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Effects of fragment size and sediment heterogeneity on the colonization and growth of *Myriophyllum spicatum*

Feng Li[a,b,c,1], Yingying Qin[c,1], Lianlian Zhu[a,b,d], Yonghong Xie[a,b,*], Shichu Liang[c,**], Cong Hu[a,b,d], Xinsheng Chen[a,b], Zhengmiao Deng[a,b]

[a] Key Laboratory of Agro-ecological Processes in Subtropical Region, The Chinese Academy of Sciences, Hunan 410125, China
[b] Dongting Lake Station for Wetland Ecosystem Research, Institute of Subtropical Agriculture, Changsha 410125, China
[c] Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection, Guangxi Normal University, Ministry of Education, 541004, China
[d] University of the Chinese Academy of Sciences, Beijing 100049, China

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ABSTRACT

Fragment colonization plays an important role in regulating the growth, reproduction, and expansion of submerged macrophytes. However, the influence of the interaction of fragment length and sediment heterogeneity on fragment colonization and growth is far from clear. Here, we investigated the effect of fragment length and sediment heterogeneity on the colonization and growth of a typical submerged macrophyte, *Myriophyllum spicatum* L. In an outdoor experiment, we examined two fragment sizes (6 cm and 12 cm in length) and three sediment types (type I, 0–12 cm sand and 12–24 cm clay; type II, 0–24 cm mixture of sand and clay at a 1:1 v/v ratio; and type III, 0–12 cm clay and 12–24 cm sand) and evaluated seven morphological traits (relative growth rate, relative elongation rate, shoot diameter, branching number, longest root length, average root length, and shoot to root ratio) and two physiological traits (total nitrogen content and total phosphorus content). Neither fragment size nor sediment type had a significant effect on the relative growth rate of *M. spicatum*. However, increased fragment size caused a significant decrease in relative elongation rate but a significant increase in shoot diameter and branching number. Fragments of the same size showed a higher branching number when grown in type III sediment than the other two sediments; furthermore, these fragments had the longest root lengths and highest average root lengths. However, they showed lower shoot to root ratios when grown in type I sediment than in type II and III sediments. Total phosphorus contents of *M. spicatum*, but not total nitrogen contents, were significantly higher when grown in type III sediment than in other two sediments. These data indicated that fragment size and sediment heterogeneity had a limited influence on colonization of *M. spicatum*. This effect might be accounted for by a high acclimation ability to these factors, mainly through adjustment of biomass allocation patterns and root characteristics.

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1. Introduction

Submerged macrophytes are important components of wetland ecosystems, since they play important roles in various processes such as water purification, biodiversity maintenance, and nutrient cycling (Li and Xie, 2009; Wang et al., 2009). Owing to their high reproductive and colonization abilities, these plants are distributed worldwide (Sondergaard et al., 2010). They propagate via different mechanisms such as seed dispersal, stolon growth, and fragmentation. In particular, fragmentation allows intermediate-to long-distance dispersal and affects other aspects of macrophytic ecology, e.g. increasing reproductive success and reducing predation risk (Madsen and Smith, 1997; Li et al., 2015). Therefore, studies on fragment colonization should help to provide a better understanding of plant establishment and growth as well as community development.

Some submerged macrophytes such as *Myriophyllum spicatum* L. exhibit two types of fragmentation: autofragmentation and allofragmentation. The former is the self-induced abscission of shoot apices, whereas the latter is mainly caused by environmental disturbance such as herbivory, wave action, river flow, boating,

* Corresponding author at: Key Laboratory of Agro-ecological Processes in Subtropical Region, The Chinese Academy of Sciences, Hunan 410125, China.
** Corresponding author.
E-mail addresses: yonghongxie@163.com (Y. Xie), gxlsc@sina.com (S. Liang).
[1] Both authors contributed equally to this work.

