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ORIGINAL ARTICLE

Effects of flooding regimes on the decomposition and nutrient dynamics of *Calamagrostis angustifolia* litter in the Sanjiang Plain of China

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Abstract From May 2005 to September 2006, the potential effects of marsh flooding regimes on the decomposition and nutrient (N, P) dynamics of *Calamagrostis angustifolia* litter were studied in the typical waterlogged depression in the Sanjiang Plain, Northeast China. The decomposition of *C. angustifolia* litter was related to four sites with different hydrologic regimes [F1 (perennial flooding, average water depth of 480 days was 40.14 ± 8.93 cm), F2 (perennial flooding 33.27 ± 6.67 cm), F3 (perennial flooding 23.23 ± 5.65 cm) and F4 (seasonal flooding 1.02 ± 1.09 cm)]. Results showed that flooding regimes had important effects on the litter decomposition, the decomposition rates differed among the four sites, in the order of F3 ($0.001820\mathrm{d}^{-1}$) > F1 ($0.001210\mathrm{d}^{-1}$) > F2 ($0.001040\mathrm{d}^{-1}$) > F4 ($0.000917\mathrm{d}^{-1}$), and the values in the perennial flooding regimes were much higher. Flooding regimes also had significant effects on the N and P dynamics of litter in decomposition process. If the perennial flooding regimes were formed in *C. angustifolia* wetland due to the changes of precipitation in the future, the litter mass loss would increase 23.28–48.88%, the decomposition rate would increase 13.41–98.47%, and the $t_{0.95}$ would decrease 1.07 yr–4.50 yr. In the perennial flooding regimes, the net N accumulated in some periods, while the net P released at all times. This study also indicated that the changes of N and P content in the litter of the four flooding regimes were probably related to the C/N or C/P ratios in the litter and the N or P availability in the decomposition environment. If the nutrient status of the decomposition environment did not change greatly, the decomposition rates depended on the substrate quality indices of the litter. Conversely, if the nutrient status changed greatly, the decomposition rates might depend on the supply status of nutrient in the decomposition environment.

Keywords Litter decomposition · Flooding regime · *Calamagrostis angustifolia* · Nitrogen · Phosphorus · Sanjiang Plain

Introduction

Nutrient cycles and energy flow are two important fields of ecosystem research. Litter decomposition is an important link of nutrient cycling, and connects the synthesis (photosynthesis) and decomposition (the breakdown of organic matter and the release of nutrient elements) of biological organisms (Peng and Liu 2002). Wetlands are the most active interfaces for energy and nutrient movement on the earth since they are the ecotones between waters and lands (Chen 1995). The decomposition rates of litter in wetland ecosystems, to a great extent, affect the accumulation rates of litter and the return of nitrogen (N), phosphorus (P) and other elements to the soil pool. This process even affects

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the germination, growth, species abundance and aboveground biomass of wetland plants, and further influences the composition of plant community and the competition among populations in the habitat (Yin et al. 1994; Peng and Liu 2002).

At present, many studies on the litter decomposition process in wetland ecosystems have been reported, and the research objects have related to freshwater marsh (Vargo et al. 1998; Villar et al. 2001; Anderson and Smith 2002; Welsch and Yavitt 2003; Xie et al. 2004), salt marsh (Mendelssohn et al. 1999; Bouchard and Lefeuvre 2000; Pereira et al. 2007), mangrove swamp (Holmboe et al. 2001; Dick and Osunkoya 2000; Tam et al. 1998; Nielsen and Andersen 2003) and peat bog (Haraguchi et al. 2002, 2003; Freeman et al. 2004; Laiho et al. 2004). Overall, the current research not only relates to the litter decomposition characteristics, the changes of organic matter composition and element [such as nitrogen (N), phosphorus (P), potassium(K), sulphur(S)] contents in litter in the decomposition process, but also focuses on the responses of litter decomposition to global changes (Cotrufo et al. 1998; Dilustro et al. 2002; Sowerby et al. 2005). Understanding the response of litter decomposition to global changes is of crucial importance in understanding soil organic matter formation and carbon sequestration in wetland ecosystems. In general, the studies on the response of litter decomposition to global changes have been widely carried out in grassland ecosystem (Owensby 1993; Wang et al. 2000; Alwyn et al. 2005), forest ecosystem (Berg et al. 2000; Finzi et al. 2001) and agroecosystem (Marhan et al. 2008; Liu et al. 2009) through long-term ground network monitoring and observation, free-air CO_2 enrichment (FACE) technique, simulating climatic change experiments in situ, cross-site decomposition experiments and application of reciprocal transplant technique across different climate zones. However, the information on the response of litter decomposition to the global changes in wetland ecosystems is still very limited.

Hydrology is suspected of a major role in litter decomposition process of wetland ecosystems, which mainly affects the transformation of organic matter indirectly through altering the aeration of litter (Cai 2000). Edward and Day (1990) studied the decomposition of roots in the periodically flooded Great Dismal Swamp, and demonstrated that the root decay was slowest on the sites with the longest duration of soil saturation (*Chamaecyparis thyoides* and *Acer rubrum-Nyssa ssp.*). But Lin et al. (2004) found that dissolved oxygen (DO) depletion associated with organic matter decomposition took place rapidly in the floodwater inundating the soils. Wrubleski et al. (1997) indicated that there were few differences in dry mass loss of four emergent macrophytes litters (*Typha glauca*, *Phragmites australis*, *Scolochloa festucacea* and *Scirpus lacustris*) in unflooded or flooded soils, and depth of flooding also had little effect on decomposition rates. The wet–dry cycles also had important effects on litter decomposition. Anderson and Smith (2002) found that the natural wet–dry cycles in playa wetland enhanced the decomposition process of *Polygonum pensylvanicum* litter. However, Laiho et al. (2004) indicated that the mass loss was faster in undrained versus drained sites for *Pinus sylvestris* litter. Generally, the effects of wet–dry cycles on litter decomposition mainly depended on the range and time of water table fluctuation. Haraguchi et al. (2003) indicated that the cellulose decomposition rates were positively correlated with the range of water table fluctuation. Anderson and Smith (2002) found that the decomposition rates of *P. pensylvanicum* litter were generally lowest in the long-term flooded conditions and highest in the short-term flooded conditions. Although the researches mentioned above have provided many important results, the information about the effects of hydrological condition on litter decomposition is unclear, and further studies are still needed.

