PRIMARY RESEARCH PAPER



Effects of sediment-borne nutrient and litter quality on macrophyte decomposition and nutrient release

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Received: 23 December 2015/Revised: 18 August 2016/Accepted: 19 August 2016/Published online: 29 August 2016 © Springer International Publishing Switzerland 2016

Abstract Macrophyte decomposition is a critical process that affects carbon and nutrient cycling, and energy flow, although the majority of the details involved in the process remain unclear. For the present study, a litter bag experiment was conducted to investigate the effects of sediment-borne nutrient and litter quality on the decomposition rates and nutrient release of four macrophyte life forms (emergent macrophyte: *Phragmites australis*, free-floating macrophyte: *Nymphoides peltata*, submerged macrophyte: *Ceratophyllum demersum*), and a species mixture. Our results indicated that litter quality significantly influenced macrophyte decomposition

Handling editor: Chris Joyce

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Keywords Decomposition · N and P release · Sediment-borne nutrient · Litter quality · Macrophytes

Introduction

The decomposition of aquatic macrophytes is an essential ecological process that influences nutrient cycling and energy flows in aquatic ecosystems (Federle et al., 1982; Hoorens et al., 2003; Debusk & Reddy, 2005). Particularly in eutrophic shallow lakes,

the incomplete decomposition of detritus leads to sediment accumulation and the acceleration of lake aging (Murray et al., 2006; Costantini et al., 2009; Yu et al., 2010).

Organic matter decomposition in aquatic ecosystems is influenced by various factors such as water temperature, pH, litter quality and complexity (i.e., interactions between different litter types), and nutrient availability (Rejmánková & Houdková, 2006; Dang et al., 2009; Song et al., 2013; Lemley et al., 2014). It has been well-documented that higher nutrient availability in the environment may directly or indirectly affect macrophyte decomposition rates and nutrient release (Royer & Minshall, 2001; Bianchini et al., 2008; Rejmánková & Houdková, 2006; Li et al., 2013). Previous studies have primarily examined the effects of nutrient availability in water columns on aquatic macrophyte decomposition (Ferreiro et al., 2011; Li et al., 2012; Song et al., 2013). Little is known about the responses of macrophyte decomposition to sediment-borne nutrients, although most dead macrophytes reside on the surface layers of lake sediments. Lake sediments with different nutrient characteristics have contrasting properties (Clarke & Wharton, 2001; Yu et al., 2010), which is reflected by their susceptibility to microbial decomposition (Gudasz et al., 2015). Thus, it is important to investigate the effects of sediment-borne nutrients on aquatic macrophyte decomposition rates and nutrient release.

Litter quality, defined as the chemical characteristics of litter, is considered as one of the critical determinants of its decomposition (Villar et al., 2001; Hoorens et al., 2003; Longhi et al., 2008). In general, high-quality litter (i.e., high initial nitrogen (N) and phosphorus (P) contents, as well as low C:N, C:P and N:P ratios), facilitates rapid decomposition (Rejmánková & Houdková, 2006; Li et al., 2012; Li et al., 2013). In addition, litters in natural environment are typically a mixture of the litterfall of diverse species (Rosemond et al., 2010; Berglund & Ågren, 2012; Chapman et al., 2013). Many previous studies have indicated that the decomposition rates of litter mixtures of diverse species may differ significantly from the anticipated rates, estimated from the additive decomposition rates of single species, most likely due to the chemical interactions between litter compounds (Lecerf et al., 2011; Berglund & Ågren, 2012). However, these studies are often conducted based only on the effects of litter quality, without taking the interactions between litter quality and sediment-borne nutrients into consideration. There exists a complex interplay between the litter quality of aquatic macrophytes and sediment-borne nutrients, possibly due to interactive effects (Murray et al., 2006; Song et al., 2013). In some cases, high concentrations of nutrient that are available in the ambient environment play a greater role than does the quality of low concentrations of nutrients and in influencing decomposition rates (Debusk & Reddy, 2005). However, due to the effects of high-quality litter and variations in microbial compositions and activities, other studies suggest that high concentrations of nutrient that are available in the ambient environment may not stimulate litter decomposition (Royer & Minshall, 2001).