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and weed cutting (Madsen and Smith, 1997; Xie and Yu, 2011). Compared with autofragmentation, allofragmentation occurs more frequently and plays an important role in plant expansion (Xie and Yu, 2011). For instance, a previous study showed that 80% of plants established in a newly created stream-bed had arisen from allofragments (Riis, 2008). The colonization of newly developed fragments is determined by several morphological traits and environmental factors (Barrat-Segretain and Bornette, 2000; Riis and Sand-Jensen, 2006; Hoffmann et al., 2015). For instance, fragments of *Potamogeton perfoliatus* with apical tips have a higher regeneration and colonization ability than those without apical tips, whereas the shoots of *Elodea canadensis* that contain three nodes have higher regeneration ability than those with one node (Riis and Sand-Jensen, 2006; Redekop et al., 2016). Some studies showed that roots and apical tips with relatively larger size facilitate fragment colonization (Riis et al., 2009; Vari, 2013; Cao and Wang, 2012); however, these results have not been consistent between reports (Umetsu et al., 2012; Li et al., 2015). Therefore, more research is needed to investigate whether there are species-specific factors that affect the colonization of fragments.

Sediment heterogeneity in space and time is a common phenomenon in both terrestrial and wetland systems, and has strong effects on plant growth and ecosystem functions (Huber-Sannwald and Jackson, 2001; Maestre and Reynolds, 2006). Plants are able to modify their root architecture (e.g., root length, root diameter, and root mass) and other morphological characteristics (e.g., shoot to root mass ratio) to adjust to nutrient heterogeneity conditions (Fransen et al., 2001). Most studies have focused on the horizontal heterogeneity of nutrients and its critical effects on plant survival, colonization, and growth (Jackson and Caldwell, 1989; Xie et al., 2007b); however, other components of soil heterogeneity, such as the vertical heterogeneity of nutrients, which frequently occurs in wetlands due to the complex hydrological processes (e.g., water level fluctuation and sedimentation), have attracted only limited attention (Xie et al., 2007a).

Fragment colonization is usually influenced by various biotic and abiotic factors simultaneously, which makes it difficult to predict fragment colonization fate on the basis of a single factor (Cao and Wang, 2012; Lin et al., 2012). Even though the influence of many biotic factors (e.g., length, root or rootless, decapitation) and abiotic factors (e.g., burial, water and sediment nutrient) on fragment colonization and growth have been investigated (Kuntz et al., 2014; Cao and Wang, 2012; Li et al., 2015), the interactive influence of fragment length and sediment heterogeneity, especially vertical heterogeneity, on fragment colonization is far from clear. Here, we aimed to elucidate the effects of these two factors on the colonization of *M. spicatum*, a typical submerged macrophyte with worldwide distribution. In this study, we examined two fragment sizes (6 cm and 12 cm) and three sediment types (type I, 0–12 cm sand and 12–24 cm clay; type II, 0–24 cm mixture of sand and clay at a 1:1 v/v ratio; and type III, 0–12 cm clay and 12–24 cm sand) and investigated their effects on seven morphological traits (relative growth rate [RGR], relative elongation rate [RER], shoot diameter [ShD], branching number [BN], longest root length [LRL], average root length [ARL], and shoot to root ratio [S:R]) and two physiological traits (total nitrogen [N] and phosphorus [P] content). We hypothesized that (1) the RGR, RER, ShD, and BN of the longer fragments grown in type III sediment would be higher than those of the shorter fragments grown in type I and II sediments; (2) the LRL and ARL of the longer fragments grown in type I sediment would be higher, but the S:R would be lower, than those of the shorter fragments grown in type II and III sediments; and (3) the total N and total P of the longer fragments in type III sediment would be higher than shorter fragments grown in type I and II sediments.

2. Materials and methods

2.1. Plant materials

Shoots of *M. spicatum* were collected from a pond at the Hunan Agricultural University, Changsha, China (28°10′49.46″, 113°04′47.01″), in April 2015. They were then transported to an experimental field at the Dongting Lake Station for Wetland Ecosystem Research, Chinese Academy of Sciences, China; and pre-incubated in tap water containing 0.511 mg L^{-1} NH_4^+-N, 1.760 mg L^{-1} NO_3^--N, and 0.527 mg L^{-1} PO_4^{3+}-P (pH 7.2) for 15 d under natural sunlight.

2.2. Treatments and growth conditions

A total of 120 apical shoots (60 apical shoots of 6 cm and 12 cm lengths, respectively) were planted in plastic pots (12 cm diameter, 24 cm height) that were filled with three different types of sediment (type I, 0–12 cm sand and 12–24 cm clay; type II, 0–24 cm mixture of sand and clay at a 1:1 v/v ratio; and type III, 0–12 cm clay and 12–24 cm sand; Fig. 1). The apical shoots were buried at a depth of 2 cm. The clay was collected from Dongting Lake and contained 2.02% organic matter, 19.49 μg g^{-1} total N, and 0.77 μg g^{-1} total P; the sand was collected from the Xiang River and contained 0.39% organic matter, 1.30 μg g^{-1} total N, and 0.30 μg g^{-1} total P.

