

Fragment growth performance of the invasive submerged macrophyte *Myriophyllum spicatum* under conditions of different water depths and sediment types

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Abstract In wetlands, many invasive plants, especially submerged macrophytes, are propagated by vegetative fragments. Fragment colonization and growth, the first step of plant invasion, strongly depend on the species and environment. In this study, the influences of water depth and sediment type on fragment growth performance of *Myriophyllum spicatum* were evaluated in an outdoor experiment. The

experiment consisted of two sediment types (mud and sand) and three water depths (20, 40, and 60 cm), with two fragment sizes (6 and 12 cm), in a factorial design. The relative growth rate (RGR), relative elongation rate (RER), shoot diameter, branching number, and total *N* and total *P* contents of plants derived from fragments of two different sizes were investigated. We hypothesized that the larger fragment size, lower water depth, and higher sediment nutrient would aid the growth of *M. spicatum* fragments. The RGR of *M. spicatum* was considerably higher for plants growing in mud than in sand. However, water depth and fragment size did not significantly influence RGR. The RER was considerably higher in plants growing in mud than in sand, and it was significantly lower when larger fragments were used. The influence of water depth on RER was found to depend on sediment type. Branching number was only affected by sediment type, and it was higher in the mud treatment than in the sand treatment. Shoot diameter was significantly larger in plants derived from the larger fragment size and grown in mud. Total *N* content was significantly lower in the higher water depth and was markedly higher in plants grown in mud compared to sand; total *P* content only decreased in the higher water depth. The results indicate that fragment size, water depth, and sediment type affect the growth performance of *M. spicatum* in different ways, providing insights into the invasiveness of *M. spicatum* under various environmental conditions.

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Introduction

Vegetative fragments, produced by various physical and biological disturbances, serve as an important means for the reproduction, invasion, and propagation of aquatic plants (Umetsu et al. 2012; Li et al. 2015). These fragments may be washed away from their site of origin by flowing water and dispersed to new habitats, where they can develop new root systems and establish rapidly in sediments (Vári 2013; Li et al. 2015). However, the eventual success of colonization and growth of fragment depends on species characteristics and environmental factors (Riis and Sand-Jensen 2006). The types of fragments that are produced vary considerably, due to differences in types and intensities of disturbance, which then determine the outcome of fragment colonization (Barrat-Segretain and Bornette 2000; Hoffmann et al. 2015). Apical fragments have been found to show higher rooting rates and length growth than stem fragments, mainly because of the presence of meristematic tissue (Vári 2013). Fragment length also determines the colonization ability. For *Hydrilla verticillata*, 10-cm-long fragments produced more roots than did 5-cm-long fragments (Umetsu et al. 2012). However, contrasting results were reported by Li et al. (2015), which could be attributed to species difference, the minimum fragment length used, and other experimental conditions (Lin et al. 2012). In any case, further studies are required.

In wetlands, the depth of the water is one of the most important factors determining plant colonization, growth, and regeneration; it can also influence other environmental factors, e.g., light and temperature (Shibayama and Kadono 2007), thereby limiting plant growth. Some studies have reported that the performance of fragments is better in shallow water than in deeper water (Lin et al. 2012). Furthermore, sediment nutrients, the primary source for plant growth, also significantly affect plant growth performance (Wang et al. 2009; Cao et al. 2012). Generally, plant growth performance is better in nutrient-rich conditions (Li et al. 2015). However, fertile sediments in eutrophic

lakes are known to substantially reduce the growth of submerged macrophytes, even leading to population degradation (Barko and Smart 1986; Wang et al. 2009). For instance, the growth of *Myriophyllum spicatum* and *Hydrilla verticillata* decreased tenfold and 20-fold, respectively, when the concentration of sediment organic matter increased (Barko and Smart 1986).

Myriophyllum spicatum is a common wetland species and is considered a typical invasive aquatic species worldwide (Madsen and Smith 1997; Li et al. 2015). This species has three mechanisms of propagation: seed production, stolon production, and fragmentation. Of these, localized propagation is mainly achieved by stolon growth, whereas fragmentation is the most common method of intermediate-to-long-distance dispersal (Madsen and Smith 1997).

