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The effects of simulated inundation duration and frequency on litter decomposition: A one-year experiment

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ABSTRACT

There is major uncertainty in the responses of litter decomposition to the inundation regimes in field studies, mainly because of the difficulties in identification of the individual effect of duration and frequency using field studies alone. The interactive role of inundation regime and litter quality also remains unclear. The responses of mass loss to simulated inundation regime (duration and frequency) and litter quality were investigated in leaves of *Carex brevicuspis* and leaves and stems of *Miscanthus sacchariflorus* from Dongting Lake, China. Three litter types differing in litter quality were incubated under seven different inundations over 360 days (three single inundations of 90, 180, and 360 days; three repeated 180-day inundations of 2, 3, and 6 times; and no inundations) in a pond near Dongting Lake. 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 were ranked in the opposite order among the three litter types. Decomposition rate was highest in *M. sacchariflorus* leaves (0.00222–0.00900 day^{-1}), intermediate in *C. brevicuspis* leaves (0.00135–0.00500 day^{-1}), and lowest in *M. sacchariflorus* stems (0.00080–0.00100 day^{-1}). The decomposition rate of both *C. brevicuspis* and *M. sacchariflorus* leaves increased with increasing inundation duration or decreasing frequency. However, both duration and frequency of inundation had no effect on decomposition of *M. sacchariflorus* stems. At the end of the incubation, N mineralization was complete in leaf litters with increasing rates with increasing inundation duration or decreasing inundation frequency, but accumulation was found in *M. sacchariflorus* stems. Organic C decayed quickly in both leaf litters compared with the stem litter. These data indicate that inundation regime has no effect on the decomposition of refractory stem litter while prolonged and stable inundation stimulates the degradation of labile leaf litter.

1. Introduction

Litter decomposition is a fundamental process influencing material cycling (e.g., C and nutrients) and energy flux in ecosystems (Hoorens et al., 2003). Limitations to decomposition include litter quality (e.g., nutrient, lignin content, and toughness) as well as physical and chemical conditions (Anderson and Smith, 2002). Litter with higher nutrient contents and lower lignin content usually decomposes more quickly and more easily (Fonseca et al., 2013).

In wetlands, the inundation regime (e.g., inundation frequency and duration) has been identified as the key driver of litter decomposition as it dictates the moisture conditions, and regulates leaching, fragmentation, and microbial activity (Anderson and Smith, 2002; Minden and Kleyer, 2015). Recently, inundation regimes have been profoundly modified in some wetlands in China by human activities, e.g. flooding reduction in Dongting Lake by the Three Gorges Project (Liu et al., 2010). It is necessary to predict the cascading responses of litter decomposition to changes in inundation regimes. However, there are major inconsistencies in current predictions. Decomposition can be hindered by anoxic conditions due to standing-water and by disturbance of decomposers under wetting and drying cycles (Lee, 1989; Gingerich et al., 2015). Conversely, it may be enhanced by physical processes (leaching or fragmentation by stream flow or dry/wet cycles) and microbial consumption (Larmola et al., 2006). Both positive and negative effects of prolonged inundation on litter decomposition have been reported by different studies, even using the same litter material, *Phragmites australis* leaves (Bedford, 2005; Christensen et al., 2009; Wallis and Raulings, 2011).

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The inconsistencies in study results might be partly due to the methodological limitations of previous studies. Many field studies have used gradient or correlative approaches (Battle and Golladay, 2001; Andersen and Nelson, 2003). Since inundation frequency often varies simultaneously with duration in natural wetlands (Baker et al., 2001; DeJager, 2012), it is difficult to identify the independent effect of each factor based on field studies. This is also the case in most hydrological manipulation studies, where duration and frequency were altered simultaneously (Day, 1983; Lockaby et al., 1996). Some studies have separated these effects by short-term (one-month) hydrological manipulations (Langhans and Tockner, 2006; Foulquier et al., 2015). However, the individual roles of duration and frequency for annual inundation in seasonal wetlands remain unclear.

