

Impacts of Soil Fauna on Litter Decomposition at Different Succession Stages of Wetland in Sanjiang Plain, China

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Abstract: Litter decomposition is the key process in nutrient recycling and energy flow. The present study examined the impacts of soil fauna on decomposition rates and nutrient fluxes at three succession stages of wetland in the Sanjiang Plain, China using different mesh litterbags. The results show that in each succession stage of wetland, soil fauna can obviously increase litter decomposition rates. The average contribution of whole soil fauna to litter mass loss was 35.35%. The more complex the soil fauna group, the more significant the role of soil fauna. The average loss of three types of litter in the 4mm mesh litterbags was 0.3–4.1 times that in 0.058mm ones. The decomposition function of soil fauna to litter mass changed with the wetland succession. The average contribution of soil fauna to litter loss firstly decreased from 34.96% (*Carex lasiocapa*) to 32.94% (*Carex meyeriana*), then increased to 38.16% (*Calamagrostis angustifolia*). The contributions of soil fauna to litter decomposition rates vary according to the litter substrata, soil fauna communities and seasons. Significant effects were respectively found in August and July on *C. angustifolia* and *C. lasiocapa*, while in June and August on *C. meyeriana*. Total carbon (TC), total nitrogen (TN) and total phosphorus (TP) contents and the C/N and C/P ratios of decaying litter can be influenced by soil fauna. At different wetland succession stages, the effects of soil fauna on nutrient elements also differ greatly, which shows the significant difference of influencing element types and degrees. Soil fauna communities strongly influenced the TC and TP concentrations of *C. meyeriana* litter, and TP content of *C. lasiocapa*. Our results indicate that soil fauna have important effects on litter decomposition and this influence will vary with the wetland succession and seasonal variation.

Keywords: wetland; invertebrate; soil fauna; litter decomposition; nutrient dynamics

1 Introduction

Wetlands are among the most productive ecosystems. The high organic matter content in macrophytes has been described as a typical characteristic of wetlands. However, only a small percentage of plant biomass is directly consumed by herbivores. Most of the litter materials enter the general pool of particulate organic matter following shoot withering and death. Plant litter decomposition is one of the least studied functions of wetland ecosystems, but represents a crucial feedback loop that recycles and transfers nutrients and helps mediate the sequestration of soil carbon (Fennessy et al., 2008). Litter decomposition has been commonly used as a pa-

rameter of ecosystem functioning (Taylor and Middleton, 2004; Fennessy et al., 2008).

Natural litter decomposition comprises several steps, i.e., leaching, mechanical fragmentation, microbial colonization and invertebrate processing. It is regulated by three factors operating at different scales: litter quality, environment characteristics (temperature, moisture and nutrition) and biotic factors (microbe and invertebrates) (Berg and Laskowski, 2006; Wu et al., 2006). The majority of studies on biotic effects on litter decomposition focused on the microbial colonization (Gessner and Chauvet, 1994; Barik et al., 2000) because microbes have exoenzymes required to degrade organic matter. The role of soil invertebrates in litter decomposition has

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been widely reported in forestry and grassland ecosystems (González and Seastedt, 2001; Bradford et al, 2002; Smith and Bradford, 2003; Song et al., 2008).

Invertebrates are essential components of wetlands and have high diversity, consisting of aquatic species and terrestrial soil fauna because wetland ecosystems consist of aquatic and terrestrial subsystems (Grimm et al., 2003; Wu et al., 2008). Although many previous studies on wetland invertebrates have described the spatial and temporal distribution, influencing factors and the indicator function to the aboveground vegetation and surrounding environment (Steinman et al., 2003; Davis et al., 2006; Genet and Olsen, 2008), wetland invertebrate function to litter decomposition has been less reported. Furthermore, little information is available concerning the effects of soil fauna on litter decomposition in Chinese wetlands.

The Sanjiang Plain is one of the freshwater marshes with integrated distribution and the largest area in China. In the past 50 years, the wetlands were seriously drained and reclaimed and thus the wetland ecosystems degenerated significantly. The process of litter decomposition of specific species (*Calamagrostis angustifolia* and *Carex lasiocapa*) has been extensively investigated in the Sanjiang Plain, including decomposition process, nutrient dynamics and abiotic influencing factors (Gao et al., 2004; Liu and Song, 2008). Yang et al. (2006) and Wu et al., (2007a) reported the different decomposition rates and main abiotic influencing factors of three types of macrophyte litter belonging to three stages of wetland succession. However, the information about the role of soil fauna to the litter decomposition was limited.

