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ORIGINAL ARTICLE

Interaction between litter quality and simulated water depths on decomposition of two emergent macrophytes

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ABSTRACT

Both water depth and litter quality are important factors influencing litter decomposition in wetlands, but the interactive role of these factors in regulating mass loss and nutrient dynamics is far from clear. The responses of mass loss and nutrient dynamics to simulated water depths and litter quality are investigated in leaves of Carex brevicuspis *and leaves and stems of* Miscanthus sacchariflorus *from the Dongting Lake, China. Three litter types differing in litter quality were incubated for 210 days at three water depths (0 cm, 5 cm, and 80 cm, relative to the water surface) in a pond near the Dongting Lake. The litter mass remaining, nitrogen (N), phosphorus (P), organic carbon (organic C), cellulose, and lignin contents were analyzed during the controlled decomposition experiment. Moreover, water properties (temperature, dissolved oxygen content, and conductivity) and fungal biomass were also characterized. Initial N and P contents were highest in* C. brevicuspis *leaves, intermediate in* M. sacchariflorus *leaves and lowest in* M. sacchariflorus *stems, whereas the organic C, cellulose, and lignin contents exhibited an opposite trend. After a 210 days incubation, decomposition rate was highest in* M. sacchariflorus *leaves (0.0034-0.0090 g* g^{-1} *DW* day^{-1}*, in exponential decay model), intermediate in* C. brevicuspis *leaves (0.0019-0.0041 g* g^{-1} *DW* day^{-1}*), and lowest in* M. sacchariflorus *stems (0.0005-0.0011 g* g^{-1}*DW* day^{-1}*). Decomposition rate of* C. brevicuspis *leaves was highest at 5 cm water depth, intermediate at 80 cm, and lowest at 0 cm. Decomposition rate of* M. sacchariflorus *leaves was higher at 5 cm, and 80 cm than at 0 cm water depths. Water depth had no effect on decomposition of* M. sacchariflorus *stems. At the end of incubation, N and P mineralization was completely in leaf litters with increasing rates along with increasing water depth, while nutrients were accumulated in* M. sacchariflorus *stem. Organic C, cellulose, and lignin decayed quickly in both leaf litters compared to the stem litter. The fungal biomass was higher in leaf than in stem litters and changed as a response to water depth in both leaf litters rather than stem ones. These data indicate that submergence has no effect on the decomposition of refractory stem litter and shallower submergence stimulates degradation of the labile leaf litter.*

Key words: Litter decomposition; water depth; Dongting Lake; wetland macrophytes; Carex brevicuspis*;* Miscanthus sacchariflorus*.*

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INTRODUCTION

Decomposition is a fundamental process influencing material cycling (*i.e.*, carbon and nutrients) and energy flux in an ecosystem (Hoorens *et al.,* 2003). Decomposition promotes nutrient return from plant litter to soil or water, which directly determines nutrient availability for plant growth (Guo *et al*., 2008). Limitations to decomposition include litter quality (*i.e.,* nutrient, lignin content, and toughness) as well as physical-chemical conditions of the medium in which the material decomposes (Newell, 2003; Ferreira and Chauvet, 2011; Fonseca *et al*., 2013). Litter with a higher nutrient and a lower lignin contents usually decays quickly and easily (Fonseca *et al*., 2013). Water level fluctuations are common phenomena in wetlands, which determine plant growth and zonation (Drew, 1997). Water depth often results in variation of physico-chemical conditions, which in turn regulates the decomposition processes of macrophyte litter (Laiho, 2006). In shallow water environments, litter decomposition is rapid due to a faster rate of leaching of dissolved organic matter and increased activities of microbes (Wallis and Raulings, 2011). In deep water ecosystems, both temperature and dissolved oxygen content are usually low limiting litter decomposition as an effect of reduced microbial activity (Torremorell and Gantes, 2010; Fonseca *et al*., 2013). Though many direct measurements of macrophyte decomposition rates in response to increase water depth have shown positive effects on decomposition process and nutrient release efficiency, also neutral or even negative results were reported (Cai *et al*., 2006; Wright *et al*., 2013; Arroita *et al*., 2015). The inconsistent effects of water depth on litter decomposition may be caused by differences in litter quality, since litter tissues (including roots, leaves, twigs and stems) used in the above-mentioned experiments differed in quality and type (Trinder *et al*., 2008). Refractory litters might be less sensitive to particular environmental conditions (*i.e.*, soil fertility and tem-

