

Effects of silt-laden water on the growth of submerged plants

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ABSTRACT

To investigate the impact of floods on aquatic plants, many studies have focused on water characteristics, such as the frequency and magnitude of water fluctuations and flooding duration. However, the silt, sand, and nutrients carried by floods have received less attention. In artificially fluctuating water with silted sediment, we grew three submerged species with similar canopy-forming growth habits in mixtures: rooted hydrilla (*Hydrilla verticillata* [L. f.] Royle), rooted Eurasian watermilfoil (*Myriophyllum spicatum* L.), and rootless coontail (*Ceratophyllum demersum* L.). We observed that silt-laden water with a higher nutrient concentration consistently enhanced the tissue nutrient concentrations of submerged plants. However, the effects of silt-laden water on plant growth differed among species and were stronger in rootless coontail than they were in rooted Eurasian watermilfoil and hydrilla. In mixed cultures, hydrilla had a competitive growth advantage over the other species because of its robust nutrient uptake and its light tolerance. Our results imply that, although turbid water significantly benefits rootless coontail, which absorbs nutrients from water, these plants cannot outcompete rooted hydrilla. To regulate the relative abundance of co-occurring, submerged species, changes in the frequency of floods carrying silt and sand, whether natural or artificial, may not be an effective strategy.

Key words: aquatic macrophyte, flood, nitrogen, nutrient, phosphorus.

INTRODUCTION

As part of our understanding of the increasing effects of climate change and human disturbance on water dynamics in wetland ecosystems (Gong and Wang 2000, Smith 2011, Lizotte et al. 2012), the impact of floods on aquatic plants has been well documented (Grace 1989, Cooling et al. 2001, Deegan et al. 2007, Zhu et al. 2012). These studies have mainly focused on water characteristics, such as the frequency and magnitude of water fluctuations and flooding duration. However, floods that carry silt, sand, and nutrients because of increased soil erosion from agricultural and forested lands (Martin 1999, Swank et al. 2001, Toda et al. 2005, Wang and Fan 2006, Liu et al. 2007) have received less attention.

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In general, silt-laden flood water increases the levels of nutrients, such as nitrogen (N) and phosphorus (P), which are resuspended from the sediments or introduced with water inputs (Izagirre et al. 2009, Gallardo and Español 2012). These nutrients are then available to the leaves of submerged plants. After flood pulses and when suspended solids are deposited, the nutrients in the surface sediment may alter the nutrient supply to the roots of submerged plants. Although the relative importance of root uptake (from sediment) vs. shoot uptake (from water) of nutrients has long been controversial (Denny 1972, Best and Mantai 1978, Carignan and Kalff 1980, Chambers et al. 1989, Robach et al. 1995, Madsen and Cedergreen 2002), with much evidence supporting a significant role for roots (Denny 1972, Best and Mantai 1978, Barko and Smart 1980, Carignan and Kalff 1980, Chambers et al. 1989). However, some results support the view that leaf uptake can be the main pathway for nutrient acquisition (Robach et al. 1995). For example, in nutrient-rich habitats, some submerged plants are able to satisfy their mineral nutrient requirements by leaf uptake alone (Madsen and Cedergreen 2002). Changes in nutrient levels in the water and sediment from floods may affect the growth of submerged plants.

Hydrilla (*Hydrilla verticillata* [L. f.] Royle), Eurasian watermilfoil (*Myriophyllum spicatum* L.), and coontail (*Ceratophyllum demersum* L.) are widespread, submerged species (Cook 1996) and are the most-frequent plants along the middle and lower reaches of the Yangtze River, China (Xing et al. 2013a). The three species have a similar tall, canopy-forming growth habit and occupy a similar range of water depths, which concentrate their leaves at or near the water surface (Chambers 1987, Chambers and Kalff 1987, Hofstra et al. 1999). The growth of these canopy-producers is primarily determined by sediments, the major source of N and P and is relatively independent of light availability (Chambers and Kalff 1987). However, a major difference among these three species is that hydrilla and Eurasian watermilfoil are rooted in sediments and rely on leaves and roots for nutrient uptake, whereas coontail is rootless and relies solely on leaves (Cook 1996).