The objectives of this study were to determine the effects of soil fauna on litter decomposition rates and nutrient cycling at different succession stages of wetland, and to reveal the change of the contributions of soil fauna communities to litter decomposition in different seasons.

2 Materials and Methods

2.1 Study site

The Sanjiang Plain as a low floodplain, located in Heilongjiang Province of Northeast China, is formed by the Heilong River, the Songhua River and the Wusuli River. The study site (47°35'N, 133°31'E) is located at the Sanjiang Mire-wetlands Experimental Station, Chi-

nese Academy of Sciences (Fig. 1). This region experiences a temperate moist monsoon climate with a mean annual temperature of 1.9°C and a mean annual precipitation of 600mm. Average monthly temperature is -21°C in January and 22°C in July. More than 60% of the annual precipitation is concentrated between July and September. The average altitude of the study area is 55m. The dish-shaped marsh is of the representative wetland type in the Sanjiang Plain. From the margin to the center, the types of vegetation vary from *C. angustifolia*-*Salix brachypoda*-*Salix myrtilloides* community, *Carex meyeriana*-*C. lasiocapa* community to *Carex lasiocapa*-*Carex pseudocuraica*-*Glyceria spiculosa* community with a zonal distribution as the depth of standing water increases significantly from no surface water, seasonal inundation to long-term submergence. Correspondingly, the dominant species are respectively *C. angustifolia*, *C. meyeriana* and *C. lasiocapa*. The three types of wetlands represent the different succession stages of natural wetlands in the Sanjiang Plain, China.

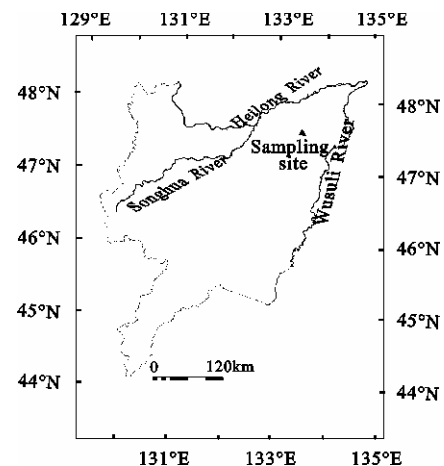


Fig. 1 Location of sampling site

2.2 Decomposition experiment

The short-term incubation experiments were conducted using the in situ litterbag technique. The litterbags with different mesh sizes were used to distinguish different soil organisms affecting decomposition. Litterbags (15cm×15cm) were made from nylon mesh with four different mesh sizes (4.000mm, 0.270mm, 0.150mm and 0.058mm). Litterbag edges were sealed by nylon thread. The largest mesh (4.000mm) allowed the entrance of all soil organism (microorganisms, microfauna, mesofauna and macrofauna) to the litterbags; the 0.270mm litterbags exclude only macrofauna, the 0.150mm litterbags

exclude macrofauna and mesofauna, whereas in the 0.058mm litterbags only microorganisms were allowed access.

Litterbag decomposition experiments were carried out in a dish-shaped marsh, along a belt of 5m wide and 45m long from the border to the center. Standing litter shoots of *C. lasiocapa*, *C. meyeriana* and *C. angustifolia* were collected from three types of wetlands, i.e., *C. lasiocapa*-*C. pseudocuraica*-*G. spiculosa* community, *C. meyeriana*-*C. lasiocapa* community and *C. angustifolia*-*S. brachypoda*-*S. myrtilloides* community, respectively, in April 2005. Shoots were washed in distilled water, cut into 10cm-long pieces and oven-dried at 60°C. Each bag contained 10g dry shoots. Every type of plant litter was placed in one litterbag and also each type of plant litter was placed in litterbags of four sizes. Four litterbags were buried randomly in the soil of 5cm deep at the same site, where the plant material had been collected, on 20 May 2005. Three litterbags of each type were retrieved from each site with total 36 bags collected respectively on 30 June, 31 July, 31 August and 31 October 2005. The incubation time was 164d. Each collected bag was further cleaned gently in deionized water baths. The materials were dried to be constant at 60°C, weighed (with 0.001g resolution) and ground to analyze the total carbon (TC), total nitrogen (TN) and total phosphorus (TP) contents using Li's method (Li, 1983).

