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ARTICLE

Morphological and Physiological Responses to Sediment Nutrients in the Submerged Macrophyte *Myriophyllum spicatum*

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Abstract To improve the understanding of morphological and physiological changes of submerged macrophytes in response to different nutrient availabilities, *Myriophyllum spicatum* (a widely used lake restoration species due to its eutrophic tolerance in China) was planted in low-nutrient (TN 0.47 mg g^{-1}, TP 0.10 mg g^{-1}) and high-nutrient (TN 2.20 mg g^{-1}, TP 1.91 mg g^{-1}) sediments. The high-nutrient treatment reflected the eutrophication conditions in most lakes in the Middle and Lower Yangzi River Basin. Our results showed that the high nutrient level significantly increased the total biomass and affected shoot morphology traits; whereas the low sediment nutrient level significantly increased the root length of *M. spicatum*. The sediment nutrient enrichment significantly decreased the plant carbohydrate concentrations. Soluble sugar was positively correlated with the plant growth; however, carbohydrate concentrations in the auto-fragments only differed throughout its production period. It is noteworthy that most traits of *M. spicatum* respond rapidly between the treatments. These data demonstrate that *M. spicatum* can achieve a trade-off between its growth and storage by adjusting the pattern of biomass allocation in response to different sediment nutrients. Our study also implies that such flexible strategies would help *M. spicatum* adapt to the eutrophic environments.

Keywords Biomass allocation · Carbohydrate storage · Morphological plasticity · *Myriophyllum spicatum* L · Sediment nutrients · Submerged macrophytes

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Introduction

Sediment is the primary source from which submerged macrophytes obtain nutrients (including both macroelements and microelements) in shallow lakes (Barko and Smart 1983; Barko et al. 1986; Barko and Smart 1986). The response of submerged macrophytes to varying nutrient availabilities is generally associated with relevant morphological and physiological adapations (Cao et al. 2011). For example, recent studies have demonstrated that nutrient availability is an important factor that leads to differences in biomass, resource allocation and reproductive strategy in submerged macrophytes (Xie et al. 2004; Xiao et al. 2006; Xie and Yu 2011a). Indeed, even small variations in nutrient availability can create large differences in plant growth and morphological output (Sugiyama and Bazzaz 1998; Bonser and Aarssen 2003). If nutrient elements are scarce, plants tend to allocate a greater proportion of their biomass to the root system (reviewed from Hermans et al. 2006; Niu et al. 2013). This shift increases the root:shoot ratio (Hermans et al. 2006). Although many studies have focused primarily on the effect of sediment nutrient on aquatic plants, experimental evidence is still limited regarding the morphological changes that occur in submerged macrophytes in response to different sediment nutrient availabilities (McFarland et al. 1992; Crossley et al. 2002; Dorken and Barrett 2004; Puijalon et al. 2007).

In submerged macrophytes, carbohydrates are the common storage molecules in multiple structures (e.g., stem fragments, turions, winter buds and rhizomes) (Titus and Adams 1979; Vojtíšková et al. 2006; Xie and Yu 2011b), and these storage molecules may serve to reduce offspring mortality and increase re-growth in habitats with frequent disturbances (Madsen 1997; Adamec 2010). Previous field observations and experimental studies have indicated that environmental

factors (e.g., mechanical stress, low nutrients and high plant density) may trigger the storage of total non-structural carbohydrates (TNCs, including soluble sugars and starch) in aquatic plants (Kimbel 1982; Puijalon et al. 2008; Xie and Yu 2011a, b). However, a recent study also indicated that the starch content varied across different submerged macrophytes under different nutrient and light availabilities in the water column (Cao et al. 2011). These results reflect our current incomplete understanding of the environmental conditions that affect energy storage in aquatic plants, particularly in the case of submerged macrophytes.