The effects of water depth and sediment type on plant growth performance have been studied widely (Cao et al. 2012; Pan et al. 2012), but their combined influence on fragments of different sizes remains unclear. The aim of this study was to evaluate the combined influence of fragment size, water depth, and sediment type on the growth performance of *M. spicatum*. To this end, *M. spicatum* fragments of two sizes were grown at three water depths and on two sediment types. Relative growth rate [RGR], relative elongation rate [RER], branching number, shoot diameter, and total *N* and total *P* contents of plants derived from the fragments were measured. We tested two hypotheses: (1) that RGR, RER, branching number, and shoot diameter in plants derived from longer fragments grown at lower water depths and on mud-based sediment would be greater than those of plants from shorter fragments grown at greater water depth and on sand-based sediment and (2) total *N* and *P* contents of plants derived from longer fragments of *M. spicatum* would be greater at lower water depths and on mud-based sediment than those in plants from shorter fragments grown at greater depth and on sand-based sediment.

Materials and methods

Plant materials

Shoots of *M. spicatum* were collected from a pond (N28°10'49.46", E113°04'47.01") at Hunan Agricultural University, Changsha, China, in April 2015. After

collection, the shoots were transported to an experimental field at Dongting Lake Station for Wetland Ecosystem Research, the Chinese Academy of Sciences, China. The shoots were pre-incubated in tap water (containing $0.411 \text{ mg L}^{-1} \text{ NH}_4^+-\text{N}$, $1.340 \text{ mg L}^{-1} \text{ NO}_3^--\text{N}$, and $0.415 \text{ mg L}^{-1} \text{ PO}_4^{3+}-\text{P}$, pH 7.1) for 15 days under natural sunlight.

Experimental design

Prior to the experiment, the dried weights (see below for methodology) of 10 fragments of each size were determined and used as the baseline for subsequent estimation of RGR. The experimental treatment groups included two sediment types (sand and mud), three water depths (20, 40, and 60 cm), and two fragment sizes (6 and 12 cm) in a factorial design, with three replicates; there were twelve treatment combinations in total. After pre-incubation, 144 apical shoots of *M. spicatum* (72 apical shoots of 6 and 12 cm each) were planted in sand- or mud-filled plastic pots (12 cm diameter \times 15 cm height) with the bottom 2 cm of the shoots being buried in the sediment. Mud was collected from Dongting Lake and contained 1.78 % organic matter, $15.32 \mu\text{g g}^{-1}$ total *N*, and $0.65 \mu\text{g g}^{-1}$ total *P*. Sand was collected from a local river (Xiang River) and contained 0.41 % organic matter, $1.15 \mu\text{g g}^{-1}$ total *N*, and $0.28 \mu\text{g g}^{-1}$ total *P*. One hundred and forty-four pots were placed in 9 cement ponds (100 cm \times 100 cm \times 100 cm) to control the water level and under natural sunlight. Three cement ponds were used for each water depth; each pond contained 4 treatments (two fragment sizes and two sediment types) and 4 subsamples for each treatment. Initially, the water depth was maintained at 20 cm. After 7 days, the level of the water was increased to the required experimental depth using tap water; after rainfall, surplus water was removed to control the water level. The water was also replenished once a week to prevent algal growth. During the experimental period, the mean air temperature was $25.41 \text{ }^\circ\text{C}$ and total precipitation was 483.0 mm (Meteorological station of Dongting Lake Station for Wetland Ecosystem Research, the Chinese Academy of Sciences).

Harvest and measurement

Plants that had formed a dense canopy in each pot were harvested after 80 days of treatment. Plant roots were

carefully dug out and cleaned with tap water. For each plant, basal shoot diameter was measured using a vernier caliper, and the number of branches was counted. Main shoot height of each plant was measured using a ruler with 0.1 cm precision. Subsequently, plant shoots (leaves and stems) and roots were separated, oven-dried at $80 \text{ }^\circ\text{C}$ for 48 h, and weighed. RGR and RER were calculated using the following equation: $\text{RGR} = (\ln w_2 - \ln w_1)/(t_2 - t_1)$ and $\text{RER} = (\ln h_2 - \ln h_1)/(t_2 - t_1)$, respectively, 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 duration.