2.3 Statistical analysis

Percentages of litter mass loss were time standardized (mass loss per day) because not all the periods comprised the same number of days. Decomposition rates were calculated by determining the percent of mass remaining at each time period and calculating K , the first-order exponential decomposition rate constant. Mass loss data were fitted to the simple exponential model according to Olson (1963):

$$W_t = W_0 e^{-kt} \quad (1)$$

where W_t is the litter dry mass remaining after time t (d), W_0 the initial mass, and K (1/d) the decomposition rate constant. The time needed to decompose 95% of the litter was inferred as:

$$t_{0.95} = 2.9957/k \quad (2)$$

Faunal effects on litter decomposition were quantified by using the formula of Seastedt et al. (1987):

$$E_{\text{fauna}} = (L_{\text{fauna}}/L_{\text{total}}) \times 100\% \quad (3)$$

where E_{fauna} (%) is faunal effect on litter loss, L_{fauna} is the percentage of litter mass loss resulting from all direct and indirect faunal activities, and obtained from the difference of the litter mass loss in the different fauna-controlled litterbags. L_{total} is the percentage of litter mass loss obtained from the 4mm mesh litterbags, and is considered as the litter natural decomposition including all the abiotic, microbial, and faunal effects.

Repeated measures analysis of variance (ANOVA) was used to determine differences in decomposition rates and TC, TN and TP concentrations for litter in different mesh litterbags. Nutrient immobilization was calculated based on the changes in litter nutrient concentrations between the initial and the collection dates. TC, TN and TP contents in each bag were assessed by multiplying the mass weight in each bag by its TC, TN or TP concentration.

Due to the highly variable nature of ecosystems and the relatively small sample sizes when using each ecosystem as an experimental unit, we report significance values at the level of $p \leq 0.10$. All statistical analyses and drawing were performed using the SPSS 13.0 and ORIGINPRO 7.5.

3 Results and Analysis

3.1 Decomposition rate

Decomposition rates of the three types of litter can be divided into two stages: higher decomposition stage in the first 41d (to the time of the first pick-up), and slight decomposition stage over the remainder of the study (Fig. 2). For the three types of litter, weight loss showed only small differences between treatments in the first 41d and then significant differences were observed. The more complex the soil fauna group was, the more significant the role of soil fauna was throughout the study (Fig. 2). At the end of the study, the average mass loss of three types of litter in the 4.000mm mesh bags was 0.3–4.1 times that in 0.058mm ones. The difference between 0.250mm and 0.170mm mesh bags were not significant at 0.05 level.

The statistics derived from the negative exponential model (Table 1) summarized the overall breakdown processes. The comparison of the decomposition constants (K) and $t_{0.95}$ showed that greater losses of litter were found in coarse mesh bags with more soil fauna effects in all the three types of litter.

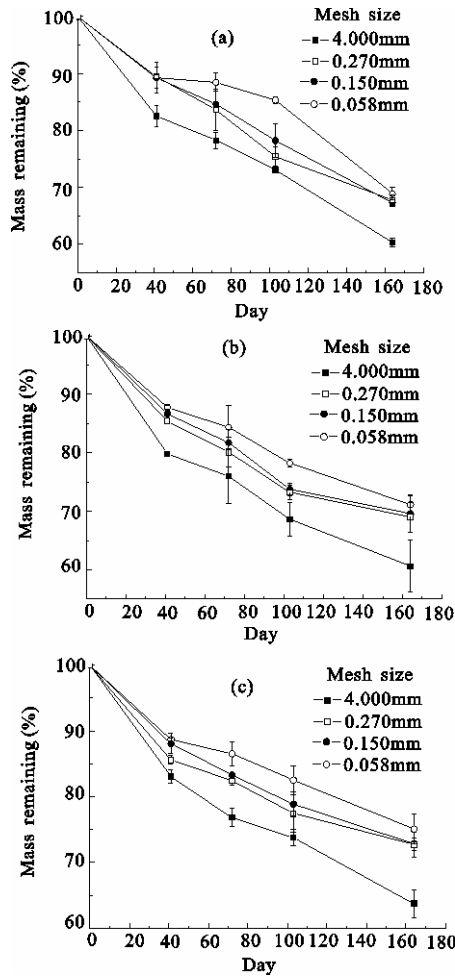


Fig. 2 Litter loss of *C. angustifolia* (a), *C. meyeriana* (b) and *C. lasiocapa* (c) in different mesh bags