In addition, the inconsistent effects may also be caused by the various different types and qualities of the litter tissues (including roots, leaves and stems) used in previous experiments (Larmola et al., 2006; Datry et al., 2011). Refractory litters might be less sensitive than labile litters to some environmental conditions (Xie et al., 2016), indicating that neutral effects may occur in refractory litters and positive or negative effects may occur in labile litters. Therefore, the inconsistent effects of inundation regime on decomposition might also result from interactions between inundation regime and litter quality.

Carex brevicuspis and *Miscanthus sacchariflorus* are two dominant species in the Dongting Lake Wetlands, the second largest freshwater lake in China. In this study, the decay of *C. brevicuspis* leaves (high nutrient contents, low organic C content), *M. sacchariflorus* leaves (low nutrient contents, high organic C content) and stem (intermediate nutrient and organic C content) was examined under different inundation durations and frequencies for one year. We hypothesized that: 1) decomposition of the leaf litters would increase with increasing inundation duration, due to the stimulation of leaching, fragmentation, and microbial activity; 2) decomposition of the leaf litters would increase with decreasing frequency because of the disturbance to microbes; and 3) decomposition of the stem litters would be insensitive to inundation regime changes because of their recalcitrant components and low nutrient contents.

2. Materials and methods

2.1. Collection and preparation of leaf material

Leaf litter from *C. brevicuspis* and leaf and stem litters from *M. sacchariflorus* were collected as standing dead litter from Dongting Lake (N29°27′2.02″, E112°47′32.28″) in November, 2012. Newly senescent brown leaves and standing stem litter were selected. After collection, the litter was air-dried to constant mass for 48 h and cut to about 10 cm length prior to litterbag construction. Weighed 5-g litter samples were placed into each 10 × 15 cm nylon bag. The bag mesh was 1 mm, which prevents macroinvertebrate colonization but allows microbial colonization and reduces litter fragment loss into the water (Langhans et al., 2008).

2.2. Experimental set-up

A litter bag experiment was established to assess the influence of inundation regime on litter decomposition. Litter bags from each litter type were randomly treated with seven different inundations: three single inundations (90, 180, and 360 days), three repeated 180-day inundations (2, 3, and 6 times), and no inundations (Fig. 1). The inundation regimes were chosen to simulate the hydrology of summer-flooded lakes in China such as Dongting Lake, with soil that is inundated from perennially to rarely, with 6 months as a common duration at seasonal sites (Liu et al., 2010). To keep similar inundation timing for Treatments 3, 4, 5, and 6, their first inundations were started simultaneously and 2 days was chosen as the non-inundation interval where necessary.

All nylon bags were placed in 21 plastic trays (100 × 100 × 10 cm) to allow three replications for each treatment. Each plastic tray contained 6-cm washed silica sand to fasten the nylon bags. A total of 24 litter bags (3 litter types × 8 harvests) 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 an 800 m^2 pond near Dongting Lake. This pond contained water that was poor in nutrients. Total organic C, total N, total P, and total K contents were 41.0, 1.10, 0.04, and 3.1 $mg\,L^{-1}$, respectively. Water temperature, dissolved oxygen content, and conductivity were recorded with a sensION156 hand-operated electrochemistry analyzer (HACH Corporation; Loveland, Colorado, USA) on the first day of incubation and on each sampling day (Fig. 2). To simulate wetting and drying cycles, trays were transferred manually from inundation to non-inundation (wet to dry) positions and vice versa. For the inundation, the trays were submerged at 5 cm depth above the sand surface; and for the non-inundation, the sand in the tray was completely wetted with pond water but with no surface pooling (Wright et al., 2013). The inundation duration and frequency were defined as the number of inundation days and number of inundation events per year, respectively (Vreugdenhil et al., 2006).

2.3. Harvest and chemical analysis

Three bags for each litter type and each treatment were randomly sampled at 15, 30, 60, 90, 180, 210, 270 and 360 days after incubation. After collection, litter samples were hand-washed gently with deionized water until the water became transparent. For ash free dry mass (AFDM) analysis, samples were dried at 60 °C for 72 h and then placed in the muffle furnace for 4 h at 550 °C to combust the organic compounds (Biasi et al., 2013).