perature) than the labile ones (Sariyildiz and Anderson, 2003; Fierer *et al*., 2005), indicating that neutral effects might happen in presence of refractory litter, whereas positive or negative effects in presence of labile one. Therefore, these inconsistent effects might also result from interaction between water depth and litter quality.

In this study, the decomposition rate, the nutrient dynamics and the fungal biomass were investigated in a pond close to the Dongting Lake (China) using three litter types as a response to a simulated water-depth gradient (0 cm, 5 cm, and 80 cm, relative to the water surface) in a 210-day long controlled experiment. The litter types include *Carex brevicuspis* leaves [high nitrogen (N) and phosphorus (P) contents, low lignin content], *Miscanthus sacchariflorus* leaves (intermediate N, P and lignin contents) and stems (low N and P contents, high lignin content). In our preliminary analyses, 5 and 80 cm depth environments were significant different in water physicochemical conditions including temperature, dissolved oxygen content, and conductivity) and could represent shallower and deeper submergence, respectively (according to Wrubleski *et al*., 1997). Both the macrophytes in analysis are dominant species in the shorelines of the Dongting Lake, that is the second largest lake in China.

Here, we tested the following hypotheses. First, decomposition would be faster in both leaf litters than in stem litter due to litter quality. Second, for leaf litters, decomposition would be stimulated at 5 cm and 80 cm depths and the effect was more significant at 5 cm than at 80 cm depth. Third, the decomposition rates of stem litter would be insensitive to water depths.

METHODS

Litter materials

Leaf litter from *C. brevicuspis* and leaf and stem litters from *M. sacchariflorus* were collected as standing dead litter from the Dongting Lake (29°27’2.02” N, 112°47’32.28” E) in November 2012. Only newly senescent brown leaf litter and standing stem litter were selected. After collection, all litters were air-dried for 48 h to achieve a constant mass and cut into about 10 cm long pieces prior to litterbag construction. Weighed litter samples (5 g) were placed into 10×15 cm nylon bags. The bag mesh size was 1 mm, which is sufficient to prevent macroinvertebrates from passing through while allowing for colonization of microbial organisms and litter fragment loss into the water (Langhans *et al*., 2008).

Experimental set-up

To assess the influence of water depth on decomposition rate, each litter type was randomly treated at three water depths: 0 cm, 5 cm, and 80 cm water depths (relative to the water surface). All nylon bags were placed in three plastic trays (100 × 100 × 10 cm), each plastic tray containing a 6-cm washed silica sand to fasten nylon bags. A total of 54 litter bags were placed in each tray. The litter bags were randomly buried to 5 cm in the sand, 5 cm apart from each other. On January 13, 2013, the trays were gently placed in a pond near the Dongting Lake. For the 0 cm treatment, the sand in tray was wetted with pond water completely but with no surface pooling. For the 5 cm and 80 cm treatments, the trays were emerged at 5 cm and 80 cm depth above the sand surface, respectively (Wright *et al*., 2013). Water depths in the trays were adjusted weekly. The experimental pond (800 m2) was fed almost exclusively by rainfall and thus water was poor in nutrients. Total organic carbon (organic C), total N, P and K were 41.0, 1.10, 0.04 and 3.1 mg L^{-1}, respectively. Other water properties (temperature, dissolved oxygen content, and conductivity) at 5 cm and 80 cm water depths were recorded with a sensION156 hand-operated electrochemistry analyzer (HACH Corporation; Loveland, CO, USA) on the first day of incubation and at each sampling day.

