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Growth and Anchorage of *Myriophyllum spicatum* L. in Relation to Water Depth and the Content of Organic Matter in Sediment

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A large body of evidence suggests that the physical and chemical characteristics of the sediment in lakes that have undergone eutrophication have been significantly altered. However, the effects of alterations in sediments on submersed macrophytes remain unknown. In this study, we present the results of an outdoor experiment that examined how the growth and anchorage of the widespread submersed macrophyte *Myriophyllum spicatum* L. responded to the enrichment of organic matter in the sediments and whether water depth affects these responses. We found that low levels of enrichment with organic matter (≤7%) enhanced the growth of *M. spicatum*. In contrast, high levels of enrichment with organic matter (from 12 to 18%) slightly inhibited its growth. Although the anchorage force of *M. spicatum* slightly decreased with an increase in the content of organic matter in the sediment, it was much higher than the hydraulic drag force on plants at a relatively high current velocity, indicating that the plants were unlikely to be uprooted in these sediments. The water depth did not alter the responses of growth and anchorage of *M. spicatum* to enrichment with organic matter. Our results suggest that *M. spicatum* could be a potential species to restore eutrophic lakes, since it can grow well and anchor stably in sediments with relatively high organic matter and manage low light stress.

Keywords: eutrophicaion, submersed macrophyte, organic matter enrichment, sediment phosphorous, lake restoration

INTRODUCTION

Submersed macrophytes are highly important for stabilizing the function and structure of freshwater ecosystems, particularly in shallow lakes (Hilt et al., 2017; Lurig et al., 2021). A high coverage and diversity of submersed macrophytes can provide positive feedback for the provision of clear water and enhance the biodiversity of shallow lakes (Scheffer et al., 1993; Law et al., 2019). Recent evidence points toward a progressive loss of submersed macrophytes during the process of lake eutrophication (Sand-Jensen et al., 2000; Zhang et al., 2017). This deterioration has primarily been attributed to an increase in the attenuation of light by phytoplankton and epiphytes following nutrient enrichment in the water column (Phillips et al., 2016). A large body of evidence suggests that the physical and chemical characteristics of the sediment had also been substantially altered as the lakes eutrophied

(Van Der Molen et al., 1998; Sand-Jensen et al., 2005; Hobaek et al., 2012), which may have a strong influence on the growth and community structure of submersed macrophytes (Barko et al., 1991; Raun et al., 2010; Bornette and Puijalon, 2011; Xie et al., 2013; Li et al., 2015). However, the effects of alteration of sediments on submersed macrophytes are still largely unknown.

One significant change in sediment with eutrophication is that the content of organic matter increased as a result of the turnover of the thriving macrophytes and sedimentation of organic particles from the production of phytoplankton (Sand-Jensen and Møller, 2014). Previous studies found that submersed macrophytes benefit from the enrichment of organic matter at low levels in the sediment, since the decomposition of organic matter can increase the concentration of nutrients in pore water (Silveira and Thomaz, 2015). However, at high levels, submersed macrophytes may suffer anaerobic and phytotoxic effects induced by organic matter (Wu et al., 2009; Pulido et al., 2011). In addition, an increase in the organic matter in sediment can reduce the strength of submersed macrophytes to anchor, and thus enhance their risk of uprooting (Sand-Jensen and Møller, 2014).

The depth of water has a profound impact on the growth of submersed macrophytes and their allocation and morphology (Fu et al., 2012; He et al., 2019). Previous studies found that water depth can alter the responses of submersed macrophytes to other stressors (Xiao et al., 2007; Xu et al., 2016). For example, Xu et al. (2016) reported that the water depth, substrate type, and wave exposure had extremely significant joint influences on the growth and morphology of *Vallisneria natans*. The negative influence of high water levels on submersed macrophytes may be aggravated by decreased belowground growth under high water levels, exposure to high waves, and high nutrient conditions (Xu et al., 2016). However, whether the water depth affects the responses of the growth and anchorage of submersed macrophytes to sediment enriched in organic matter remains unclear.

In this study, we aimed to investigate how the submersed macrophyte growth and anchorage responded to the enrichment of organic matter in the sediment and whether water depth affects these responses. To answer these questions, we conducted an outdoor experiment in which we evaluated the response of the widespread submerged macrophyte *Myriophyllum spicatum* L. to the individual and combined effects of water depth and enrichment of organic matter in the sediment. We hypothesized the following: 1) Low levels of enrichment in organic matter in the sediment would enhance the growth of the plant, while high levels of organic matter would inhibit the plant growth. 2) The anchorage force would decrease with an increase in the content of organic matter in the sediment. 3) The negative effects of high content of organic matter on the plant would be stronger in deep water than shallow ones, since the plant may allocate more resources to the elongation of shoots at deeper sites.

MATERIALS AND METHODS

Plant Species

M. spicatum is a rooted submersed aquatic plant that forms canopies. It has spread from its native Eurasia to become an invasive plant worldwide (Aiken et al., 1979). This species occurs at a wide range of water and sediment conditions (Sondergaard et al., 2010; Su et al., 2019), and the plant strongly morphologically and physiologically responds to changing environmental conditions, such as variations in temperature, light, nutrients, and dissolved inorganic carbon availability (Strand and Weisner, 2001; Wang et al., 2008; Hussner and Jahns, 2015; Hussner and Heidbuchel, 2021).