The samples for litter quality determination were ground to powder and passed through a 0.5-mm mesh screen to analyze litter quality. Organic C content was analyzed using the H_2SO_4-$K_2Cr_2O_7$ heat followed by $FeSO_4$ titration, N and P contents using H_2SO_4-$HClO_4$ digestion followed by colorimetric analysis, and cellulose and lignin contents using hydrolysis of H_2SO_4 followed by $Na_2S_2O_3$ titration (Zhou et al., 2015; Xie et al., 2016).

2.4. Calculation and data analysis

Decomposition rate (k) for each litter type was calculated by the following single exponential model:

$$-kt = ln\,(W_t/W_0),$$

where W_0 is the initial AFDM and W_t the AFDM at time t (days) (Olson, 1963). AFDM were calculated as % of the initial mass. The single exponential model was chosen because it had the lowest regression coefficient (r^2) among the studied models. Decomposition rates were compared among litter types by three-way analysis of covariance (ANCOVA), with litter type and inundation duration or frequency as main factors, and time as the covariate. For each litter type, decomposition rates were compared using a two-way ANCOVA with inundation duration or frequency as main effects, and time as covariate, to test the specific effect of inundation treatment. The difference between litter quality and decomposition rate of the three litter types was evaluated by the least significant deviation (LSD) at the 0.05 significance level. All values were ln-transformed to homogenize variances prior to statistical analysis if necessary. All the statistical analyses were performed using the software SPSS statistics 21.

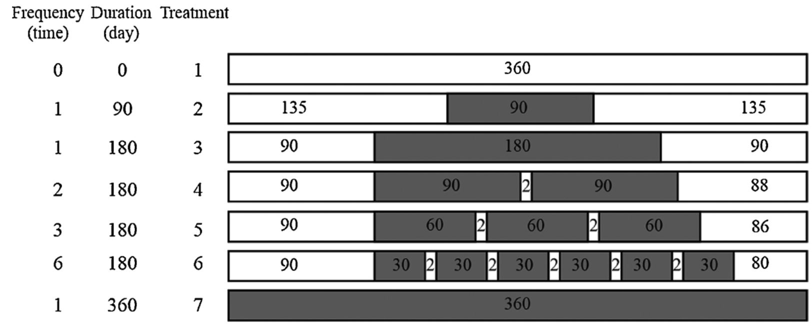

Fig. 1. Experimental design: 7 treatments with different durations (day) and frequencies (time). For the boxes: white represents dry periods; gray represents wet periods; the number in each box represents the duration (days).

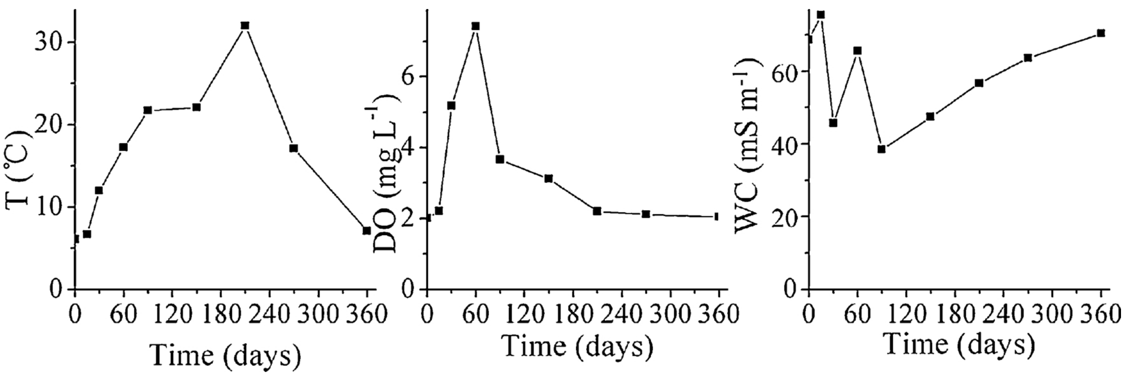

Fig. 2. Dynamics of water properties in the pond. T, temperature; DO, dissolved oxygen content; WC, water conductivity.