Harvest and chemical analysis

Three bags for each litter type and water depth were randomly sampled at day 11, 30, 60, 90, and 210 from the start of incubation. Simultaneously, another 9 samples (3 replicates for the 3 litter types in analysis) were sampled to measure ergosterol content at each harvest day. After collection, litter samples were hand-washed gently with deionized water until the water became transparent, then oven-dried to constant weight for a week at 60°C to measure the remaining dry mass (with 0.01 g accuracy). The samples were ground to powder and passed through a 0.5-mm mesh screen to analyze litter quality. Organic C content was analyzed using the H2SO4-K2Cr2O7 heat method, N and P contents using Kjeldahl digestion followed by colorimetric analysis, and cellulose and lignin contents using hydrolysis of H2SO4 followed by Na2S2O3 titration (Graça *et al*., 2005). Initial litter qualities were determined by colorimetric analysis as described above. Fungus, especially aquatic hyphomycetes, play a fundamental role in litter decomposition in aquatic environments, and the activities of decomposer can be indicated by the fungal biomass by measuring ergosterol content (Ferreira and Chauvet, 2011). The decomposed litter samples were frozen at -30°C after sampling. Ergosterol content was determined by high-performance liquid chromatography (Graça *et al*., 2005). For analyses, the litter material was lyophilised and ground. The extraction was done in alkaline methanol at 80°C. Solid-phase extraction through C18 cartridges was used for purification. Dry, unprocessed litters were used for blank values. This material was stored dry at room temperature. In addition to ergosterol concentration, we calculated the fungal biomass at the peak time with the conversion factor of 5.5

mg ergosterol g^{-1} fungal biomass, and values were expressed as mg g^{-1} dry weight (DW).

Data analysis and statistics

The decomposition rate (k) was calculated using the following equation:

$$-kt = ln\ (Wt/W0) \quad \text{(eq. 1)}$$

where:
$W0$ is the initial litter mass;
Wt is the mass remaining at time t (days) (Olson, 1963).

The remaining mass was calculated as the percentage of the initial mass, and the remaining litter components (N, P, organic C, cellulose, and lignin) as the litter mass × litter components content. Decomposition rate, remaining mass, and remaining litter components were compared among the three litter types by three-way analysis of variance (ANOVA), with litter type, water depth, and time as the main factor. Values were log-transformed to homogenize the variances among groups. Within each litter type, the response variables were compared using two-way ANOVA with water depth and time as the main factors to test the treatment effect. Fungal biomass was compared by two-way ANOVA, with litter type and water depth as the main factor. The difference between initial litter quality and mass remaining (including dry mass, N, P, organic C, cellulose, and lignin) of the three litter types was evaluated by LSD at the 0.05 significance level. All statistical analyses were performed using the statistical software SPSS 21 (Sun *et al*., 2012).

RESULTS

Initial litter quality and water properties

One-way ANOVA showed the initial N (F=109.4, P<0.01), P (F=47.3, P<0.01), organic C (F=38.5, P<0.01), cellulose (F=7.0, P<0.05), and lignin (F=14.9, P<0.05) contents differed among the three litter types (Tab. 1). N and P contents were highest in *C. brevicuspis* leaves, intermediate in *M. sacchariflorus* leaves, and lowest in *M. sacchariflorus* stems (F=20.3, P<0.05), whereas the organic C, cellulose, and lignin contents ranked in the opposite order among the three litter types (F=22.6, P<0.05). The ratios of C:N, C:P, and lignin:N were lowest in *C. brevicuspis* leaves, intermediate in *M. sacchariflorus* leaves, and highest in *M. sacchariflorus* stems. These results demonstrated that decomposition potential was highest in *C. brevicuspis* leaves, intermediate in *M. sacchariflorus* leaves, and lowest in *M. sacchariflorus* stems (Tab. 1). The Student's *t*-test showed that the temperature and dissolved oxygen content in water were significantly higher at 5 cm than at 80 cm depth, while water conductivity was significantly higher at 80 cm than at 0 cm depth (Fig. 1) (F=3.2, P<0.05).