The above species frequently co-occur in natural communities (Cheng and Li 2000, Xiong et al. 2006, Gao et al. 2011) and rarely form monospecies communities. Their relative abundances vary within communities, and any of the species may be dominant, depending on environmental conditions and plant growth traits (Cheng and Li 2000, Xiong et al. 2006, Gao et al. 2011). Of the environmental factors affecting plant growth, nutrient and water levels are very important (Ma et al. 2003, Xiong et al. 2006). Therefore, in this study, we used artificial, silt-laden water that involved changes in nutrient and water levels simultaneously to

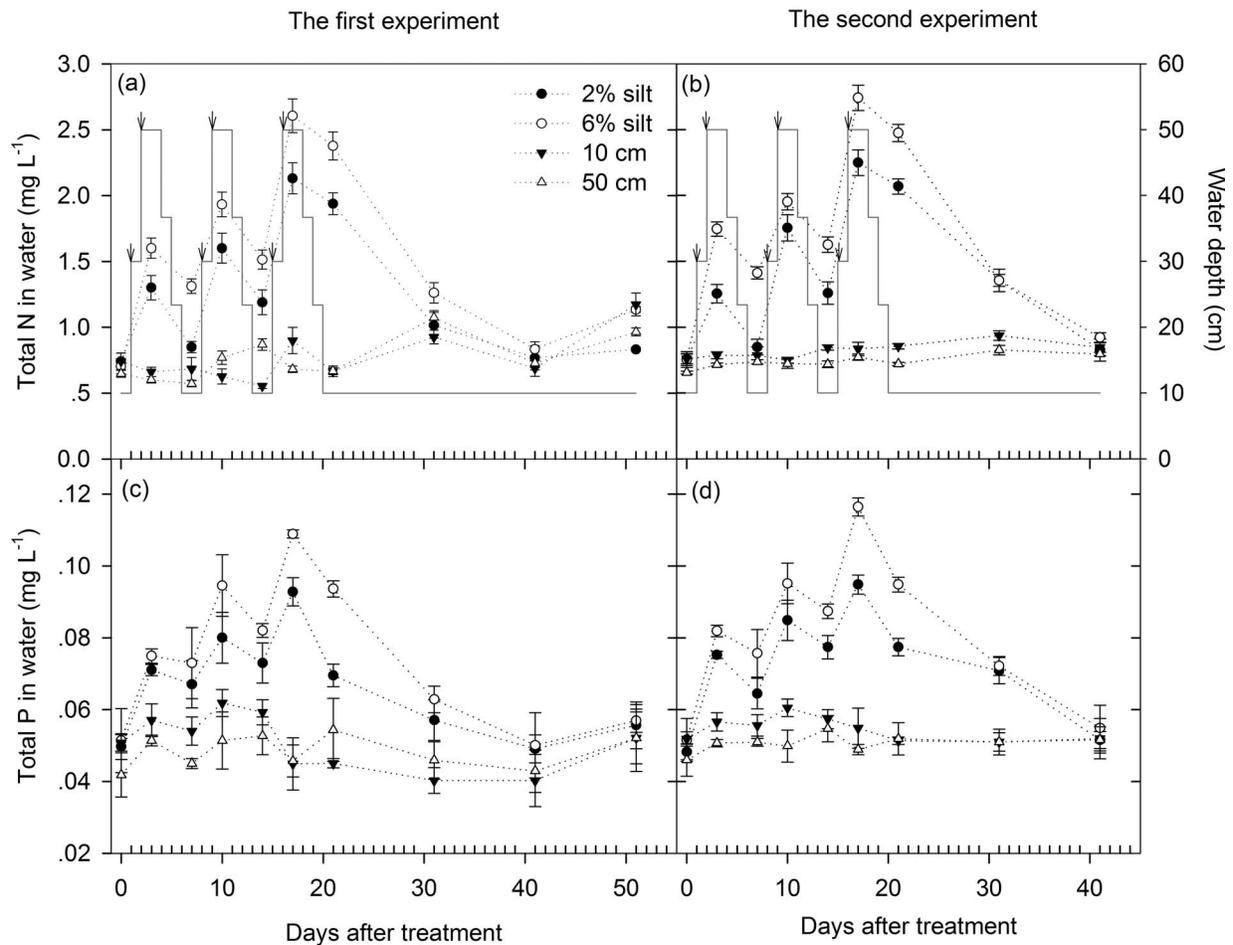


Figure 1. Total nitrogen (N) and phosphorus (P) content in the water in the two fluctuating treatments of artificial silt-laden water (2 and 6% silt by weight) and two control treatments without silt-laden water (constant water depths of 10 and 50 cm). The grey line denotes the changes in water depth. Arrows indicate the addition of silt-laden water.

simulate the effects of turbid flood water on the growth of submerged plants in mixed cultures. Our aims were to determine 1) whether silt-laden water improves the growth of submerged plants because of changes in environmental nutrient levels, and 2) whether differences were from the effects of turbid water on the growth of rooted and rootless, mixed, submerged plants with similar growth habits.

MATERIALS AND METHODS

We conducted an experiment in summer 2012 and repeated it in summer 2014. The experiments were conducted in the experimental garden at the South-Lake Campus of Central China Normal University (30°30'N; 114°21'E) in Wuhan, Hubei, China.

The first experiment

