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Does light heterogeneity affect structure and biomass of submerged macrophyte communities?

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ABSTRACT. Environmental heterogeneity is universal and occurs at various spatial scales. Many studies have examined effects of environmental heterogeneity on growth of individual species, but few have tested the effects on species composition and biomass of plant communities, especially those consisting of submerged macrophytes. Moreover, no study has tested effects of scale of heterogeneity on plant communities. We constructed communities with four submerged macrophytes (i.e., *Ceratophyllum demersum, Hydrilla verticillata*, *Egeria densa* and *Myriophyllum verticillatum*) and subjected the communities to three homogeneous light treatments (100%, 65% and 30% of full light and coded as high, medium and low light treatment, respectively) and two heterogeneous light treatments differing in patch size (large *vs.* small patch treatment). The total amount of light received by the whole communities in the two patchy treatments was the same as that in the homogeneous medium light treatment. Under homogeneous treatments, decreasing light intensity significantly decreased total biomass, total number of nodes and total shoot length of the submerged macrophyte communities and of *H. verticillata* and *E. densa*, but did not significantly affect growth of *M. verticillatum* or *C. demersum*. Light heterogeneity, i.e., light patchiness or patch scale, did not affect these three growth variables of the community as well as those of the individual macrophytes. Therefore, light intensity can affect structure and biomass of submerged macrophyte communities, but light heterogeneity may not.

Keywords: Aquatic plants; Clonal plants; Environmental heterogeneity; Patch scale.

INTRODUCTION

Environmental heterogeneity is an important feature of natural habitats and occurs in different temporal and spatial scales (Kotliar and Wiens, 1990; Stuefer, 1996). It is ubiquitous in both terrestrial (Huber-Sannwald and Jackson, 2001) and aquatic ecosystems (Cronk and Fennessy, 2001; Scheffer, 2004), and commonly shown by non-uniform distributions of the essential resources (e.g. light, water and soil nutrients) required by plants (Caldwell and Pearcy, 1994; Hutchings and Wijesinghe, 1997; Fitter et al., 2000).

Environmental heterogeneity can significantly affect the fitness of plants (Hutchings and Wijesinghe, 1997) and some plants even develop strategies to benefit from it (Stuefer et al., 1996; Alpert, 1999; Yu et al., 2004, 2008, 2009; Zhou et al., 2012). So far, however, most studies testing the ecological significance of environmental heterogeneity have focused on individual plant species (Jonsdottir and Watson, 1997 for a review; Alpert, 1999; Chen et al., 2004; Yu et al., 2004, 2008; Gomez et al., 2007; Roiloa et al., 2007; Janecek et al., 2008; Nilsson and D'Hertefeldt, 2008; Zhang and He, 2009), and few have tested the effects on plant communities (Maestre et al., 2005; Wijesinghe et al., 2005; Maestre and Reynolds, 2006; Yu et al., 2010). Because plant species differ in the ability to capture resources, they may also differ in the ability to respond to heterogeneity in resource supply (Huber-Sannwald and Jackson, 2001; Hutchings et al., 2003). As a result, environmental heterogeneity may affect interactions between co-occurring species (Hutchings and Wijesinghe, 2000; Hutchings et al., 2003) and thus modify species diversity, composition and biomass of the communities (Facelli and Facelli, 2002; Yu et al., 2009, 2010). For instance, soil nutrient heterogeneity was found to be able to modify competitive intensity between *Briza media* and *Festuca ovina* (Day et al., 2003) and between *Carex hartmanii* and *Molinia caerulea* (Janecek et al., 2004), and alter biomass or species composition of terrestrial plant communities (Hutchings et al., 2003; Maestre et al., 2005; Wijesinghe et al., 2005; Maestre and Reynolds, 2006, 2007; Yu et al., 2010). So far, however, we know very little about the effects of environmental heterogeneity on species composition and biomass of submerged plant communities.

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Spatial scale is an essential component of environmental heterogeneity, and heterogeneity showing at different scales may have dramatically different effects on individual plant species and communities (Kotliar and Wiens, 1990; Stuefer, 1996). Wijesinghe and Hutchings (1997) studied the effects of spatial scale of soil nutrient heterogeneity on the growth of the stoloniferous herb *Glechoma hederacea* by growing the plants under six types of heterogeneous environments differing in patch size (ranging from 50 cm × 50 cm to 6.25 cm × 6.25 cm). They found that growth of *G. hederacea* was the largest at the medium patch-size treatment (25 cm × 25 cm) and decreased significantly at smaller patch-size treatments (Wijesinghe and Hutchings, 1997). However, to our knowledge, no study has tested the effects of spatial scale of heterogeneity at community level.