3. Results

3.1. Initial litter quality

Initial N, P, organic C, cellulose, and lignin contents differed among the three litter types ($P < 0.05$, Table 1). The N and P contents were highest in *C. brevicuspis* leaves, intermediate in *M. sacchariflorus* leaves, and lowest in *M. sacchariflorus* stems ($P < 0.05$). The orders of organic C, cellulose, and lignin among the three litter types were opposite to that of nutrient contents ($P < 0.05$). 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.

3.2. Decomposition

AFDM of the three litter types decreased slowly within the initial 60-day incubation, and then increased gradually. Decomposition rates differed with litter type, inundation regime, time, and inundation

Table 2
Regression statistics (r^2) for exponential rates of decomposition (k) in 7 inundation regime treatments at the end of the experiment.

Treatment	*Carex brevicuspis* leaves		*Miscanthus sacchariflorus* leaves		*Miscanthus sacchariflorus* stem	
	k	r^2	k	r^2	k	r^2
1	0.00228	0.6408	0.00267	0.6381	0.00081	0.7508
2	0.00290	0.9062	0.00397	0.8961	0.00084	0.7451
3	0.00352	0.9263	0.00502	0.8732	0.00083	0.8123
4	0.00289	0.8071	0.00484	0.9046	0.00085	0.9466
5	0.00184	0.7221	0.00349	0.8907	0.00100	0.9617
6	0.00234	0.9442	0.00288	0.9128	0.00087	0.8689
7	0.00520	0.9532	0.00820	0.8517	0.00092	0.7586

k is a decomposition constant (day^{-1}) based on an exponential model.

Table 1
Initial quality of three types of plant litter.

Parameter	Litter type		
	Carex brevicuspis leaves	*Miscanthus sacchariflorus* leaves	*Miscanthus sacchariflorus* stems
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 ± 0.02 c
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 b
Lignin (%)	30.75 ± 1.41 a	32.42 ± 0.91 b	34.47 ± 2.64 c
C:N (mol mol^{-1})	58.36 ± 3.80 a	125.69 ± 31.85 b	419.84 ± 97.68 c
C:P (mol mol^{-1})	1120.73 ± 71.95 a	2437.30 ± 596.03 b	9130.35 ± 1562.92 c
N:P (mol mol^{-1})	19.31 ± 2.41 a	19.64 ± 4.30 a	21.94 ± 3.70 b
Lignin:N (g g^{-1})	40.07 ± 2.09 a	80.99 ± 20.76 b	253.04 ± 63.35 c

All values are means of three replicates, expressed on a dry-mass basis. Different lowercase letters (a, b, c) within rows indicate significant difference in initial litter quality among the three litter types (LSD test, $P < 0.05$).