Dynamics of mass remaining

Mass remaining of the three litter types decreased slowly within the initial 90-day incubation, and then increased gradually. Decomposition rates differed with litter type (F=89.6, P<0.01) and water depth (F=22.7, P<0.01) (Tab. 2). At the same water depth, the decomposition rate in the three litter types decreased in the order *M. sacchariflorus* leaves (0.0062 g g^{-1} DW day^{-1}) > *C. brevicuspis* leaves (0.0030 g g^{-1} DW day^{-1}) > *M. sacchariflorus* stems (0.0008 g g^{-1} DW day^{-1}). Decomposition was fastest in *M. sacchariflorus* leaves at 5 cm depth (0.0087 g g^{-1} DW day^{-1}), and slowest in *M. sacchariflorus* stems at 80 cm depth (0.0006 g g^{-1} DW day^{-1}).

Two-way ANOVAs showed a significant interaction between litter type and water depth, indicating that the effect of water depth differed among the three litter types

Tab. 1. Initial nitrogen (N), phosphorus (P), organic carbon (Organic C), cellulose, lignin contents, ratios of C:N, C:P, N:P, and lignin:N of three types of litters.

Parameter	Litter type		
	C. brevicuspis leaves	*M. sacchariflorus* leaves	*M. sacchariflorus* stem
N (mg g^{-1})	7.68±0.18[a]	4.15±0.85[b]	1.40±0.25 c
P (mg g^{-1})	0.89±0.10[a]	0.48±0.13[b]	0.14±0.02c
Organic C (%)	38.37±1.77[c]	43.13±0.85[b]	49.12±1.70[a]
Cellulose (%)	14.61±0.31[a]	18.56±2.53[b]	18.48±0.14[c]
Lignin (%)	30.75±1.41[a]	32.42±0.91[b]	34.47±2.64[c]
C:N	50.02±3.26[a]	107.73±27.30[b]	359.86±83.73[c]
C:P	433.87±27.85[a]	943.47±230.72[b]	3534.33±605.00[c]
N:P	8.72±1.09[b]	8.87±1.94[a]	9.97±1.67[c]
Lignin:N	40.07±2.09[a]	80.99±20.76[b]	253.04±63.35[c]

Values are means±standard deviation, are expressed on a dry mass basis, and are means of three replicates. [a,b,c]Different letters indicate a significant difference in initial leaf chemistry among the three litter types; the differences were compared by least significant deviation at the 0.05 significance level.

(F=9.7, P<0.01) (Fig. 2). Decomposition rates were only affected by water depth (F=29.9, P<0.01) in both leaf litters rather than stem litter, ranked in the following order: 5 cm ≥80 cm >0 cm.

Dynamics of litter chemical components

At the same water depth, the litter N and P contents of the three litter types increased in the order *M. sacchariflorus* stems < *M. sacchariflorus* leaves < *C. brevicuspis* leaves, while the order for litter C, lignin, and cellulose contents was: *M. sacchariflorus* leaves < *C. brevicuspis* leaves < *M. sacchariflorus* stems (Fig. 3). Both leaf litters released N and P at the end of incubation, while *M. sacchariflorus* stems showed an accumulation of these nutrients. Similar to the mass loss, litter C, cellulose, and lignin were released slowly in *M. sacchariflorus* stems (F=35.9, P<0.01). Two-way ANOVAs showed that the release of C, P, and lignin of the two leaf litters was significantly promoted by increasing water depth (F=46.9, P<0.01). The lignin content of *M. sacchariflorus* stems was also affected by water depth (F=4.6, P<0.05). Other litter chemical components were not affected by water depth (F=1.6, P>0.05).

Fungal biomass

Among the three litter types, fungal biomass was higher in *C. brevicuspis* leaves, and lower in *M. sacchariflorus* stems (F=58.7, P<0.05) (Fig. 4). At the end of the experiment, the fungal biomass of both leaf litters rather than stem litter was significantly affected by water depth (F=58.7, P<0.01) (Fig. 4). Two-way ANOVAs showed a significant interaction between litter type and water depth, indicating that the effect of water depth differed among the three litter types (F=3.3, P<0.05) (Fig. 4). Fungal biomass was only affected by water depth (F=6.9, P<0.05) in both leaf litters rather than stem litter, ranked in the following order: 5 cm ≥ 80 cm > 0 cm.