Calamagrostis angustifolia wetland is the main wetland type (accounts for 34.45% of the wetland) in the Sanjiang Plain of Northeast China (He 2000), which is predominated by *C. angustifolia* species (>83%), with the remaining of the vegetation (<17%) constituted by *Salix myrtilloides*, *Sium suave* and *Gentiana scabra*, etc (Ji 2004). The *C. angustifolia* wetland is located on the edge of waterlogged depression which is the most typical distribution in the Sanjiang Plain. In general, the waterlogged depression is relatively closed and usually separated by embankments or ditches resulting from human activities (Lu et al. 2008). There is almost no water imported by runoff, and precipitation is the main source of marsh water. Therefore, the *C. angustifolia* wetland is very sensitive to the changes of water conditions caused by precipitation. At present, some studies on the decomposition of *C. angustifolia* litter already have been reported, but these studies mainly focused on the research of decomposition characteristics and common affecting factors (Liu et al. 2000; Gao et al. 2004; Yang et al. 2006; Wu et al. 2007), and the relative studies about the effects of flooding regime on *C. angustifolia* litter decomposition are very scarce. According to the studies using IPCC AR4 models (under scenarios A2 and B1) (IPCC 2007), precipitation in northeast China in the future presents increasing tendency (Wang et al. 2009), and extreme precipitation events or precipitation intensity also will be increased (Jiang et al. 2009), indicating that the water conditions of *C. angustifolia* wetland are likely to change greatly in the future. Therefore, in the background of global change, how to predict the effects of flooding regimes, caused by the changes of precipitation, on the decomposition of *C. angustifolia* litter is an important question in understanding the ecological process and mechanism of *C. angustifolia* wetland in the future.

In this paper, the litterbag technique was used, and the natural flooding regimes in the waterlogged depression were applied to simulate the changes of water conditions in *C. angustifolia* wetland. The purposes of this paper were (i) to predict the potential effects of different flooding regimes, caused by the changes of precipitation in the future, on the decomposition of *C. angustifolia* litter; (ii) to study the probable dynamic characteristics of nutrient (N, P) in *C. angustifolia* litter as the different flooding regimes were formed in the future.

Materials and methods

Study site

The experiment was carried out at the Ecological Experiment Station of Mire Wetland in the Sanjiang Plain, Chinese Academy of Sciences (47°35′N, 133°31′E), which is located in northeast of Heilongjiang province of China (Chen 1996). The experimental field (about 1,000 ha^2) is located in the floodplain between Bielahong River and Nongjiang River, at an altitude of 56 m. The experimental field is of typical continental monsoon climate, summer is warm and rainy while winter is long-term cold. The frozen depth of soil in winter is about 1.8–2.2 m. The annual average temperature is 1.9°C, and the effective accumulative temperature is about 2,300°C. The annual evaporation is 542–580 mm, the annual precipitation is 565–600 mm and about 60% of precipitation occurs between June and August (Liu et al. 2003). The experimental field is a waterlogged depression which is the most typical distribution in the Sanjiang Plain. From centre to outside, the vegetations in the waterlogged depression are circularly distributed with *Carex pseudocuraica*, *Carex lasiocarpa*, *Carex meyeriana* and *C. angustifolia*. Because the water adaption ranges differed among the four communities, in the order of *C. pseudocuraica* > *C. lasiocarpa* > *Carex meyeriana* > *C. angustifolia*, the distribution and succession of different communities are significantly affected by the changes of water conditions caused by precipitation (Yang and Lu 1996). If water condition in a community exceeds its adaption range, the vegetation will disappear and be replaced by other vegetations gradually (Zhang 1988). The soils at the experimental field are of humus marsh soil and meadow marsh soil, and the characteristics of topsoil (0–20 cm) in different communities are showed in Table 1. In this study, the annual average production of *C. angustifolia* litter is 1,027.7 ± 202.9 g m^{-2}, and the total carbon (TC), total nitrogen (TN), total phosphorus (TP) and total sulfur (TS) contents in *C. angustifolia* litter are 41.24 ± 2.81%, 4,505.7 ± 100.3, 656.2 ± 67.6 and 752.2 ± 141.7 mg kg^{-1}, respectively.

Study method

As the flooding conditions of waterlogged depression, from centre to outside, represents different hydrologic regimes, it can be used to study the different changes of water regimes in *C. angustifolia* wetland caused by precipitation in the future. From May 2005 to September 2006, the decomposition experiment of *C. angustifolia* litter was conducted with litterbag technique in four different sites (F1, F2, F3 and F4) in waterlogged depression. The water regime in each site was classified, based on 480 days, water depth (only determined in unfrozen period) and flooding time, as F1 (perennial flooding, average water depth of 480 days was 40.14 ± 8.93 cm), F2 (perennial flooding, 33.27 ± 6.67 cm), F3 (perennial flooding, 23.23 ± 5.65 cm) and F4 (seasonal flooding, the abundant precipitation, in the growing season, generally occurs in summer (between June and August), and the *C. angustifolia* community is usually flooded by shallow water. While in early spring (May) and autumn (September and October), the community usually has no standing water due to the low precipitation, (1.02 ± 1.09 cm), according to the natural hydrologic conditions observed during the study (Fig. 1). The four water regimes (represented by water depth) during the experiment had significant different ($p < 0.01$). Precipitation during the