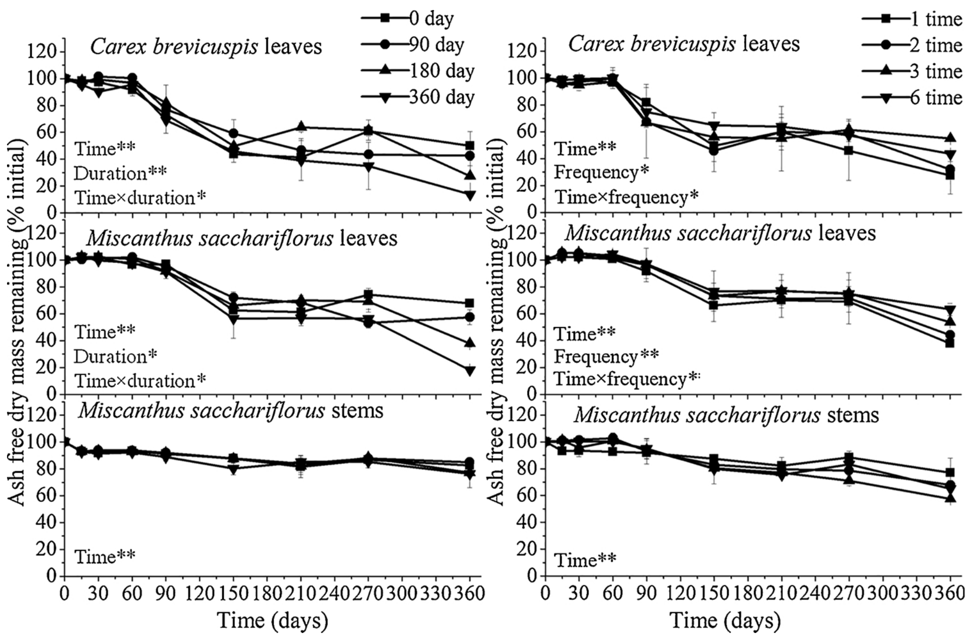

Fig. 3. Dynamic of ash free dry mass (% initial) in response to inundation duration (*Duration*, day) and frequency (*Frequency*, time). * $P < 0.05$; ** $P < 0.01$.

regime × time ($P < 0.05$ or $P < 0.01$, Table 2, Fig. 3). Under the same inundation regime, the decomposition rate in the three litter types decreased in the order *M. sacchariflorus* leaves (0.00444 day^{-1}) > *C. brevicuspis* leaves (0.00300 day^{-1}) > *M. sacchariflorus* stems (0.00087 day^{-1}) (Table 2). Decomposition was fastest in *M. sacchariflorus* leaves at 360-day inundation (0.0082 day^{-1}), and slowest in *M. sacchariflorus* stems at 0 days inundation (0.00081 day^{-1}).

Two-way ANCOVA showed a significant interaction between litter type and inundation regime, indicating that the effect of inundation regime differed among the three litter types ($P < 0.05$ or $P < 0.01$, Fig. 3). Decomposition rates were affected by inundation regime ($P < 0.05$ or $P < 0.01$) in both leaf litters but not in the stem litter ($P > 0.05$). The effects of decomposition rates on the leaf litters were ranked in the following order: 360 days > 180 days > 90 days > 0 days, and 1 time > 2 times > 3 times > 6 times for duration and frequency treatments, respectively.

Organic C decayed quickly in both leaf litters compared with the *M. sacchariflorus* stems ($P < 0.05$, Fig. 4). Both leaf litters released N at the end of incubation, while the stem litters showed nutrient accumulation ($P < 0.05$). One-way ANOVA showed that the release of litter C and N was significantly promoted by increasing inundation duration or decreasing inundation frequency ($P < 0.05$).

4. Discussion

4.1. Litter quality and decomposition

At the same inundation duration or frequency, decomposition rates among the three litter types decreased in the order *M. sacchariflorus* leaves > *C. brevicuspis* leaves > *M. sacchariflorus* stems. The initial litter qualities of the three litter types suggested that decomposability was highest in *C. brevicuspis* leaves, intermediate in *M. sacchariflorus* leaves, and lowest in *M. sacchariflorus* stem. The lowest initial N and P contents and the highest ratios of C:N, C:P, and lignin:N among litter types 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 decayed at a slower rate than *M. sacchariflorus* leaves with lower N and P contents. However, 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).

4.2. Inundation duration and leaf litter decomposition

Decomposition rates for both leaf litters increased with increasing inundation duration, suggesting a stimulation effect by submergence in labile litters, which is consistent with our first hypothesis. Promotion by prolonged inundation has also been reported in other studies (Capps et al., 2011; Sun et al., 2012). Baker et al. (2001) suggested that litter decomposition might be accelerated when moisture is adequate rather than excessive. For both leaf litters, the fast decay indicates that the moisture might not be excessive, therefore a stimulation effect of prolonged inundation was observed. Furthermore, by increasing leaching and physical fragmentation (Wallis and Raulings, 2011), prolonged inundation also accelerated litter decomposition through the stimulation of decomposers in litters (Langhans and Tockner, 2006). Actually, fungal biomass in both leaf litters of *M. sacchariflorus* and *C. brevicuspis* was stimulated by inundation, as shown in our previous experiment (Xie et al., 2016).