Plant materials. Twelve cylindrical, plastic buckets were used for plant cultivation. In each bucket, 10-cm-thick sediment ($1.312 \pm 0.025\%$ total N, $0.067 \pm 0.011\%$ total P, and $6.562 \pm 0.985\%$ organic matter; 23.52% sand, 51.11% silt, and 25.37% clay by dry weight) collected from Lake

Donghu in Wuhan, China, was placed on the bottom. Above the sediment was 10 cm (nine buckets) or 50 cm (three buckets) of tap water. After the tap water was exposed to sunshine for 3 d to dissipate chlorine gas, three vegetative fragments each of hydrilla, coontail, and Eurasian watermilfoil were collected from a pond in our experimental garden and were placed into each bucket on July 11, 2012. We used mixtures of species, rather than monocultures, to simulate natural situations more closely. Each fragment was about 10 cm long. Fresh weights of the fragments were 1.75 ± 0.34 g for hydrilla, 1.53 ± 0.54 g for coontail, and 2.97 ± 0.91 g for Eurasian watermilfoil.

Experimental design. We designed two treatments of artificial, silt-laden, fluctuating water (silt content: 2 and 6% by weight; fluctuating amplitude: 40 cm) with an initial water depth of 10 cm, and two control treatments of constant water (shallow: 10 cm; deep: 50 cm) without silt-laden water. Each treatment had three replicates (three buckets: height 70 cm, diameter 50 cm). The water depths were intentionally shallow because 50 cm is the average transparency in many eutrophic lakes (Xing et al. 2013a). By using this as our maximum depth, variation in light intensity had minimal effects on plant growth. Silt content

Table 1. SUMMARY (*F* VALUES) OF ONE-WAY ANOVA OF THE EFFECTS OF EXPERIMENTAL TREATMENTS (TWO FLUCTUATING TREATMENTS OF ARTIFICIAL SILT-LADEN WATER AND TWO CONSTANT-CONTROL TREATMENTS OF 10 AND 50 CM) ON GROWTH TRAITS OF EURASIAN WATERMILFOIL (*MYRIOPHYLLUM SPICATUM* [Ms]), HYDRILLA (*HYDRILLA VERTICILLATA* [Hv]), AND COONTAIL (*CERATOPHYLLUM DEMERSUM* [Cd]) IN TWO REPEATED EXPERIMENTS.