Plant *N* and *P* content

Four subsamples from each treatment group from each cement pond were combined for the measurement of plant *N* and *P* contents. Plant above-ground parts were ground to powder and mixed together to prepare samples. All samples were digested with $\text{H}_2\text{SO}_4\text{--H}_2\text{O}_2$, and plant *N* and *P* contents were measured by a colorimetric analysis on a TU-1901 spectrophotometer (Shi 1994; Xie et al. 2007). Three replicate measurements were taken.

Statistical analysis

Mean values of four subsamples from each treatment in each pond were used for data analysis. The data were fitted to a generalized linear model, with fragment size, sediment type, and water depth as the main factors to determine their effects on RGR, RER, shoot diameter, branching number, and total *N* and total *P* contents. Multiple comparisons of means were performed using Duncan's test at the 0.05 significance level. Data were \log_{10} -transformed if required to reduce the heterogeneity of variance. Normality and homogeneity were tested using Lilliefors and Levene's tests, respectively. All analyses were performed using the SPSS 15.0 software package for Windows.

Results

RGR and RER

The RGR of *M. spicatum* plants was markedly higher in those produced by fragments grown in mud compared

to sand (Table 1; Fig. 1a, b). However, neither water depth nor fragment size had a significant influence on RGR. The highest RGR was observed in 6-cm fragment in the 20-cm water depth + mud treatment ($0.033 \pm 0.00 \text{ g g}^{-1} \text{ day}^{-1}$; Fig. 1b). This value was 1.42-fold higher than the lowest RGR, which was observed in 12-cm fragments in the 60-cm water depth + sand treatment ($0.023 \pm 0.00 \text{ g g}^{-1} \text{ day}^{-1}$; Fig. 1a).

Sediment type, water depth, and fragment size all had a significant influence on RER (Table 1; Fig. 1c, d). Higher RERs were observed in fragments grown in mud than in sand; RERs were significantly lower for larger fragments. The influence of water depth on RER was dependent on the sediment type. In the sand treatment, the RER of 6-cm fragments was significantly lower in the higher water depth, whereas in the mud treatment, it was significantly higher in the higher water depth treatment (Table 1; Fig. 1d).

Shoot diameter and branching number

Shoot diameters varied significantly among the different sediment treatments and fragment sizes (Table 1; Fig. 2a, b), but were not affected by water depth. Plant derived from 12-cm fragments and grown in mud had significantly larger shoot diameters. The 12-cm fragments in the 40-cm water depth + mud treatment produced the largest shoot diameter ($0.37 \pm 0.01 \text{ cm}$; Fig. 2b), which was 1.54-fold larger than the smallest shoot diameter, which was observed for 6-cm fragments grown in the 20-cm water depth + sand treatment ($0.24 \pm 0.03 \text{ cm}$; Fig. 2a).

Branching number was only significantly affected by sediment type (Table 1; Fig. 2c, d), and it was higher in the mud treatments than in the sand treatments. The highest branching number was observed in the 12-cm fragment grown in the 20-cm water depth + mud treatment (4.44 ± 0.80 ; Fig. 2d), and it was 2.17-fold higher than the lowest branching number that was found in 6-cm fragments grown in the 20-cm water depth + sand treatment (2.05 ± 0.19 ; Fig. 2c).

Total *N* and total *P* contents

Total *N* content was significantly affected by sediment type and water depth, but not by fragment size (Table 1; Fig. 3a, b). Mud and low-water-depth

treatments gave a higher total *N* content than sand and high water depth treatments. The highest total *N* content was recorded for 12-cm fragments grown in the 20-cm water depth + mud treatment ($10.53 \pm 0.40 \text{ mg g}^{-1}$; Fig. 3b), which was 1.50-fold higher than the lowest value recorded for 12-cm fragments grown in the 60-cm water depth + sand treatment ($7.00 \pm 0.33 \text{ mg g}^{-1}$; Fig. 3a).

