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Decomposition of reed leaf and non-leaf litter in the air and on the ground in the Yellow River Delta, China

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Abstract The decomposition of standing litter is a vital but easily neglected process. Most studies always focused on the decomposition of leaf litter on the surface of soil or sediment, whereas the decomposition of leaf and non-leaf litter in the air is often overlooked. A field experiment was conducted in the Yellow River Delta to investigate the decomposition of leaf and non-leaf (culm and sheath) litter (*Phragmites australis*) in the air and on the ground. The results showed that the litter on the ground decomposed faster than the standing litter due to its larger enzyme activities, and the remaining mass of litter on the soil surface was 73–87% of the standing litter. The culm litter had the largest mass remaining among three types of litter owing to the lowest enzyme activities and the largest initial C/N and C/P of the culm litter. Concerning the dynamics of nutrient, nitrogen and phosphorus in leaf and non-leaf litter were first released and then enriched at two decomposition interfaces. Of the three types of litter, the culm litter had the highest N remaining after 360 days of decomposition due to the largest initial C/N of the culm litter. Our findings emphasize the importance of standing litter decomposition in the wetlands of the Yellow River Delta, and suggest that the decomposition of non-leaf (culm and sheath) litter of emergent macrophytes should not be ignored in wetlands.

Keywords Standing litter · Mass loss · Nutrient dynamics · Reed · Yellow River Delta

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Introduction

Coastal wetland is an important carbon (C) pool due to rapid C sequestration in soil compared to terrestrial ecosystems, sequestering 30–70 Tg C yr^{-1} (Lovelock and Reef 2020; Kirwan et al. 2023). Litter decomposition regulates the recycling of C, nitrogen (N), and phosphorus (P), which plays a vital role in maintaining wetland function and global C balance (Stoler and Relyea 2020; Tuomei et al., 2009). Emergent macrophytes, such as *Phragmites*, are common species in many wetlands and produce a large proportion of the annual biomass (Mitsch and Gosselink 2000). Litter decomposition of emergent macrophytes usually

consists of two phases, aerial decomposition (i.e., standing litter decomposition, Kuehn et al. 2004) and subsequent decay on the soil surface. Although previous studies have suggested that standing litter is an important process of nutrient cycling and C fluxes (see, e.g., Kuehn et al. 2004 and 2011; Gessner 2001), most studies have investigated litter decomposition on the ground (see, e.g., Knorr et al. 2005; Wang et al. 2017a), but have ignored the aerial decay process. Furthermore, the decomposition rates of litter in the air and on the ground remain unclear, with similar (Mao et al. 2021), larger (Wang et al. 2017b), and smaller (Zhang et al. 2014b) decomposition rates for standing litter compared to litter on the ground. Therefore, clarifying the decomposition of litter in the air and on the ground is helpful in comprehensively evaluating the decomposition of litter.

Litter decomposition is usually controlled by biotic and abiotic factors (Knorr et al. 2005; Hebert et al. 2021). There is growing evidence that microorganisms begin to colonize and decompose litter when they are standing (see, e.g. Wang et al. 2017b; Zhang et al. 2014a; Kuehn et al. 1999, 2004). Litter traits (e.g., lignin content and stoichiometry) can regulate fungal biomass and decomposition of standing litter (see, e.g., Knorr et al. 2005; Hebert et al. 2021). Differences in environmental factors (for example, relative humidity) between two decomposition interfaces (i.e., in the air and on the soil surface) can alter microbial activity and thus regulate litter decomposition at two interfaces (Wang et al. 2017b). Furthermore, differences in litter traits of different plant organs (e.g., leaf and culm) can adjust microbial activities and their decomposition (Kuehn et al. 1999, 2004; Zhang et al. 2014b). However, most studies have focused on the decomposition of leaf litter on the surface of soil or sediment, while the decomposition of standing litter, especially non-leaf litter, has not received sufficient attention. Thus, understanding the differences in decomposition of leaf and non-leaf litter can accurately evaluate the litter decomposition process and its impact on nutrient cycling.