Myriophyllum spicatum L. is a submersed macrophyte that is native to Europe and Asia and is dominant in freshwater regions throughout China (Aiken et al. 1979; Xie et al. 2007; Xie and Yu 2011a). However, this species is now considered one of the most troublesome weeds in North America (Grace and Wetzel 1978; Smith and Barko 1990; Buchan and Padilla 2000) and North Africa (Ali and Soltan 2006). Invasion by this species results in various ecological consequences, such as interference with water-based recreation, disruption of water flow (Boylen et al. 1999) and a decrease in the relative abundance and richness of the native species in the communities (Madsen 1997). *M. spicatum* occurs in various sediment types and can tolerate extremely eutrophic environments (Xie et al. 2007). The asexual propagation of *M. spicatum* occurs predominantly via mechanical breakage of stem fragments (also called allo-fragments) and self-formed stem fragments (also called auto-fragments) that are produced through the development of an abscission layer (Smith and Barko 1990; Madsen 1997; Santamaría 2002; Xie and Yu 2011a). The dispersal of stem fragments is an efficient mechanism for population expansion between different water bodies (Madsen and Smith 1997; Xie et al. 2010; Sarneel 2012; Xie et al. 2013). The stem fragments of *M. spicatum* have great regeneration, colonization and overwintering abilities (Kimbel 1982; Barrat-Segretain 1996; Barrat-Segretain et al. 1999). Most likely, these abilities result from the high content of carbohydrates in the stem fragments (Kimbel 1982; Smith et al. 2002; Xie and Yu 2011a).

In this study, we evaluated the morphological and physiological responses of *M. spicatum* at two different levels of sediment nutrients across three harvesting times. The following hypotheses were examined: (1) in a high nutrient sediment, greater and faster shoot growth (particularly the lateral branches) of *M. spicatum* is expected, and more carbohydrates will be allocated to shoot to sustain the shoot growth; and (2) in a low nutrient sediment, longer roots and a greater proportion of their biomass (versus the shoots) is expected, and carbohydrates will be allocated to the roots to support the root growth and storage because of the nutrient deficiencies.

Methods

Materials

This study was conducted at the National Observation and Research Field Station for Lake Ecosystem in Liangzi Lake, China (30°5′–30°18′ N, 114°21′–114°39′ E). In mid-April 2007, 150 apical shoots (approximately 7 cm long) of *M. spicatum* were collected from different individuals in Liangzi Lake. The water depths at the collection sites were 0.5 to 2.3 m and the sites were covered with monospecific stands of *M. spicatum*. The substratum at the collection sites was mud, with a total nitrogen (TN) content of 0.47±0.16 mg g^{-1} (mean ± s.e.) and a total phosphorus (TP) content of 0.10±0.07 mg g^{-1} (mean ± s.e.). The nutrient contents of Liangzi Lake sediment are lower than those in the eutrophic lakes in Middle and Lower Yangzi River Basin (e.g., Taihu Lake TN 1.47 mg g^{-1} and TP 0.80 mg g^{-1}; Chaohu Lake TN 1.57 mg g^{-1} and TP 0.62 mg g^{-1}) (Ye et al. 2009; Zhang et al. 2012). The apical shoots were transplanted into containers filled with sand and water at a 20-cm depth in a greenhouse (water temperature 26.76±3.65 °C; light intensity 1252.22±34.28 μmol photons m^{-2} s^{-1}, mean ± s.e.) for approximately 2 weeks until the plants had well-developed root systems.

Experimental Design

The experiment was conducted from 29 April 2007 to 07 July 2007. During the experimental period, the plants were cultivated in mud sediments with two nutrient levels and were harvested 3 times. Each treatment was replicated eight times (n=8); therefore, a total of 48 plant individuals of similar sizes were used (fresh weight, 0.2794±0.014 g; length, 22.66±0.87 cm with a root length 5.15±0.19 cm, mean ± s.e.). To create sediments with two different nutrient levels, commercial fertilizer (Osmocote®-1, smart-release fertilizer containing 14 % N, 14 % P, 14 % K, Scotts Miracle-Gro, Marysville, OH, USA) was mixed with the sediment, which was obtained from the lake. For the low nutrient level, the treatment consisted of 4 kg of pure sediment (without Osmocote™-1), with a TN of 0.37±0.07 mg g^{-1} (mean ± s.e.), a TP of 0.077±0.05 mg g^{-1} (mean ± s.e.) and 8.3 % organic matter. The high nutrient level treatment contained 52.5 g Osmocote™-1 (with an initial concentration of TN 7.35 g, TP 7.35 g and TK 7.35 g) mixed into 4 kg of sediment (final sediment nutrient concentration of TN 2.20±0.12 mg g^{-1}, TP 1.91±0.10 mg g^{-1}). Each individual plant was placed in 4 kg of substratum, and each substratum was placed in a plastic bag to prevent the release of nutrients into the water. Each bag of substratum was then placed in a fiberglass tank (100×100×100 cm, randomly placed) filled to a 100-cm depth with lake water (TN 0.71±0.06 mg l^{-1}, TP 0.04±0.01 mg l^{-1}); 48 tanks were used at the start of the