Total *P* content was only affected by water depth (Table 1; Fig. 3c, d). The highest total *P* content was recorded in plants from 12-cm fragments grown in the 20-cm water depth + mud treatment ($1.42 \pm 0.26 \text{ mg g}^{-1}$; Fig. 3d). It was 1.38-fold greater than the lowest value recorded in plants from 12-cm fragments grown in the 60-cm water depth + sand treatment ($1.03 \pm 0.02 \text{ mg g}^{-1}$; Fig. 3c).

Discussion

The finding of greater shoot diameters of plants derived from 12-cm fragments of *M. spicatum* was consistent with the first hypothesis outlined in the Introduction. However, contrary to expectations, RGR and branching number did not change significantly with fragment size. These results are discordant with those of other studies, which confirmed that larger fragments were better for colonization and plant growth (Riis et al. 2009; Lin et al. 2012). For instance, larger fragments of *Potamogeton crispus* produced plants with higher dry weights than smaller fragments (Jiang et al. 2009). Larger fragments contain higher amounts of photosynthetic tissue and reserves (e.g., carbohydrates), thereby facilitating new tissue production, especially in the initial stage of plant growth (Riis et al. 2009; Li et al. 2015). However, our results are consistent with those of Umetsu et al. (2012) who found that 5- and 10-cm fragments of *Hydrilla verticillata* produced plants with similar shoot number and shoot dry weight. One possible explanation for the similar RGRs found here for the two fragment sizes was that both the selected lengths (6 and 12 cm) ensured enough resources were available for *M. spicatum* to produce new tissues. In natural conditions, fragments of various lengths are produced due to the different types and intensities of disturbances. Similar RGRs for different fragment lengths suggested that *M. spicatum* has a relatively high colonization ability for the invasion of a new habitat. Furthermore, analysis of

Table 1 Summary of the data analysis for the relative growth rate, relative elongation rate, branching number, shoot diameter, total *N* content, and total *P* content of *Myriophyllum*

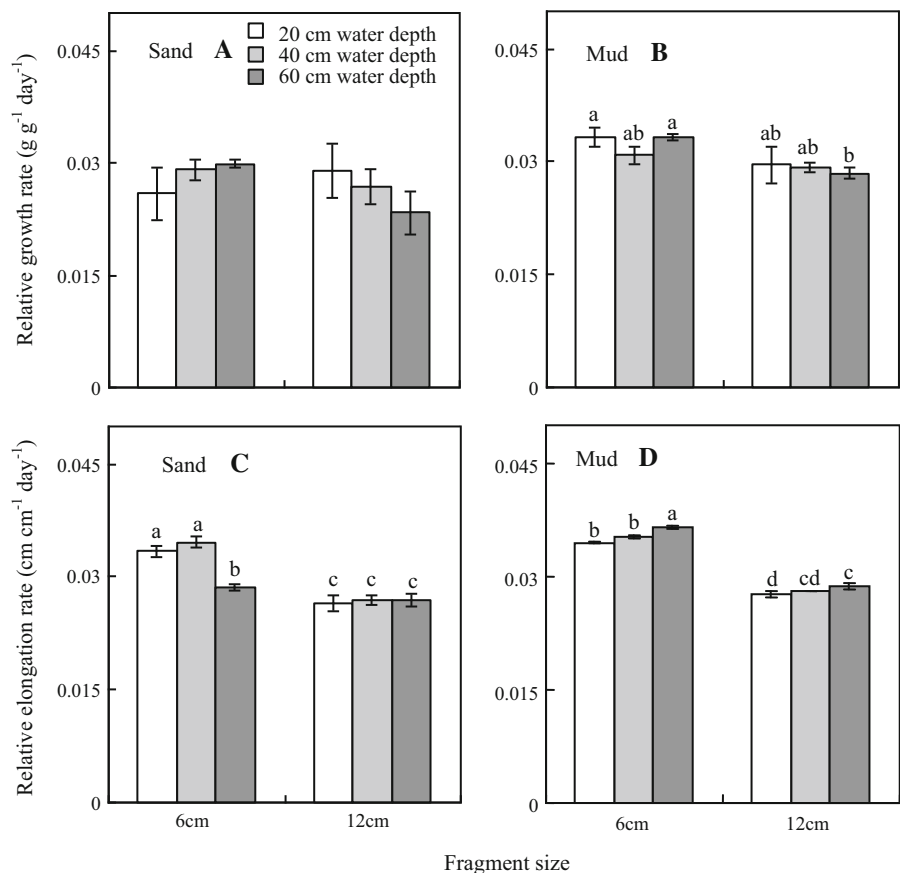
spicatum fragments with different sizes growing in three water depths and two sediment types (*F* values)