4.3. Inundation frequency and leaf litter decomposition

Decomposition rates for leaf litters decreased with increasing inundation frequency, suggesting an inhibition effect of repeated inundation in labile litters, which is consistent with our second hypothesis and with the findings of Datry et al., (2011). A general explanation might be the disturbance to microbes caused by wetting and drying cycles, since a stable environment is necessary for microbes to inhabit and consume the litter (Andersen and Nelson, 2003; Datry et al., 2011). Drying events not only strongly reduce breakdown processes when they occur, but also persistently affect leaf litter breakdown processes long after wet conditions have resumed (Corti et al., 2011). In the present experiment, litters under repeated inundation treatments were inundated again at 280 days, but still decomposed more slowly than those under the single inundation.

The response of leaf litter to inundation frequency in one-month incubations in previous studies (Langhans and Tockner, 2006; Foulquier et al., 2015) was different from the findings of our study. Therefore, our one-year experiment might offer a valuable prediction

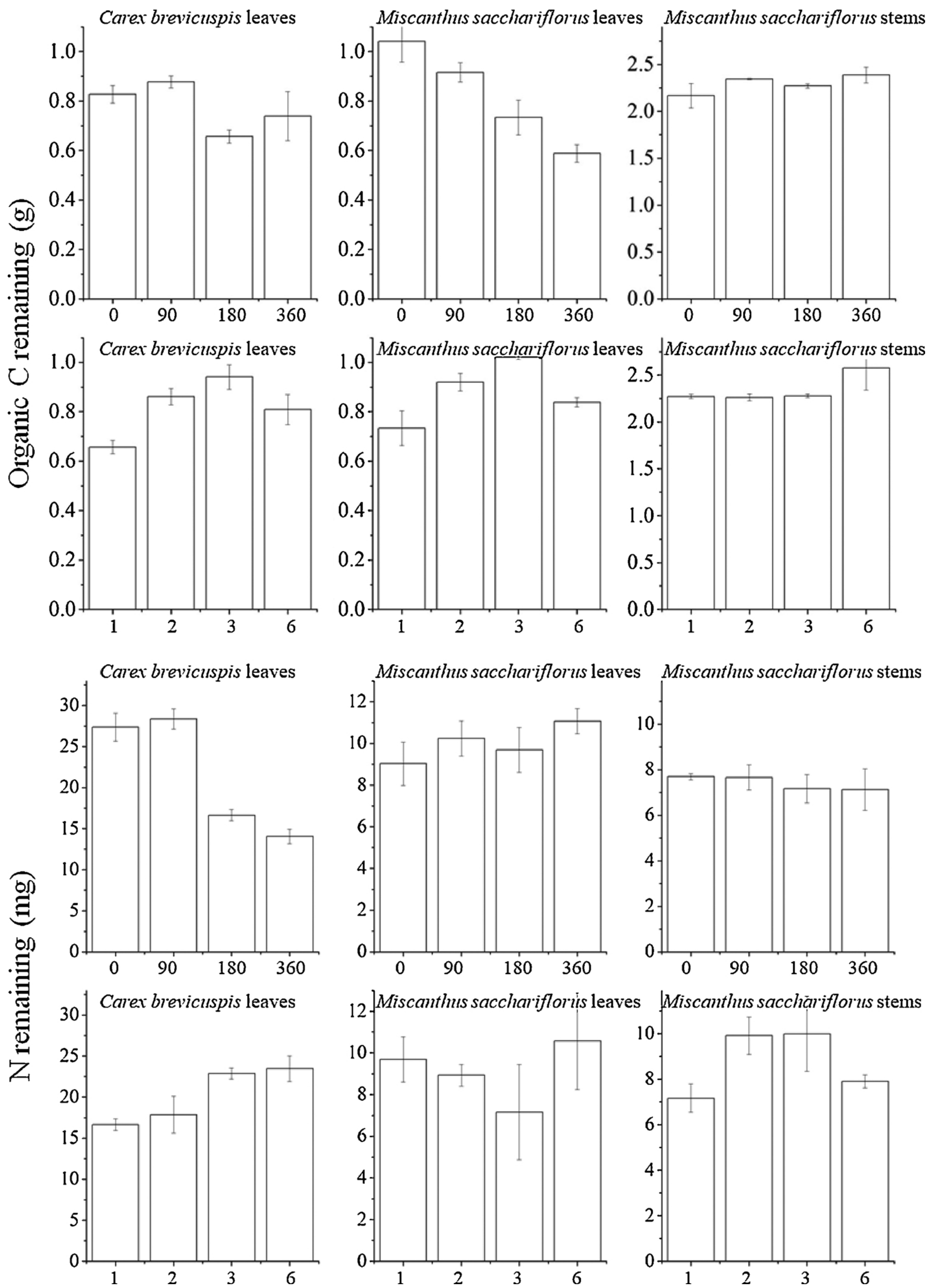

Fig. 4. Dynamic of litter organic C (g) and N (mg) remaining in response to inundation duration (0, 90, 180, and 360 days) and frequency (1, 2, 3, and 6 times).

about the dynamic response of litter to seasonal inundation regimes.

To simulate the wetting and drying cycles, 2-day interval was chosen as the non-inundation interval. This interval occurs in many natural wetlands including Dongting Lake (Liu et al., 2010; Wallis and Raulings, 2011) and has also been used in previous experiments (Langhans and Tockner, 2006; Foulquier et al., 2015). Actually, most of the water held in litter pores will drain out after 2 days (Tietema et al., 2007).

4.4. Inundation regime and stem litter decomposition

Both inundation duration and frequency had no impact on the decomposition of *M. sacchariflorus* stems, suggesting that decomposition of refractory litters might primarily be regulated by their poor quality and insensitivity to environmental fluctuations (Fonseca et al., 2013). This is consistent with our third hypothesis. Similarly, other studies have also found the insensitivity of some low-quality litters (mainly stem litters) to particular