Table 1 Basic characteristics of topsoil (0–20 cm) in different communities

Communities	Soil types	Soil bulk density (g cm^{-3})	pH	Organic matter (%)[a]	Total phosphorus (g kg^{-1})[a]	Total nitrogen (g kg^{-1})[a]	Ammonium nitrogen (mg kg^{-1})[a]	Nitrate nitrogen (mg kg^{-1})[a]
Calamagrostis angustifolia	Meadow marsh soil	0.91	5.37	14.03 ± 6.00	99.59 ± 35.38	806.77 ± 396.83	18.97 ± 11.20	0.97 ± 0.19
Carex meyeriana	Humus marsh soil	0.73	5.93	29.80 ± 8.05	137.76 ± 3.71	1,592.60 ± 308.34	38.87 ± 24.54	1.04 ± 0.25
Carex lasiocarpa	Humus marsh soil	0.57	5.36	51.24 ± 3.53	96.21 ± 12.65	2,247.30 ± 175.26	31.79 ± 3.54	2.29 ± 0.21
Carex pseudocuraica	Humus marsh soil	0.35	6.37	53.79 ± 0.13	112.11 ± 3.38	1,456.05 ± 24.00	28.98 ± 2.65	2.40 ± 0.14

[a] Values are means (±SD, $n = 5$)

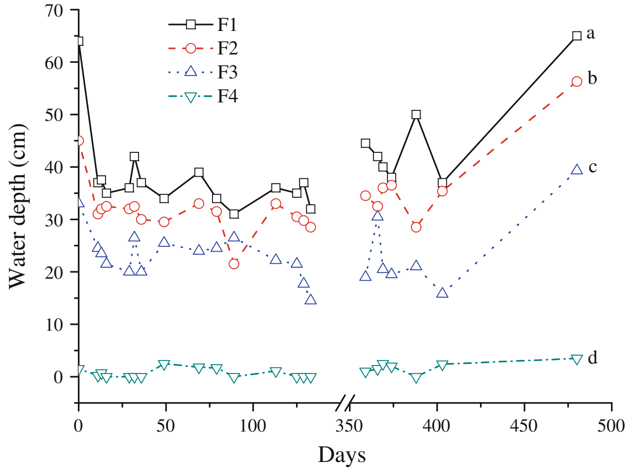

Fig. 1 Water depth through time for four sites with varying flooding regimes [F1 (perennial flooding, average water depth of 480 days was 40.14 ± 8.93 cm), F2 (perennial flooding, 33.27 ± 6.67 cm), F3 (perennial flooding, 23.23 ± 5.65 cm) and F4 (seasonal flooding, 1.02 ± 1.09 cm)] in the waterlogged depression, 25 May 2005–25 September 2006. Values with the same letters are not significantly different at $p < 0.05$

growing season (May–October) in 2005 and 2006 were 388.6 and 518.7 mm, respectively.

The *C. angustifolia* litter was collected from the *C. angustifolia* community at the end of April 2005. In order to weaken the fragmentation impact of heavy snowfalls and strong winds in winter, the standing litter was selected for use in this study. The litter was washed in distilled water, cut into 10 cm segments and oven-dried at 80°C for 48 h. Each 20 cm × 20 cm litterbag was made of nylon netting (0.5 mm mesh) and was filled with 15 g (oven-dried weight) litter. The litterbags were randomly placed on the ground of above-mentioned sites (more than 36 litterbags were placed in each site) on May 25, 2006. Five litterbags were regularly retrieved from each sampling site during the following 480 days, with a total of 20 litterbags for each time. After retrieval, these litterbags were immediately taken back to the laboratory, and the plant roots, lichen, sediment and macro-invertebrates were removed from the remaining litter. Finally, all litterbags were further cleaned gently in deionized water. The samples were dried at 80°C for 48 h, weighed and ground (<0.25 mm) using a Wiely mill and analyzed for TC, TN contents by element analyzer (Elementar Vario Micro, Germany) and TP content by molybdate-ascorbic acid colorimetry (digested by H_2SO_4-H_2O_2) (The Committee of Agro-chemistry of the Chinese Society of Soil Science 1983).

Determination of environmental factors

During the experiment, the atmospheric temperature, ground/water temperature (0, 5, 10, 20 cm depth) and soil/water pH were periodically determined. Marsh water was sampled per month in F1, F2 and F3 for analyzing the TN, TP, NH_4^+-N, NO_3^--N, NO_2^--N and PO_4^{3-}-P contents with conventional methods (The Committee of Agro-chemistry of the Chinese Society of Soil Science 1983). Since the majority dates of the water samples from April to September in 2006 were incomplete, the corresponding dates used in this study were from May to September in 2005.

Calculation and statistical analysis

Litter decomposition rate was calculated by the following exponential model (Olson 1963):

$$W_t/W_0 = e^{-kt}$$

where W_0 is the original dry mass (g), W_t is the mass remaining at time "t", k is the decay constant and t is decomposition time in days. Differences in decomposition rates among the flooding regime treatments were determined by comparing the decay constant "k".

The N accumulation index (NAI) and P accumulation index (PAI) were used to express the accumulation or release status of nutrient (N, P) in litter in decomposition process, which could be calculated by the following equation:

$$\mathrm{AI} = \frac{M_i \cdot X_i}{M_0 \cdot X_0} \times 100\%$$

where M_0 is the original dry mass, X_0 is the original nutrient content in litter, M_i is the dry mass at time "i" and X_i is the nutrient content in litter at time "i". AI > 100% indicated that net nutrient accumulated in litter, whereas AI < 100% indicated that net nutrient released from litter.