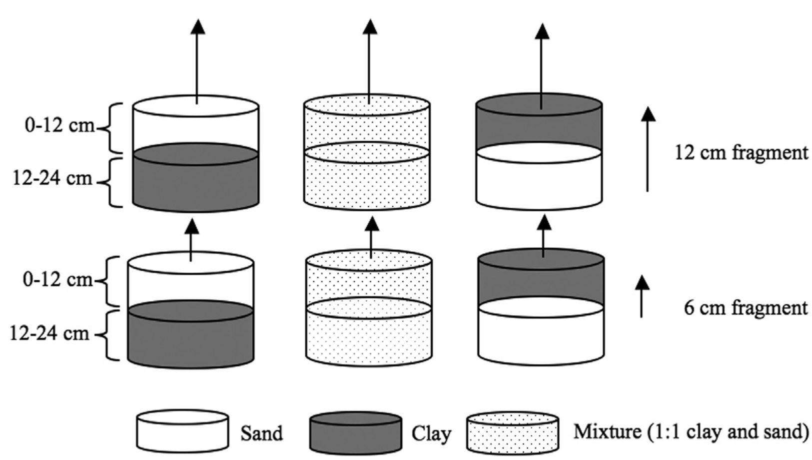

Fig. 1. Schematic representation of the experimental arrangement used in this study. Apical shoots of *Myriophyllum spicatum* with different fragment sizes (6 cm and 12 cm) were planted in three different sediment types (type I: 0–12 cm sand and 12–24 cm clay; type II: 0–24 cm mixture of sand and clay at a 1:1 v/v ratio; and type III: 0–12 cm clay and 12–24 cm sand).

Four pots per treatment (24 pots in total) were placed in a separate cement pond (five ponds in total; 100 cm × 100 cm × 100 cm) to control the water level under natural sunlight. Therefore, the experiment contained six treatments (four subsamples for each treatment) with five replications. The initial water level was 20 cm, but it was raised to 50 cm with tap water at 7 d after planting. Surplus water was removed after rainfall to control the water level. We also replenished the water once a week to prevent algal growth. During the experimental period, the mean air temperature was 25.41 °C and total precipitation was 483.0 mm (Meteorological station of Dongting Lake Station for Wetland Ecosystem Research, the Chinese Academy of Sciences).

2.3. Evaluation of morphological traits

Before planting, the biomass of 10 shoots from each fragment size was measured for later calculation of RGR. Plants were harvested after 80 days. This treatment time was based on previous studies (Xie et al., 2007b; Li et al., 2015). Plant roots were carefully removed from the soil and washed with tap water. The ShD of each plant was measured with a Vernier caliper, and their BN was counted. The height of the main shoot was measured using a ruler with a 0.1-cm precision. The longest root and 7–10 representative full-grown roots were selected from each plant to measure LRL and ARL, respectively, using a Vernier caliper (Pan et al., 2012). Then, the plants were separated into shoots (leaves and stems) and roots, oven dried at 80 °C for 48 h, and weighed. S:R was determined as the ratio of shoot dry mass to root dry mass. RGR and RER were calculated as follows:

$$\mathrm{RGR} = (\ln w_2 - \ln w_1)/(t_2 - t_1)$$

$$\mathrm{RER} = (\ln h_2 - \ln h_1)/(t_2 - t_1),$$

where w_1 is the initial dry mass, w_2 is the dry mass at harvest time t_2, h_1 is the initial height, h_2 is the height at harvest time t_2, and $(t_2 - t_1)$ is the experimental time.

2.4. Analysis of total N and P content

Four subsamples of each treatment from each cement pond were combined for the measurement of plant N and P contents. Shoots and roots were ground into powder and mixed together to measure the total N and P. All samples were digested with H_2SO_4-H_2O_2 and analyzed using the colorimetric method (Shi, 1994; Xie et al., 2007a) with a TU-1901 spectrophotometer (Beijing Purkinje General Instruments, Beijing, China). All measurements were repeated in triplicate.