Variables	<i>N</i>	Sediment type (<i>S</i>)	Fragment size (<i>F</i>)	Water depth (<i>W</i>)	<i>S</i> × <i>F</i>	<i>S</i> × <i>W</i>	<i>F</i> × <i>W</i>	<i>S</i> × <i>W</i> × <i>F</i>
Relative growth rate (g g ⁻¹ day ⁻¹)	3	8.276**	3.278 ^{ns}	0.116 ^{ns}	0.357 ^{ns}	0.317 ^{ns}	1.719 ^{ns}	1.209 ^{ns}
Relative elongation rate (cm cm ⁻¹ day ⁻¹)	3	12.336**	5.288*	502.457***	0.338 ^{ns}	0.278 ^{ns}	1.216 ^{ns}	0.043 ^{ns}
Branching number	3	14.782**	3.216 ^{ns}	0.039 ^{ns}	0.071 ^{ns}	1.666 ^{ns}	0.821 ^{ns}	0.107 ^{ns}
Shoot diameter (cm)	3	8.875**	54.656***	0.422 ^{ns}	1.079 ^{ns}	0.372 ^{ns}	3.685*	1.630 ^{ns}
Total <i>N</i> content (mg g ⁻¹)	3	4.880*	1.934 ^{ns}	32.844***	3.351 ^{ns}	0.227 ^{ns}	1.188 ^{ns}	3.596*
Total <i>P</i> content (mg g ⁻¹)	3	0.146 ^{ns}	0.660 ^{ns}	7.050**	2.012 ^{ns}	0.896 ^{ns}	0.562 ^{ns}	3.831*

N the replication for the data analysis

^{ns} *P* > 0.05; * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001

Fig. 1 Relative growth rate (mean ± SE, *n* = 3) and relative elongation rate (mean ± SE, *n* = 3) of *Myriophyllum spicatum* fragments of different sizes growing in two sediment types and three water depths. Different letters indicate a significant difference between treatments at the 0.05 significance level



the total *N* and total *P* contents suggested that nutrient content was also similar in fragments of different sizes.

High water levels might hamper plant growth, mainly because of the limited light availability in the higher water depths (Cao et al. 2012). The results of

the present study suggested that water depth did not have a significant influence on RGR, branching number, or shoot diameter, but did significantly reduce the nutrient contents of *M. spicatum* plants. This result is contrary to our hypothesis 1 and with the results of other studies (Nielsen et al. 2006; Lin et al. 2012). One