The Yellow River Delta (YRD) is a typical coastal wetland in China. Reed (*Phragmites australis*) is one of the main plant species in the YRD. According to field investigation, aerial decay of reed (especially its culm) can last until the end of the next growing season in the YRD. Although several field investigations and laboratory incubation have examined the litter decomposition in the YRD (see, e.g., Zhai et al. 2021; Tao et al. 2019 and 2023; Sun and Mo 2016), the comparison of mass loss and nutrient dynamics between leaf and non-leaf litter (i.e., sheath and culm) at two decomposition interfaces is still less known in the YRD. The aim of this field investigation is to examine the difference in decomposition of leaf and non-leaf litter in the air and on the ground, thereby providing some valuable data for the management of coastal wetland.

Materials and methods

Site description and experiment design

The field experiment was conducted in the buffer zone (that is, a non-tidal wetland) of the Yellow River Delta National Nature Reserve (119.006 E, 37.730 N). Detailed information of the YRD was listed in Tao et al. (2019 and 2023) and Zhai et al. (2021). Leaf, sheath, and culm samples were collected at the end of October 2020 and oven-dried at 70 °C for 72 h to constant weight. 96 litterbags (3 litter types × 4 replicates × 2 decomposition interfaces × 4 sample dates) were prepared and placed at the original sample site in early November 2020. Each nylon litterbag (20 cm × 20 cm, 1 mm mesh size) contained ten grams of litter sample. For each litter type, half of the litterbags were fixed on the soil surface and the other half were suspended at 3/4 of the average height of the reeds according to Zhang et al. (2014a), that is, the litterbags in the air were suspended at a height of 1 m in this field experiment. Twelve litterbags (3 litter types × 4 replicates) were collected on days 90, 180, 270, and 360 at each decomposition interface and stored at 4 °C. Litter samples were gently cleaned with a soft brush, half of which was used to test enzyme activities, and the other half was oven-dried at 70 °C for 72 h and then crushed through a 0.25-mm mesh to test the content of organic carbon (OC), total N and P and litter moisture. The OC content was tested with the Multi N/C 2100 analyzer (Analytik Jena, Germany). Total N in the litter was measured using a Kjeltec Auto Analyzer (Foss 8400, Denmark). The litter was digested by H_2SO_4–H_2O_2 and the total P content was determined by the ammonium molybdate method (Kuo 1996). The activities of phosphatase and urease were measured using the method of Guan

(1986) and expressed as mg g^{-1} h^{-1}. The diel air temperature and relative humidity were measured when collecting litterbags and are listed in Tao et al. (2023). The mean air temperature and relative humidity analyzed in this paper were calculated from the diel air temperature and relative humidity of Tao et al. (2023) and were listed in Fig. S1. The initial characteristics of the litter sample are listed in Table S1.

Statistical analysis and calculation

The remaining litter mass (%) was calculated by dividing the residual mass by the initial mass. The remaining nutrients in the litter (that is, N and P) was calculated by dividing the residual N or P (that is, the N or P content multiplied the litter mass) by the initial N or P (that is, the initial N or P content multiplied the initial litter mass). Differences in litter mass remaining, litter nutrients remaining, enzyme activities, stoichiometry, air temperature, and relative humidity were determined separately by one-way analysis of ANOVA (Tukey's HSD test) at a significant level of $P < 0.05$. The effects of the decomposition interfaces and litter types were measured by two-way repeated measures ANOVA. According to the normality test (Shapiro-Wilk test), all data were converted by logarithmic transformation ($\log_{10}$) before applying repeated measures ANOVA. SPSS 25.0 (IBM Crop, USA) was used for statistical analyzes, and Origin 9.0 (Originlab, USA) was used for drawing figures. Redundancy analysis (RDA) was performed by Canoco software for Windows 5.0 (Microcomputer Power, Ithaca, NY).

Results

Litter mass dynamics

The decomposition interface and the type of litter significantly influenced the remaining litter mass ($P < 0.001$; Table 1). The litter on the ground decomposed faster than the standing litter, that is, the standing litter had a larger litter mass remaining than the litter on the ground ($P < 0.05$). The remaining mass of the ground litter was equivalent to 84.73% (leaf), 86.77% (culm) and 73.65% (sheath) of standing litter after 360 days of decomposition (Fig. 1). According to Olson's equation (Table 2), the time required for the 50% mass loss was 2.27 a for standing litter and 1.45 a for litter on the ground; and the time required for the 95% mass loss was 9.35 a for standing litter and 5.55 a for litter on the ground; indicating that the phase of standing litter decomposition should not be ignored.