In most aquatic environments, light is a limiting factor for submerged macrophytes (Kirk, 1994; Cronk and Fennessy, 2001; Scheffer, 2004), and it is also commonly heterogeneously distributed in the horizontal plane due to non-uniform distributions of e.g. floating and emergent plants, plankton, periphyton and suspended load. Because most submerged macrophytes are clonal (Les, 1988; Grace, 1993; Cronk and Fennessy, 2001) and they may differ greatly in the ability to adapt to light heterogeneity, we hypothesize that patchy distributions of light can affect species composition and biomass of submerged macrophyte communities.

We constructed experimental plant communities with four co-occurring submerged macrophytes and subjected the communities to three homogeneous light treatments (high, medium and low) and two patchy light treatments differing in patch scale. Specifically, we address the following questions: do changing light availability under homogeneous conditions, environmental heterogeneity in light supply and patch scale affect the growth of the four submerged macrophytes and thus modify the structure and biomass of the submerged macrophyte communities?

MATERIALS AND METHODS

Experimental community

The experimental community assembled in this study consisted of four submerged macrophytes, i.e., *Ceratophyllum demersum* L., *Hydrilla verticillata* (L.f.) Royle, *Egeria densa* Planch. and *Myriophyllum verticillatum* L. All of them are perennial macrophytes and capable of clonal growth, i.e., stem/stolon fragments can develop into whole plants. They can co-occur in freshwater lakes, e.g., in the lakes at the Winter Palace in Beijing (Q. Zhang personal observation).

Ceratophyllum demersum (Ceratophyllaceae) commonly occurs in still water or slow-flowing water (Stephens and Dowling, 2002). This species grows better in water with high nutrients and can tolerate low light and turbidity but not salinity (DiTomaso and Healy, 2003). In China, *C. demersum* flowers from June to July, and fruits from August to October (Zhang, 2009). *H. verticillata* and *E. densa* belong to the Hydrocharitaceae family (DiTomaso and Healy, 2003). *H. verticillata* is probably native to warmer regions of Asia, and can grow under a wide range of conditions from oligotrophic to eutrophic water (Cook and Luond, 1982). It has 3 to 6 or 8 linear or narrowly strap-shaped whorled leaves, and its shoots can grow very long when it grows in deep water (Langeland, 1996). This species is widely distributed from temperate to tropical regions (Wu et al., 1994), and reproduces asexually by stolons, stem fragments, stem turions and subterranean tubers. In China, it flowers and fruits from May to October. *E. densa* has 3-8 whorled leaves and propagates vegetatively by stolons and stem fragments, but only fragments with more than one node develop into new plants (DiTomaso and Healy, 2003). *M. verticillatum* belongs to the Haloragaceae family, and its shoots rarely branch (Wu et al., 1994). Each node of *M. verticillatum* has 4 - 6 whorled leaves. This species commonly grows in still water and can grow vigorously in eutrophic water.

Sampling and experiment

Plants of all the four species were collected in the lakes of Winter Palace in Beijing in mid-July 2010, and vegetatively propagated in a greenhouse at Forestry Science Co, Ltd. of Beijing Forestry University. On 9 August 2010, 110 mature shoot fragments of each species were selected and all side branches were removed. Each fragment of *C. demersum* and *H. verticillata* had ten nodes with intact leaves, while each fragment of *M. verticillatum* and *E. densa* contained eight nodes. Of the 110 fragments, ten were used for initial measurement; the average dry mass of the fragment was 57.1, 30.5, 29.2 and 43.4 mg for *C. demersum*, *H. verticillata*, *M. verticillatum* and *E. densa*, respectively.

The communities were assembled in 25 plastic boxes (34 cm long × 34 cm wide × 53 cm high) and light could not penetrate the wall of the boxes. Each box was filled with a 1:1 (v:v) mixture of washed river sand and yellow loam to a depth of 18 cm as the sediment, and then covered by additional 2-cm-deep river sand to reduce turbidity. On 11 August 2010, 16 fragments, i.e., four shoot fragments of each species, were planted in each box, arranged in four rows and four columns. The distance between two adjacent rows/columns was 7 cm. After planting, all boxes were filled with tap water to a depth of 30 cm above the surface of the sediment.