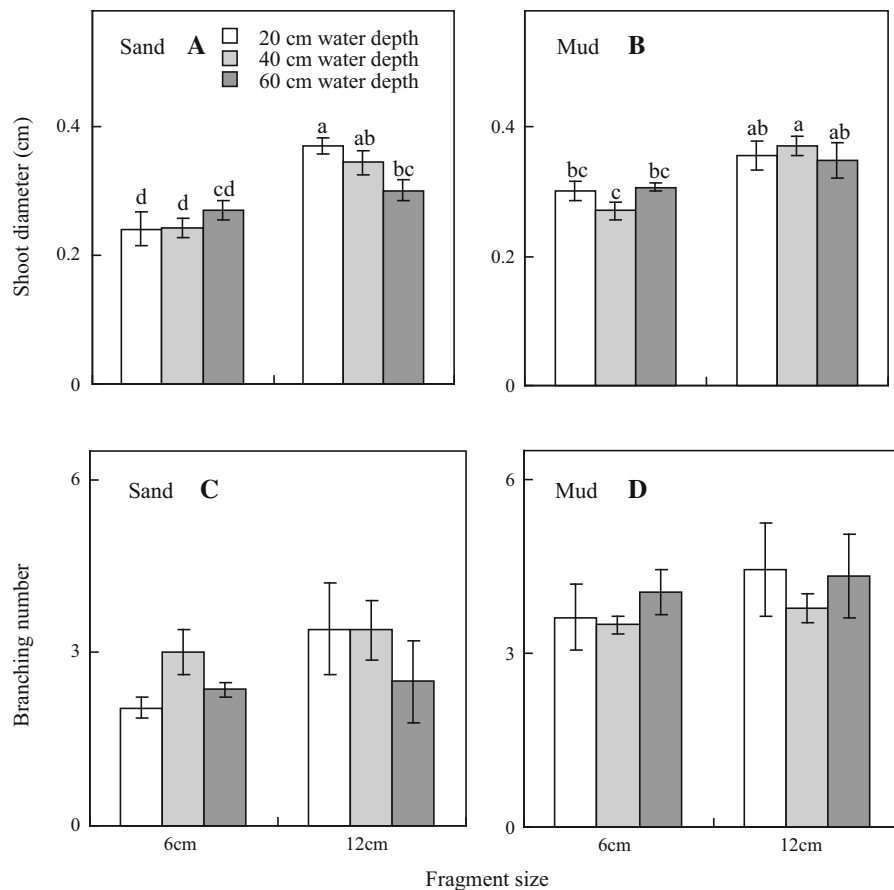


Fig. 2 Shoot diameter (mean \pm SE, $n = 3$) and branching number (mean \pm SE, $n = 3$) of *Myriophyllum spicatum* fragments of different sizes growing in two sediment types and three

water depths. Different letters indicate a significant difference between treatments at the 0.05 significance level

possible reason could be that the highest water depths used in our study (60 cm) was too low to inhibit the growth of *M. spicatum*. At the end of the study, the lengths of *M. spicatum* plants in the different treatments ranged from 90.0 to 118.8 cm, which is considerably greater than the highest water depths used in our experiment. Moreover, tap water was used in our experiment; therefore, the light attenuation effect is limited. Another possible explanation is that *M. spicatum* may be able to adapt to increased water depths through possession of low-light-compensation point and a high maximum photosynthetic rate, which could result in a high growth rate (Yang et al. 2004). The lower total N and total P contents of *M. spicatum* in the higher water depths might be due to the dilution effect. Some sediment nutrients are water soluble; thus, greater water depth might result in lower nutrient

concentrations in both the sediment and the water column. However, we did not measure sediment nutrient changes after the experiment.

Higher RGR, RER, shoot diameter, and branching number in fragments grown in mud indicated that the growth of *M. spicatum* is significantly enhanced by sediments that have a higher nutrient content; this conclusion is consistent with our first hypothesis (see Introduction) and with the results of previous studies (Xie and Yu 2011; Cao et al. 2012; Li et al. 2015). For instance, plant length and biomass of *Urochloa arrecta* increased significantly with increasing sediment nutrient (Fasoli et al. 2015). Moreover, total N content was also considerably higher in the mud treatment than in the sand treatment, which is consistent with our second hypothesis (see Introduction). Higher levels of nutrients can promote shoot