Experiment Establishment

A two-by-five factorial design experiment was conducted with two levels of water depth and five levels of the addition of organic matter to the sediment. Each treatment included seven replicates. The experiment was performed using a concrete pond (length 6 m × width 4 m × depth 1.6 m) located outdoors at the Biological Gardens of Nanchang University (Nanchang, China) (28°39′ N, 115°48′ E) and filled with tap water. No further water was added after the beginning of the experiment (except for precipitation). Sediment was collected from Poyang Lake, air-dried, and mixed. The contents of total nitrogen (TN), total phosphorus (TP), and organic matter in the sediment were 0.54 ± 0.02 g kg^{-1}g, 0.25 ± 0.01 g kg^{-1}, and 0.81 ± 0.01% dry weight (dw), respectively. A gradient of 4, 8, 12, and 16% dry weight treatments of organic matter were produced by adding commercial peat soil (Compo, Germany) to the lake sediment. Lake sediment without the addition of organic matter was used as control. Three sediment samples were taken randomly from each gradient to analyze the actual initial organic matter and contents of TN and TP. Three healthy and clean apices of *M. spicatum* (15 cm in length) were planted in each pot (diameter = 15 cm, height = 10 cm) filled with 8 cm of sediment. Ten plant apices of similar sizes were randomly selected to determine their initial dry weight. Half of the pots were placed at 0.8 m water depth on a steel frame submersed in the pond water. The other pots were placed on the bottom of the pond (without sediment). The pots just covered 5% area of the pond, and the volume of the sediment was only 0.25% of the water; thus, the dissolved organic matter release from the sediment would not strongly influence the plant performance.

Monitoring

Three sites were established to monitor the water parameters in the pond. Two of the sites were next to the middle of the long sides, while one was beside the middle of the short side. The concentration of phytoplankton chlorophyll *a* (chl-*a*) and water temperature in the pond were measured weekly using a BBE algae analyzer (AlgeaTorch, Moldaenke, Germany). Dissolved oxygen, pH, and conductivity were measured weekly at 10 cm below the water surface using a multiparameter water quality instrument (HI9829, Hanna, Italy). Photosynthetically active radiation (PAR) was measured weekly at intervals of 0.5 m water depth from the subsurface to 1 m of the water column using a Li-COR UWQ-9525 sensor coupled with a Li-1500 data logger (LI-COR, Lincoln, NE, United States). The attenuation coefficient of light (K) in the water column was calculated based on the PAR at different depths as described by Duarte et al. (1986). Water samples were collected from the pond biweekly to analyze the levels of TN, TP, ammonium nitrogen (NH_4^+-N), and nitrate nitrogen (NO_3^--N). Samples filtered through Whatman GF/C glass fiber filters were used to determine the amount of NH_4^+-N using Nessler's reagent colorimetric method and NO_3^--N using ultraviolet spectrophotometric methods (State Environmental Protection Administration of China, 2002). TP and TN were analyzed from unfiltered water using the ammonium molybdate spectrophotometric method after digestion with $K_2S_2O_8$ solution and the ultraviolet spectrophotometric method after digestion with $K_2S_2O_8$ and the addition of HCl (State Environmental Protection Administration of China, 2002), respectively.

Plant Harvest and Anchorage Force Measurement

The experiment ended when some of the plants at 0.8 m deep reached the water surface. The duration of the experiment was from August 25, 2019, to October 9, 2019, a period of 45 days. The plant height and anchorage force were measured immediately when the pots were removed from the pond. The anchorage force was measured by wrapping a cotton rope around the stem just above the sediment, connecting it via a metal string to a digital force gauge and gradually increasing the pull until the plant was dislodged (Sand-Jensen and Møller, 2014). The maximum pull registered by digital force gauge was registered as the anchorage strength. A few measurements were discarded where the plant broke. The plant shoots and roots of each pot were collected and then dried at 60°C for 48 h for dry weight measurements. The plant relative growth rate (RGR) was calculated as follows:

$RGR = \ln(W_t/W_0)/t$,

where W_0 is the initial dry weight of *M. spicatum* (g), W_t is the dry weight (including shoots and roots) of *M. spicatum* at the end of the experiment (g), and t is the duration of experiment (days).

Calculation of Hydraulic Forces

To evaluate whether the plant will be uprooted in lakes, we calculated the hydraulic force (F) on *M. spicatum* as described by Schutten and Davy (2000):

$F = A \times biomass \times velocity^{1.5}$, where A is a species-specific factor that incorporates the roughness that arises from shoot geometry and surface characteristic. In this study, we used the species-specific factor A = 2564 for *M. spicatum* delineated by Schutten and Davy (2000) and the velocity = 0.6 m s^{-1} as described by Schutten et al. (2005). This value of velocity was relatively high compared with that in lakes under normal conditions (Schutten et al., 2005; Qin et al., 2007), but it may occur in extreme conditions, such as during a storm (Schutten et al., 2005).

Sediment and Plant Sample Analyses

The contents of TN, TP, and organic carbon (OC) of the sediment taken at the beginning of the experiment were analyzed using standard methods (Shi, 1994), i.e., the $K_2Cr_2O_7$–H_2SO_4 oxidation method for OC, the Kjeldahl acid-digestion method for TN, and the molybdenum blue colorimetric method for TP. The total organic matter of the sediment was determined by multiplying OC with Van Bemmelen's factor of 1.724. At the end of the experiment, sediment samples were taken from each pot to analyze the water content and dry density analysis as described by Barko and Smart (1986). The contents of C, N, and P of *M. spicatum* shoots were analyzed after being ground into powder as described above.

TABLE 1 | Physical, chemical, and biological parameters of water in the pond during the experiment.