For litter types, the culm litter decomposed more slowly than the leaf and sheath litter regardless of the decomposition interface ($P < 0.05$; Fig. 1). Leaf litter had a similar decomposition rate to sheath litter on the ground, while its decomposition rate was higher than that of sheath in the air ($P < 0.05$; Fig. 1). After 360 days of decomposition, the rate of decomposition of
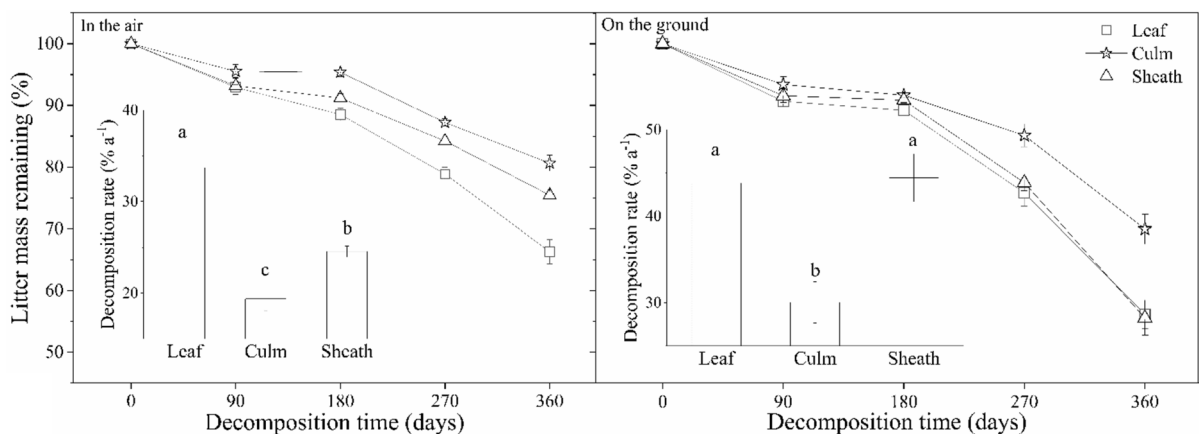

Fig. 1 Remaining mass of litter and decomposition rate during 360 days at two interfaces. Data are means and standard deviation (n = 4). Different lowercase letters represent significant differences among three types of litter ($P < 0.05$)

Table 1 Results of two-way repeated measures ANOVA on the effect of decomposition interfaces and litter types on litter decomposition

Items	Litter mass remaining		N remaining		P remaining		Phosphatase	
	F	P value	F	P value	F	P value	F	P value
Type	276.051	<0.001	11.741	0.001	3.351	0.058	441.763	<0.001
Interface	375.595	<0.001	0.705	0.412	8.206	0.100	227.223	<0.001
Type × Interface	14.97	<0.001	2.356	0.123	8.801	0.003	18.118	<0.001
Items	C/N		C/P		N/P		Urease	
	F	P value	F	P value	F	P value	F	P value
Type	214.120	<0.001	71.88	<0.001	99.404	<0.001	63.082	<0.001
Interface	3.071	0.097	0.095	0.762	2.423	0.137	223.418	<0.001
Type × Interface	0.199	0.822	12.446	<0.001	4.902	0.020	8.171	0.003

Table 2 Relationship between remaining mass and decomposition time based on the Olson's equation (Olson 1963)

Items	Equation	DR (g g^{-1} yr^{-1})	P value	T$_{50\%}$ (yr)	T$_{95\%}$ (yr)
Litter in the air	$Y = 1.045e^{-0.325T}$	0.325	<0.001	2.27	9.35
Litter on the ground	$Y = 1.127e^{-0.561T}$	0.561	<0.001	1.45	5.55

Y represents remaining litter mass, %. T represents decomposition time, yr. DR represents decomposition rate. T$_{50\%}$ represents time of half decomposition, yr. T$_{95\%}$ represents time of 95% decomposition, yr

non-leaf litter was equivalent to 72.87% (sheath) and 57.49% (culm) of that of leaf litter in the air; while decomposition rate of non-leaf litter was equivalent to 101.40% (sheath) and 68.55% (culm) of that of leaf litter on the ground; indicating a non-negligible role of non-leaf organs in litter decomposition.