Despite widespread concerns regarding detritus decomposition in aquatic ecosystems, few studies have explored effects of sediment-borne nutrients and their interactions with litter quality on the macrophyte decomposition. In order to assess the impacts of sediment-borne nutrients and their interactive effects with litter quality on the decomposition of macrophytes, we present data here from an experimental study with three sediment treatments which represent different sediment-borne nutrient levels. We hypothesized that (1) higher sediment-borne nutrients enhance the decomposition of macrophytes; (2) litter quality has greater important than sediment-borne nutrients in affecting the macrophyte decomposition and nutrient release.

Materials and methods

Experimental materials and litter bags

Four common macrophyte species, emergent macrophyte *Phragmites australis* (Cavanilles) Trinius ex Steudel, free-floating macrophytes *Hydrocharis dubia* (Blume) Backer, floating-leaved macrophytes *Nymphoides peltata* (S. G. Gmelin) O. Kuntze, and submerged macrophytes *Ceratophyllum demersum* Linnaeus, were employed to examine the effects of sediment-borne nutrients and litter quality on macrophyte decomposition and nutrient release. On June 12, 2014, intact plants (including roots, stems, and leaves) were collected from Shahu Lake (114°21′E, 30°35′N), a eutrophic lake that is typical of the lakes in Wuhan City, in Hubei Province, China, with area of 3.08 km^2 and depth of 1.5 m. The plants were then carefully washed to remove sediment residues and micro-invertebrates, air dried at room temperature, and then oven dried to a constant weight at 70°C for 48 hours. The dried plant material was subsequently cut into sections (2 to 4 cm in length) prior to further use.

Precisely 4 g litter was placed into mesh bags $(10 \text{ cm} \times 10 \text{ cm}; \text{pore size: } 500 \text{ }\mu\text{m})$ which were then sewn shut using nylon thread. In order to test the interaction of species, the litterbags were filled with both single species and a mixture thereof. In singlespecies bags, the entire bodies of *H. dubia*, *N. peltata*, and C. demersum were used, respectively, while P. australis was employed following the mixing of stems, leaves, and roots with a dry weight ratio of 1:2:1. In species mixture bags, the four species were combined at a dry weight ratio of 1:1:1:1. In total, 240 bags were prepared for five types of samples (four single species and one species mixture, with one sample from each type bonded together as a cluster using a plastic clip), three sediment treatments, four replicates, and four sampling times.

Experimental set up

Three types of sediments (lake sediment sludge collected from the Shahu Lake, washed river sand, and a mixture of the sludge and sand at a ratio of 1:1) were employed to investigate the effects of sedimentborne nutrients on the macrophyte decomposition. The experimental system consisted of 12 plastic aquaria (48 cm \times 32 cm \times 22 cm), including three sediment treatments (ca. 10 cm thick) by four replications situated in an open area. On July 3, tap water was used due to relatively low concentration of TN and TP, and slowly added to each plastic container with the water level being maintained at 11 cm.

On July 14, four litterbag clusters (each cluster containing five types of litter) were randomly placed into each plastic aquarium. Weights were attached to the litterbags so as to sink them into the surface of the sediment. During the experiment, phytoplankton was removed via a plankton net with a mesh size of 76 μ m, to minimize their impact on light and oxygen conditions. Tap water was added every two days to maintain water level, whereas the ambient air temperature was recorded twice a day at 8 AM and 7 PM.

Measurement and chemical analyses

Following 14, 35, 49, and 63 days, one litterbag cluster from each plastic aquarium was removed for the determination of carbon (C), nitrogen (N), phosphorus (P), and the remaining dry weight. The sampled litterbags were gently rinsed with tap water to remove any contaminants that were attached to their outer surfaces. The materials that remained in the litterbag were carefully transferred into the Kraft paper bags, and oven dried to constant weight at 70°C for 48 h. Subsequently, these remaining materials were ground to a fine powder with a mortar.

The total C and N contents of the remaining litter were determined with 5–6 mg of homogeneously ground materials using an Elemental Analyzer (NA2500, Carlo Erba Reagenti, Milan, Italy). The total P content of the remaining litter was measured colorimetrically with an AutoAnalyzer (Bran + Luebbe GmbH, Inc., Germany), utilizing the ammonium molybdate ascorbic acid method (Agriculture industry standard of the people's Republic of China 2017-2011 NY/T).