2.5. Statistical analysis

Mean values of four subsamples from each treatment in each pond were used for data analysis. A two-way analysis of variance (ANOVA) in conjunction with Duncan's test was performed to determine the effects of fragment size and sediment type on the RGR, RER, ShD, BN, LRL, ARL, S:R, total N, and total P of *M. spicatum*, with the significance level set at $P < 0.05$. Data were $\log_{10}$-transformed, when necessary, to reduce the heterogeneity of variance. Normality and homogeneity were tested using Lilliefors and Levene's tests, respectively. All analyses were performed using SPSS 15.0 for Windows (IBM Corp., Chicago, IL, USA).

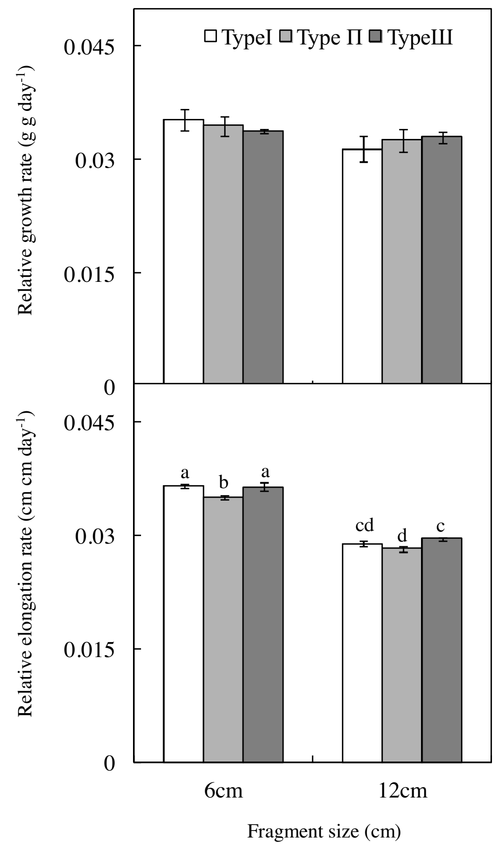

Fig. 2. Relative growth rate and relative elongation rate of *Myriophyllum spicatum* with different fragment sizes (6 cm and 12 cm) grown in three different sediment types (type I: 0–12 cm sand and 12–24 cm clay; type II: 0–24 cm mixture of sand and clay at a 1:1 v/v ratio; and type III: 0–12 cm clay and 12–24 cm sand). Error bars represent one standard error (n = 5). Different letters indicate significant differences among treatments at the 0.05 significance level.

3. Results

3.1. Effects of fragment size and sediment type on morphological traits

Neither fragment size nor sediment type had a significant effect on the RGR of *M. spicatum* (Table 1; Fig. 2). However, RER decreased significantly for the larger sized fragment, although RERs were lowest for both fragment sizes when grown in type II sediment compared to type I and III sediments.

ShD significantly increased for the larger sized fragment (Table 1; Fig. 3). These fragments showed the highest ShD when grown in type III sediment (0.45 ± 0.01 cm; Fig. 3); this average was 1.29-fold greater than that of 6 cm fragments grown in the same sediment type (0.35 ± 0.02 cm; Fig. 3).

Both fragment size and sediment type had significant effects on BN (Table 1; Fig. 3). The 12 cm fragments had higher BNs than those of 6 cm fragments regardless of sediment type. Fragments of the same size had the highest BNs when grown in type III sediment compared with type I and II sediments.

LRL was only affected by sediment type (Table 1; Fig. 4). The 12 cm fragments grown in type I sediment had the highest LRL (29.53 ± 2.17 cm), which was 1.54-fold greater than the LRL obtained from fragments of the same length grown in type II sediment (19.21 ± 0.98 cm).

ARL displayed a similar pattern as LRL and was only significantly affected by sediment type (Table 1; Fig. 4). The 12 cm fragments grown in type I sediment showed the highest ARL (19.44 ± 0.67 cm),

Table 1
Two-way analysis of variance (ANOVA) for the relative growth rate, relative elongation rate, shoot diameter, branching number, longest root length, average root length, shoot to root ratio, total nitrogen (N) content, and total phosphorus (P) content of *Myriophyllum spicatum* with different fragment sizes (6 am and 12 cm in length) grown in three different sediment types (type I: 0–12 cm sand and 12–24 cm clay; type II: 0–24 cm mixture of sand and clay at a 1:1 v/v ratio; and type III: 0–12 cm clay and 12–24 cm sand).