experiment. The experiment was performed outdoors, and the water temperature and light intensities were recorded at noon every 3 days (the water temperature was 25.23±2.38 °C and the light intensity was 1,533±31.13 μmol photons m^{-2} s^{-1}, mean ± s.e.). To reduce the influence of algae on the plant growth, the water in the tanks was changed weekly.

The experimental period coincided with active growth of *M. spicatum* in China. Morphological traits that respond to different environmental gradients can be expressed across a short-time period (Xie et al. 2005). Therefore, subsequent harvests were conducted at 3-week intervals, i.e. weeks 3, 6 and 9. Eight randomly selected plants from each nutrient treatment were carefully harvested. Upon harvest, the total number of branches was counted, the shoot and root lengths were measured and the internode length of the longest stem was also measured. These traits are commonly used to study the morphological responses of *M. spicatum* to different environmental conditions (Starand and Weisner 2001; Cao et al. 2012; Zhang et al. 2012). The plant individuals were then segmented and categorized into roots, main stem, branches and auto-fragments. The auto-fragments were collected (every 3 days) and time of abscision from the parent plant was recorded. The plant tissue samples were dried at 80 °C for 72 h and then weighed. All auto-fragments from each parent plant were placed together in a mixed sample for the carbohydrate analysis.

Chemical Analysis

The perchloric acid/anthrone method (Morris 1948) was used for analyzing the soluble sugars and starch fractions in the shoots and roots, respectively. The soluble sugar and starch concentrations were reported as mg g^{-1} dry weight (DW). For further details on the sample preparation and analytical methods, please see Xie and Yu (2011a).

Statistical Analysis

The total plant biomass and carbohydrate storage traits (i.e., soluble sugar and starch concentrations in the shoots, roots and auto-fragments of *M. spicatum*) between the nutrient treatments over the three harvest times were analyzed with a generalized linear model (GLM) ANOVA, with the sediment nutrients as the fixed factor and the harvest times as the random factor. For the morphological traits (i.e., the total branch number, shoot internode length, and shoot and root length), the differences were analyzed with GLM ANCOVA, with the sediment nutrients as the fixed factor, the harvest times as the random factor and the total plant biomass as the covariate (Xie and Yu 2011a). All of the possible interaction terms were first introduced into the model, and the non-significant interaction terms were eliminated from the model to obtain the final model. A Duncan test was used to compare the levels within the factors for significance (P<0.05). All of the experimental data were transformed using the log (x + 1) or arcsine (x) function to ensure homogeneity of the variance or a normal distribution of residuals and were then analyzed. All of the data were analyzed with SPSS 19.0 software (SPSS, Chicago, IL, USA).

Results

Plant Growth and Biomass Allocation

During the entire experimental period, the water temperature at noon was approximately 25 °C, which is representative of the natural growing conditions of *M. spicatum*. There were significant differences in the total plant biomass between the nutrient treatments ($F_{1,\ 44}$=79.627, P<0.001), and the total plant biomass also differed significantly among the weeks of harvest ($F_{2,\ 44}$=68.072, P<0.001) (Fig. 1). In general, the plants that grew at the high level of nutrients produced comparatively more branch fractions ($F_{1,\ 44}$=96.685, P<0.001), whereas those that grew in the low-nutrient sediment produced more root fractions ($F_{1,\ 44}$=21.829, P<0.001) and main stems ($F_{1,\ 44}$=19.884, P<0.001); this trend was observed throughout the entire experiment period (Table 1). For the plants grown in the high- and low-nutrient sediments, the main stem biomass fractions decreased ($F_{2,\ 44}$=28.348, P<0.001), and the branch biomass fractions increased during the experimental weeks ($F_{2,\ 44}$=61.896, P<0.001). However, the root biomass fractions of the plants in both nutrient sediments did not show significant variations within study period ($F_{2,\ 44}$=1.233, P=0.301). Moreover, the auto-fragment biomass fractions showed significant differences across the