The samples were presented as means over the replications, with standard deviation (SD). The analysis of variance (ANOVA) tests (SPSS for windows 11.0) was employed to determine if treatments differed significantly ($p < 0.05$). If ANOVA showed significant differences, multiple comparison of means was undertaken by Tukey's test with a significance level of $p = 0.05$.

Results

Dynamics of nutrient contents in marsh water of the four sites

The dynamics of TN, TP, NH_4^+-N, NO_3^--N, NO_2^--N and PO_4^{3-}-P contents in the marsh water of F1, F2 and F3 from May to September in 2005 showed that the N and P nutrient status of the three sites were different (Fig. 2), but the differences were not significant. In general, the TN content was higher in F3 site, while in F1 site, the TP content was much higher.

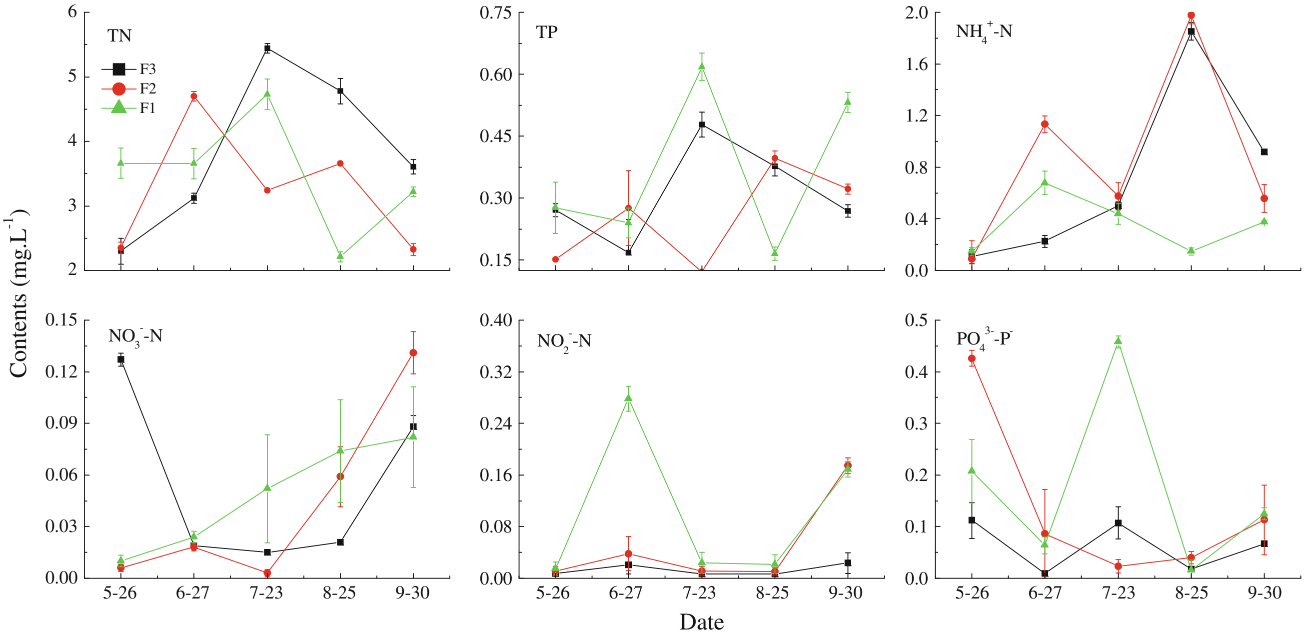

Fig. 2 Changes of TN, TP, NH_4^+-N, NO_3^--N, NO_2^--N and PO_4^{3-} contents in marsh water of the four sites with varying flooding regimes [F1 (perennial flooding, average water depth of 480 days was 40.14 ± 8.93 cm), F2 (perennial flooding, 33.27 ± 6.67 cm), F3 (perennial flooding, 23.23 ± 5.65 cm) and F4 (seasonal flooding, 1.02 ± 1.09 cm)] in the waterlogged depression from May to September in 2005. Values are means (±SD, $n = 3$)

Dynamics of litter decomposition

The mass loss of *C. angustifolia* litter in the four sites were rapid in summer and fall (accounting for 58.74, 54.99, 85.14 and 90.87% of annual loss for F4, F3, F2 and F1, respectively), while slow or even inactive in winter and early spring except F4 and F3 (Fig. 3). After 480 days, the percent of dry mass remaining was 59.01 ± 7.50% for F4, 38.97 ± 8.60% for F3, 49.47 ± 0.72% for F2 and 47.65 ± 1.76% for F1. The mass loss of litter in different sites presented F2 $\approx$ F1 > F3 > F4 from 0 to 220 days and F3 > F2 $\approx$ F1 > F4 from 220 to 480 days, indicating that flooding regime had important effects on the litter decomposition. The decomposition rates differed among the four sites, in the order of F3 (0.001820d^{-1}) > F1 (0.001210d^{-1}) > F2 (0.001040d^{-1}) > F4 (0.000917d^{-1}) and the values in the perennial flooding regimes were much higher (Table 2). If the perennial flooding regimes were formed in *C. angustifolia* wetland in the future, the litter mass loss would increase 23.28–48.88%, the decomposition rate would increase 13.41–98.47%, and the $t_{0.95}$ would decrease 1.07 yr–4.50 yr.

Nutrient dynamics in litter decomposition process

Dynamics of total nitrogen and total phosphorus content

The TN content in *C. angustifolia* litter of F4 had no significantly changed except for one obvious decline occurred in 420 days (Fig. 4a), and after 480 days, the value was very close to the initial one. Comparatively, the TN content in the litter of F3, F2 and F1 changed consistently with a significant peak observed in 120 days, and over 480 days, the values were 1.80, 1.13 and 1.43 times the initial ones, respectively. ANOVA showed that the TN contents in litter of the four flooding regimes had no significant difference ($p > 0.05$).