Variables	N	Sediment type (S)	Fragment size (F)	S × F
Relative growth rate ($g\,g^{-1}\,d^{-1}$)	5	0.011^{ns}	3.848^{ns}	0.724^{ns}
Relative elongation rate ($cm\,cm^{-1}$)	5	**8.735****	**650.324*****	0.801^{ns}
Branching number	5	**7.823****	**4.733***	0.994^{ns}
Shoot diameter (cm)	5	1.857^{ns}	**15.081****	2.509^{ns}
The longest root length (cm)	5	**13.401*****	0.222^{ns}	1.393^{ns}
Mean root length (cm)	5	**31.028*****	0.140^{ns}	**3.750***
Shoot: root ratio	5	**5.283***	1.099^{ns}	0.002^{ns}
Total N content ($mg\,g^{-1}$)	5	1.336^{ns}	**18.922*****	2.047^{ns}
Total P content ($mg\,g^{-1}$)	5	**24.821*****	2.94^{ns}	0.751^{ns}

$^{NS}P > 0.05$.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

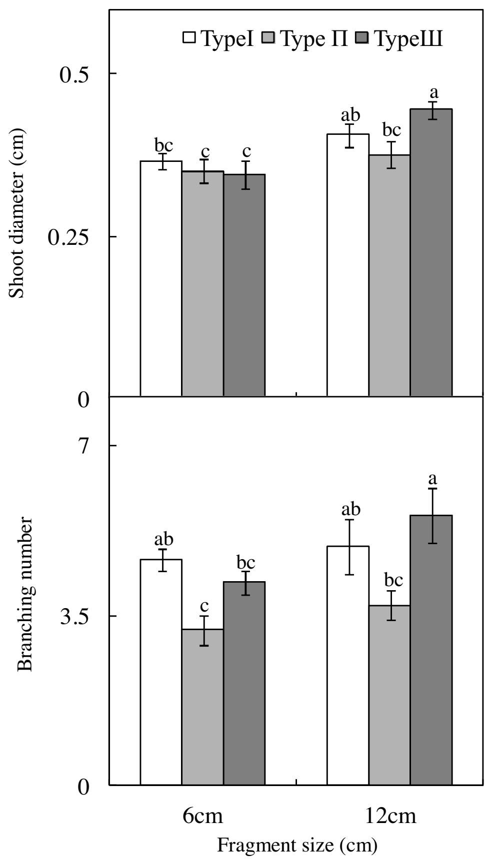

Fig. 3. Branching number and shoot diameter of *Myriophyllum spicatum* with different fragment sizes (6 cm and 12 cm) grown in three different sediment types (type I: 0–12 cm sand and 12–24 cm clay; type II: 0–24 cm mixture of sand and clay at a 1:1 v/v ratio; and type III: 0–12 cm clay and 12–24 cm sand). Error bars represent one standard error (n = 5). Different letters indicate significant differences among treatments at the 0.05 significance level.