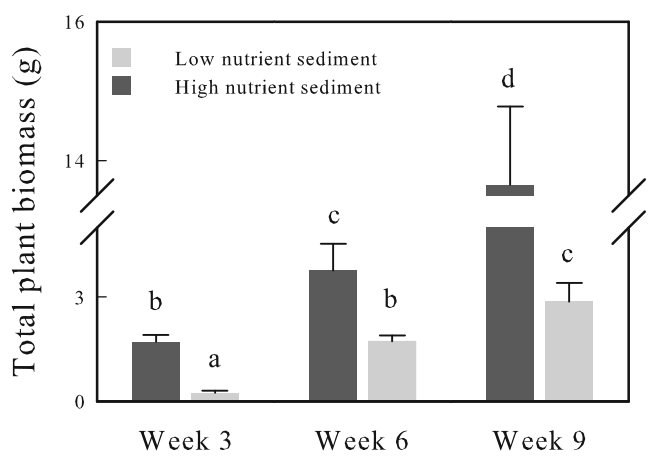

Fig. 1 Total plant biomass for the two sediment nutrient treatments across the three harvest times; the total plant biomass data are the means ± s.e. (n=8). The *bars sharing different letters* indicate significant differences among treatments (P<0.05). The data were transformed using a log (x + 1) function

harvest times ($F_{2, 44}$=5.641, P=0.007) and in between nutrient sediments ($F_{1, 44}$=12.241, P=0.001), and the plants grown in low nutrients sediment did not produce any auto-fragments in the first harvest, i.e., week 3 (Table 1).

Morphological Responses

During the experimental period, the shoot internode length and shoot length of *M. spicatum* were strongly correlated with the total plant biomass, and the relationships were significantly affected by the sediment nutrient treatments (Table 2). The plants grown at the high level of nutrients produced longer shoots and shoot internodes than the plants grown at the low level of nutrients across the three harvest times (Fig. 2b and c). Although the branch number and root length did not correlate with the total plant biomass, the sediment nutrient treatments still significantly affected these two traits (Table 2). The *M. spicatum* plants grown in the high-nutrient sediment produced more branches, whereas the plants grown in the low-nutrient sediment produced longer roots (Fig. 2a and d). All of the morphological traits at the low nutrient level significantly increased during the experiment, but this trend was only observed for the total branch number and shoot length in the high-nutrient treatment (Fig. 2).

Carbohydrate Storage Responses

The sediment nutrients also significantly affected the carbohydrate storage in the shoots, roots and auto-fragments of *M. spicatum* (Table 3). Over the three harvest times, the plants grown in the low-nutrient sediment had significantly higher soluble sugar and starch concentrations in the shoots and roots than the plants grown in the high-nutrient sediment. However, neither the soluble sugar nor the starch concentration in the auto-fragments differed between the two sediment nutrient levels (Fig. 3). Except for the roots at the high nutrient level, the soluble sugar concentration increased in the shoots and roots of *M. spicatum* in both treatments across the three harvest times (Fig. 3a and c; Table 3). A similar trend was also observed for the starch concentrations in the shoots and roots of *M. spicatum* in both nutrients treatments, and the starch concentration in the roots was higher than in the shoots (Fig. 3b and d; Table 3). For the auto-fragments, the soluble sugar and starch concentrations were low in week 3 compared with weeks 6 and 9 (Fig. 3e and f; Table 3).