The TP content in litter of F4 increased rapidly to 2.15 times the initial value at the first month, and then changed steadily from 30 to 60 days (Fig. 4b). After that, the TP content decreased although little fluctuation was observed from 90 to 360 days, and the value in litter, over 480 days, was only 0.35 times the initial one. Comparatively, the TP content in the litter of F3, F2 and F1 changed consistently from 0 to 120 days, accounting for 34.60–89.57, 49.99–90.14 and 55.04–77.98% of the initial value, respectively. From 120 to 480 days, the values of F3, F2 and F1 changed differently and, over 480 days, an obvious increase observed in F3 and F2, while a significant decrease occurred in F1. ANOVA showed that the TP contents in litter of the four flooding regimes had significant difference ($p < 0.05$).

Dynamics of C/N and C/P ratio

In the perennial flooding regimes (F1, F2 and F3), C/N ratios were much lower and C/P ratios were generally

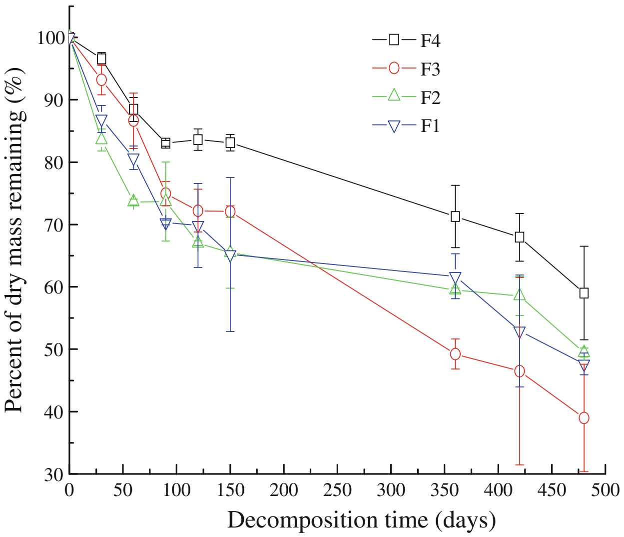

Fig. 3 Percent of dry mass remaining of *C. angustifolia* litter in the four sites with varying flooding regimes [F1 (perennial flooding, average water depth of 480 days was 40.14 ± 8.93 cm), F2 (perennial flooding, 33.27 ± 6.67 cm), F3 (perennial flooding, 23.23 ± 5.65 cm) and F4 (seasonal flooding, 1.02 ± 1.09 cm)] in the waterlogged depression, 25 May 2005–25 September 2006. Values are means (±SD, $n = 5$)

higher than those in the seasonal flooding regime (Fig. 5), but the C/N or C/P ratios in litter of the four flooding regimes had no significant differences ($p > 0.05$). The C/N ratios in litter during the decomposition were 83.46–225.52% for F4, 53.23–124.27% for F3, 46.77–140.13% for F2 and 62.60–114.82% for F1 compared with the initial values, and the C/P ratios in litter of the four flooding regimes accounted for 46.26–265.14, 100.00–278.25, 100.00–195.85 and 100.00–228.41% of the initial values, respectively, indicating that, in the perennial flooding regimes, N might accumulate more in the litter, while P might release from the litter at all times.

Dynamics of nitrogen or phosphorus accumulation index

The NAI and PAI of *C. angustifolia* litter in the four flooding regimes had different change characteristics (Fig. 6). In general, the variations of NAI or PAI in F3, F2 and F1 were consistent, while those in F4 were different. During the decomposition, the net N released from the litter at all times in F4, while in F3 and F2, the net N accumulated only in 30 and 120 days. Similarly, in F1, the net N accumulation only occurred in 120 days. In contrast with that, the net P released from the litter in F3, F2 and F1 at all times, while in F4, the net P release predominated although P accumulation occurred in 30 and 60 days. ANOVA showed that the NAI of *C. angustifolia* litter in the four sites had no significant differences, while the differences of PAI were significant ($p < 0.05$). The percent of mass remaining (W_t/W_0) had significantly positive correlation with PAI in the four sites ($p < 0.05$ or $p < 0.01$), while the correlation between W_t/W_0 and NAI was significant only in F4 ($p < 0.05$) (Table 3), indicating that the changes of P absolute amount in litter of the four sites, to a great extent, probably depended on the mass remaining amount, while those of N absolute amount in litter of F3, F2 and F1 might depend on other affecting factors, such as N sources in decomposition environment, microbe immobilization and exchange adsorption of organic matter.

Discussion

Dynamics of litter decomposition

This study showed that flooding regimes had important effects on the decomposition of *C. angustifolia* litter, the decomposition rates differed among the four water regimes, in the order of F3 > F1 > F2 > F4, and the values in the perennial flooding regimes were much higher. Lin et al. (2004) found that dissolved oxygen (DO) depletion associated with organic matter decomposition took place rapidly in the floodwater inundating the soils. Neckles and Neill (1994) also indicated that the litter in wetland generally decomposed faster when flooded than un-flooded or infrequently flooded, and the positive effect of flooding on litter decomposition might be due to the maintenance of adequate soil moisture for microbial/fungal colonization and activity. In general, water condition affects the decomposition rate of organic matter indirectly through altering the aeration of litter (Cai 2000), and the effect of water condition change on the decomposition depends on the potential change magnitude as well as the current water condition (Chen 1999). If the current water condition is favor for litter decomposition, then the significant water condition change may result in a decrease in decomposition. However, if water is the limiting factor,

Table 2 Linear equations and parameters between the natural logarithm (y) of mass remaining and decomposition days (t)

Sites	Equations	k	R^2	p	Decomposition time (days)	$t_{0.95}$ (yr)
F1	$y = -0.14280-0.001210t$	0.001210	0.8694	0.0002	480	6.88
F2	$y = -0.17715-0.001040t$	0.001040	0.8162	0.0008	480	8.00
F3	$y = -0.05080-0.001820t$	0.001820	0.9825	<0.0001	480	4.57
F4	$y = -0.04359-0.000917t$	0.000917	0.9442	<0.0001	480	9.07