Parameter	Mean ± SD	Parameter	Mean ± SD
TN (mg L^{-1})	0.387 ± 0.226	Conductivity (μs cm^{-1})	167.97 ± 15.58
TP (mg L^{-1})	0.030 ± 0.012	DO (mg L^{-1})	10.28 ± 1.86
NH_4^+-N (mg L^{-1})	0.073 ± 0.028	Temperature (°C)	29.21 ± 2.82
NO_3^--N (mg L^{-1})	0.281 ± 0.240	Chlorophyll-*a* (μg L^{-1})	3.58 ± 1.83
pH	9.48 ± 0.51	K	0.012 ± 0.002

TN, total nitrogen; TP, total phosphorous; DO, dissolved oxygen; K, light attenuation coefficient.

Data Analyses

The relationship between TN, TP, water content along with the density, and the content of organic matter in the sediment was examined using linear regression analyses to assess the effects of addition of organic matter on the characteristics of the sediment. The effects of water depth, enrichment in organic matter, and their interaction on the sediment and plant parameters were tested using two-way analyses of variance (ANOVAs). GAMs (generalized additive models) were used to fit the relationship between the content of organic matter and plant parameters at 0.8 and 1.6 m, respectively. GAMs were also used to fit the relationship between shoot N, shoot P, and the plant RGR. The GAMs were constructed with the function "gam" in package "mgcv" using penalized regression splines as the smoothing function, Gaussian error distribution, and automatic calculation of smoothing parameters. All the analyses were performed in R (R Core Team, 2020). The results were considered to be significant at $p < 0.05$.

RESULTS

Water Characteristics in the Pond

The water conditions were suitable for the growth of submersed macrophytes. There were low concentrations of water nutrients, resulting in a low abundance of phytoplankton and high transparency in the pond (**Table 1**). The warm temperatures were beneficial to plant growth (**Table 1**). In addition, warm temperatures can maintain high levels of decomposition of the organic matter in the sediment, which is crucial to properly evaluate the addition of organic matter on the growth of submersed macrophytes.

Effects of the Addition of Organic Matter on the Sediment Characteristics

Both the TN and TP of the sediment increased linearly as the content of organic matter increased (**Figures 1A,B**; $R^2 = 0.992$, $p < 0.001$ for N and $R^2 = 0.973$, $p = 0.001$ for P). The addition of organic matter had strong effects on the water content of the sediment (**Table 2**, $p < 0.001$) and sediment density (**Table 2**, $p < 0.001$). With the addition of organic matter, the mean water content of sediment increased from 36 to 71% (**Table 3**,

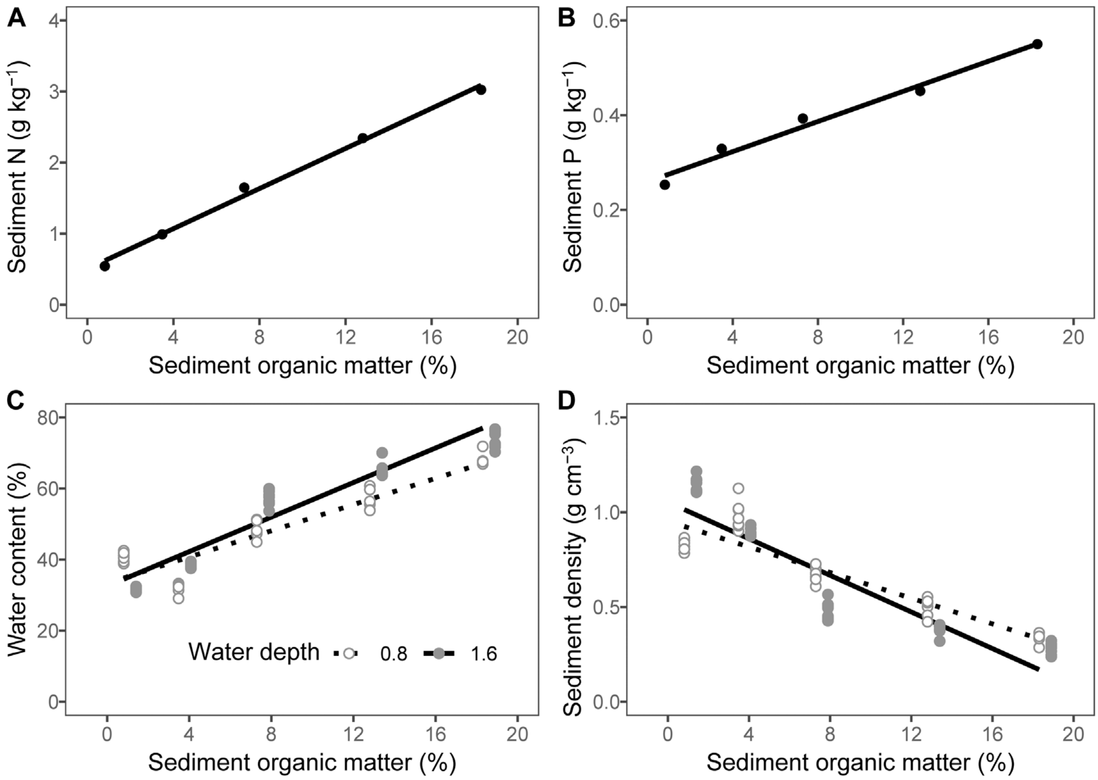

FIGURE 1 | Relationship between the sediment organic matter and **(A)** sediment total nitrogen (N), **(B)** sediment total phosphorous (P), **(C)** sediment water content, and **(D)** sediment density. The lines are predicted by linear models. The points of 1.6 m water depth were moved 0.6% to the right to avoid overlapping.