After ten days for recovery, the 25 assembled communities were randomly subjected to three homogeneous and two heterogeneous light treatments (Figure 1). There were five replicates in each treatment. The three homogeneous light treatments were high light (full light in the greenhouse), medium light (about 65% of high light by covering the box with a black, neutral shading net without changing the red light to far red light ratio) and low light (30% of high light by covering the boxes with a different type of black, neutral shading

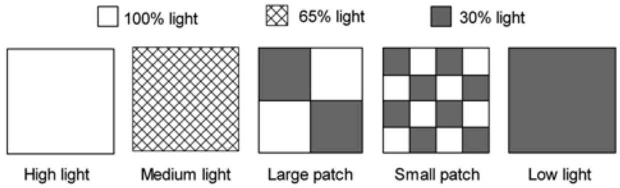

Figure 1. Schematic representation of the experimental design. The experiment consisted of three homogeneous treatments (High light - the whole community in the container received 100% light in the greenhouse; Medium light - the whole community received 65% light; Low light - the whole communities received 30% light) and two heterogeneous treatments (Large patch - the whole community was divided into four large patches; two patches received 100% light and the other two 30% light. Small patches - the whole community was divided into 16 small patches; eight patches received 100% light and the other eight 30% light). The light received by the whole communities in the two patchy treatments was the same as that in the homogeneous medium light treatment.

net (Figure 1). The two heterogeneous light treatments were coded as large patch treatment (each box consisted of four large patches) and small patch treatment (each box having 16 small patches), respectively (Figure 1). The shading net that allows 30% light to pass through (used in the homogeneous low light treatment) was used in both patchy treatments. In the large patch treatment, the shading net covering the top of each box was divided into four 17 cm × 17 cm patches, and in two patches the shading net was removed so that 100% light could pass through these two patches. In the small patch treatment, the shading net covering the top of each box was divided into 16 8.5 cm × 8.5 cm patches, and in eight patches the shading net was removed so that 100% light could pass through these patches (Figure 1). Therefore, the total amount of light received by the whole communities in the two patchy treatments was the same as that in the homogeneous medium light treatment.

The experiment lasted ten weeks and ended on 22 October 2010. During the experiment, water was added to each box every four or five days to compensate for the loss by evaporation, and water in each box was also partly replaced three times to renew its quality. In the greenhouse the temperature was 21.8 ± 0.1°C and relative humidity 77.0 ± 0.3% (mean ± SE; measured hourly by two Hygrochron temperature/humidity loggers, iButton DS1923; Maxim Integrated Products, USA).

Harvest and measurements

On 22 October 2010, the surviving plants in each box were harvested and sorted into three groups, i.e., (1) *M. verticillatum*, (2) *C. demersum* and (3) the two species in the Hydrocharitaceae family (*H. verticillata* and *E. densa*). We combined plants of *H. verticillata* and *E. densa* because at the end of the experiment it was rather difficult to precisely distinguish and separate plants of *H. verticillata* from those of *E. densa*, which was unexpected when the experiment was set up. Despite this defect, we still could address the questions raised in the introduction as long as we treated the two species as one group. For each plant group, we counted number of nodes and measured total shoot length. Then the plants in each group were harvested, oven-dried at 70°C for at least 48 h and weighed.

Data analyses

Biomass, number of nodes and shoot length of each plant group were collected and the data of the three plant groups were summed up as the values of the communities. The data were statistically tested for differences by the analysis of variance (one-way ANOVA) followed by five planned comparisons (Sokal and Rohlf, 1995) using the Contrast options of SPSS (SPSS, Chicago, IL, USA). The first three contrasts (i.e., high *vs.* medium light treatment, high *vs.* low light treatment and medium *vs.* low light treatment) tested the effects of light intensity under homogenous treatments on the three growth variables of the communities as well as on those of each plant group. The fourth contrast [i.e., medium light treatment *vs.* (large and small patch treatment)] tested the overall effects of light heterogeneity on the growth variables, and the fifth contrast (i.e., large *vs.* small patch treatment) examined the effects of the patch scale. All analyses were conducted with SPSS 16.0 software (SPSS, Chicago, IL, USA).