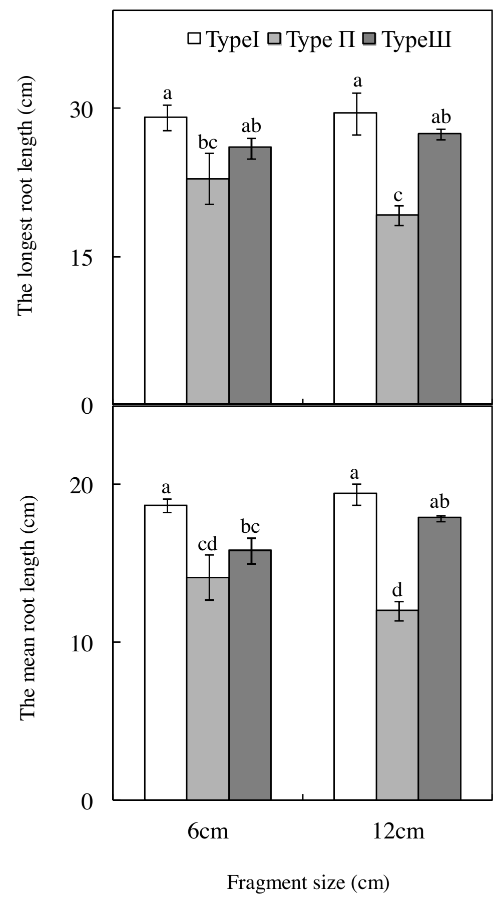

Fig. 4. The longest root length and the mean root length of *Myriophyllum spicatum* with different fragment sizes (6 cm and 12 cm) grown in three different sediment types (type I: 0–12 cm sand and 12–24 cm clay; type II: 0–24 cm mixture of sand and clay at a 1:1 v/v ratio; and type III: 0–12 cm clay and 12–24 cm sand). Error bars represent one standard error (n = 5). Different letters indicate significant differences among treatments at the 0.05 significance level.

which was 1.61-fold greater than the ARL obtained from fragments of the same length grown in type II sediment (12.05 ± 0.62 cm).

S:R was only affected by the sediment type (Table 1; Fig. 5). Fragments of the same size had a lower S:R when grown in type I sediment than when grown in type II and III sediments. The 12 cm fragments grown in type III sediment had the highest S:R (10.63 ± 1.33), which was 1.79-fold greater than the S:R obtained from 6 cm fragments grown in type I sediment (5.94 ± 0.52).

3.2. Effects of fragment size and sediment type on physiological traits

Fragment size had a significant effect on the total N content. Plants derived from 6 cm fragments and grown in type II and III sediments had higher total N contents than 12 cm fragments in the same sediment types (Table 1; Fig. 6). However, sediment type had no significant influence on the total N content.

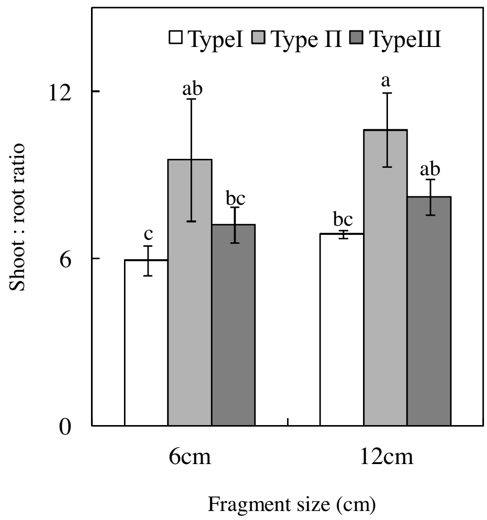

Fig. 5. Biomass allocation pattern of *Myriophyllum spicatum* with different fragment sizes (6 cm and 12 cm) grown in three different sediment types (type I: 0–12 cm sand and 12–24 cm clay; type II: 0–24 cm mixture of sand and clay at a 1:1 v/v ratio; and type III: 0–12 cm clay and 12–24 cm sand). Error bars represent one standard error (n = 5). Different letters indicate significant differences among treatments at the 0.05 significance level.

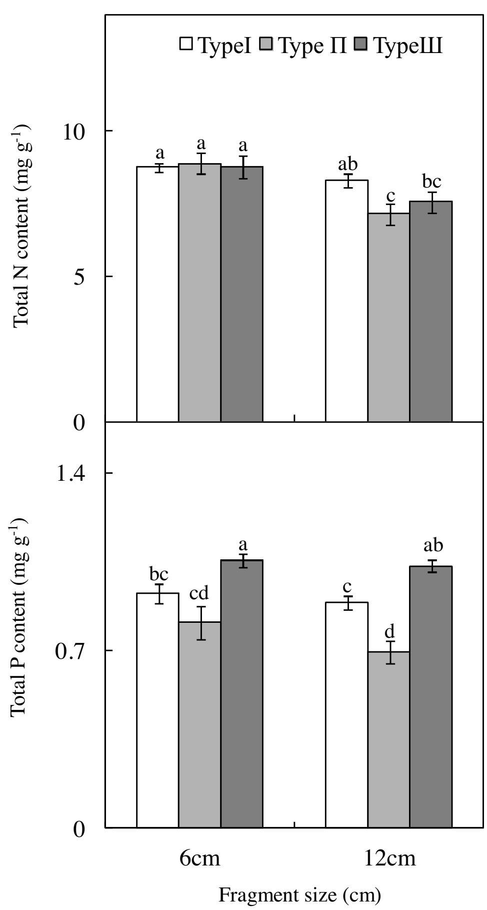

Fig. 6. Total nitrogen (N) and total phosphorus (P) contents of *Myriophyllum spicatum* with different fragment sizes (6 cm and 12 cm) grown in three different sediment types (type I: 0–12 cm sand and 12–24 cm clay; type II: 0–24 cm mixture of sand and clay at a 1:1 v/v ratio; and type III: 0–12 cm clay and 12–24 cm sand). Error bars represent one standard error (n = 5). Different letters indicate significant differences among treatments at the 0.05 significance level.