Trait	First Experiment			Second Experiment		
	Ms	Hv	Cd	Ms	Hv	Cd
Total biomass (g)	28.4***	24.7***	430.6***	9.0**	87.1***	299.2***
No. of branches	9.4**	5.8*	55.5***	0.6	49.4***	16.1***
Total No. of nodes	33.6***	33.5***	157.0***	177.5***	311.8***	72.6***
Length of longest stem (cm)	3.1	19.5***	110.9***	37.4***	137.7***	127.7***
Average length of internodes (cm)	14.8**	11.3**	59.8***	66.6***	20.0**	98.8***
Total N content at end of water fluctuation cycles (%)	37.8***	7.7**	24.2***	88.2***	68.7***	68.7***
Total N content at harvest (%)	9.9**	9.8**	21.4***	123.1***	135.6***	100.2***
Total P content at end of water fluctuation cycles (%)	127.8***	9.0**	7.9**	190.7***	39.3***	55.5***
Total P content at harvest (%)	16.5***	11.3**	0.9	116.8***	74.1***	76.5***

N = nitrogen, P = phosphorus.
 ****P* < 0.001, ***P* < 0.01, **P* < 0.05.

was based on Wang and Fan (2006), who found that natural floodwaters contained 2.32 to 6.05% silt. The silty water was a mix of tap water exposed to sunshine for 3 d and silted sediment ($0.081 \pm 0.010\%$ total N, $0.053 \pm 0.012\%$ total P, $5.01 \pm 0.51\%$ organic matter; $86.13 \pm 4.32\%$ sand, $13.35 \pm 3.10\%$ silt, and $0.52 \pm 0.01\%$ clay by dry weight) collected from a local river in Wuhan.

After 1 wk of plant preculture, fluctuation treatments began in three cycles (Figure 1). Each cycle began with a 20-cm increase in water depth per day for 2 d, to a final depth of 50 cm, where the water level was maintained on the third day. On the following 3 d, the water depth decreased 13.3 cm per day, and was maintained at 10 cm on the seventh day. After three consecutive cycles (3 wk), water depth was maintained at 10 cm for 30 d. To raise the water level, the appropriate water and sediment were mixed in a plastic basin and immediately poured into the center of the experimental buckets from a height of about 20 cm above the water surface. To lower the water depth, plastic pipes (2.5 cm in diameter) were used to draw water to minimize disturbance.

We recorded water pH, temperature, electrical conductivity,¹ and underwater light intensity² at a depth of 5 cm at about 1300 hours every 4 d. Throughout the experiments, these parameters in all buckets were in the range of 7.02 to 7.43, 24.0 to 28.1 C, 107 to 427 $\mu\text{S cm}^{-1}$, and 406.2 to 523.8 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, respectively.

Measurements. Samples of overlying water and surface sediment were collected from each bucket to measure total N and total P on the third and seventh day of each fluctuation cycle and every 10 d during the 30-d stasis period. Total N and total P in plant tissues were measured on the last day of the third fluctuation cycle and on harvest day. At the first measurement, a small quantity of leaf material (fresh weight: 3.53 to 4.19 g; dry weight: 0.201 to 0.205 g) were collected from each bucket. On the 51st (last) day of treatment, all plants were harvested to measure the longest stem length, branch number, node number, and internode length. Then, all plants were dried at 80 C to weigh biomass. Nutrients (total N and total P) in water and plants were measured according to SEPA (2002) and Cao and Wang (2012), respectively. Total N and P in sediment were determined by the UV absorption photometric method and the molybdenum–antimony (Mo–Sb) antispec-

trophotometric method after potassium persulfate ($\text{K}_2\text{S}_2\text{O}_8$) digestion, respectively (SEPA 2002).

The second experiment

The repeated experiment started on July 27, 2014, when plants were cultivated into buckets. In the second experiment, the following protocols were the same as the first experiment of 2012: experimental treatments, time of plant preculture, size of buckets, sediment collection site, plant sample collection, parameter measurement, water pretreatment, and routine management. However, the replicates of each treatment were increased to five. Additionally, the number of days maintaining a water depth at 10 cm after three consecutive fluctuation cycles was shortened to 20 d before harvest (Figure 1) to prevent the dropping temperature from negatively affecting plant growth in mid September. Water pH, temperature, electrical conductivity,¹ and underwater light intensity² at a depth of 5 cm were in the range of 7.11 to 7.35, 23.4 to 27.2 C, 126 to 411 $\mu\text{S cm}^{-1}$, and 489.3 to 591.7 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, respectively, throughout the experiment.