TABLE 2 | Results of two-way ANOVAs for water depth and the addition of organic matter on sediment and plant parameters.

	Water depth (A)			Organic matter (B)			A×B		
	df	F	*p*	df	F	*p*	df	F	*p*
Sediment water content	1	68.4	<0.001	4	837	<0.001	4	51.6	<0.001
Sediment density	1	3.74	0.058	4	222	<0.001	4	38.2	<0.001
Relative growth rate	1	1.98	0.165	4	9.92	<0.001	4	0.18	0.947
Shoot biomass	1	2.01	0.163	4	8.27	<0.001	4	0.72	0.584
Root biomass	1	3.04	0.087	4	8.02	<0.001	4	3.16	0.021
Plant height	1	193	<0.001	4	9.99	<0.001	4	0.97	0.430
Shoot C	1	11.6	0.001	4	1.16	0.340	4	4.60	0.003
Shoot N	1	26.2	<0.001	4	2.63	0.045	4	0.58	0.675
Shoot P	1	13.6	0.001	4	228	<0.001	4	1.73	0.157
Shoot C:N	1	34.6	<0.001	4	3.38	0.016	4	1.73	0.158
Shoot C:P	1	26.7	<0.001	4	217	<0.001	4	0.31	0.871
Shoot N:P	1	0.00	0.985	4	260	<0.001	4	3.03	0.026
Anchorage force	1	0.05	0.828	4	1.37	0.256	4	0.45	0.770

C, carbon; N, nitrogen; P, phosphorous.

Figure 1C), whereas the mean sediment density decreased from 0.99 g cm^{-3} to 0.30 g cm^{-3} (**Table 3**, **Figure 1D**).

Effects of Water Depth and the Addition of Organic Matter on Plant Growth

There was no interactive effect of water depth and organic matter addition on the plant growth parameters with the exception of the root biomass (**Table 2**; p = 0.947 for the relative growth rate, p = 0.584 for shoot biomass, p = 0.430 for plant height and p = 0.021 for root biomass). The water depth had no effect on the plant RGR (**Table 2**; p = 0.165) and shoot biomass (**Table 2**; p = 0.163), whereas the effect on plant height was significantly positive with much taller plants at a depth of 1.6 m compared with those at a depth of 0.8 m (**Table 2**, **Figure 2D**; $p < 0.001$). The plant RGR increased in parallel with the content of organic matter of the sediment from 0.81 to

TABLE 3 | Relationship between the organic matter in sediments and plant traits and sediment parameters based on linear or generalized additive models.

	Model	Water depth	N	Df/edf	F	R^2	*p*
Sediment N	lm	-	5	1	497	0.99	<0.001
Sediment P	lm	-	5	1	148	0.97	0.001
Sediment water content	lm	0.8	32	1	156	0.83	<0.001
		1.6	34	1	406	0.92	<0.001
Sediment density	lm	0.8	32	1	133	0.81	<0.001
		1.6	34	1	173	0.84	<0.001
Relative growth rate	gam	0.8	31	3.35	6.93	0.44	0.001
		1.6	33	2.30	3.69	0.21	0.043
Shoot biomass	Gam	0.8	31	3.27	4.44	0.31	0.013
		1.6	32	2.43	5.74	0.33	0.005
Root biomass	Gam	0.8	29	3.35	7.18	0.47	0.001
		1.6	33	1.48	3.77	0.19	0.026
Plant height	Gam	0.8	33	2.56	4.72	0.30	0.008
		1.6	33	3.57	5.93	0.38	0.002
Shoot C	Gam	0.8	33	1.69	5.00	0.23	0.012
		1.6	33	1	4.16	0.39	0.050
Shoot N	Gam	0.8	31	1	6.32	0.15	0.018
		1.6	29	1.78	1.92	0.11	0.161
Shoot P	Gam	0.8	32	3.83	111	0.93	<0.001
		1.6	32	3.95	132	0.94	<0.001
Shoot C:N	Gam	0.8	32	1.27	9.97	0.29	0.003
		1.6	28	1.63	0.83	0.03	0.46
Shoot C:P	gam	0.8	32	3.69	87.4	0.92	<0.001
		1.6	34	3.53	114	0.93	<0.001
Shoot N:P	gam	0.8	32	3.78	150	0.95	<0.001
		1.6	29	3.45	141	0.95	<0.001
Anchorage force	lm	0.8	31	1	0.63	0.02	0.434
		1.6	32	1	4.31	0.13	0.047

lm, linear model; gam, generalized additive model; C, carbon; N, nitrogen; P, phosphorous.

7.29% and tended to slightly decrease when the content of organic matter in the sediment was higher at both water depths (**Table 3**, **Figure 2A**; $p = 0.001$ for 0.8 m and $p = 0.043$ for 1.6 m). The plant shoot biomass responded similarly to the content of organic matter in the sediment with that of plant RGR (**Table 3**, **Figure 2B**; $p = 0.013$ for 0.8 m and $p = 0.015$ for 1.6 m). The plant height increased in parallel with that of organic matter in the sediment at the lower end of the gradient at both water depths (**Figure 2D**, $p = 0.008$ for 0.8 m and $p = 0.002$ for 1.6 m). At higher levels of sediment organic matter, the plant height was constant at a water depth of 1.6 m but tended to decrease at a water depth of 0.8 m (**Figure 2D**, $p = 0.008$ for 0.8 m and $p = 0.002$ for 1.6 m).