DISCUSSION

Litter quality and decomposition

At the same water depth, decomposition rates among

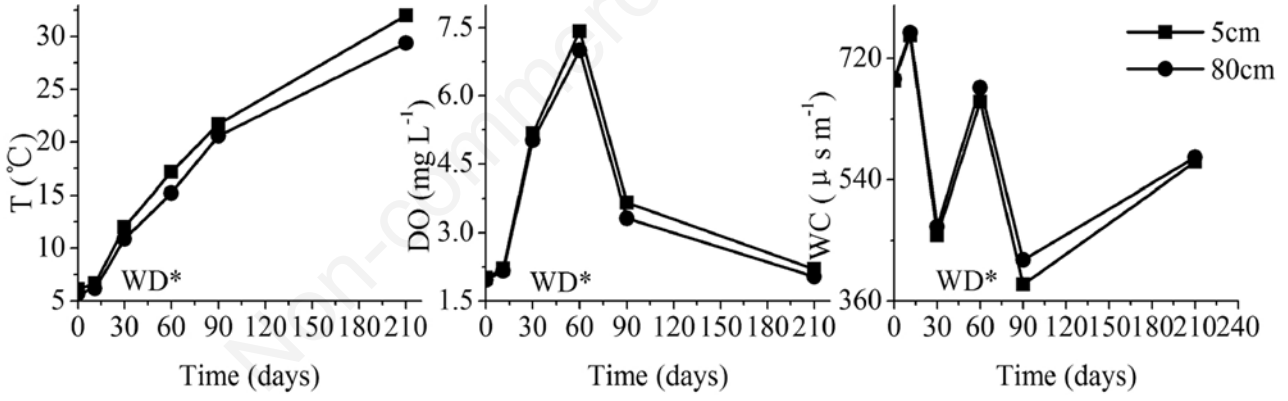

Fig. 1. Dynamics of water properties at 5 cm and 80 cm water depths (WD). *P<0.05. T, temperature; DO, dissolved oxygen content; WC, water conductivity.

Tab. 2 Decomposition rates (*k*) of three types of litters at 0 cm, 5 cm and 80 cm water depth at the end of the experiment.

	k (g g^{-1} dry mass day^{-1})				
	0 cm	5 cm	80 cm	Mean	SD
Carex brevicuspis leaves	0.0018^{d} (0.009)	0.0041^{b} (0.0005)	0.0031^{c} (0.0004)	0.0030	0.0011
Miscanthus sacchariflorus leaves	0.0036^{c} (0.0006)	0.0087^{a} (0.0024)	0.0062^{ab} (0.0026)	0.0062	0.0028
Miscanthus sacchariflorus stem	0.0007^{e} (0.0001)	0.0010^{de} (0.0005)	0.0006^{e} (0.0001)	0.0008	0.0003
Mean	0.0021	0.0046	0.0033		
SD	0.0014	0.0036	0.0027		

Values are means±standard deviation, and are means of three replicates. The numbers in brackets are estimated standard deviations. a-eDifferent letters indicate a significant difference in litter decomposition rates among the three litter types; the differences were compared by least significant deviation at the 0.05 significance level.

the three litter types decreased in the order *M. sacchariflorus* leaves > *C. brevicuspis* leaves > *M. sacchariflorus* stem, which is consistent with our first hypothesis. The slowest decomposition and highest C content in the *M. sacchariflorus* stems might reflect a N or P limitation (Freschet *et al*., 2012). In addition, also the lower initial N and P contents and the higher ratios of C:N, C:P, and lignin:N contribute to make the *M. sacchariflorus* stems recalcitrant to decay (Lan *et al*., 2006; Pettit *et al*., 2012). It is surprising that *C. brevicuspis* leaves with higher N and P contents decay at a lower rate than do *M. sacchariflorus* leaves with lower N and P contents. Actually, nutrient content is not the sole factor in determining decomposition rate of aquatic macrophytes (Gijsman *et al*., 1997). Other aspects, such as lower toughness and higher initial cellulose content, can explain the faster lignin decay observed (Moorhead and Sinsabaugh, 2006; Fonseca *et al*., 2013).