environmental factors (e.g. soil fertility, temperature, and water depth) (Sariyildiz and Anderson, 2003; Fierer et al., 2005). One reason for this phenomenon might be the low nutrient contents in litters. In a previous study the immobilization of nutrients and slow releases in C, lignin, and cellulose during decomposition of *M. sacchariflorus* stem litters indicated that the fungus could not assimilate sufficient nutrients from the stem litter to utilize the organic C (Xie et al., 2016). Therefore, fungal consumption of stem litter can be limited by nutrients at all inundation levels; however, litter decay took place under different water conditions in the various inundation regimes. Another reason might relate to the fragmentation of litters. Previous studies have suggested that highly recalcitrant components, such as cellulose and lignin, would make the stem more resistant to physical abrasion than the leaf (Fonseca et al., 2013). In the present study, lignin, cellulose, and C contents were highest in *M. sacchariflorus* stems among the three litter types, indicating a strong resistance of this stem litter to water abrasion.

5. Conclusions

Effects of inundation regime on macrophyte decomposition yield consistent results. Using a one-year experiment, we quantitatively indicated that decomposition of emergent macrophytes was dependent on the interaction between litter quality and the inundation regime. The inundation regime had no effect on the decomposition of refractory stem litter because of its low nutrient contents and high resistance to physical abrasion. Hence, labile leaf litter decayed faster at longer inundation periods than at shorter ones because of the stimulation of leaching, fragmentation, and microbial consumption. Repeated inundation decelerated degradation of the labile leaf litter compared with single inundation, indicating that decomposers could not adapt to the wetting and drying cycles from repeated inundation.

Our study suggests that the labile litters require more attention than refractory litters during evaluation of the nutrient recycle responses to changes in the hydrological regime. Given the sampling timing in our experiment, it is difficult to distinguish between the effects of dry–wet and wet–dry alternation on decomposition of labile leaf litter.

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