Discussion

Over the three harvest times, nutrient enrichment of the sediment positively affected the growth of *M. spicatum*. This result was consistent with our previous studies on this species and other species of submerged macrophytes in Liangzi Lake (Xie and Yu 2011a, b). As a competitive-strategy species (Kautsky 1988; Murphy et al. 1990), *M. spicatum* grows rapidly after it is established in a favorable environment and reaches a large size to capture more light, thus reducing the soil nutrient uptake by neighboring plants (Smith and Barko 1990). The total biomass differences between the two levels of nutrient sediments were primarily due to the production of branches. This result is similar to those of several previous studies in both terrestrial and aquatic plant species. In these studies the plants that grew in more favorable environments tended to have greater lateral expansion (Bonser and Aarssen 2003; Wang and Yu 2007; Xie et al. 2013). In contrast, the branch development of *M. spicatum* may be constrained under unfavorable conditions because a greater proportion of the biomass is allocated to the root system (Hermans et al. 2006). Moreover, it is common that perennial plants may reallocate resources for storage in an adverse environment instead of utilizing them for vegetative growth processes (Suzuki and Stuefer 1999; Hangelbroek et al. 2003). Our results also showed that the plants grown in the high-nutrient sediment produced more auto-fragments than the plants grown in the low-nutrient sediment across the three harvest times. This finding is in agreement with previous studies in which the production of auto-fragments is correlated with the shoot biomass (or plant size) of *M. spicatum* (Madsen 1997; Smith et al. 2002; Xie and Yu 2011a). Nevertheless, the detachment of auto-fragments may be closely related to the

Table 1 Biomass allocation of *M. spicatum* as affected by different sediment nutrient treatments across three harvest times (week 3, week 6 and week 9; means ± SE n=8)

Dependent variable	High-nutrient treatment			Low-nutrient treatment		
	Week 3	Week 6	Week 9	Week 3	Week 6	Week 9
Root mass fraction (%)	10.77±0.84^{a}	7.98±1.06^{a}	5.78±0.60^{a}	23.64±7.49^{bc}	16.23±1.82^{ab}	27.77±2.65^{c}
Main stem mass fraction (%)	52.17±4.91^{b}	14.59±2.14^{a}	8.03±1.45^{a}	66.41±7.91^{c}	49.10±8.51^{b}	22.40±2.78^{a}
Branch mass fraction (%)	27.99±3.41^{b}	62.52±1.77^{d}	71.97±1.96^{e}	9.96±4.67^{a}	23.49±4.24^{b}	44.69±2.64^{c}
Auto-fragment mass fraction (%)	9.06±4.14^{bc}	14.91±1.50^{c}	14.22±2.03^{c}	0^{a}	11.18±3.75^{bc}	5.13±1.42^{ab}

The different letters indicate significant differences among the treatments (P<0.05). All of the data were transformed using an arcsine (x) function

Table 2 The *F* and *P* values for the sediment nutrients (S) for the total branch number, shoot internode length, shoot length and mean root length using the total biomass (C) as a covariate and the harvest week as a random factor

Dependent variable	Sediment nutrient (S)			Total biomass (C)			S × C			Harvest week		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
Total branch number	1, 44	318.569	<0.001	1, 42	1.170	0.286	–	–	–	2, 44	18.330	<0.001
Shoot internode length	1, 42	13.927	0.001	1, 42	15.349	<0.001	1, 42	35.187	<0.001	2, 42	2.945	0.064
Shoot length	1, 42	52.946	<0.001	1, 42	51.249	<0.001	1, 42	35.497	<0.001	2, 42	6.450	0.004
Mean root length	1, 44	59.518	<0.001	1, 42	0.318	0.576	–	–	–	2, 44	3.075	0.056

All of the data were transformed using a log (x + 1) function

lignin content. Because a zone of "partially lignified cells" is formatted at the last node and causes the abscission of auto-fragment (Aiken et al. 1979; Xie and Yu 2011a). Indeed, the internal regulation mechanism describing the management of the production of auto-fragments by *M. spicatum* in response to variable environmental conditions requires further study.