The total C, N, and P contents of the initial litter samples, along with the sediment samples, prior to immersion, were measured in a similar manner. The total N and P contents of tap water were determined using a potassium persulfate digestion UV spectrophotometric method, and ammonium molybdate spectrophotometric method (The national environmental protection standard of the people's Republic of China 636-2012 HJ), respectively.

Environmental variables

During the experiment, the daily mean air temperatures varied from 18.5 to 33°C (Fig. 1). The total P and N concentrations of the tap water were generally below 0.01 and 0.05 mg/L, respectively, which were the detection limit for our analyses.

Data analysis

One-way analysis of variance (ANOVA) was applied to determine the statistical significance of the differences of C, N, and P contents among species, as well as sediments. Three-way ANOVA was used to examine the effects of the treatments and species on decomposition and C, N and P release. Three-way ANOVA was



Fig. 1 Mean daily air temperatures in Wuhan, China, during the experimental period

also employed to examine the effects of species mixtures on litter decomposition.

Pearson correlation analysis was used to test the relationship between the initial nutrients and remaining mass by analyzing the initial N%, P%, C:N, C:P, and N:P in litter and average residual mass of three sediments at each time interval.

Results

The initial C%, N%, and P% in sludge, river sand, and their mixtures differed significantly. The C% and N% in the sludge and sediment mixtures were approximately tenfold and sixfold higher than those in river sand, respectively. The P content of the sludge was highest among the three sediments; however, significant differences in the P content were observed only between the sludge and river sand (Table 1).

Table 1 Initial content (Mean \pm SD, n = 4) of carbon (C), total nitrogen (TN), and total phosphorus (TP) of the sediments at the beginning of the experiment (significant differences between means within rows evaluated by LSD at P < 0.05 are indicated by different letters)

Sediment type	C (%)	TN (%)	TP (%)
Sludge	$3.53\pm0.05a$	$0.30\pm0.01a$	$0.07\pm0.03a$
Mixture	$3.51\pm0.13a$	$0.29\pm0.02a$	0.05 ± 0.02 ab
Sand	$0.34\pm0.04b$	$0.05\pm0.01b$	$0.02\pm0.001\mathrm{b}$

The initial C%, N%, P%, C:N, C:P, and N:P in different types of litter differed significantly (Table 2). Specifically, submerged macrophyte *C. demersum* exhibited the highest N% and P% and the lowest C:N and C:P ratios, followed by the species mixture, while emergent macrophyte *P. australis* exhibited the lowest N% and P%, albeit the highest C:N and C:P ratios. Both the N% and P% of *C. demersum* were more than three times higher than those of *P. australis*. However, no discernible difference in N:P was observed between these two litter types. Further, no differences in N% and P% and the C:N ratio were observed between *N. peltata* and *H. dubia*, although significant differences were found in the C% and N:P ratio between them (Table 2).

Decomposition process

The dry weight loss of all litters exhibited similar patterns, wherein most of the weight loss occurred within the first 14 days (Fig. 2), after which the decomposition rates were reduced (Fig. 2). As a consequence, the decomposition rates for the first 14 days for all litter types were much higher than those for the entire experimental period. The dry weight loss rates of different litter types followed a decreasing order as, Н. dubia (81.40%) > N.peltata (79.04%) > C. demersum (73.00%) > species mixture (68.67%) > P. australis (41.55%). Three-way ANOVA showed that there was no significant difference in the decomposition rates between single species and species mixtures (Table 3; Fig. 4).

Carbon, nitrogen, and phosphorus dynamics in decomposing litter

The C% for all litter types exhibited slight increases (from ~39 to 44%) during the first 14 days, and then showed a slow decrease (to ~41%) (Fig. 3). In contrast, the P% of all litter types obviously decreased (from ~0.41 to 0.16%) over the first 14 days and leveled off thereafter (to ~0.15%). The N% of *H. dubia*, *N. peltata*, and *C. demersum* increased over the initial 14 days (from 2.55 to 5.83%, 2.79 to 5.19%, and 4.58 to 6.10%, respectively), yet slowly decreased (to 4.96, 3.99, and 5.03%, respectively) thereafter, while the N% of *P. australis* and the litter mixture decreased (from 1.33 to 0.93% and 3.19 to 2.70%,