Litter nutrient dynamics

For the remaining nutrients, after 360 days of decomposition, three types of litter first released N and P and subsequently enriched these two elements at two interfaces (Fig. S2 and S3). Three types of litter released P from the beginning of the experiment to day 180, and then enriched P from day 270 to the end of the experiment. Three types of litter mainly released N from the beginning of the experiment to day 270, and then enriched N at the end of the experiment. The culm litter had the highest remaining N among the three types of litter on day 360 ($P<0.05$). Litter types significantly affected stoichiometry ($P<0.001$). Regardless of the decomposition interface, the C/N, C/P and N/P of three litter types decreased during litter decomposition. Of the three types of litter, culm litter had the highest C/N and C/P and the lowest N/P ($P<0.05$).

Litter enzyme activities

The types of litter and the decomposition interface significantly affected the activities of phosphatase (Fig. 2) and urease (Fig. 3) ($P<0.001$). Regardless of the decomposition interface, the culm had the lowest urease and phosphatase activities among three types of litter ($P<0.05$). Across the three types of litter and the two decomposition interfaces, the activities of urease and phosphatase were greater on days 270 and 360 than on days 90 and 180 ($P<0.05$). Concerning the interface, the litter on the ground had a higher urease activity than the standing litter ($P<0.05$). The phosphatase activities of the litter did not differ between two interfaces on days 90 and 180, and the litter on the ground had higher phosphatase activities than the standing litter on days 270 and 360 ($P<0.05$).

Relationships between litter decomposition and biotic and abiotic factors

The remaining litter mass had a negative relationship with urease, phosphatase, mean air temperature, and relative humidity and a positive relationship with C/N, C/P, and N/P (Fig. 4; $P<0.05$), that is, the mass