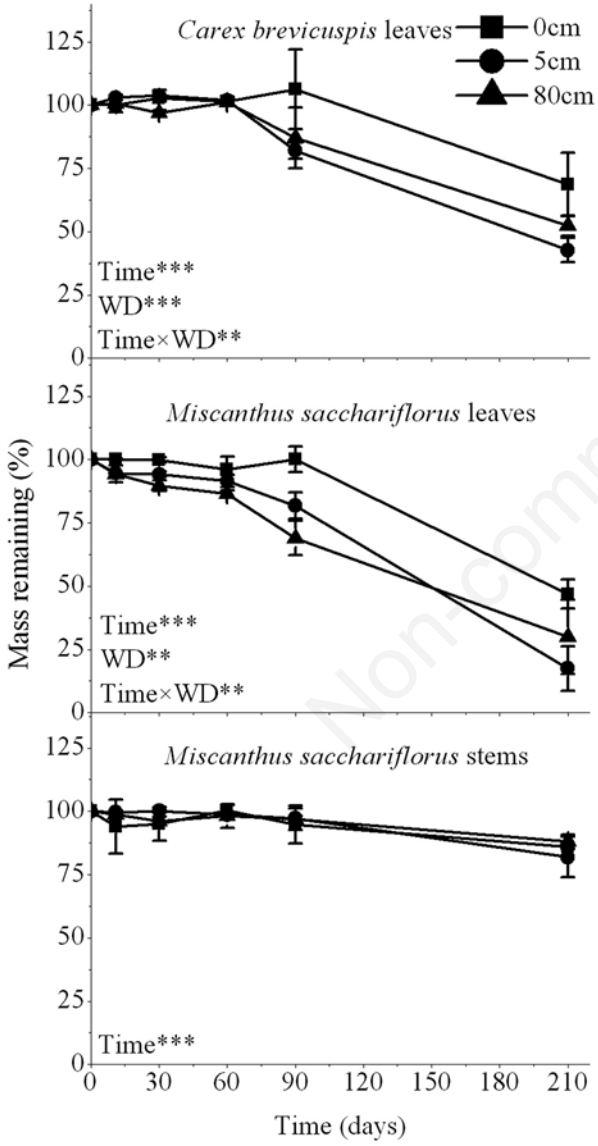

Fig. 2. Decomposition (expressed as the percentage of mass remaining respect to initial dry mass) of different litter types in response to water depth (WD) at 0, 5, and 80 cm. *P<0.05; **P<0.01; ***P<0.001.

Water depth and leaf litter decomposition

The decomposition rates of both leaf litters among the three water depths were decreased in the order 5 cm > 80 cm > 0 cm for C. *brevicuspis* leaves and 5 cm ≥ 80 cm 0 80 cm for *M. sacchariflorus* leaves. This result is partially consistent with our second hypothesis. The decomposition rates of both leaf litters were slowest at 0 cm, suggesting a stimulation effect by submergence in liable litters. Inhabitation or promotion by water depth have also been reported in other studies (Wallis and Raulings, 2011; Sun *et al*., 2012). Besides by increasing leaching and physical fragmentation resulting from submergence itself (Torremorell and Gantes, 2010; Wallis and Raulings, 2011), water depth variation might also affected litter decomposition through the decomposer. Generally, litter decomposition rate depended on the utilization rate of decomposer (Beth *et al*., 2012).