RESULTS

Effects at community level

Under homogeneous treatments, decreasing light intensity significantly decreased total biomass, total number of nodes and total shoot length of the communities (Figure 2, Table 1). However, total biomass, total number of nodes or total shoot length did not differ significantly among the three medium light treatments (i.e., the homogeneous medium light treatment, the large patch treatment and the small patch treatment; Figure 2, Table 1), suggesting that light heterogeneity did not affect these three variables of the community.

Effects at species level

Under homogeneous treatments, total biomass, total number of nodes and total shoot length of the *H. verticillata* - *E. densa* group decreased greatly with decreasing light intensity (Figure 3, Table 1). However, none of the three variables of the *H. verticillata* - *E. densa* group differed significantly among the homogeneous medium light treatment, the large patch treatment and the small patch treatment, suggesting that light heterogeneity had no effect on these three parameters of the *H. verticillata* - *E. densa* group (Figure 3, Table 1). Neither *C. demersum* nor *M. verticillatum* showed significant differences in total biomass, total number of nodes or total shoot length among the five light treatments (Figures 4 and 5, Table 1), suggesting neither light intensity nor spatial heterogeneity affected growth of these two macrophytes.

DISCUSSION

Effects of light availability

Light availability is a major factor determining the growth of submerged macrophytes (Tanaka and Nakaoka, 2006). In the experiment, the submerged macrophyte communities showed the highest shoot growth and total biomass accumulation under full light condition. The results suggest that light availability significantly affects the growth of submerged macrophyte communities, which is consistent with the findings of the studies on individual macrophytes (Cronin and Lodge, 2003; Xie et al., 2007). These studies showed that high light intensity increased growth of rhizomes and floating leaves and biomass accumulation of submerged macrophytes. As the four macrophytes selected in our study produced only a few adventitious roots, the changes in total biomass was quite similar with the changes in total number of nodes and total shoot length, indicating that large biomass is allocated to shoot development to increase vegetative propagation.

In the submerged macrophyte communities, the four submerged macrophytes exhibited different responses to light availability (Figures 3-5, Table 1). The changes in total number of nodes, total shoot length and total biomass of the *H. verticillata* - *E. densa* group were largely accordant with the changes in the submerged macrophyte communities (Figures 2 and 3, Table 1); however, plants of *C. demersum* or *M. verticillatum* did not show significant dif-

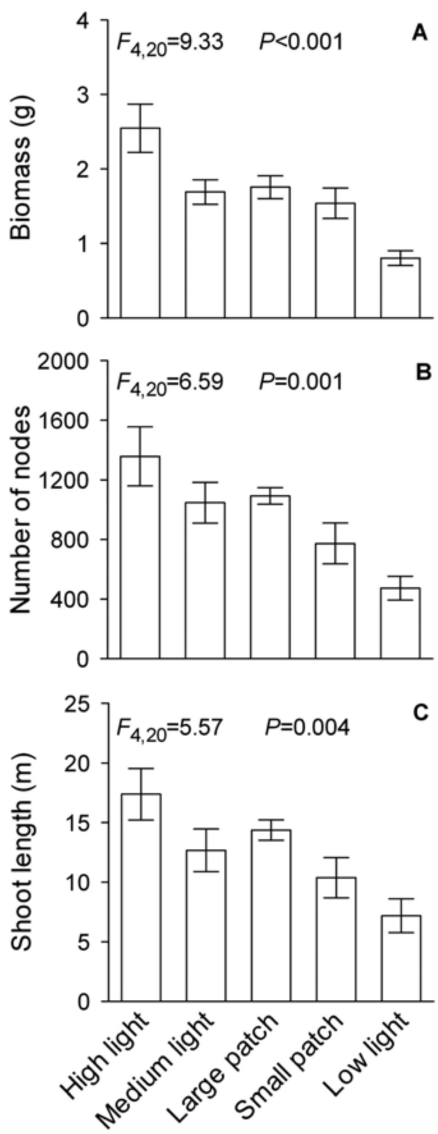

Figure 2. (A) Total biomass, (B) total number of nodes and (C) total shoot length of the experimental submerged plant communities under the three homogeneous light treatments and the two heterogeneous light treatments differing in patch size. Bars and vertical lines are means and SE. See Table 1 for statistical results.

