$0.26 \pm 0.09$	$67.9 \pm 5.5$	$0.61 \pm 0.04$	$112.3 \pm 5.4$

(root/rhizome) had not developed well in most of these species, the growth analysis in this study was restricted to the above-ground plant parts. Biomass invested in roots was not taken into account (with the exception of *V. natans*); therefore, the reported NAR is less than the whole-plant NAR. All analyses were conducted with STATISTICA version 6.0 (Statsoft Inc., Tulsa, OK, USA) and differences were significant at  $p < 0.05$ .

## Results

RGR of the 11 macrophytes ranged from 17.4 to  $94.5 \text{ mg g}^{-1} \text{d}^{-1}$ , with *P. crispus* having the highest RGR and *P. malaianus* the lowest RGR. NAR of the plants was  $0.26-1.13 \text{ g m}^{-2} \text{d}^{-1}$ , LAR was  $47.5-192.5 \text{ m}^2 \text{kg}^{-1}$ , LMR was  $0.48-0.83 \text{ g g}^{-1}$  and SLA was  $84.7-347.5 \text{ m}^2 \text{kg}^{-1}$  (Table 1). *H. verticillata* showed the highest LAR ( $192.5 \text{ m}^2 \text{kg}^{-1}$ ) and SLA ( $347.5 \text{ m}^2 \text{kg}^{-1}$ ) and *P. pectinatus* showed highest LMR ( $0.83 \text{ g g}^{-1}$ ).

Across the macrophytes, RGR was strongly positively correlated with NAR (Figure 2a); the  $\text{GRC}_{\text{NAR}}$  ranged from 0.7 to 0.94 and was significantly different from zero (Figure 3). NAR accounted for the most variation of RGR. In contrast, RGR was never significantly correlated with LAR, LMR, or SLA (Figure 2b-d), and the GRC values of these parameters were not significantly different from zero (Figure 3). No significant correlations were found between NAR and LAR ( $r = -0.15$ ,  $p = 0.97$ ) or SLA ( $r = -0.09$ ,  $p = 0.80$ ). SLA accounted for the most variation of LAR ( $r = 0.96$ ,  $p < 0.0001$ ).

## Discussion

We examined the growth of 11 morphologically diverse species, which were representative of submersed macrophytes in general, under moderately high light conditions during spring, and found great variability in RGR and its components (NAR, LAR, SLA, and LMA) among species. This result is consistent with previous