	C%	N%	Р%	C/N	C/P	N/P
Ceratophyllum demersum	$37.04 \pm 1.58a$	$4.58\pm0.16a$	$0.71\pm0.13a$	$8.09\pm0.15a$	$54.01 \pm 11.02a$	6.68 ± 1.36a
Nymphoides peltatum	$42.00\pm0.52b$	$2.79\pm0.37b$	$0.32\pm0.03b$	$15.24\pm2.11\mathrm{b}$	$131.22 \pm 13.49b$	$8.67\pm0.87\mathrm{b}$
Hydrocharis dubia	$35.40\pm0.77c$	$2.55\pm0.11\mathrm{b}$	$0.39\pm0.02b$	$13.90\pm0.41\mathrm{b}$	$89.53\pm4.86c$	$6.44\pm0.34a$
Phragmites australis	$41.55\pm0.31b$	$1.33\pm0.06c$	$0.20\pm0.03c$	$31.32 \pm 1.30 \mathrm{c}$	$209.11 \pm 25.54d$	$6.68\pm0.84a$
Species mixture	$38.59\pm0.69d$	$3.19\pm0.38d$	$0.44\pm0.04d$	$12.25\pm1.89d$	$88.58 \pm 10.69c$	$7.25\pm0.25a$

Table 2 Initial nutrient characteristics (mean \pm SD, n = 4) of four macrophytes and species mixtures (significant differences between means within rows evaluated by LSD at P < 0.05 are indicated by different letters)

respectively) over the initial 14 days, and then increased slightly (to 0.84 and 2.75%, respectively).

Three-way ANOVA analysis revealed that there were significant differences in N% and P% between single species and species mixture for the three sediment treatments (Table 3; Fig. 4).

Effects of litter quality and sediment-borne nutrients on decomposition and nutrient release

Three-way ANOVA analysis showed that litter quality strongly influenced the macrophyte decomposition rate (Table 3). However, there was an insignificant effect of sediment-borne nutrients on the litter decomposition rate (Table 3), although the interactions between litter quality and sediment-borne nutrients were significant as it relates to the litter decomposition rate (Table 3).

Both litter quality and sediment-borne nutrients significantly influenced litter resident C and P dynamics (Table 3). Higher *F*-values for the litter quality than that for the sediment-borne nutrients indicated that litter quality had a greater effect on C and P dynamics than sediment-borne nutrient effects (Table 3).

Pearson correlation analysis indicated that the remaining biomass was positively associated with the initial C:N and C:P ratios, but not with the initial N% and P% or N:P ratio, over the entire experimental period (Table 4).

Discussion

Effects of litter quality and sediment-borne nutrients on decomposition rates

Our study indicated that the decomposition rates of four different macrophyte species differed significantly.

Among them, P. australis (lower quality litter species) decomposed the slowest, while H. dubia (higher quality litter species) decomposed most rapidly. The quality of litter has widely been thought to be a good indicator of decomposition rates (Rejmánková & Houdková, 2006; Li et al., 2012, 2013). Some studies have suggested that the decomposition rate was negatively related to the initial litter C:N, C:P, and N:P ratios, and positively related to the N and P contents (Rejmánková & Houdková, 2006; Li et al., 2012). However, other studies have argued that the N and P contents, as well as C:P and C:N ratios, were not related to the decomposition rate (Lan et al., 2012; Li et al., 2013), and thus the initial nutrient content alone could not explain the differences in the decomposition rates across species (Longhi et al., 2008). Our results revealed that the decomposition rate was negatively related to the initial C:N and C:P ratios, rather than initial N and P contents, or N:P ratio. A potential explanation for this pattern was that a larger proportion of refractory or non-biodegradable carbon materials (e.g., cellulose, lignin, etc.) may have inhibited microbial activity (Pagioro & Thomaz, 1999; Li et al., 2014). Therefore, our study suggested that only the initial C:N and C:P ratios of litter could be effective indicators for the decomposition rate of macrophytes.