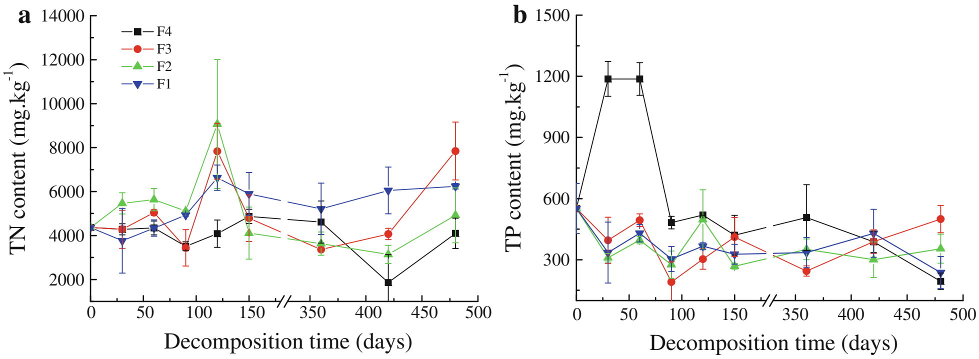

Fig. 4 Changes of TN (**a**) and TP (**b**) content in the *C. angustifolia* litter in the four sites with varying flooding regimes [F1 (perennial flooding, average water depth of 480 days was 40.14 ± 8.93 cm), F2 (perennial flooding, 33.27 ± 6.67 cm), F3 (perennial flooding, 23.23 ± 5.65 cm) and F4 (seasonal flooding, 1.02 ± 1.09 cm)] in the waterlogged depression, 25 May 2005–25 September 2006. Values are means (±SD, *n* = 5)

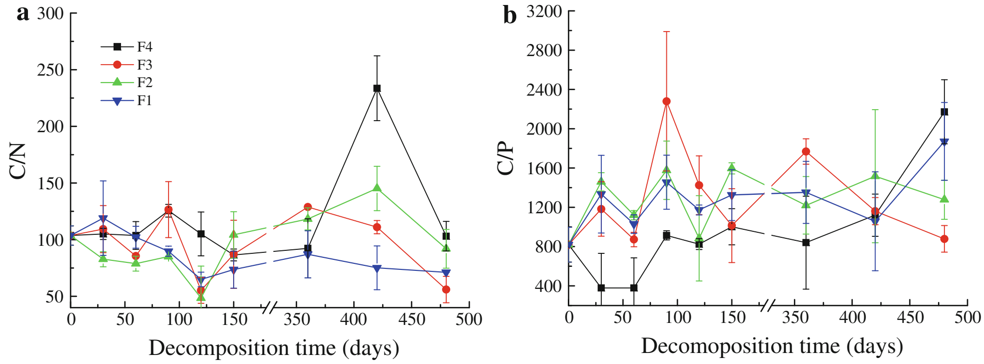

Fig. 5 Changes of C/N ratio (**a**) and C/P ratio (**b**) in the *C. angustifolia* litter in the four sites with varying flooding regimes [F1 (perennial flooding, average water depth of 480 days was 40.14 ± 8.93 cm), F2 (perennial flooding, 33.27 ± 6.67 cm), F3 (perennial flooding, 23.23 ± 5.65 cm) and F4 (seasonal flooding, 1.02 ± 1.09 cm)] in the waterlogged depression, 25 May 2005–25 September 2006. Values are means (±SD, *n* = 5)

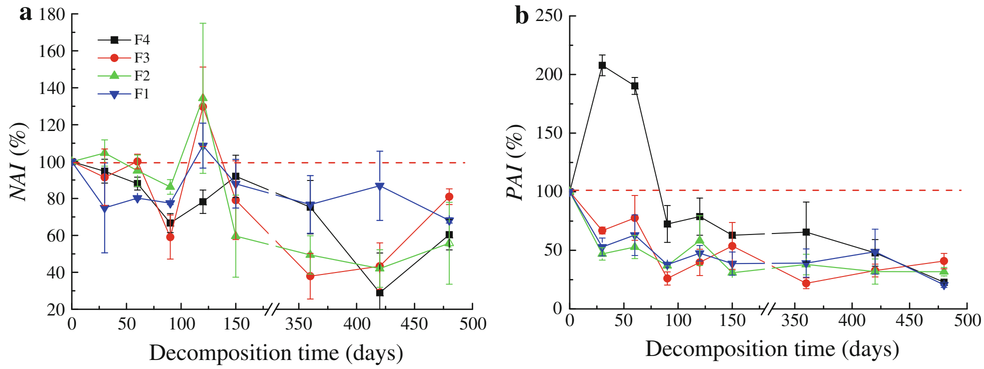

Fig. 6 Changes of *NAI* (**a**) and *PAI* (**b**) of *C. angustifolia* litter in the four sites with varying flooding regimes [F1 (perennial flooding, average water depth of 480 days was 40.14 ± 8.93 cm), F2 (perennial flooding, 33.27 ± 6.67 cm), F3 (perennial flooding, 23.23 ± 5.65 cm) and F4 (seasonal flooding, 1.02 ± 1.09 cm)] on the waterlogged depression, 25 May 2005–25 September 2006. Values are means (±SD, *n* = 5)

then the increase of water condition will enhance decomposition (Chen et al. 2001). In current water condition (F4), the *C. angustifolia* litter decomposed slowest, while in weak perennial flooding regimes (F3), the decomposition rate rapidly increased. This showed that water was a limiting factor in F1, and the proper increase of water

Table 3 Correlation coefficients between percent of mass remaining (W_t/W_0) and accumulation index (AI)