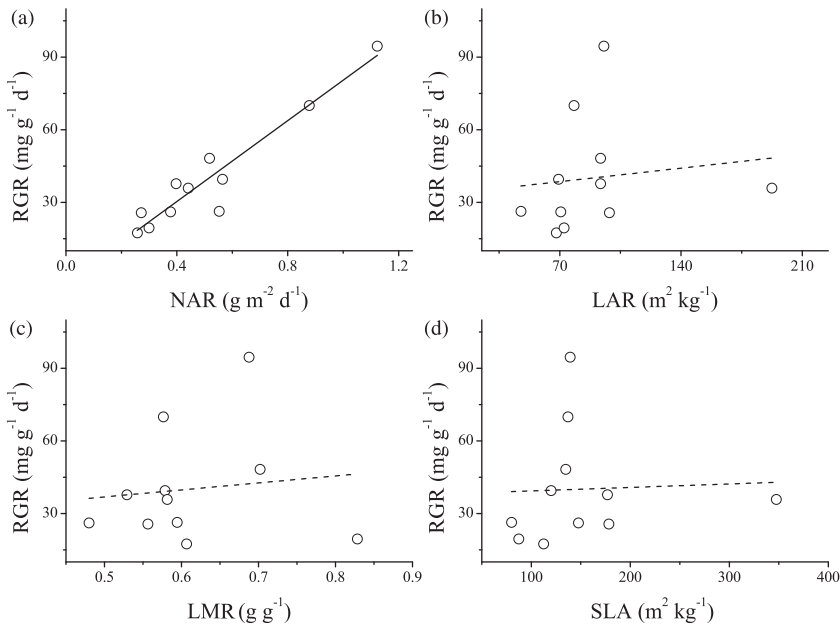


Figure 2. Mean relative growth rate (RGR) of 11 submersed macrophyte species as a function of (a) net assimilation rate (NAR), (b) leaf area ratio (LAR), (c) leaf mass ratio (LMR), and (d) specific leaf area (SLA). Lines are the linear regression lines (for NAR:  $p < 0.001$ ,  $r^2 = 0.9$ , for LAR:  $p > 0.05$ ,  $r^2 = -0.09$ , for LAR:  $p > 0.05$ ,  $r^2 = -0.1$ , for LAR:  $p > 0.05$ ,  $r^2 = -0.1$ ).

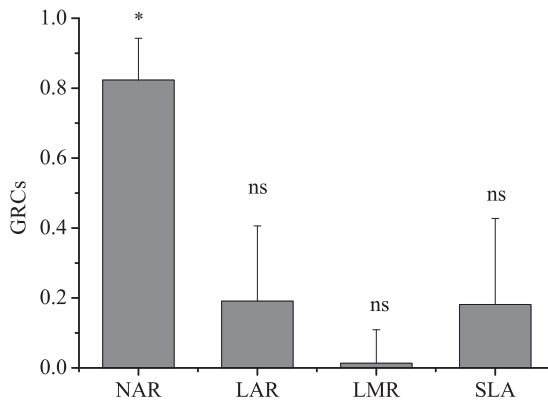


Figure 3. Growth response coefficient (GRC, mean  $\pm$  SE) of net assimilation rate (NAR), leaf area ratio (LAR), leaf mass ratio (LMR) and specific leaf area (SLA) for 11 submersed macrophyte species. The GRC indicates how a growth parameter responds to an observed difference in relative growth rate (RGR). \*indicates that the  $GRC_{NAR}$  is significantly different from 0 ( $p < 0.05$ ) and the difference in RGR is significantly related to the variation in NAR; “ns” indicates the  $GRC_{LAR}$ ,  $GRC_{LMR}$  and  $GRC_{SLA}$  are not significantly different from 0 ( $p > 0.05$ ) and the change in RGR is not significantly related to the variation in LAR, LMR and SLA.

findings in the laboratory during summer (Nielsen and Sand-Jensen 1991), whereas the rank order of species with respect to RGR was not consistent between two studies. For example, Nielsen and Sand-Jensen reported that *P. pectinatus* ( $0.094 \text{ mg g}^{-1} \text{ d}^{-1}$ ) had much higher RGR than *P. crispus* ( $0.052 \text{ mg g}^{-1} \text{ d}^{-1}$ ) in contrast to our study. The difference in the season might contribute to those differences in RGR between studies, as the two species have different growth cycles with *P. crispus* usually blooming earlier than *P. pectinatus*. In addition, the lower DIC concentration (2.52–2.85 mM) and higher light availability ( $500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) relative to their study (DIC: 3.3–3.8 mM and light:  $250 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) could also contribute to the differences in RGR between studies.

*H. verticillata* showed the highest LAR, largely explained by the greatest SLA, which helps plants form a dense canopy and enhance photosynthetic area with the lowest resource investments. Furthermore, the inherent variation in SLA is closely related to leaf anatomy, morphology and chemical composition. The great variability in leaf surface area to volume ratio (SA:V, Nielsen and Sand-Jensen 1990) and leaf thickness (Nielsen et al. 1996) across macrophyte species should contribute to the observed differences in SLA and thus LAR. In this study, *P. pectinatus* had the highest LMR and usually concentrated its leaf tissues on the water surface, which might promote photosynthetic rate. The high leaf dry mass, however, means large carbon loss due to leaf respiration, resulting in very low RGR for *P. pectinatus*.