Litter diversity is a further critical factor that influences macrophyte decomposition rates due to the mixing effect (Berglund & Ågren, 2012; Chapman et al., 2013). A mechanism has been proposed to explain this phenomenon within litter mixtures, where nutrients may be transferred between litter types (Lecerf et al., 2011; Li et al., 2012). Several studies have suggested that when there is more slowly decomposing litter than rapidly decomposing litter in a mixture, the decomposition rate for the mixture must be slower than the average of the two individual litters, due to the release of inhibitory compounds (Chapman



Fig. 2 Remaining biomass (mean \pm SD, n = 4) of the litter of the four single species and the species mixture

Source of variation	Df	Remaining biomass		C%		N%		P%	
		F	Р	F	Р	F	Р	F	Р
Single species									
Sediment	2	2.12	>0.05	9.73	< 0.001	0.68	>0.05	5.4	< 0.05
Species	3	1280.65	< 0.001	87.75	< 0.001	924.33	< 0.001	375.1	< 0.001
Time	4	40.99	< 0.001	25.85	< 0.001	81.04	< 0.001	385.16	< 0.001
Sediment × Species	6	4.55	< 0.001	2.50	< 0.05	2.99	< 0.05	1.35	>0.05
Sediment × Time	6	2.73	< 0.05	2.39	< 0.01	1.81	>0.05	2.35	< 0.05
Species \times Time	9	4.19	< 0.001	2.83	< 0.01	20.62	< 0.001	50.49	< 0.001
Species mixture									
Sediment	2	3.22	>0.05	0.30	>0.05	0.06	>0.05	3.14	>0.05
Mixture versus single	1	0.21	>0.05	0.57	>0.05	175.47	< 0.0001	99.16	< 0.001
Time	1	86.09	< 0.001	44.14	< 0.0001	22.96	< 0.0001	0.26	>0.05
Sediment \times mixture versus single	2	0.33	>0.05	7.92	< 0.001	3.22	< 0.05	5.05	< 0.01
Sediment × time	2	5.9	< 0.01	3.35	< 0.05	0.37	>0.05	0.27	>0.05
Mixture versus single \times time	1	0.25	>0.05	4.07	< 0.05	27.54	< 0.0001	15.32	< 0.001

 Table 3
 Three-way ANOVA of effects of sediment-borne nutrient, species and time on remaining biomass and nutrient contents for single-species litters and mixtures versus single litter treatments during the entire experiment

et al., 1988; Berglund & Ågren, 2012). However, in contrast to these studies, our investigation demonstrated that no significant differences in the decomposition rate were found between litter mixtures and single-species litters. One possible explanation is that the inhibitory effect on microbial activities caused by recalcitrant materials in low-quality species (*P. aus-tralis*) may offset the stimulatory effects of nutrients that are provided by high-quality species (*H. dubia*, *N. peltata* and *C. demersum*) (Kominoski et al., 2007; Jonsson & Wardle, 2008; Abelho, 2009; Li et al., 2012).

Ambient environments may impact litter decomposition through the influence of microbial compositions and activities (Rejmánková & Houdková, 2006; Li et al., 2012). A number of studies have shown that the availability of nutrients in the environment may significantly impact the litter decomposition rate, particularly for submerged and floating macrophytes (Li et al., 2013). However, our results indicated that sediment-borne nutrients had little effect on the litter decomposition rates, although interactions between litter quality and sediment-borne nutrients were observed. This result agrees with one of our hypotheses, which suggests that litter quality has a stronger effect on macrophyte decomposition than sedimentborne nutrients, although it is contrary to our other hypothesis, which suggests that higher levels of sediment-borne nutrients leads to higher macrophyte decomposition rates. This may be explained by that the effect of the initial nutrient content of litters on decomposition rate being more potent than that of the nutrients that may be available in the ambient environment (Li et al., 2012).

Effects of litter quality and sediment-borne nutrients on nutrient dynamics

The litter quality strongly influences its nutrient dynamics. Our studies showed that N% increased in *C. demersum*, *N. peltata*, and *H. dubia*, but decreased in *P. australis* at an early stage. The increase of N% in high-quality species may be attributed to rapid leaching of other dissolved materials, as well as the immobilization of N by microorganisms (Pagioro & Thomaz, 1999; Li et al., 2014). The decrease of N% of low-quality species *P. australis* in the leaching phase may be attributed to high C:N (31.3:1) and non-biodegradable carbon materials, such as cellulose and lignin, which may impede the immobilization of nitrogen by the microorganisms (Pagioro & Thomaz, 1999; Li et al., 2014). Litter diversity may