Table 1 Regression parameters of relation between litter mass remaining and decomposition days

	<i>K</i>	<i>F</i>	<i>p</i>	<i>R</i> ²	<i>t</i> _{0.95}
<i>C. angustifolia</i>					
4.000mm	0.0029	131.926	0.001	0.978	2.83
0.270mm	0.0024	281.261	0.000	0.989	3.42
0.150mm	0.0024	1026.628	0.000	0.997	3.42
0.058mm	0.0021	37.225	0.009	0.925	3.91
<i>C. meyeriana</i>					
4.000mm	0.0029	55.049	0.005	0.948	3.16
0.270mm	0.0022	41.474	0.008	0.933	4.32
0.150mm	0.0022	50.497	0.006	0.944	4.32
0.058mm	0.0020	125.713	0.002	0.977	4.83
<i>C. lasiocapa</i>					
4.000mm	0.0026	67.166	0.004	0.957	3.15
0.270mm	0.0019	33.817	0.010	0.919	4.32
0.150mm	0.0019	72.938	0.003	0.961	4.32
0.058mm	0.0017	87.782	0.003	0.967	4.83

The significant effects of soil fauna to litter decomposition rates vary according to the litter substrata and seasons. Significant effects on *C. angustifolia* and *C. lasio-*

capa were respectively found in August and July, while on *C. meyeriana* in June and August (Table 2).

Table 2 *F* values for ANOVA of mesh sizes for litter decomposition rates

	Litter loss percent			
	30 June 2005 (41d)	31 July 2005 (72d)	31 August 2005 (103d)	31 October 2005 (164d)
<i>C. angustifolia</i>	3.15ns	3.92ns	9.42**	0.21ns
<i>C. meyeriana</i>	93.32***	1.04ns	5.43*	0.41ns
<i>C. lasiocapa</i>	0.74ns	4.28*	2.34ns	1.83ns

Notes: *df*=3 in all comparisons; ns: *p*>0.10; * 0.05<*p*<0.10; ** 0.01<*p*<0.05; *** *p*<0.01

3.2 Soil fauna contribution to litter loss

The contribution rates of soil fauna communities were significantly different among various litter substrata and seasons (Fig. 3). The total average contribution from direct and indirect effects of soil fauna accounted for