Data analysis

Before analysis, the average internode length of the three species in the two experiments was square root–transformed to achieve homoscedasticity. One-way ANOVA tests were used to analyze differences in growth traits among treatments for each species and among species for each treatment. For traits in which significant differences (*P* < 0.05) were detected, Tukey's tests among treatments and among species were performed. Statistical analyses were performed using STATISTICA 6.0 software,³ and figures were drawn in SigmaPlot 10.0 software.⁴

RESULTS AND DISCUSSION

Silt-laden water enhances the nutrient content of water and submerged plant tissues

During water-fluctuation cycles, total N and P content in the overlying water was higher in the silty-water treatments

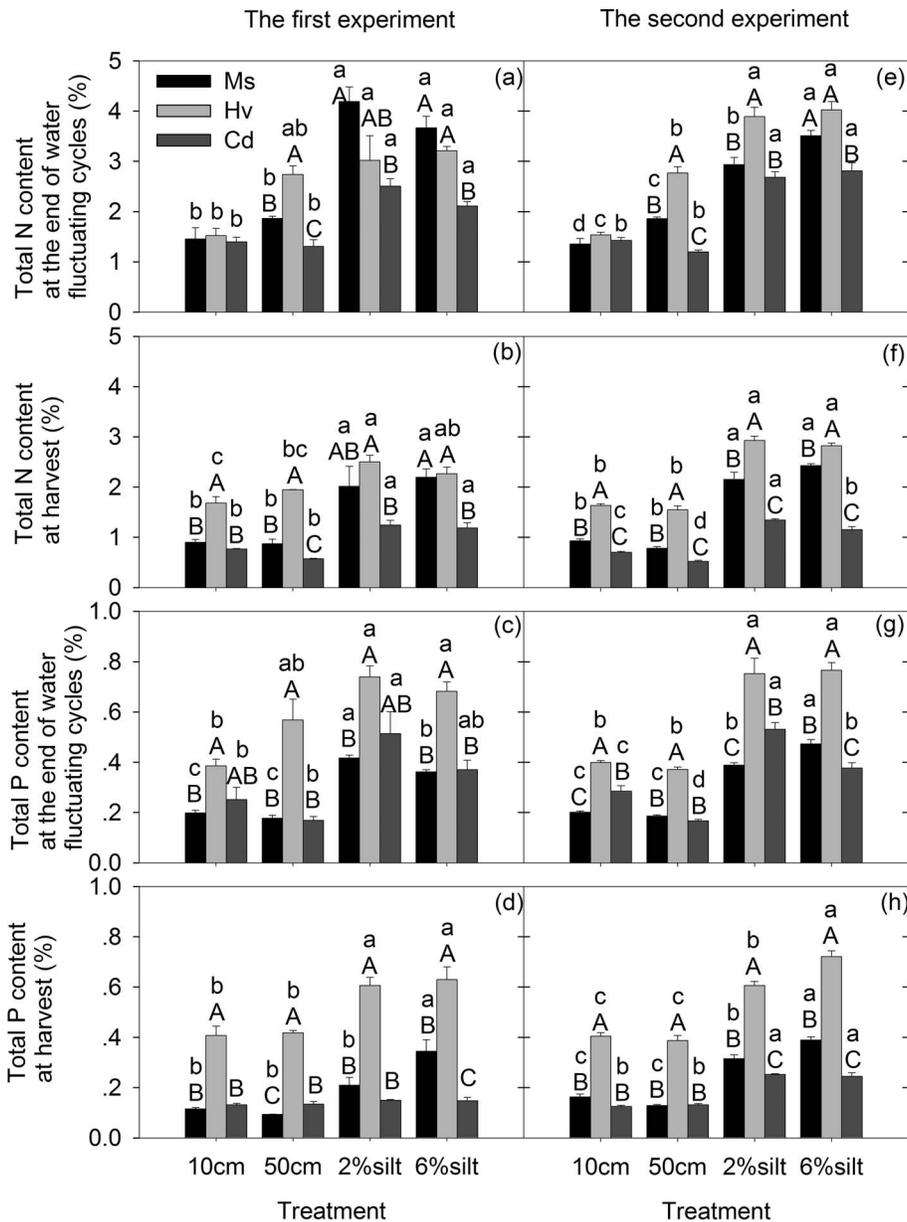


Figure 2. Total nitrogen (N) and phosphorus (P) content in Eurasian watermilfoil (*Myriophyllum spicatum* [Ms]), hydrilla (*Hydrilla verticillata* [Hv]), and coontail (*Ceratophyllum demersum* [Cd]) in two fluctuating treatments of artificial silt-laden water (2 and 6% silt by weight) and two control treatments without silt-laden water (constant water depths of 10 and 50 cm). Different lowercase and uppercase letters denote significant differences among the four treatments for each species and among the three species in each treatment, respectively (Tukey's tests, $P < 0.05$). Significance levels are not shown for traits in which no significant differences ($P > 0.05$) were detected by ANOVA.

than it was in the constant-water controls (Figure 1). Moreover, total N and P content was higher in the 6% silty-water treatment than it was in the 2% treatment. However, differences among the four treatments became negligible after water fluctuations ceased. Similar increases in water nutrient concentrations were observed in channels subjected to a pulse of clay in a study into the effects of siltation in streams and rivers on periphyton (Izagirre et al. 2009). Solute concentrations frequently increase in natural streams and rivers because of soil erosion from agricultural and forested lands in many regions of the world (Martin 1999, Swank et al. 2001, Wang and Fan 2006, Liu et al. 2007).

N and P content in the three submerged species were generally higher in the two silty-water treatments than it was in the two constant-water controls, both at the end of the fluctuation cycles and at harvest (Table 1; all P values, except one, were less than 0.01; Figure 2). Thus, the effects of silt-laden water on tissue nutrient content of the rooted and rootless plants were similar. These relationships between water and tissue nutrients agree with previous findings that the levels of elements, including N and P, in submerged macrophytes are positively correlated with those in water but not in the sediment (Robach et al. 1995, Xiong et al. 2010, Xing et al.