Accumulation index (AI, %)	Percent of mass remaining (%) in the four sites			
	F1	F2	F3	F4
NAI	0.366	0.593	0.574	0.776*
PAI	0.855**	0.829**	0.780**	0.727*

* Correlation is significant at the 0.05 level

** Correlation is significant at the 0.01 level

Table 4 Correlation coefficients between environment temperature and relative decomposition rate

Items	F1	F2	F3	F4
Atmospheric temperature	0.677	0.218	0.598	0.440
Surface ground/water temperature	0.584	0.390	0.581	0.643
5 cm ground/water temperature	0.265	0.146	0.441	0.700
10 cm ground/water temperature	0.208	−0.109	0.403	0.584
20 cm ground/water temperature	0.235	−0.003	0.234	0.436

condition in F3 was in favor of decomposition. On the other hand, the litter decomposition rate in strong or medium perennial flooding regime (F1, F2) was much lower than that in weak perennial flooding regime (F3), indicating that the water regime in F3 was favor for decomposition, and the significant increase of water condition in F2 and F1 resulted in obvious decrease in decomposition through affecting the status of O_2 and CO_2 in litter. With the great increase of water in decomposition environment, the O_2 in litter would be depleted rapidly and the metabolism of decomposition microbes would be restrained (Laiho et al. 2004). In addition, the lower decomposition rates of litter also might be attributed to the low rate of enzymic decomposition (Freeman et al. 2004). As the devoid of molecular oxygen, the enzymes such as phenol oxidase, which required molecular oxygen for their activity, were rarely active, and thus inhibited the decomposition of organic matter. Anderson and Smith (2002) studied the effect of flooding regimes on decomposition of *P. pensylvanicum* litter in playa wetlands, and also found that the litter decomposition rates were generally lowest in the strong or medium flooded conditions and highest in the weak flooded conditions.

The litter decomposition rates are also significantly affected by environment temperature, and the values generally increased with increasing temperature (Cai 2000). Our study showed the similar result. In summer and fall, the *C. angustifolia* litter decomposed rapidly, while in winter and early spring, the litter decomposed slowly, and the correlation between environment temperature and decomposition rate in the four sites were mostly positive (Table 4). The acidity-alkalinity status also may have great effects on litter decomposition as microbes all have different optimum pH ranges, and higher or lower pH may significantly inhibit microbe activities (Cai 2000). Hohmann and Neely (1993) indicated that the increase of acidity could inhibit the decomposition of *Sparganium eurycarpum* litter, and the dry weight remaining after 200 days at pH 4, 6 and 8 were 47.5, 27.9 and 7.3%, respectively. Leuven and Wolfs (1988) found that the pH particularly influenced the decomposition rate of *Juncus bulbosus* L. litter, and in control media with pH 3.5 and 5.6, the total organic weight losses after 37 days were 55 and 59%, respectively. In this study, the pH of water or soil in the four sites ranged from 5.36 to 6.37, implying that the acidity status of decomposition environments might have different effects on the litter decomposition, but these effects still need to be studied.

In general, the chemical properties of litter (mainly include N, P, lignin and cellulose contents, C/N, lignin/N and C/P ratios) are the main control factors of decomposition. Among them, the C/N and lignin/N ratios are the best predication indices of decomposition rate as they reflect the ratio of carbohydrate and lignin to protein in litter (Harmon et al. 1990; Hobbic 1996; Chen 1999). However, the predication indices of decomposition in different stages differ with the changes of litter substrate quality. Alerts and Caluwe (1997) found that the litter decomposition was strongly limited by C/P ratio in the initial stage, while closely correlated with the ratios of phenolic compounds/N and phenolic compounds/P in long-term decomposition. In this experiment, the C/N and C/P ratios had different effects on the litter decomposition in the four sites. In most instances, the C/N or C/P ratios had negative correlations with decomposition rates (Table 5), which indicated that the higher of C/N or C/P ratios, the slower of decomposition rates and the result was close to the reports mentioned previously (Harmon et al. 1990; Hobbic 1996; Chen 1999; Yang et al. 2006; Wu et al. 2007). On the other hand, the C/N or C/P ratios, in F3 and F1, had positive correlations with decomposition rates and the correlation in F1 was significant ($p < 0.05$), implying that the status of N and P nutrient in the decomposition environment probably influenced the litter decomposition. Davis (1991) studied the decomposition of *Cladium jamaicense* and *T. domingensis* litters in Florida Everglades, and found that the decomposition was lowest under non-enriched conditions and reached a maximum under a moderate level of enrichment. Verhoeven and Arts (1992) studied the *Carex* litter decomposition in mires with different water chemistry, and found that the conditions for cellulose decay are much more suitable in the groundwater fed (base-rich) fen dominated by *Carex diandra* than in the rainwater fed (base-poor) fen with *Carex acutiformis*. In addition, the increase of N and P supply in the decomposition environment also have great

Table 5 Correlation coefficients between C/N or C/P ratio and relative decomposition rate

Items	F1	F2	F3	F4
C/N	0.779*	−0.517	0.377	−0.083
C/P	−0.017	−0.282	0.561	−0.110

* Correlation is significant at the 0.05 level

effects on the litter decomposition as this increase may alter the C/N or C/P ratios of litter. Aerts and Caluwe (1994) indicated that, in the area of abundant N deposition, the increase of N import might accelerate the litter decomposition. Xie et al. (2004) studied the effects of N and P availability on the decomposition of aquatic plants, and found that the elevation of P-availability greatly increased the decomposition rate of *Eichhornia crassipes* by 68–87%, whereas the impact of N-availability was insignificant, implying that the responses of decomposition to nutrient availability depended on nutrient type. As mentioned previously, the N and P nutrient status in the marsh water of F3, F2 and F1 were different, which might affect the corresponding litter decomposition rate. In addition, the physiognomy of waterlogged depression was declined in turn along with the direction of F3 → F2 → F1, indicating that the exchange of marsh water in the three sites might occur if the flooding regimes changed significantly resulting from the increase or decrease of precipitation during the experiment. During the exchange of marsh water, the nutrient among the three sites would be changed simultaneously, and the ultimate results caused the nutrient status in the marsh water of each decomposition site, compared with its original environment, changed greatly. Therefore, based on above-mentioned analysis, we could conclude that the decomposition rates, to some extent, depended on the substrate quality indices of the litter if the nutrient status of decomposition environment did not change greatly. Conversely, if the nutrient status changed greatly due to nutrient deposition and nutrient exchange among marsh water, the decomposition rates, to a great extent, depended on the supply status of nutrient in the decomposition environment.