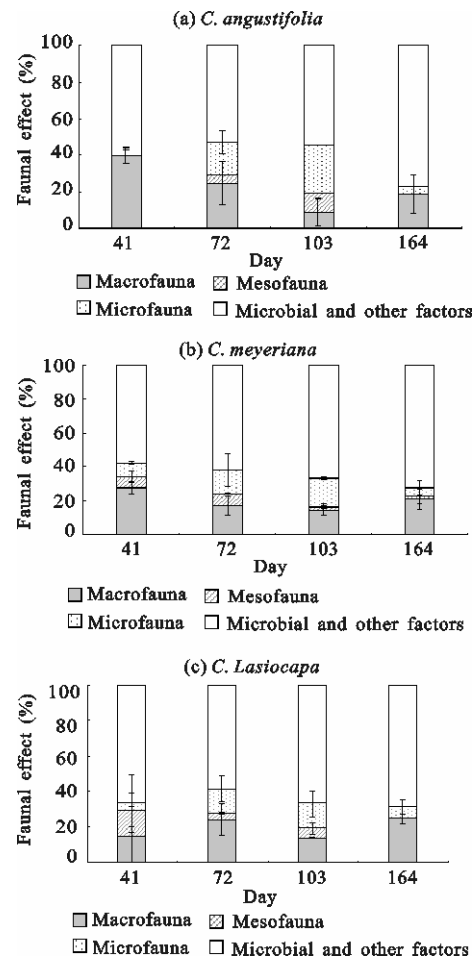


Fig. 3 Faunal effect of different fauna communities on litter loss

35.35% of mass loss of three types of litter. In *C. angustifolia*-*S. brachypoda*-*S. myrtilloides* wetland, the total average effect of soil fauna reached 38.16% of *C. angustifolia* litter loss and the maximum and minimum values appeared on the day 72 and day 164, respectively. On the day 41 and the day 164, the macrofauna effect was dominant; and on the day 72, the macrofauna and microfauna effects were leading; while on the day 103, it was mainly microfauna. In *C. meyeriana*-*C. lasiocapa* wetland, the *C. meyeriana* mass loss rate by soil fauna showed a decreased tendency and the maximum value was 39.45% on the day 41; the average contribution of whole experimental period was 32.94%. The macrofauna effect was dominant in the whole decomposition process and microfauna effect was also important on day 72 and day 103. However, the total average concentration of soil fauna reached 34.96% of *C. lasiocapa* litter loss in *C. lasiocapa*-*C. pseudocuraica*-*G. spiculosa* wetland and the dominant soil fauna communities

significantly changed (Fig. 3).

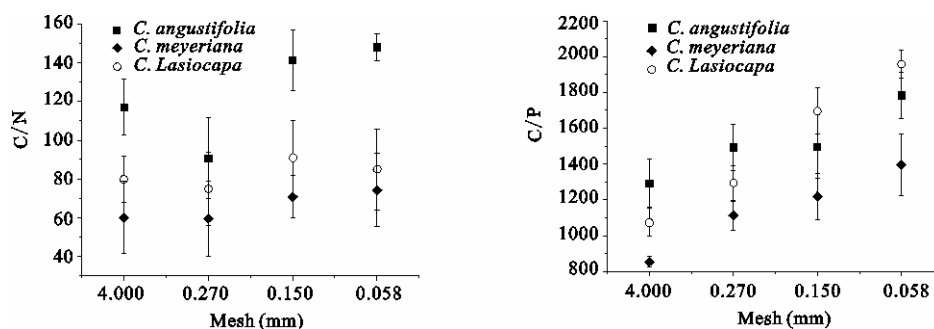
3.3 Soil fauna effects on litter TC, TN and TP dynamics

During the whole litter decomposition processes, significant differences in the changes of TC, TN and TP contents were observed in different mesh litterbags, which exhibited a similar trend. Table 3 showed TC, TN and TP concentrations at the end of the study. The results indicated that different soil fauna communities strongly influenced the TC ($p < 0.01$) and TP ($p < 0.01$) contents of *C. meyeriana* litter, also TP ($p < 0.05$) concentration of *C. lasiocapa*.

The C/N and C/P ratios of three types of litter were also affected to different degrees by different soil fauna communities because they influenced TC, TN and TP content and litter remaining percent. Fig. 4 showed that the C/N and C/P ratios were substantially different among different mesh bags for each litter type.

Table 3 TC, TN and TP concentration in different mesh litterbags at end of the study (31 October 2005)

	Mesh size				F	p
	4.000mm	0.270mm	0.150mm	0.058mm		
TC (%)						
<i>C. angustifolia</i>	42.63±0.90	43.30±0.51	43.40±0.75	44.60±0.84	0.31	0.818
<i>C. meyeriana</i>	43.56±0.81	44.49±0.92	45.12±0.53	47.48±0.77	6.10	0.009
<i>C. lasiocapa</i>	46.14±0.37	46.57±0.95	47.48±0.53	48.94±1.45	0.22	0.882
TN (g/kg)						
<i>C. angustifolia</i>	3.64±0.36	4.78±0.40	3.07±0.30	3.01±0.59	1.01	0.438
<i>C. meyeriana</i>	7.26±0.71	7.48±0.55	6.38±0.32	6.40±0.37	0.08	0.969
<i>C. lasiocapa</i>	5.78±0.56	6.22±0.46	5.22±0.16	5.76±0.26	1.25	0.333
TP (g/kg)						
<i>C. angustifolia</i>	0.33±0.023	0.29±0.046	0.29±0.019	0.25±0.015	2.27	0.133
<i>C. meyeriana</i>	0.51±0.021	0.40±0.033	0.37±0.034	0.34±0.021	6.76	0.003
<i>C. lasiocapa</i>	0.43±0.037	0.36±0.031	0.28±0.011	0.25±0.015	5.77	0.011