With increasing sediment nutrients, *M. spicatum* tended to produce longer shoot internodes and taller shoots and was associated with decreased root elongation. In general, the elongation of shoots is a common strategy that allows submerged macrophytes to adapt to low light (Starand and Weisner 2001; Pilon and Santamaría 2002; Yu and Yu 2009). In the present study, the shoot internode length was significantly higher by week 3 than at the other two time points (week 6 and week 9) in the high-nutrient sediment, indicating that *M. spicatum* responded rapidly to grow toward the water surface to capture more light and carbon via shoot elongation (Starand and Weisner 2001; Yang et al. 2004; Zhang et al. 2012). When the plants in the high-nutrient sediment reached the water surface (100 cm), the lateral expansions of branches resulted from increases in the branch number and biomass. In contrast, none of the plants in the low-nutrient sediment reached the water surface throughout the 9-week period. The total branch number, shoot internode length and shoot length remained low because of the nutrient deficiencies. However, these plants produced longer roots at the low nutrient level, and the root length increased during the 9-week period, which is consistent with the adaptive responses of *M. spicatum* and other submerged macrophytes to infertile environments (Wang and Yu 2007; Xie et al. 2007). Although many studies have indicated that morphological adaptations to a new environment take time to occur, most of the differences in the morphological traits developed rapidly in our study (within 3 weeks). These results were consistent with previous studies that showed that submerged macrophytes (*M. spicatum* and *Vallisneria natans* (Lour.) Hara) can adjust its root morphology in response to the fertility of the sediment in a short-time (14–35 days) (Xie et al. 2005, 2007). One possible explanation would be that *M. spicatum* has a high light compensation point, a high light saturation level, and a high maximum photosynthetic rate. This species can adapt

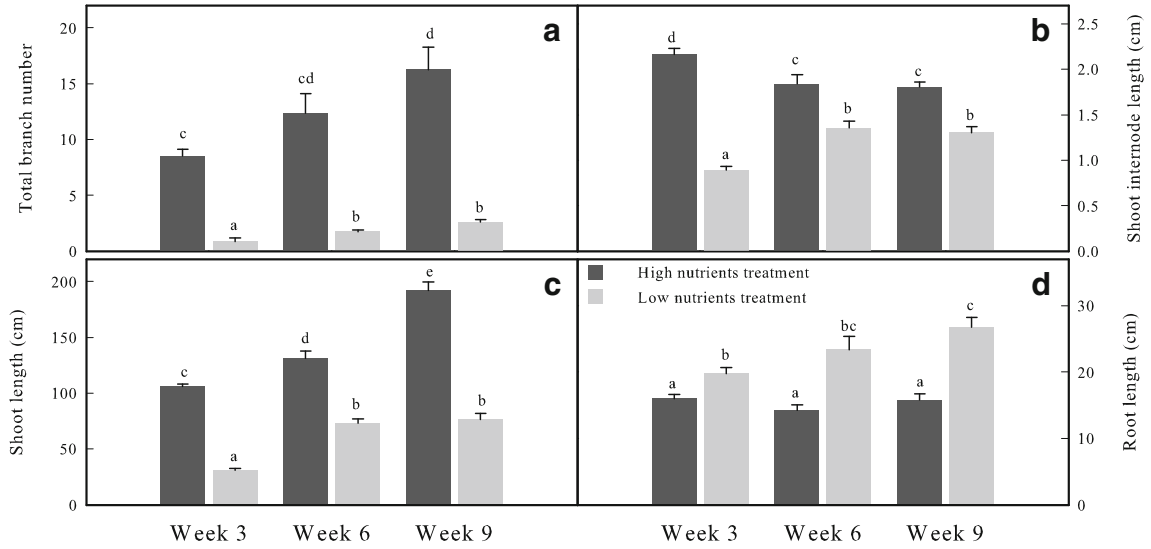

Fig. 2 Total branch number (**a**), shoot internode length (**b**), shoot length (**c**) and root length (**d**) for the two sediment nutrient treatments across three harvest times; the data are presented as the means ± s.e. (n=8). The *bars sharing different letters* indicate significant differences among the treatments (P<0.05). The data were transformed using a log (x + 1) function