In the present study, NAR was the only factor that was strongly correlated with RGR and it explained most of the variability of RGR of all the macrophytes. These results support our hypothesis that NAR is the primary component determining RGR across the macrophytes but is not consistent with previous results for terrestrial plants (Poorter 1989; Poorter and Remkes 1990; Lambers and Poorter 1992; Cornelissen et al. 1998), in which SLA rather than NAR was the most important determinant of RGR under low light conditions. The mechanisms responsible for the differences may be attributed to different strategies (i.e., physiological or morphological) between aquatic and terrestrial plants to enhance net photosynthesis (Bowes and Salvucci 1989; Madsen and Sand-Jensen 1991). Previous studies have indicated that the diffusion rate of  $\text{CO}_2$  in water is 10,000 times lower than that in air, commonly limiting photosynthesis of submersed macrophytes (Raven 1970). Thus,  $\text{CO}_2$  availability in water is one of the most important factors determining NAR of macrophyte species that have developed diverse carbon concentration mechanisms (CCM, Maberly and Madsen 2002). The differences in CCM among macrophyte species may be critical in explaining the variations of RGR. Furthermore, Nielsen and Sand-Jensen (1991) demonstrated that carbon affinity was the most important attribute affecting RGR of 14 macrophyte species. In addition, submersed macrophytes exhibit very different physiological attributes, such as light-saturated net photosynthesis rates and  $\text{CO}_2$  compensation or saturation points (Kadono 1980; Allen and Spence 1981; Bowes and Salvucci 1989). Biochemical resistance (i.e., carboxylation resistance, photorespiration and dark respiration), may be also important for net carbon accumulation and potential growth rates (Black et al. 1981; Maberly and Spence 1989). These differences in physiology and biochemistry could account for the variation in NAR among macrophyte species and, thereby, influence RGR.

Remarkably, no correlations were found between RGR and its morphological components, which was in agreement with the results of Nielsen and Sand-Jensen



(1991) for 14 submersed macrophytes. SLA, instead of LMR, explained most of the LAR variation, consistent with the results for terrestrial plants (Poorter 2001). Furthermore, all morphological parameters were almost invariant with regard to RGR. Although the changes in these parameters can be important in the adaptive responses of macrophytes to environmental stress, such as light and DIC (Barko and Smart 1981; Madsen et al. 1996), our results and others (Nielsen and Sand-Jensen 1991) suggest that morphological traits explained much less variation in RGR under certain light availabilities ( $500$  and  $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and DIC concentrations ( $2.52$ – $2.85$  and  $3.3$ – $3.8$  mM).

In the present study, the invariable SLA across the 11 macrophytes was impressive but probably reasonable. First, submersed macrophytes have simplified leaf structure with little waxy cuticle and lignin and thus much higher SLA than terrestrial plants (Poorter et al. 2009), which may inhibit further thinning of the submersed leaves. Second, further changes in the SLA may have little economic return, probably because dense epiphytes on the leaf surface of submersed macrophytes would reduce light penetration into the leaf and discount the plant photosynthesis (Phillips et al. 1978). Finally and most importantly, SLA changed in response to light availability but was independent of species identity (Spence et al. 1973), despite the specific ranges of SLA showed by different submersed macrophytes (Spence and Chrystal 1970).

Generally, most macrophyte species exhibit a high degree of plasticity in morphology as adaptive responses to freshwater environment. Such morphological plasticity can promote plant fitness in specific ranges of environmental conditions within species, representing a trade-off with RGR. For example, *Potamogeton obtusifolius* increased its shoot length and specific leaf area but decreased shoot growth with increased water depth (Maberly 1993). In the present study, despite the great differences in morphological traits among species, the role of morphology was no significant in determining neither the interspecific nor the intraspecific variations in RGR. Our results suggest that the physiological components (NAR) would be the main determinant of RGR in submersed macrophytes, which might be related to the differences in their ability to enhance net carbon gain including CCM (e.g., utilization of sediment  $\text{CO}_2$  by *V. natans*,  $\text{C}_4$  pathway for *H. verticillata* and pH-polarity mechanism of *P. lucens* and *H. verticillata*), carbon affinity and biochemical resistance (Bowes and Salvucci 1989; Bowes et al. 2002; Maberly and Madsen 2002). The differences in photosynthetic carbon assimilation may be more intrinsic among species than those in morphology, which highlights the importance of net assimilation rate in explaining differences in macrophyte species performance in freshwater habitat.

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