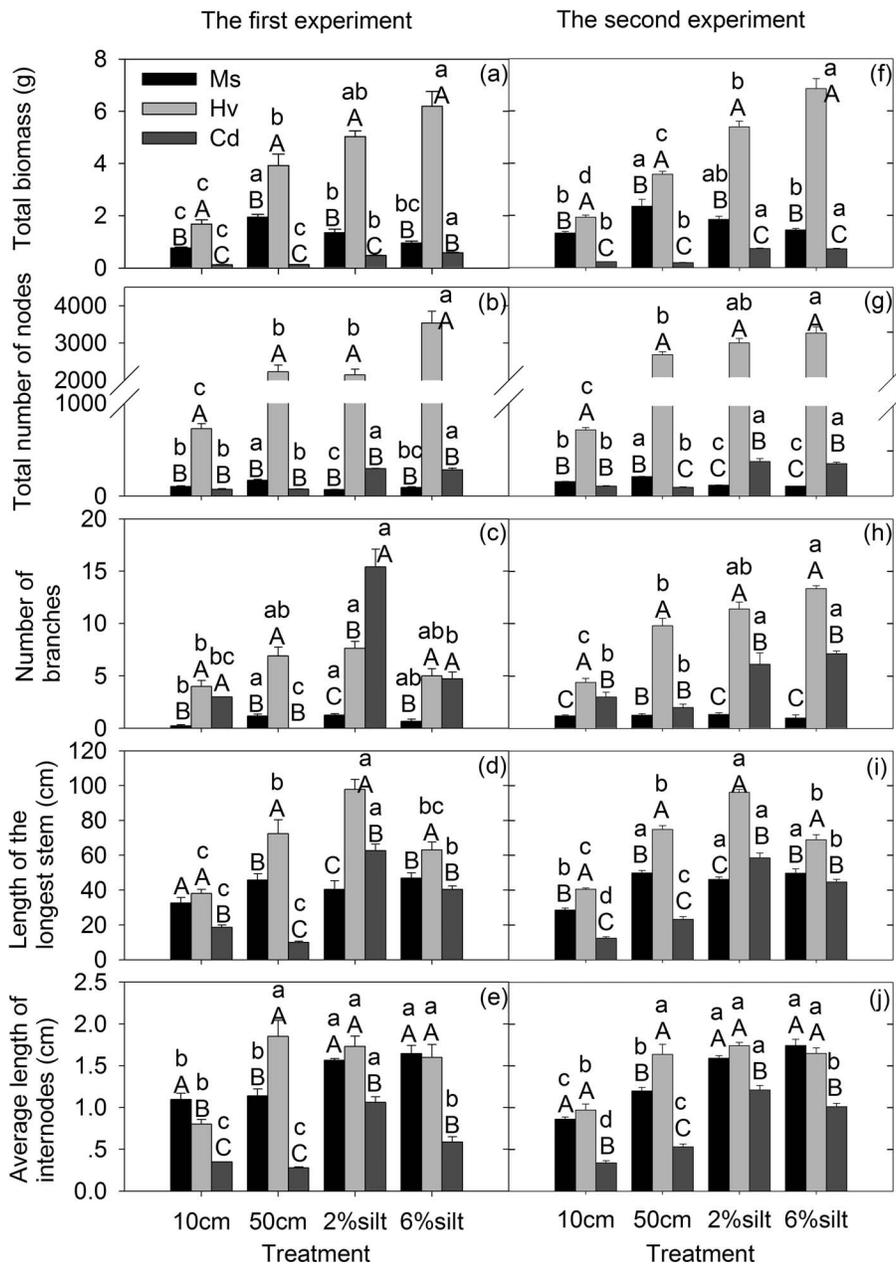


Figure 3. Total biomass and morphological traits of Eurasian watermilfoil (*Myriophyllum spicatum* [Ms]), hydrilla (*Hydrilla verticillata* [Hv]), and coontail (*Ceratophyllum demersum* [Cd]) in two fluctuating treatments of artificial silt-laden water (2 and 6% silt by weight) and two control treatments without silt-laden water (constant water depths of 10 and 50 cm). Different lowercase and uppercase letters denote significant differences among the four treatments for each species and among the three species in each treatment, respectively (Tukey's tests, $P < 0.05$). Significance levels are not shown for traits in which no significant differences ($P > 0.05$) were detected by ANOVA.

2013a,b). The significant effects of external nutrient concentrations on plant tissue levels have been discussed in previous studies on aquatic vascular plants, including submerged species (Demars and Edwards 2007), and on terrestrial plants (Sabine 2004). Although the relationship between external and plant-tissue N and P concentrations is often considered weak (Güsewell and Koerselman 2002, Demars and Edwards 2007), nutritional changes resulting from silt-laden water should not be neglected.

Different growth rates of the three submerged plants in silt-laden water

With increased plant tissue N and P concentrations in the silt-laden water treatments (Figure 2), coontail showed enhancement of total biomass and all morphological traits (Table 1, all P values less than 0.001), and hydrilla had more total biomass, but Eurasian watermilfoil did not exhibit any positive growth responses, except for internode length (Table 1; Figure 3). These patterns indicate that the

relationship between growth and tissue nutrients is species specific. Similar species-specific relationships were reported by Li et al. (2013) who found that, with increased water depth, coontail had increased N and P concentrations in leaves and stems, but its growth rate was unaffected; meanwhile, four other rooted macrophytes, including hydrilla and Eurasian watermilfoil, had reduced growth rates but maintained N and P concentrations. Nevertheless, whether the correlations among coontail growth and nutrient levels in plant tissues and surrounding water are related to a plant's rootlessness remains an open question.