Table 3 The *F* and *P* values for the sediment nutrients for the soluble sugar and starch concentrations in the shoots, roots and auto-fragments using the harvest week as a random factor

Dependent variable	Sediment nutrient			Harvest week		
	d.f.	*F*	*P*	d.f.	*F*	*P*
Soluble sugar concentration in shoots	1, 44	58.905	<0.001	2, 44	21.523	<0.001
Starch concentration in shoots	1, 44	52.606	<0.001	2, 44	17.207	<0.001
Soluble sugar concentration in roots	1, 44	124.677	<0.001	2, 44	1.769	0.182
Starch concentration in roots	1, 44	36.453	<0.001	2, 44	7.259	0.002
Soluble sugar concentration in auto-fragments	1, 44	2.280	0.138	2, 44	12.121	<0.001
Starch concentration in auto-fragments	1, 44	0.501	0.483	2, 44	12.473	<0.001

All of the data were transformed using a log (x + 1) function

rapidly to new environment, and these characteristics promote its high growth rate.

Carbohydrate storage plays an important role in plant performance (e.g., survival, sprouting and spread) under variable environmental conditions (Spencer and Ksander 1996; Suzuki and Stuefer 1999; Weber and Noodén 2005). Carbohydrates are also important in the processes that sustain plant growth, such as the construction of new cell walls (Huber et al. 2012). Over the three harvest times, the *M. spicatum* plants grown in low-nutrient sediment stored higher concentrations of TNC (soluble sugars and starch) in both shoots and roots than the plants grown in the high-nutrient sediment. In high-nutrient sediment, an average concentration of 113 mg g^{-1} DW starch was stored in 8 % root fractions; while in low-nutrient sediment, an average concentration of 210 mg g^{-1} DW starch was stored in 23 % root fractions. These findings were in agreement with previous studies (Kimbel 1982; Madsen and Smith 1997; Smith et al. 2002), and our results supported the important role of the root tissues as structural storage organs for *M. spicatum* (Madsen 1997). In plants grown at low levels of nutrients sediments, a large amount of TNC storage may allow the re-allocation of carbohydrates from the shoots into the roots for storage and root growth; conversely, a large TNC was allocated into shoot growth in the plants grown at the high nutrient level. These results indicated a trade-off between current growth and resource investment in *M. spicatum* in