Effects of Water Depth and the Addition of Organic Matter on the Elemental Content of Plant Shoots

There was no interactive effect between the water depth and the addition of organic matter on the elemental content of the plant shoots with the exception of the shoot C and shoot N:P ratio (**Table 2**; $p = 0.675$ for shoot N, $p = 0.157$ for shoot P, $p = 0.158$ for shoot C:N, $p = 0.871$ for shoot C:P, $p = 0.003$ for shoot C, and $p = 0.026$ for shoot N:P). The contents of shoot N and P of the plant shoots were slightly higher at a water depth of 1.6 m than that at 0.8 m (**Table 2**, **Figure 3 B, C**; $p < 0.001$ for shoot N and $p = 0.001$ for shoot P). However, the shoot C, shoot C:N ratio, and shoot C:P ratio were lower at a water depth of 1.6 m than that at 0.8 m (**Table 2**, **Figures 3A,D,E**; $p = 0.001$ for shoot C, $p < 0.001$ for shoot C:N, and $p < 0.001$ for shoot C:P). There was no significant effect of water depth on the shoot N:P ratio (**Table 2**, $p = 0.985$). The content of shoot C increased in parallel with an increase in the content of organic matter at a water depth of 0.8 m, whereas it showed an inverse trend at a water depth of 1.6 m (**Table 3**, **Figure 3A**; $p = 0.012$ for 0.8 m and $p = 0.050$ for 1.6 m). The shoot N content decreased with an increase in the sediment organic content at a water depth of 0.8 m, while it remained unchanged at a water depth of 1.6 m (**Table 3**, **Figure 3B**; $p = 0.018$ for 0.8 m and $p = 0.161$ for 1.6 m). The content of shoot P rapidly increased in parallel with that in the organic matter in the sediment up to 7.29% but remained unchanged at greater values of organic matter at both water depths (**Table 3**, **Figure 3C**; $p < 0.001$ for 0.8 m and $p < 0.001$ for 1.6 m). The shoot C:N ratio increased as the sediment organic content increased at a water depth of 0.8 m, while it remained constant at a water depth of 1.6 m (**Table 3**, **Figure 3D**; $p = 0.003$ for 0.8 m and $p = 0.460$ for 1.6 m). The shoot C:P and N:P ratios decreased with an increase in the organic matter in the sediment from 0.81 to 7.29%, but they remained unchanged at greater values of organic content at both water depths (**Table 3**, **Figures 3E,F**, $p < 0.001$).

Relationship between the Shoot N, Shoot P, and Plant Relative Growth Rate

The plant RGR decreased as the content of shoot N at a water depth of 0.8 m, whereas there was no measurable significant relationship between the plant RGR and the content of shoot

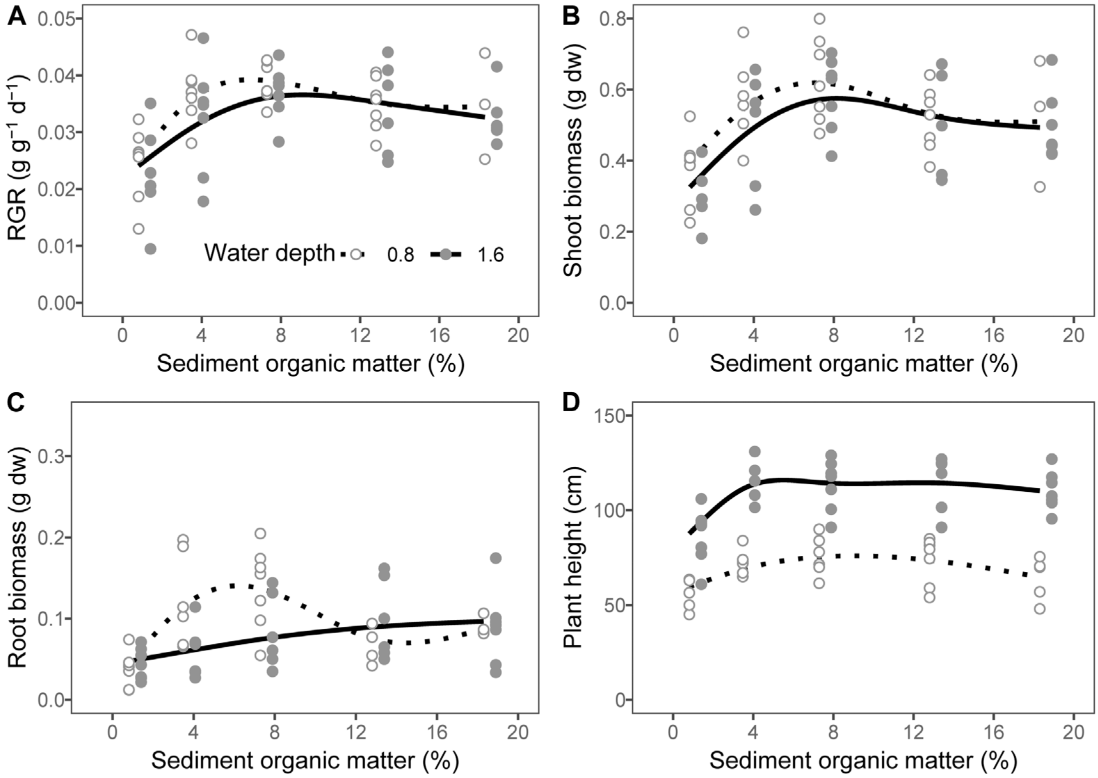

FIGURE 2 | Relationship between sediment organic matter and **(A)** plant relative growth rate (RGR), **(B)** shoot biomass, **(C)** root biomass, and **(D)** plant height. The lines are predicted by generalized additive models. The points of 1.6 m water depth were moved 0.6% to the right to avoid overlapping dw, dry weight.