In this experiment, fungal biomass was affected by litter type, water depth and their interaction. Fungus must assimilate nutrients from available resources to maintain the balance in component composition (Beth *et al*., 2012). Both leaf litters released C, N, P and lignin during litter incubation, indicating that nutrient demands of fungus is satisfied by litter decomposition (Xie *et al*., 2004). However, fungal biomass of both leaf litters was higher at 5 cm and 80 cm than at 0 cm water depths, which might be resulted from an adaptive response of fungal growth and reproduction to adequate moisture by submergence (Wallis and Raulings, 2011; Sun *et al*., 2012;). The faster release of nutrients, lignin and cellulose as a response to submergence also reflected that fungus utilized litter more efficiently (Fonseca *et al*., 2013). As a result, we observed both leaf litters decay faster at submergence than at 0 cm water depth.

C. *brevicuspis* leaves decayed slower at 80 cm than at 5 cm water depths, implying a less stimulation at 80 cm water depths. This phenomenon might result from the harsher water condition at 80 cm, including lower temperature and dissolved oxygen content and higher conductivity. In such environment, fungus might be impeded from colonization due to lower nutrients uptake ability and enzymatic activity (Battle and Golladay, 2001). Therefore, the fungal biomass was lower at 80 cm due to slower C, P, and lignin releases. However, both 5 cm and 80 cm water depth showed similar stimulation in the most fast-decaying litter of *M. sacchariflorus* leaves, indicating that the de-

composition of some litter types was too fast to be limited by harsh environmental conditions (Gijsman *et al*., 1997; Straková *et al.*, 2010). Though releases of C, P, and lignin were slower at 80 cm than at 5 cm water depths, no difference in fungal biomass was observed between them, indicating that fungus activity was not inhibited by the harsher condition at 80 cm water depth. Any decomposers (fungi and invertebrates) associated with the highly decomposable leaf litter would also be effective in deep water as reported by Pozo *et al.* (1998). Fungus could also change its functional composition, *i.e.* from terrestrial fungus to aquatic hyphomycetes, to adapt to hypoxic-submergence environments (Peltoniemi *et al*., 2012).

Water depth and stem litter decomposition

Water depth had no impact on the decomposition of *M. sacchariflorus* stems, suggested that decomposition of refractory litters might be primarily regulated by its poor quality and was insensitive to environmental condition variation (Fonseca *et al*., 2013). This is consistent with our third hypothesis. Other studies have also reported the insensitivity of refractory litters to temperature and soil fertility (Sariyildiz and Anderson, 2003; Fierer *et al*., 2005). One reason might result from the lower nutrient contents in stem litters. Stem litters showed immobilization in nutrients and slow releases in organic C, lignin and cellulose, indicating that the fungus could not assimilate enough N and P from the poor-nutrients stem litter to utilize the organic C (Beth *et al*., 2012). Though litter decay at three water depths experienced different submergence conditions, the nutrients accumulation were unaffected by water depth. Therefore, fungal consumption of stem litter can be limited by nutrients at all water depths, as supported by the lower and unchanged fungal biomass (Ferreira and Chauvet, 2011). Another reason might result from the recalcitrant component including cellulose and lignin in stem litter. A previous study has suggested that highly recalcitrant components, such as cellulose and lignin, would make the stem more resistant to physical abrasion compared to the leaf (Fonseca *et al*., 2013). Our evidence suggests that the loss of cellulose and C of *M. sacchariflorus* stems were also unaffected by water depth. Therefore, the insensitiveness of stem decomposition to water depth might also result from its highest cellulose and C contents.

CONCLUSIONS

Effects of increasing water depth on macrophytes decomposition yield consistent results. This study provided quantitative support that decomposition of emergent macrophytes depended on interaction between litter quality and water depth. Submergence has no effect on the decomposition of refractory stem litter, due to litter's lower nutrients content and resistance to physical abrasion. Hence, *C. brevicuspis* leaves decayed slower at deeper submergence than at shallower submergence, implying a less stimulation at 80 cm water depths, due to the harsher water condition at deeper water. Submergence stimulates degradation of the labile leaf thanks to the fact that the nutrients demand and the activities of decomposers increase in proportion to the increase in moisture levels.