Although the growth of rootless coontail was promoted by silt-laden water, it exhibited the lowest biomass accumulation among the three species in mixed cultures, independent of treatment (Figure 3). Similarly, Hofstra et al. (1999) found that coontail growth was extremely disadvantaged relative to cocultured hydrilla in terms of surface cover, dry weight, and tuber number. The poor growth of coontail may be partially attributed to the repressive effect of vigorous hydrilla, which had the greatest total biomass, total node number, and longest stem length among our focal species (Figure 3). The strong competitive ability of hydrilla has been observed repeatedly when this species is grown with other submerged plants (Chambers et al. 1993, Hofstra et al. 1999, Umetsu et al. 2012, Zhang et al. 2013, Zhang et al. 2014).

The competitive advantage of hydrilla may be related to its strong ability to accumulate nutrients, especially P. Among the three species, hydrilla had the greatest concentrations of P at the end of the fluctuation cycles and at harvest (Figure 2). The idea that hydrilla has high nutrient-uptake ability is supported by results from Xing et al. (2013a), in which hydrilla plants directly collected from natural populations had higher N concentrations than five other submerged species, including Eurasian watermilfoil and coontail. Meanwhile, the tissue P concentration of hydrilla was higher than that of four species and only slightly lower than coontail. Relatively high nutrient levels give hydrilla a growth advantage.

In addition to its capacity for nutrient uptake, the vigorous growth of hydrilla can be partially attributed to its advantage in light capture, as implied by its long stems (Figure 3). Furthermore, hydrilla has a low-light compensation point (Van et al. 1976) and a wide tolerance to changing light levels (Hofstra et al. 1999), so its growth is little affected by changes in light availability resulting from water depth and turbidity. In mixtures of the three species, tall hydrilla plants inevitably shaded the other two species. Additionally, both coontail and Eurasian watermilfoil prefer high-light conditions (Van et al. 1976, Su et al. 2004). Reduced light intensity resulting from turbidity and the dense canopy of hydrilla may have limited the growth of coontail and Eurasian watermilfoil.

Compared with hydrilla, low N and P content (Figure 2) may also have limited the growth of coontail. However, its nutrient limitation was not due simply to its rootlessness because rooted Eurasian watermilfoil had a similar nutrient content (especially P) to coontail in many situations (Figure 2). With similar light compensation points that are higher than that of hydrilla (Van et al. 1976), coontail and Eurasian

watermilfoil were inferior to hydrilla in terms of photosynthetic rates from the start of their mixed cultures. The lower photosynthetic rates in these two species might have further limited their biomass production. Thus, although the three species have similar canopy-forming growth habits (Chambers 1987, Chambers and Kalff 1987, Hofstra et al. 1999), hydrilla gradually prevailed in direct competition for reasons in addition to its superiority in nutrient uptake. The extreme advantage of hydrilla over coontail and Eurasian watermilfoil might mask differences between rootless and rooted species.

In conclusion, silt-laden water, with a high nutrient concentration, consistently enhanced the tissue nutrient concentrations of the submerged plants. However, its effects on plant growth traits differed among species and were more notable in the rootless coontail than in the rooted Eurasian watermilfoil and hydrilla. Comparing their performances in mixed cultures, hydrilla had a competitive advantage in growth over the other two species, independent of treatments. The superior performance of hydrilla may be related to its robust nutrient uptake and light capture. Our results imply that, although silt-laden water significantly benefits nutrient absorption by rootless coontail, that species is unlikely to outcompete the rooted hydrilla when these species co-occur. To regulate the relative abundance of co-occurring, submerged species, changes in the frequency of floods carrying silt and sand, whether natural or artificial, may not be an effective strategy. This study is the start of our research into the effects of increasing flooding on aquatic communities and future work will involve examining the influence of silt-laden water on communities with more-diverse species and different life forms. We expect these results will provide valuable references for the effective management of wetland ecosystems.

SOURCES OF MATERIALS

¹Waterproof ECTestr, Eutech Instruments, Thermo Fisher Scientific, 81 Wyman St., Waltham, MA 02451.

²LI-193SA underwater irradiance sensor, LI-COR, 4647 Superior St., Lincoln, NE 68504.

³STATISTICA 6.0 software, StatSoft, 2300 E. 14th St., Tulsa, OK 74104.

⁴SigmaPlot 10.0 software, Systat Software, 225 W. Washington St., Suite 425, Chicago, IL 60606.

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