N at a water depth of 1.6 m (**Table 4**, **Figure 4A**; p = 0.027 for 0.8 m and p = 0.237 for 1.6 m). The plant RGR increased when the content of shoot P was as high as 4 mg g^{-1}, while it remained unchanged with a further increase in the content of P (**Table 4**, **Figure 4B**; p = 0.007 for 0.8 m and p = 0.011 for 1.6 m).

Effects of Water Depth and the Addition of Organic Matter on the Plant Anchorage Force

Neither the water depth nor the addition of organic matter had an effect on the plant anchorage force based on the two-way ANOVA test (**Table 2**, p = 0.828 for water depth and p = 0.256 for organic matter addition), while the results of GAMs suggested that the plant anchorage force decreased with the content of organic matter in the sediment at a water depth of 1.6 m (**Table 3**, **Figure 5A**; p = 0.047). The plant anchorage force was larger than the hydraulic forces in all the treatments. This indicated that there was no risk of *M. spicatum* becoming uprooted in these sediments when the current velocity was below 0.6 m s^{-1} (**Figure 5B**).

DISCUSSION

Our findings revealed two important aspects with respect to how the enrichment of organic matter in sediment affects the submersed macrophytes. First, low levels of the enrichment of organic matter in the sediment (≤7%) enhanced the growth of *M. spicatum* by increasing the supply of phosphorus, whereas high levels of organic matter in the sediment inhibited its growth. Second, although the anchorage forces of *M. spicatum* decreased slightly as the amount of organic matter increased in the sediment, they were much higher than the hydraulic drag force on the plant at a relatively high current velocity. Therefore, our results suggest that the risk of uprooting *M. spicatum* is very low even in lakes that have high levels of organic matter in their sediment. In contrast to our hypothesis, the water depth did not alter the responses of plant growth and root anchorage of *M. spicatum* to the enrichment of organic matter.

Effects of the Addition of Organic Matter on Plant Growth

The growth of *M. spicatum* benefited from the enrichment in low levels of organic matter in the sediment. After a threshold of organic matter was reached, the growth rate of *M. spicatum* decreased. The optimum level of organic matter (≈7%) for the growth of *M. spicatum* is consistent with that identified by Barko and Smart (1986) and similar to that of *Hydrilla verticillata* (Silveira and Thomaz, 2015). The mechanism behind the enhancement of enrichment of organic matter on plant growth