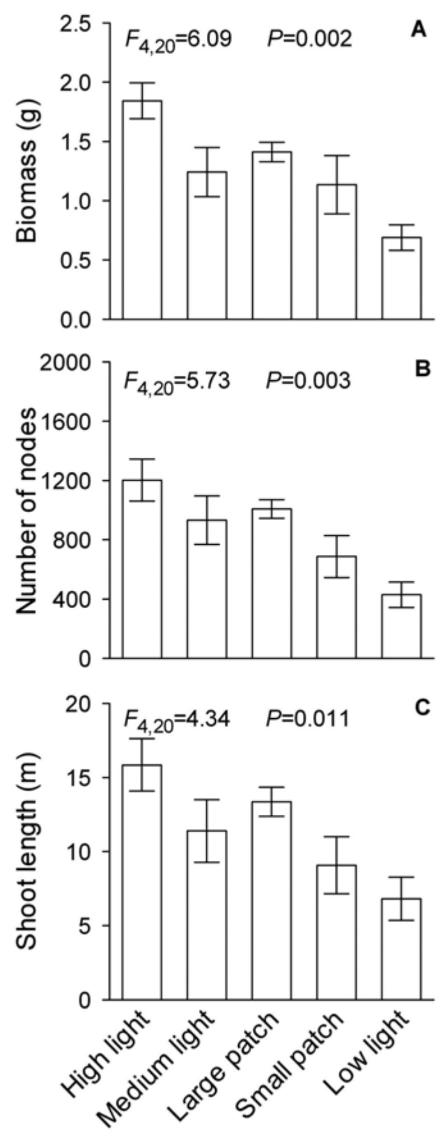

Figure 3. (A) Total biomass, (B) total number of nodes and (C) total shoot length of the *H. verticillata* - *E. densa* group under the three homogeneous light treatments and the two heterogeneous light treatments differing in patch size. Bars and vertical lines are means and SE. See Table 1 for statistical results.

Table 1. The five planned comparisons of the effects of light intensity and light heterogeneity on the three growth measures of the whole community (A) and of each of the three species groups (B-D).

		High *vs.* Medium	High *vs.* Low	Medium *vs.* Low	Medium *vs.* (Large + Small)	Large *vs.* Small
(A) Community						
Biomass	*t*	**2.98**	**6.06**	**3.08**	0.18	0.75
	P	**0.007**	**<0.001**	**0.006**	0.863	0.460
No. of nodes	*t*	1.67	**4.76**	**3.09**	0.71	1.72
	P	0.110	**<0.001**	**0.006**	0.487	0.101
Shoot length	*t*	2.03	**4.39**	**2.36**	0.14	1.72
	P	0.056	**<0.001**	**0.028**	0.887	0.101
(B) *Hydrilla verticillata - Egeria densa*						
Biomass	*t*	**2.50**	**4.80**	**2.30**	0.15	1.15
	P	**0.021**	**<0.001**	**0.032**	0.881	0.265
No. of nodes	*t*	1.52	**4.37**	**2.84**	0.55	1.81
	P	0.142	**<0.001**	**0.010**	0.587	0.085
Shoot length	*t*	1.86	**3.77**	1.91	0.08	1.79
	P	0.078	**<0.001**	0.071	0.934	0.090
(C) *Myriophyllum verticillatum*						
Biomass	*t*	0.85	**2.12**	1.27	0.39	0.20
	P	0.404	**0.047**	0.220	0.702	0.847
No. of nodes	*t*	0.76	1.92	1.16	0.44	0.19
	P	0.455	0.070	0.261	0.663	0.852
Shoot length	*t*	0.22	1.50	1.28	0.28	0.55
	P	0.825	0.150	0.217	0.779	0.591
(D) *Ceratophyllum demersum*						
Biomass	*t*	1.06	1.65	0.59	0.16	0.26
	P	0.302	0.114	0.559	0.876	0.795
No. of nodes	*t*	0.24	0.73	0.97	1.24	1.19
	P	0.811	0.475	0.344	0.228	0.250
Shoot length	*t*	1.19	1.59	0.39	0.75	1.03
	P	0.248	0.129	0.697	0.465	0.314

ferences among different light availabilities (Figures 4 and 5, Table 1). These results suggest that light availability can affect the structure of the submerged macrophyte communities. If we compare the increase of total number of nodes in the high light treatment, plants of the *H. verticillata* - *E. densa* group, *C. demersum* and *M. verticillatum* increased about 60, 12 and 3 times, respectively (Figures 3-5, Table 1). The results suggest the dominancy of *H. verticillata-E. densa* group in the submerged macrophyte communities, which may be due to their stronger capacities of vegetative propagation and photosynthesis, as compared with plants of *C. demersum* and *M. verticillatum* (Cui et al., 2000; DiTomaso and Healy, 2003; Yuan et al., 2006; Rodrigues and Thomaz, 2010).