Total P content was affected by the sediment type but not fragment size (Table 1; Fig. 6). Fragments of the same size had significantly higher total P content when grown in type III sediment than in type I and II sediments. The 6 cm fragments grown in type III sediment showed the highest total P content (1.05 ± 0.03 mg g^{-1}), which was 1.52-fold greater than the lowest total P content obtained from 12 cm fragments in type II sediment (0.69 ± 0.05 mg g^{-1}).

4. Discussion

Our study showed that 12 cm fragments of the submerged macrophyte *M. spicatum* had higher ShD and BN than 6-cm fragments, suggesting that longer fragments have better colonization ability than shorter ones. However, fragment size did not have a significant effect on RGR. These results were partly consistent with our first hypothesis and our previous study (Li et al., 2015), but disagreed with the outcomes of other studies (Wu et al., 2007; Riis and Sand-Jensen, 2006; Lin et al., 2012). Umetsu et al. (2012) suggested that the photosynthetic tissues and reserves (e.g., carbohydrates stored as biomass) of relatively short fragments are limited compared with those of long fragments, hampering subsequent plant growth. The similar RGR found here for 6- and 12-cm fragments could be explained if the shorter fragments invested sufficient energy into plant growth. The short fragments showed a higher RER that enabled them to increase their vertical growth, and consequently, increase both their light acquisition and biomass, leading to a similar RGR as the long fragments.

The sediment type did not have a significant effect on RGR and ShD, indicating that nutrient heterogeneity does not affect the colonization of *M. spicatum*. This conclusion is not in agreement with the prediction of our first hypothesis, but is consistent with previous studies. For instance, *Vallisneria natans* did not show any significant changes in biomass accumulation when grown in two heterogeneous sediments or homogeneous mud (Xie et al., 2007b) and *Prosopis glandulosa* did not show any significant changes in biomass or seedling morphology under spatially heterogeneous conditions (Maestre and Reynolds, 2006). These findings support the view that *M. spicatum* has high acclimation ability in response to heterogeneous conditions in the sediment, owing to its morphological plasticity.

Plants can root into nutrient-rich zones to obtain the necessary nutrients (Schenk, 2006; Mommer et al., 2011). In this study, LRL and ARL were highest in type I sediment, suggesting that *M. spicatum* can reach fertile sediments by penetrating infertile top-layers. These results were supported by the similar total N content between fragments grown in type I and type III sediments. Additionally, plants can also alter their root distribution patterns to acclimate to heterogeneous sediment conditions, as shown in previous studies (Xie et al., 2007a; Zou and Wang, 2010). Xie et al. (2007b) reported that nutrients in the mud layer are usually released to the sand layer by water transfer, which might be another explanation of the similar RGR of *M. spicatum* fragments grown in different sediment types. Plants can decrease the ratio of the shoot to root, in order to increase their root mass fraction and, consequently, the acquisition of nutrients (Balestri et al., 2010). In this study, the lowest S:R was obtained from fragments grown in type I sediment, indicating that *M. spicatum* allocates more biomass to the roots when the top layer is sandy loam, in order to maximize nutrient absorption in an infertile environment (Xie et al., 2007a).

In conclusion, the present study showed that fragment size and sediment heterogeneity had limited influence on the colonization and growth of *M. spicatum*. Our results may account for the high acclimation ability to fragment size and sediment heterogeneity through adjustment of biomass allocation patterns and root characteristics. *M. spicatum* is considered a major threat to the ecological balance of many aquatic ecosystems in North America, North Africa, and China (Smith et al., 2002; Ali and Soltan, 2006). Overall, this study provides new insights into the morphological plasticity of *M. spicatum* that may help to develop effective management plans for controlling the invasion of this species.

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