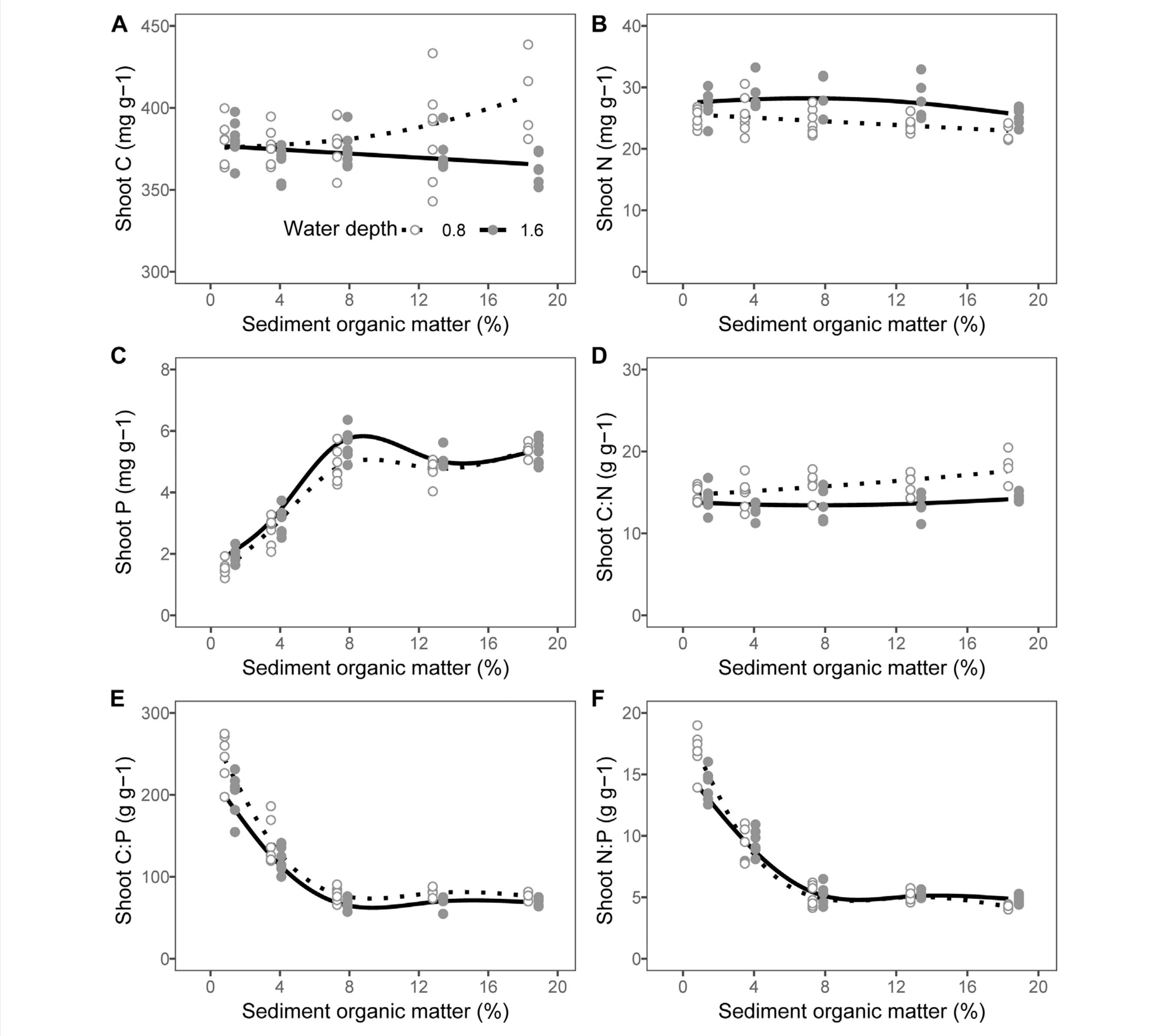

FIGURE 3 | Relationship between sediment organic matter and **(A)** shoot carbon (C), **(B)** shoot nitrogen (N), **(C)** shoot phosphorous (P), **(D)** shoot C:N ratio, **(E)** shoot C:P ratio, and **(F)** shoot N:P ratio. The lines are predicted by generalized additive models. The points of 1.6 m water depth were moved 0.6% to the right to avoid overlapping.

TABLE 4 | Relationship between shoot nitrogen (N), phosphorous (P), and plant relative growth rate based on generalized additive models.

	Predictor	Water depth	N	Df/edf	F	R^2	p
Relative growth rate	N	0.8	30	1.18	4.37	0.17	0.027
		1.6	28	1	1.46	0.02	0.237
	P	0.8	31	2.04	5.60	0.31	0.007
		1.6	31	2.11	4.58	0.29	0.011

could be that the supply of phosphorus increased in parallel with that of the organic matter in sediment. This is confirmed by the results that the contents of shoot P in *M. spicatum* increased in parallel with that in the content of organic matter (<7%), and the growth rate of *M. spicatum* increased with the content of shoot P (<4%). Richter and Gross (2013) also found that *M. spicatum* grows poorly when the supply of phosphorus is low. However, the positive effect of increased phosphorus supply was counteracted by other stressors when the organic matter reached a high level. The stressor was not likely to be the deficiency of nutrients in sediments

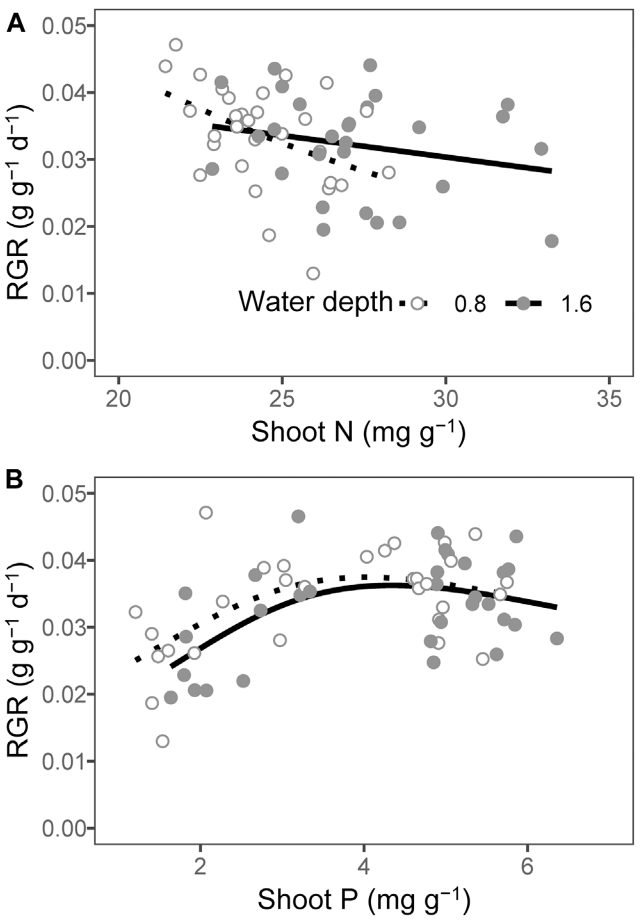

FIGURE 4 | Relationship between **(A)** shoot nitrogen (N), **(B)** shoot phosphorous (P), and the plant relative growth rate (RGR). The lines were predicted by generalized additive models.