Fig. 2 The phosphatase activity in the air and on the ground. Data are means and standard deviation (n = 4). Different lowercase letters represent significant differences among three types of litter ($P < 0.05$). Different capital letters represent significant differences between two interfaces for each type of litter ($P < 0.05$)
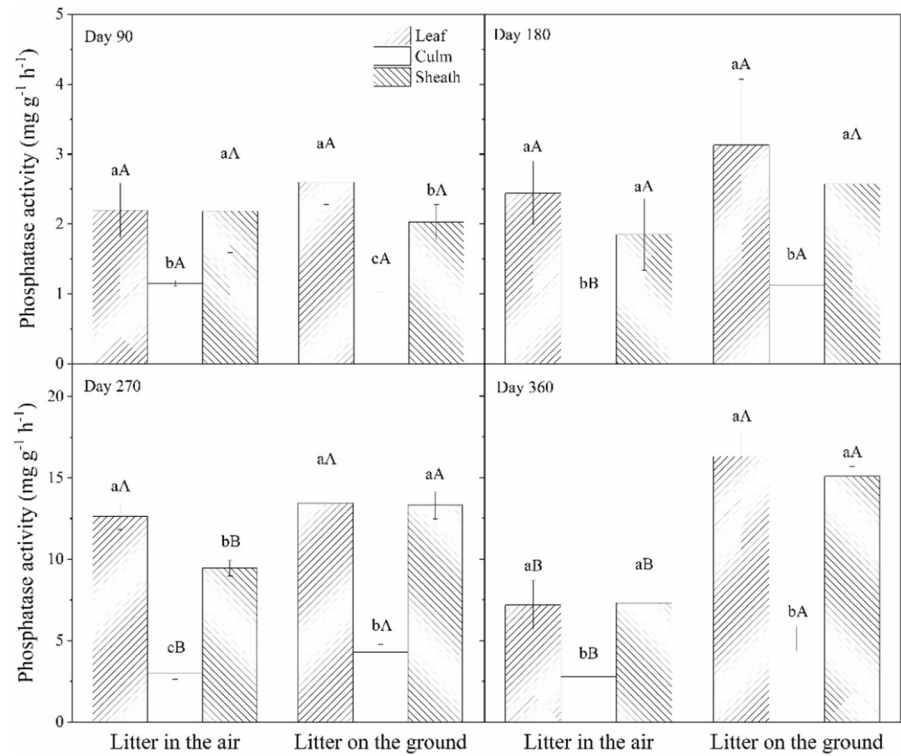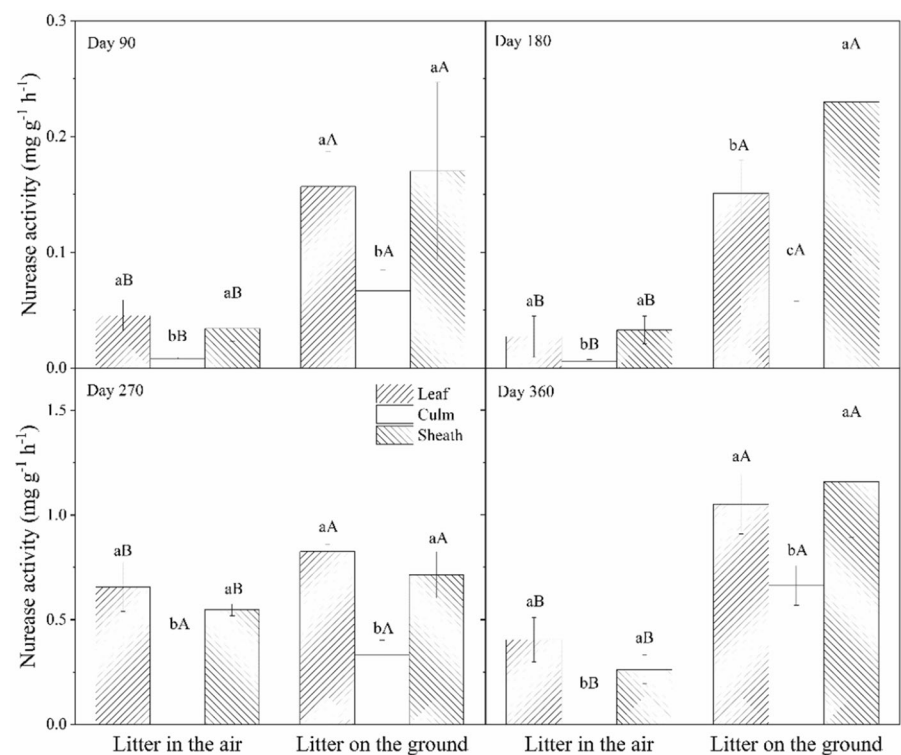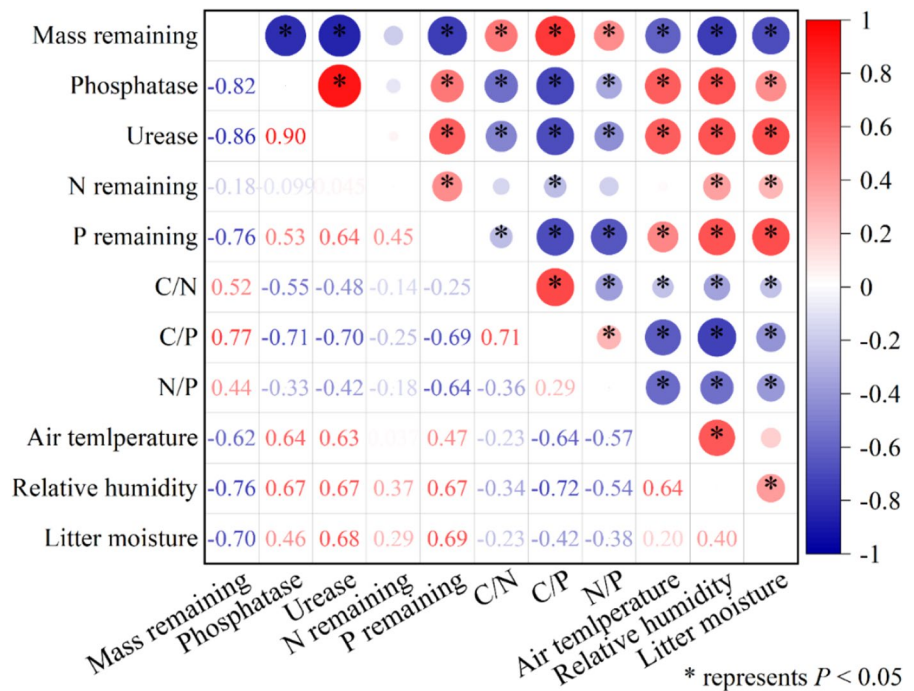

Fig. 3 The urease activity in the air and on the ground. Data are means and standard deviation (n = 4). Different lowercase letters represent significant differences among three types of litter ($P < 0.05$). Different capital letters represent significant differences between two interfaces for each type of litter ($P < 0.05$)

Fig. 4 Results of Pearson correlation analysis (n = 96)

loss was positively related to enzyme activities, mean air temperature and relative humidity and negatively correlated with stoichiometry (i.e., C/N, C/P, and N/P; Fig. S4). Urease and phosphatase activities were negatively related to C/N, C/P, and N/P and positively correlated with mean air temperature and relative humidity (Fig. 4; $P < 0.05$).