Effects of light heterogeneity

Contrary to our expectations, patchy distributions of light (i.e., light patchiness or patch scale) did not affect structure or biomass accumulation of submerged macrophyte communities or growth of individual macrophytes

(Figures 2-5, Table 1). The effects of heterogeneity on biomass accumulation are determined by a combination of local responses to growing conditions and modification of these responses due to physiological integration with other parts of the plant growing in contrasting conditions (Stuefer et al., 1996; Alpert, 1999; Yu et al., 2004, 2008; de Kroon et al., 2005). In this study, the branches of submerged macrophytes in light-rich patches may increase the photosynthetic capacity by foraging responses to light, but the other parts of macrophytes under light-poor conditions may accelerate the anaerobic respiration to maintain the underwater metabolism, which is energy-consuming compared with aerobic respiration (Gibbs and Greenway, 2003). Thus, the photoassimilates acquired by light-rich patches might be completely offset by an equally large consumption in the light-poor patches through physiological integration, especially when patch size was small (Hutchings and Wijesinghe, 2008), resulting in no significant differences between the homogeneous and heterogeneous medium light treatment (Figures 2-5, Table 1).

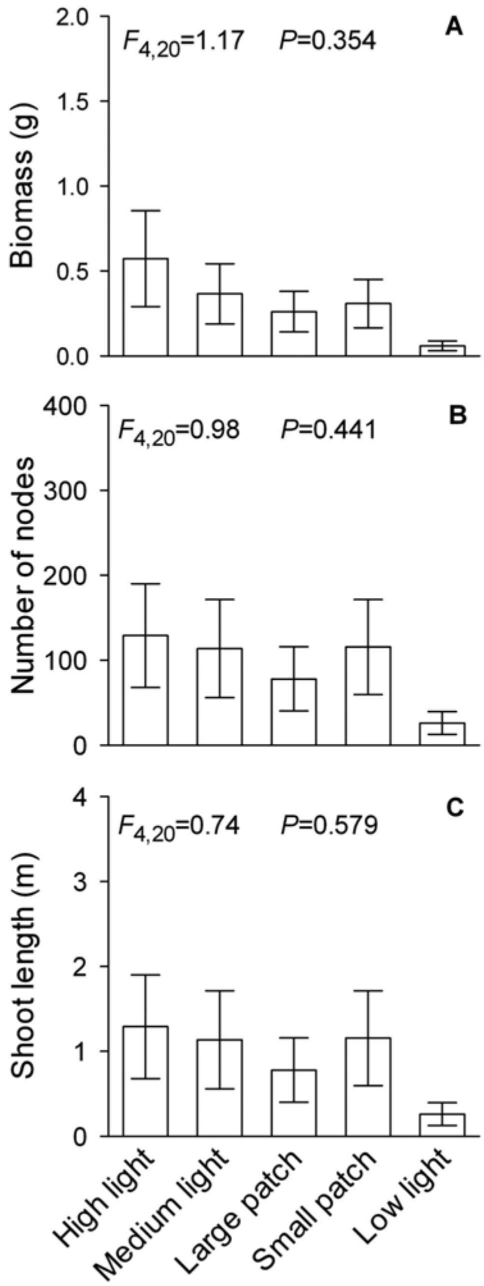

Figure 4. (A) Total biomass, (B) total number of nodes and (C) total shoot length of *M. verticillatum* under the three homogeneous light treatments and the two heterogeneous light treatments differing in patch size. Bars and vertical lines are means and SE. See Table 1 for statistical results.