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◄ Fig. 3 Litter carbon (C), nitrogen (N), and phosphorus (P) dynamics on three sediments and among five litter types. **a**-**c** correspond to litter C%, N%, and P% (as mean values of the percentage of the initial content for five litter types on each sediment; mean \pm SD, n = 20). **d**-**f** correspond to litter C%, N%, and P% (as mean values of the percentage of the initial content for each species on three sediments; mean \pm SD, n = 12)

significantly influence N dynamics in litter mixtures. Our studies showed that N% in single-species samples decreased sharply following the first few days; while in litter mixtures, N% exhibited a slow increase during the second and third sampling intervals. This result may be explained by the fact that the inhibitory effect provided by recalcitrant materials in *P. australis* on microbial activities was more potent than the stimulatory effects initiated by nutrients in high-quality species (*H. dubia*, *N. peltata*, and *C. demersum*) (Kominoski et al., 2007; Jonsson & Wardle, 2008; Li et al., 2012). Several studies concluded that N is released when C:N < 25, while it is immobilized if C:N > 25 (Paul & Clark., 1989; Heal et al., 1997;



Fig. 4 Remaining biomass and nutrient dynamics of single species and species mixtures. Changes in biomass (a), carbon (b), nitrogen (c), and phosphorus (d) content (as mean values of the percentage of the initial content). The solid line corresponds

to single species (mean value of the four macrophytes; mean \pm SD, n = 16). The *dotted line* corresponds to species mixtures (observed value of species mixture; mean \pm SD, n = 12)

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Table 4 Pearson correlation coefficients (r) between averageresidual biomass and initial litter quality factors during thedecomposition period

Factor	Remaining biomass at each sampling time							
	Day 14	Day 35	Day 49	Day 63				
N %	0.43	0.54	0.49	0.50				
Р %	-0.41	-0.53	-0.49	-0.49				
C/N	0.83**	0.89**	0.88**	0.87**				
C/P	0.74**	0.83**	0.80**	0.79**				
N/P	-0.38	-0.26	-0.31	-0.29				

* P < 0.05, ** P < 0.01

Rejmánková & Houdková, 2006). In our study, similar patterns were found only in the four single species, rather than in litter mixtures due to the combined effect of species mixtures on N dynamics (Fig. 4). In agreement with other studies, our results revealed that the P% of all litter types decreased sharply in the early stage, and then leveled off (Pagioro & Thomaz, 1999; Carvalho et al., 2005; Longhi et al., 2008; Lan et al., 2012; Li et al., 2014). A small number of studies have reported that the C:P ratio of 80 divides net P mineralization (<80) and P immobilization (>80) (Canfield et al., 2005; Rejmánková & Houdková, 2006). However, this pattern of P dynamics was not observed in our study. Hence, our studies suggested that we should be cautious in the use of the initial C:N and C:P of litter as a predictor of N and P release.

Sediment-borne nutrients significantly influence litter C, N, and P releasing dynamics. Previous studies have demonstrated that increased nutrient supplies in the ambient environment might stimulate litter P mineralization (Rejmánková & Houdková, 2006), which may explain the relatively high net P mineralization of litter on sludge. However, the values of the P content of litter on the three sediment types became similar at the end of experiment (Fig. 3). This indicated that the availability of nutrients in the ambient environment insignificantly impacted the net P mineralization of litter for the long-term decomposition (Li et al., 2012). Compared to the effects of sedimentborne nutrients on P dynamics, our results showed that the effect of sediment-borne nutrient on N dynamics was relatively weak. This suggested that the microbes involved in decomposition may obtain the majority of their N requirements from litter (Li et al., 2012).

Conclusion

In conclusion, our study indicated that sediment-borne nutrients insignificantly affected macrophyte decomposition rates, but strongly influenced the N and P releasing dynamics. There are significant interactions that occur between litter quality and sediment-borne nutrients on macrophyte decomposition, where litter quality has a stronger influence on the decomposition than sediment-borne nutrients. Litter quality, in conjunction with sediment-borne nutrients, may be a factor controlling the macrophyte decomposition in shallow lakes.

Acknowledgments This study was supported by the National Natural Science Foundation of China (31270261) and (31570366).

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