Bars indicate standard error

Fig. 4 C/N and C/P of remaining litter in different mesh litterbags at end of the study (31 October 2005)

4 Discussion

The effects of soil fauna communities (size-classes) on

litter decomposition were greatly different for the same litter, even in the same season. We believe that the variation can be primarily attributed to soil fauna com-

munity compositions and their effect mechanisms. Paris et al. (2008) suggested that macrofauna, mainly earthworms, termites and ants, affects the decomposition either directly through digestion or indirectly by their alteration of soil physicochemical properties; mesofauna, which includes mites and collembolans, alters the microbial community by selective feeding, dispersal, and activation of microorganisms; and microfauna, mainly comprising free-living nematodes, can regulate decomposition processes and nitrogen mineralization. Although we did not give the concrete contribution value of soil fauna communities to nutrient cycle, the different results of element concentrations between different mesh litterbags have proven the sizeable role on nutrient mineralization of soil fauna.

For different succession stages of wetland, whether the soil faunal effects were also significantly depended on litter substrate and timing of litter retrieved. The different effects can be attributed to direct and indirect roles of soil fauna, including the interactions between soil fauna and other factors. Soil fauna affect decomposition processes both directly through the comminution of litter material, and indirectly by altering microbial function through grazing of the soil microbial biomass and through excretion of nutrient rich wastes. Meantime, litter and soil environment as the food or living spaces also influence soil fauna community. This indicated that soil fauna and other factors are interacting with each other and affect the litter decomposition processes.

Some previous studies have revealed that the changes in land use modify soil environmental conditions and alter the community of soil fauna (Liang et al., 2005). Our results further proved that the alteration of soil fauna community also lead to the changes of soil faunal decomposition function. Dominant groups of soil fauna varied with changing environmental factors: Acariformes, Stylommatophora and Cellembola in *C. angustifolia-S. brachypoda-S. myrtilloides* wetland; Coleoptera adult, Nemata, Stylommatophora and Acariformes in *C. meyeriana-C. Lasiocapa* wetland; Acariformes, Stylommatophora and Cellembola in *C. lasiocapa-C. pseudocuraica-G. Spiculosa* wetland.

Relationships between soil fauna diversity and ecosystem function have been investigated by categorizing fauna by species, trophic group, body size, habitat preference or successional community (Cole et al., 2006).

Body size provides a good functional classification because it correlates with metabolic rate, generation time, population density and food size. We manipulated soil fauna community composition by constraining access by organism body size using the different mesh litterbags. But this approach has some limitations: the soil fauna surrounding the litterbag remain unchanged and thus may indirectly affect the litter decomposition, involving soil fauna mediating the abiotic environment and the decomposer assemblage (Cole et al., 2006; Wu et al., 2007b). Therefore, the results may magnify the contribution of soil fauna to litter decomposition; also, such a manipulation does not necessarily simulate how soil fauna community composition changes spatially and temporally, or responses to environmental factor variations (Smith et al., 2003; Wu et al., 2007b). It is also important to note that this study is a fundamental investigation of soil fauna affecting litter decomposition as a good example of interactions of below-ground food webs and wetland processes. The influencing ratio and mechanism should be further revealed by long-term investigations.

5 Conclusions

Through examining the impacts of soil fauna on litter-decomposition rates and nutrient fluxes at three succession stages of wetland in the Sanjiang Plain, Northeast China using different mesh litterbags, this article drew following conclusions.

(1) In each succession stage of wetland, soil fauna obviously increase litter decomposition rates. The more complex the soil fauna group, the more significant the role of soil fauna, and this role becomes more obvious in the late stage of the decomposition (from the day 41 to the day 164). The contributions of soil fauna to litter decomposition rates include direct and indirect effects, and vary according to the different litter substrata, soil fauna communities and seasons. The decomposition functions of soil fauna to litter mass loss change with the wetland succession.

(2) TC, TN and TP contents and the C/N and C/P ratios of decaying litter can be influenced by soil fauna. At different wetland succession stages, the effects of soil fauna on nutrient elements also differ greatly, which shows the significant difference of influencing element types and degrees.

Our results indicate that soil fauna have important effects on litter decomposition and this influence varies with the wetland succession and seasonal variation

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