Discussion

Litter mass loss

Our results showed that the mass loss of standing litter was equivalent to 55–77% of that on the ground, indicating that the decomposition of standing litter of emergent macrophytes should not be overlooked and implying that the traditional method of placing litterbags directly on the surface of soil or sediment may overestimate the decomposition of reed litter in the YRD. Microbial decomposition is a key process of litter decomposition (Knorr et al. 2005; Hebert et al. 2021). When emergent macrophytes die and stand in the air, microorganisms begin to colonize the standing litter (Kuehn et al. 1999). However, the litter in the air and on the ground had different

microbial activities (Wang et al. 2017b), implying a different rate of litter decay between two interfaces. Non-rainfall moisture, such as humidity and dew, is a vital factor in regulating litter decomposition, especially for standing litter (Wang et al. 2017b; Evans et al. 2020; Tao et al. 2023). Higher humidity and lower temperatures at night help dew production in the YRD (Tao et al. 2023), which supplies moisture for microorganisms in the litter. Additionally, precipitation and resulting surface ponding can adjust the moisture content of the litter, especially on the ground. We found that the ground litter had a higher moisture content than the standing litter on days 90 and 360 (Fig. S5). Our results showed that the soil litter had higher activities of β-glucosidase, invertase (Tao et al. 2023), phosphatase (Fig. 2) and urease (Fig. 3), implying a higher microbial activity and a faster decomposition of soil litter. We also observed a negative relationship between the remaining litter mass and the moisture content, and a positive relationship between enzyme activities and the moisture content (Fig. 4). Thus, we speculate that a higher moisture content of ground litter may lead to a higher microbial activity and the resultant rapid decomposition of the litter in contrast to standing litter.

As litter types, the decomposition of the culm litter was slower than that of the leaf and sheath litter at two interfaces (Fig. 1), which is similar to the results of Koukoura et al. (2003) and may be due to the following reasons. First, microbial activity regulates litter decomposition (see, e.g., Knorr et al. 2005; Hebert et al. 2021). Our results showed that the culm litter had lower activities of phosphatase, urease (Figs. 2 and 3), invertase and β-glucosidase (Tao et al. 2023), and the activities of phosphatase and urease had a negative relationship with the remaining mass of the litter (Fig. 4). Moreover, labile organic carbon (LOC) is one of the main energy sources for microorganisms (De Graaff et al. 2010). Our recent results showed that leaf and sheath litter had a higher LOC loss ratio than culm litter (Tao et al. 2023), implying rapid microbial utilization of LOC in leaf and sheath litter and the resulting higher microbial activities. Thus, the sheath and leaf litter decomposed faster than the culm litter as a result of higher enzyme activities. Second, litter quality (e.g., C/N and C/P) is also a crucial factor influencing litter decomposition (Kuehn et al. 2004; Liao et al. 2008). Previous studies found a negative relationship between litter composition

rate and stoichiometry (C/N and C/P; Koukoura et al. 2003; Hebert et al. 2021). We also observed that litter stoichiometry (C/N and C/P) was positively related to the remaining litter mass (Fig. 4), while litter stoichiometry was negatively correlated with litter mass loss (Fig. S4). Therefore, larger C/N (Fig. 5) and C/P (Fig. 6) of the culm litter than leaf and sheath litter can result in a slow decomposition rate.

A previous study adjacent to our research site revealed that the biomass of the reed culm was 2.9 times that of the leaf (Zan et al. 2011). Although our results showed that culm litter had a lower decomposition rate than leaf litter, culm litter may play a non-ignorable role in litter decomposition and nutrient cycling due to its larger biomass compared to leaf litter. Therefore, subsequent studies should focus on the decomposition of non-leaf litter.