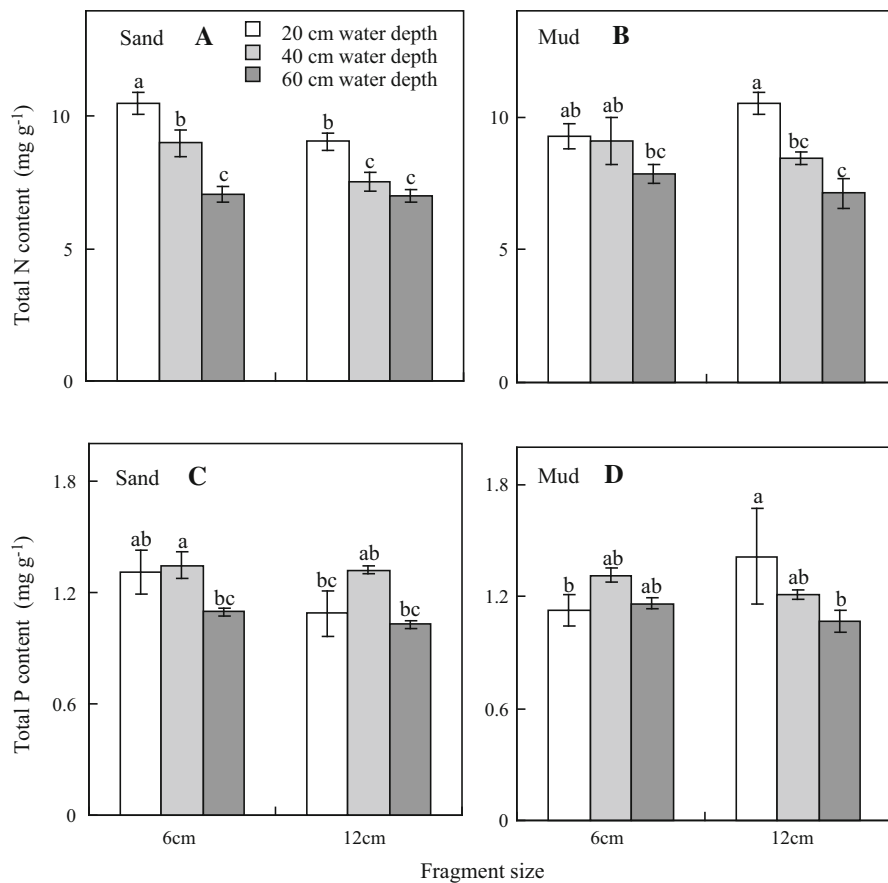


Fig. 3 Total N and total P contents (mean \pm SE, $n = 3$) of *Myriophyllum spicatum* fragments of different sizes growing in two sediment types and three water depths. Different letters indicate a significant difference between treatments at the 0.05 significance level

production and increase the tensile strength of rooted submerged macrophytes (Brewer and Parker 1990; Xie and Yu 2011; Cao et al. 2012). Furthermore, several studies have indicated that increased nutrient supply helps plants to acclimate to other environmental stresses (Xie et al. 2008). In the present study, the RER of *M. spicatum* increased significantly with increasing water depth in the mud treatment, which suggests that it is probably beneficial for *M. spicatum* to grow beyond the water surface for light acquisition. However, in the sand treatment, RER showed a contrasting pattern, indicating that lower nutrient levels are not suitable for shoot elongation in *M. spicatum*.

Aquatic systems are particularly vulnerable to invasion by non-native species, which negatively affect the aquatic environment and reduce native

biodiversity through a variety of mechanisms, including competitive exclusion from preferred habitats, predation, and hybridization (Umetsu et al. 2012; Thomaz et al. 2015). Generally, invasive species own higher competitive ability and environmental tolerance ability than native species, which would benefit their invasion into a new habitat (Silveira et al. 2009). Recently, the propagation of *M. spicatum* in lakes has caused many ecological problems in North America, North Africa, and China (Smith et al. 2002; Ali and Soltan 2006). The results of the present study suggest that fragment size, water depth, and sediment type all affect the growth performance of *M. spicatum* in different ways. Similar RGR at different fragment sizes and water depths indicated that this species had a high ability to acclimate to these two factors, which might be a major reason for its wide distribution.

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