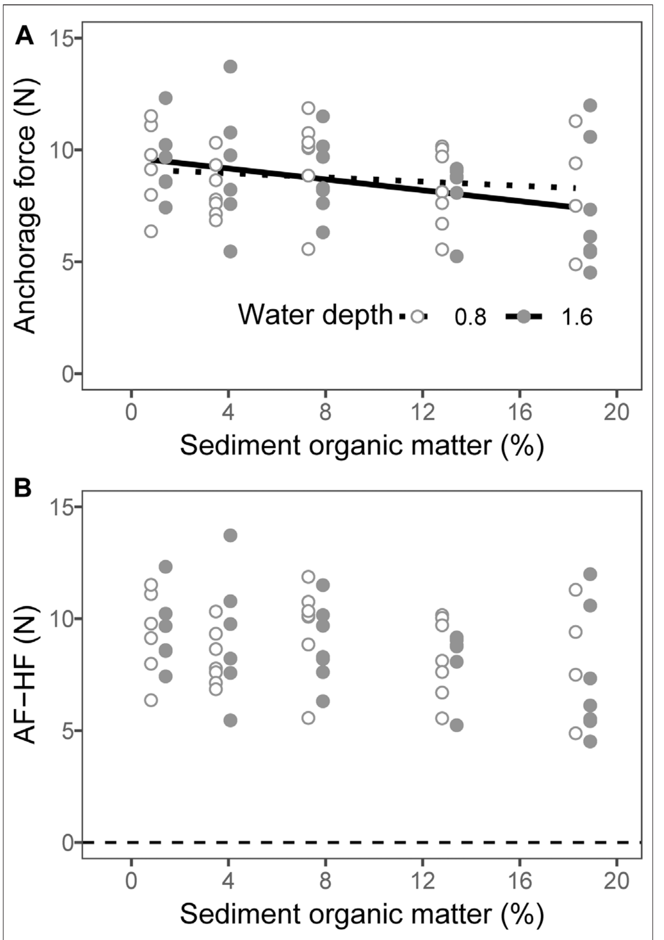

FIGURE 5 | Relationship between the sediment organic matter and plant anchorage force **(A)**. The lines are predicted by linear models. Anchorage force minus hydraulic force (AF-HF) for the sediment with different organic matter contents **(B)**. The points of 1.6 m water depth were moved 0.6% to the right to avoid overlapping.

with a high content of organic matter as described by Barko et al. (1991), since the shoot N and P of *M. spicatum* growing in sediments with a high content of organic matter were comparable to those growing in moderate ones. Instead, toxicity or the anaerobic conditions induced by the high organic matter may be responsible for the decrease in growth of *M. spicatum* (Barko et al., 1991; Wu et al., 2009; Silveira and Thomaz, 2015). However, we found that the growth rate of *M. spicatum* was quite high in our experiment even in the treatment with the highest content of organic matter, indicating that *M. spicatum* has a high tolerance to the enrichment of organic matter in the sediment. This is consistent with the results of Lemoine et al. (2012), who found that *M. spicatum* can survive in anaerobic sediments and maintain similar photosynthetic rates with those under aerobic conditions by increasing their root porosity and radial loss of oxygen.

Effects of the Addition of Organic Matter on Plant Anchorage

Anchorage in the sediment is crucial for the survival and growth of submersed macrophytes in lakes (Schutten et al., 2005). The enrichment in organic matter reduced the anchorage of roots of submersed macrophytes by impairing root development and reducing the cohesive strength of the sediment (Sand-Jensen and Møller, 2014). In our study, the force of root anchorage clearly showed a slight tendency to decrease with increasing organic matter in the sediment as predicted at a water depth of 1.6 m. The root anchorage force was primarily determined by the size of plant root and the characteristics of the sediment (Sand-Jensen and Møller, 2014). No significant reduction of the root system in the sediment that contained a high content of organic matter was observed in our experiment. Thus, the reduction of anchorage force in the sediment that had a high content of organic matter was primarily owing to falling mass density and the falling cohesive binding between root surfaces and the surrounding sediment (Sand-Jensen and Møller 2014). Consistent with a previous study (Schutten et al., 2005), we demonstrated that *M. spicatum* had a very low risk of uprooting even in the sediment with the highest content of organic matter (18%) in our experiment because the anchorage force of the plants was much higher than the hydraulic force that the plant may be exposed in lakes (Schutten et al., 2004).

Effects of Water Depth on the Response of Plant Growth and Root Anchorage to Enriched Organic Matter

Overall, the water depth did not alter the response of plant growth and root anchorage to the enrichment of organic matter in the sediment. *M. spicatum* elongated its shoots to avoid low light stress and increased the contents of shoot N and P to enhance the photosynthetic efficiency at high water depths, which resulted in a similar biomass at the end of the experiment. Similar responses to low light condition were also identified in *M. spicatum* (Strand and Weisner, 2001) and other canopy-forming species (He et al., 2018; He et al., 2019). The canopy-forming species elongate their stems as a major strategy to respond to low light conditions, which can help these species to concentrate their leaves closer to the water surface (He et al., 2019). Increased leaf chlorophylls at low light conditions, which resulted in higher N and P contents in leaves (He et al., 2018), could further enhance their ability to absorb light (Strand and Weisner, 2001; Hussner and Heidbuchel, 2021). Interestingly, the plastic responses of *M. spicatum* to low light stress did not weaken its ability to manage the stresses induced by high organic matter in the sediment. Therefore, we demonstrated that *M. spicatum* could maintain the ability to assimilate and allocate the resources to both support growth and resist the stress of enrichment of organic matter through morphological and physiological adjustments in deep water. The ability to tolerate high amounts of organic matter in the sediment and effectively manage low light stress could be the reason for the ability of this species to survive eutrophication in lakes (Qiu and Wu, 1996; Cao et al., 2011).

In conclusion, our data showed that *M. spicatum* had a high tolerance to the enrichment with organic matter and could anchor without the risk of uprooting in sediments with a wide range of organic matter content. In addition, *M. spicatum* can effectively manage low light stress through morphological and physiological adjustments. Thus, we suggest that *M. spicatum* could be a potential species for the restoration of eutrophic lakes since it can grow well and anchor stably in sediments with a relatively high amount of organic matter and effectively manage low light stress.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding authors.

AUTHOR CONTRIBUTIONS

LH and GG conceived the idea and proposed the method. LH and RW contributed to conduct the experiment. LH, HZ, YL, MZ, GZ, TC, and LN wrote the manuscript. All authors read and approved the final manuscript.

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