Litter nutrient dynamics

Generally, litter releases N when the C/N is less than 25 or 30 (Moore et al. 2006; Jacob et al. 2009). A previous study has observed that large C/N (that is, 46–238) led to net N accumulation during litter

Fig. 5 C/N ratio of litter in the air and on the ground. Data are means and standard deviation (n = 4). Different lowercase letters represent significant differences among three types of litter (P < 0.05). Different capital letters represent significant differences between two interfaces for each type of litter (P < 0.05)
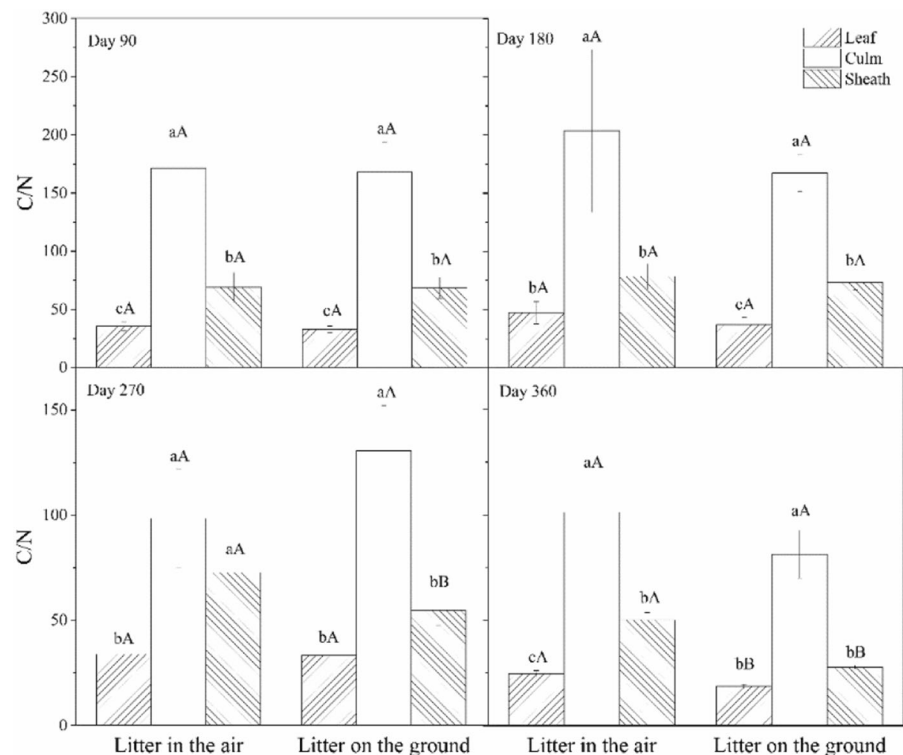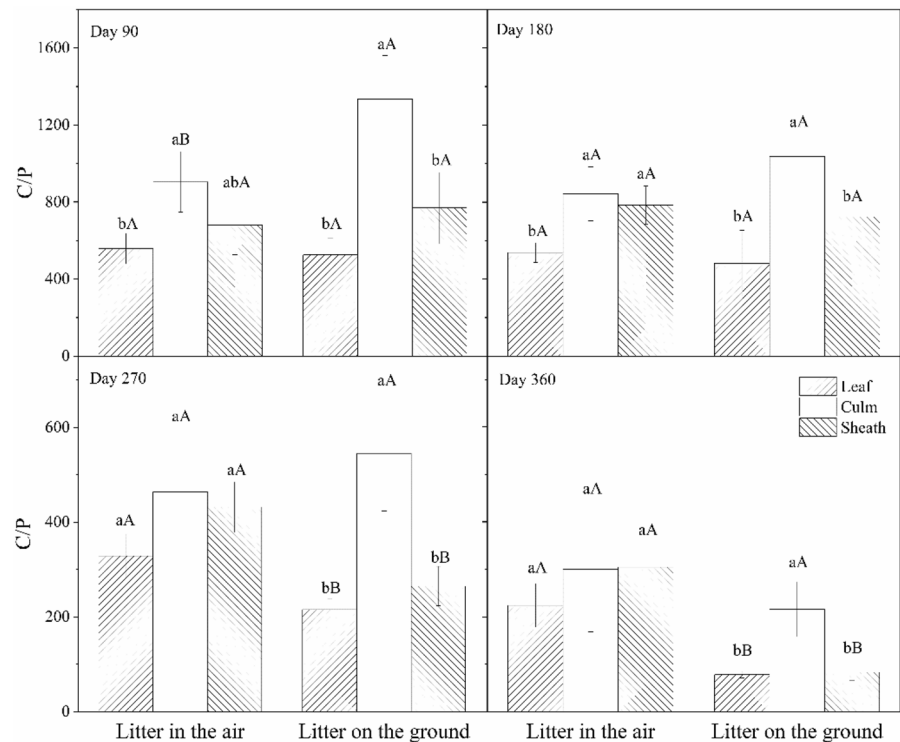
Fig. 6 C/P ratio of litter in the air and on the ground. Data are means and standard deviation (n = 4). Different lowercase letters represent significant differences among three types of litter (*P* < 0.05). Different capital letters represent significant differences between two interfaces for each type of litter (*P* < 0.05)