The analysis of aquatic ecosystem functions should take into account the interaction between litter quality and water depth because of their importance in biogeo-

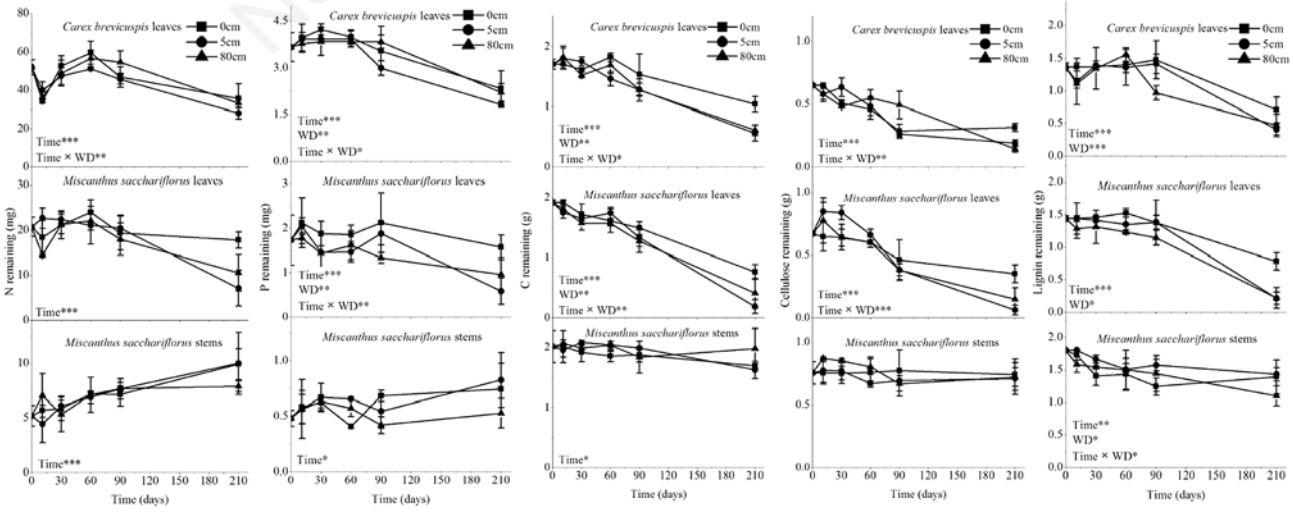

Fig. 3. Dynamics of the litter component contents on a dry mass basis at 0, 5, and 80 cm water depths (WD). *P<0.05; **P<0.01; ***P<0.001.

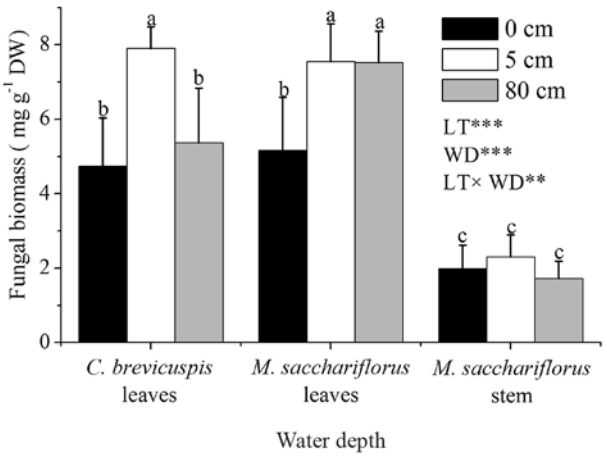

Fig. 4. Fungal biomass of three litter types (LT) at 0, 5, and 80 cm water depths (WD).**P<0.01; ***P<0.001. Different letters (a,b,c) indicate a significant difference in fungal biomass among the three water depths.

chemical processes. The Three Gorges Project, the largest hydropower of construction scale in the world, has changed the hydrology of some lakes such as the Dognting Lake. Our study suggested that the labile litters required more attention than refractory ones in evaluation the nutrient recycle responses to hydrological changes. Given that our study was only 210 days long, and our findings are exclusively related to the early stages of decomposition and cannot predict long-term decomposition rates, we needed to further explorations of the response of litter decomposition to water depth changes in experiments of several years.

ACKNOWLEDGMENTS

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