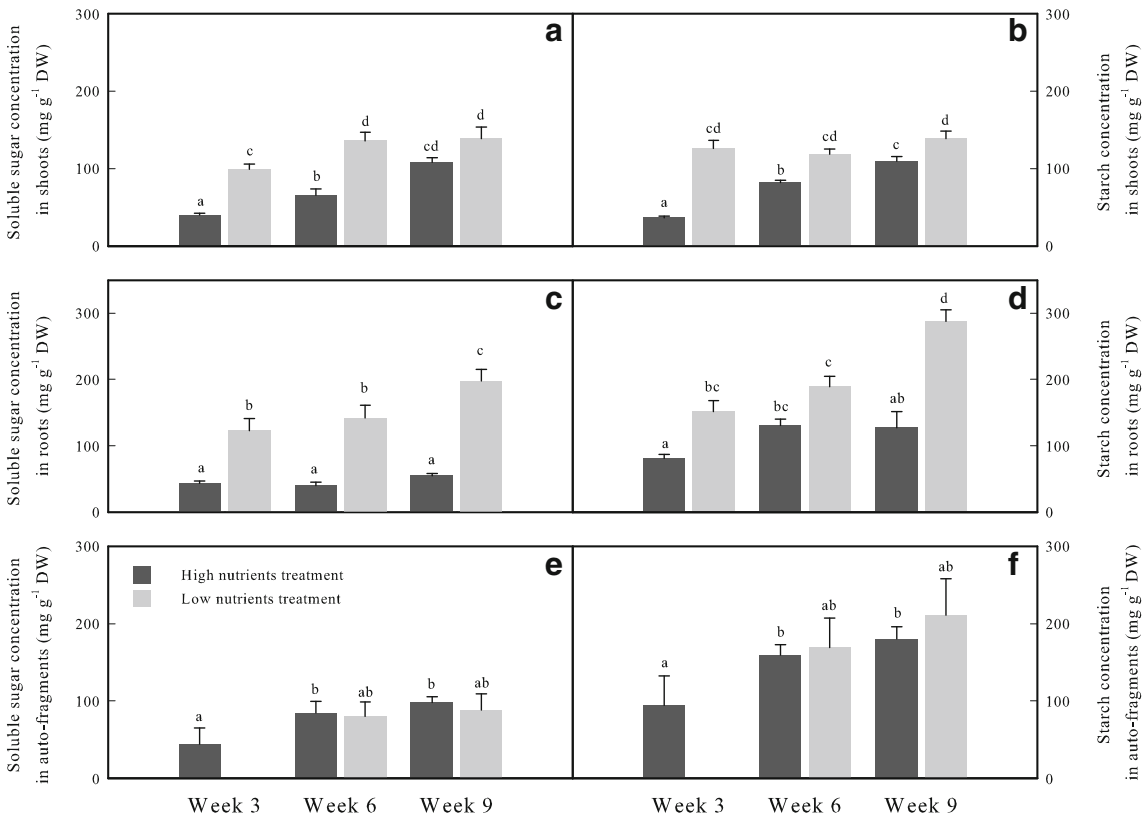

Fig. 3 Soluble sugar concentration and starch concentration in the shoots (**a** and **b**), roots (**c** and **d**) and auto-fragments (**e** and **f**) of *M. spicatum* for the two sediment nutrient treatments across three harvest times; the data are presented as means ± s.e. (n=8). The *bars sharing the different letters* indicate significant differences among the treatments (P<0.05). The data were transformed using a log (x + 1) function

response to different sediment nutrient conditions, and they also indicated that the carbohydrate concentration correlated positively with the elongation of the plant tissues (root and shoot elongation in this case) (Huber et al. 2012). Furthermore, in both nutrient sediments, the increase in the soluble sugar concentration was positively associated with the shoot and root growth of *M. spicatum* throughout the study. This result was in agreement with previous reports that soluble sugar concentration is related to tissue growth and may regulate hormone concentrations to modify the plant's morphology (Huber et al. 2012; Deng et al. 2013). Indeed, the soluble sugar is a successful resource supply in maintaining plant growth rather than starch. Because starch cannot be utilized directly by the plant and must be transformed to soluble sugar for utilization (Karunagaran and Ramakrishna Rao 1991; Hajirezaei et al. 2003). However, whether this sugar accumulation in our study is a downstream response to different nutrient levels or part of a systemic signaling system in the regulation of plant growth requires further investigation. Moreover, neither the soluble sugar nor the starch concentrations in auto-fragments different significantly between the sediment nutrient levels across the three harvest times, a result consistent with in our previous study (Xie and Yu 2011a). This result may be explained by the induction of the ability to recovery TNC by rapid photosynthesis (Kimbel 1982) and by the storage of a sufficient amount of TNC in the auto-fragments (Smith et al. 2002).

Conclusion

The enrichment of the sediment nutrients triggered an increase in the total biomass accumulation of *M. spicatum*, particularly the branch biomass, throughout our 9-week experiment. *M. spicatum* tended to produce more branches, longer shoot internodes and taller shoots, changes associated with unchanged root elongation, in response to the sediment nutrient enrichment. Additionally, the sediment nutrient enrichment significantly decreased the shoot and root TNC (soluble sugar and starch) concentrations in *M. spicatum*. The soluble sugar concentrations in the plants from both nutrient levels were positively correlated with the growth of *M. spicatum*. However, neither the soluble sugar nor the starch concentration in the auto-fragments differed significantly between the nutrient levels. Interestingly, most of these morphological and physiological traits responses of *M. spicatum* to the different sediment nutrients occurred within a short time period (within 3 weeks). These data indicate that *M. spicatum* can achieve a rapid trade-off between current growth and carbohydrate storage by adjusting the structure of the shoots and the pattern of biomass allocation in response to the sediment nutrients. Such flexible growth and storage strategies would help *M. spicatum* to adapt to the different environments and to prevent the extinction of its population.

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