decomposition in a freshwater marsh (Zhang et al. 2014a). Rodríguez Pleguezuelo et al. (2009) also observed that larger initial C/N (31 and 32) led to N enrichment of litter, while lower C/N (12.1 and 27.2) resulted in N release from the litter. Atmospheric N deposition, soil, and litter itself are the main sources of N immobilized by microorganisms (Gessner 2001; van Ryckegem et al. 2006). For P, previous studies found an enrichment in P in *Juncus effusus* litter (C/P = 4300; Kuehn and Suberkropp 1998) or net release of P from the litter of four emergent macrophytes (C/P ranging from 798 to 2934; Zhang et al. 2014a). However, we found the opposite result that N and P were first released and then enriched during litter decomposition among three litter types at two interfaces (Fig. S2 and S3), which may be due to the following reasons. A previous study suggested that nutrient accumulation in litter was largely dependent on microbial activity (Chen and Stark 2000). In this study, enzyme activities on days 90 and 180 were lower than those on days 270 and 360, which implies that microbial activity and demand for N and P were lower during the first 180 days of the experiment, which can lead to the release of N and P from litters. On days 270 and 360, enzyme activities were

enhanced probably due to the increase in temperature, and we also observed a positive relationship between enzyme activities and air temperature (Fig. 4). Thus, we speculated that the increase in microbial activity on days 270 and 360 increased the microbial demand for N and P and thus began to fix N and P.

For litter types, the culm litter had the highest N remaining at the end of the field experiment (Fig. S2). Litter quality may affect microbial immobilization of N. An earlier study showed that microbial demand for N was greater in more recalcitrant litter compared to labile litter (Melillo et al. 1982). We observed that the remaining N (Fig. S2) and the initial C/N (Tao et al. 2023) were the highest for the culm litter among the three types of litter, which implies that the largest initial C/N of the culm litter (Tao et al. 2023) can result in the highest microbial demand for N and thus the largest remaining N. Of the decomposition interface, the leaf and sheath litter had larger P remaining on the ground that in the air on day 360. Previous studies have found a common phenomenon that the P content of the litter was increased at the later stage of decomposition due to the increasing demand of decomposers for P to promote their own growth (Pagioro and Thomaz

1999; Ozalp et al. 2007; Zhang et al. 2014b). In this study, the ground litter had higher enzyme activities than the standing litter, especially on days 270 and 360 (Figs. 2 and 3), which may promote the demand for P and immobilization by microorganisms in the ground litter. Moreover, N/P is an effective indicator to determine whether N or P limits graminoid litter decomposition, with a threshold value of 25 (Güsewell and Verhoeven 2006). Our results showed that the N/P of the reed litter was much less than 25 (Fig. S6), indicating that the litter decomposition in the YRD may be limited by N.

Conclusion

Although the mass loss of litter on the ground was greater than that in the air due to its larger enzyme activities, the mass loss of standing litter is equivalent to 55–77% of that on the ground, emphasizing the importance of standing litter decomposition. Culm litter slowly decomposed than leaf and sheath litter due to its smaller enzyme activities and larger C/N and C/P, while the mass loss of culm litter was equivalent to 57-79% of leaf and sheath litter, indicating that non-leaf litter played an important role in litter decomposition. If a larger biomass of reed culm compared with leaf is considered, the importance of non-leaf litter may be further enhanced. This research suggests that subsequent studies should focus on the decomposition of standing litter, especially non-leaf litter.

Author contributions BT designed the study, performed the research, analyzed data, and wrote the paper. JW and QC performed the research. YJ, BZ, and HY wrote the paper.

Declarations

Competing interests The authors declare no competing interests.

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