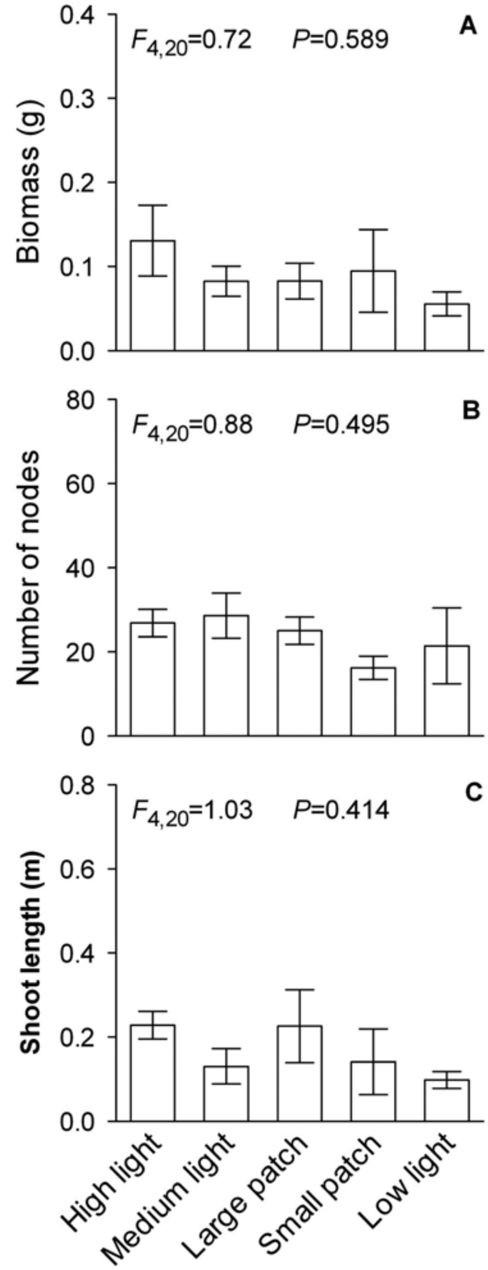

Figure 5. (A) Total biomass, (B) total number of nodes and (C) total shoot length of *C. demersum* under the three homogeneous light treatments and the two heterogeneous light treatments differing in patch size. Bars and vertical lines are means and SE. See Table 1 for statistical results.

Previous studies also demonstrated that heterogeneity did not always increase the biomass accumulation of plants compared with homogenous conditions providing the same amount of resources, because the biomass accumulation is strongly dependent on environmental context such as patch size and contrast; for the macrophyte communities, the submerged condition also needs to be taken into account (Wijesinghe et al., 2001; Hutchings et al., 2003; Baer et al. 2004; de Kroon et al., 2005; Hutchings and Wijesinghe, 2008). Further studies on the effects of heterogeneous distributions of light on submerged macrophyte communities will focus on performance of plants in light-rich and light-poor patches to elucidate their compensative actions in submerged macrophyte communities, which was not considered in the present study.

In conclusion, light availability significantly affects the structure and productivity of the submerged macrophyte communities. The *H. verticillata* - *E. densa* group plays a dominant role in such conditions, as compared with the other two species. However, there is no indication that heterogeneous distributions of light can affect the structure and productivity of submerged macrophyte communities as well as individual macrophytes.

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光照異質性是否影響沉水植物群落的結構和生物量？

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環境異質性在各種空間尺度普遍存在。目前已開展了很多有關異質性對植物個體生長影響的研究，但有關異質性對群落物種組成和生物量影響的研究卻十分缺乏，尤其是對沉水植物群落的研究。我們構建了一個由四種常見沉水植物（金魚藻、黑藻、水蘊草和狐尾藻）組成的水生植物群落，並將這些群落進行三種同質性光照處理（即 100%、65% 和 35% 的全光照，分別記作高、中和低光處理）以及兩種斑塊尺寸不同的異質性光照處理（即大斑塊和小斑塊處理）。在整個實驗過程中，異質性光照處理下的群落所接收的光照總量與同質中光照處理相同。在同質光照處理下，群落的總生物量、總節數和總莖長隨光照強度的降低顯著減小；黑藻和水蘊草生物量、節數和莖長表現出與整個群落相同的變化趨勢，但光照強度對狐尾藻和金魚藻的生長卻未產生顯著影響。光照異質性（斑塊性和斑塊尺度）並不顯著影響整個群落以及每個植物種的生長。這些結果表明，光照強度可以改變沉水植物群落的結構和生物量，但光照異質性卻似乎沒有這種效應。

關鍵詞：水生植物；克隆植物；環境異質性；斑塊尺度。