Nutrient dynamics in litter decomposition process

This study showed that flooding regimes also had important effects on the N and P dynamics of *C. angustifolia* litter in decomposition process, and in the perennial flooding regimes, the N might accumulate more in the litter, while P might release from the litter at all times. Some relative studies also showed similar results. Dick and Osunkoya (2000) found that the C and N contents in *Avicennia marina* litter were much higher in tidal wetland than those of landward wetland as the difference in water conditions. Wrubleski et al. (1997) found that the P in litters (*T. glauca*, *P. australis*, *S. festucacea* and *S. lacustris*) in different flood conditions (1–30 cm, 31–60 cm and >60 cm water depths) exhibited significant losses (46.3–92.7%) during the first 112 days. In this experiment, the changes of N and P content in the litter of the four sites might be related to the different nutrient status in marsh water (Fig. 2). Sun et al. (2006) found that the N/P ratio of *C. angustifolia* was 5.99 ± 0.20, indicating that the marsh was limited by N (Tessier and Raynal 2003). Therefore, in some periods, the increase of N content in litter in the perennial flooding regimes might be attributed to the N immobilization by microbes from marsh water (Liu et al. 2000). Similarly, Gessner (2000) found that the N concentrations tended to increase in the leaf, culm and sheath of *Pragmites australis* litter, and the reasons were mainly related to the external biological immobilization from lake water. Another study by Gessner (2001) indicated that the microbial immobilization was a very important process controlling the nutrient dynamics of litter during decomposition, which was mainly regulated by the C/N ratios in the litter and the N availability in the decomposition environment (Berg 1986; Köchy and Wilson 1997). The C/N ratios had significant negative correlations with N contents ($p < 0.01$) (Table 6), but the correlations between C/N ratios and P contents were not significant, indicating that the C/N ratios might control the N dynamics in the litter of the four sites. The C/N ratios in the litter of the four sites were all much lower, and the N in the litter could meet the demand of organisms, thus the superfluous N would release from the litter in most periods.

As analyzed previously, the net P released from the litter in F3, F2 and F1 at all times, while in F4, the net P release predominated although P accumulation occurred in 30 and 60 days, and the reasons were related to the P loss by leaching (Puriveth 1980). Previous studies indicated that the P was easily lost due to leaching because P mainly existed in phosphates in plant tissues (Wen et al. 1998). Based on above analysis, the marsh was not limited by P, and

Table 6 Correlation coefficients between C/N or C/P ratio and nitrogen or phosphorus

Items	N				P			
	F1	F2	F3	F4	F1	F2	F3	F4
C/N	−0.989**	−0.923**	−0.968**	−0.977**	0.357	−0.369	−0.442	−0.205
C/P	0.330	−0.486	−0.390	−0.177	−0.949**	−0.979**	−0.954**	−0.807**

** Correlation is significant at the 0.01 level therefore, the demand of decomposers was not limited by P supply during the decomposition. As a result, superfluous P would retard microbial activities, causing P to release from the litter. In this study, the C/P ratios had significant negative correlations with P contents ($p < 0.01$) (Table 6), but the correlations between C/P ratios and N contents were not significant, indicating that the C/P ratios might control the P dynamics in the litter of the four sites. This study also showed that, in the perennial flooding regimes, the net P release amounts were much higher than those in the seasonal flooding regime (Fig. 6b), and the reasons were mainly related to the P nutrient status in the decomposition environment. In general, the lower the C/P ratios, the more the P release (Yang et al. 2006). Although the C/P ratios in the litter of the perennial flooding regimes were higher than those in the seasonal flooding regime (Fig. 5b), the relatively abundant P nutrient in marsh water might reduce the C/P ratios, and thus cause the litter release more P.

Conclusion

The decomposition experiment of *C. angustifolia* litter in different flooding regimes has demonstrated that: (i) flooding regimes had important effects on the litter decomposition, the decomposition rates differed among the four sites, in the order of F3 > F1 > F2 > F4. Flooding regimes also had significant effects on the N and P dynamics of litter in decomposition process; (ii) If the perennial flooding regimes were formed in *C. angustifolia* wetland in the future, the litter mass loss would increase 23.28–48.88%, the decomposition rate would increase 13.41–98.47%, and the $t_{0.95}$ would decrease 1.07 yr–4.50 yr. In the perennial flooding regimes, the net N accumulated in some periods, while the net P released at all times; (iii) the decomposition rates in the four flooding regimes depended on the substrate quality indices of the litter if the nutrient status of the decomposition environment did not change greatly. Conversely, if the nutrient status changed greatly, the decomposition rates probably depended on the supply status of nutrient in the decomposition environment; (iv) the changes of N and P content in the litter of the four flooding regimes were related to the C/N or C/P ratios in the litter and the N or P availability in the decomposition environment. In the perennial flooding regimes, the increase of N content in the litter in some periods might be attributed to the N immobilization by microbes from marsh water, while more P released from the litter might be related to the alteration of C/P ratios in the litter due to the change of P nutrient in the decomposition environment.

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