The overall decomposition of the spring-detached litter is faster than the autumn-detached litter in a steppe ecosystem

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Abstract

In the grasslands, a large proportion of plant shoots senesces into standing dead materials in autumn and stays over the winter period instead of becoming detached litter immediately. However, the information on the decomposition of plant standing dead materials during the winter period and its impacts on their subsequent decomposition after littering in coming spring remain unavailable. We conducted a two-year experiment in Inner Mongolia to compare the decomposition process of the litters detached in autumn versus that detached in spring of two dominant plant *Leymus chinensis* and *Stipa grandis*. Throughout the whole decomposition period, the autumn litter was directly positioned upon the soil surface, while the spring litter suspended as standing dead for the first 7 months of winter before being detached. We found that the overall decomposition rate of spring litter was faster than the autumn litter over the experimental period. The decomposition rate was correlated positively with the N content, but negatively with the C/N ratio, lignin concentration and lignin/N ratio in litters. The spring litter showed a sharp decrease in lignin remaining during the standing-dead stage, while the autumn litter did not, which suggests an important role of photodegradation in the breakdown of lignin over the winter period that facilitates the litter decomposition in subsequent stages. These findings highlight the difference in the decomposition rates of the litters detached in autumn versus in spring, and suggest to incorporate the effects of the standing-dead stage in calculating or modeling the nutrient turnover rates in semi-arid steppe ecosystems.

1. Introduction

The decomposition of plant litter represents a crucial process for nutrient transfer from plants to soil, and has significant implications for ecosystem carbon pool, soil fertility, and plant growth (Berg and McClaugherty, 2020). Plant litter quality and microbial community composition determines litter decomposition to a great degree at the site scale (Bradford et al. 2016; Yue et al. 2018; Joly et al. 2023). High quality litter with high-nutrient and low-lignin contents decomposes faster than the low quality litter (Zhang et al. 2008). Microbial decomposers break down plant residues into soil humus, carbon dioxide, and other inorganic compounds (Gartner and Cardon 2004; Moorhead and Sinsabaugh 2006; Veen et al. 2019). A change in microbial community composition affects litter carbon (C) and nitrogen (N) losses (Bray et al. 2012), although this effect may only be significant during the early phases of litter decomposition (Liao et al. 2022). The status of plant dead materials, i.e., either being standing in the field or detached on soil surface, matters much for decomposition process (Lin and King 2014; Almagro et al. 2015). Many grassland plants retain senescent shoots as standing dead for months or even longer, before they eventually detach from the plants and become the litter on the soil surface, and this plant standing-dead stage affects much their decomposition (Wang et al. 2017; Jiang et al. 2023). The implications of the standing-dead stage for plant material decomposition and ecosystem nutrient cycling have not yet been fully explored, including the decomposition process in the standing-dead stage and its impacts on the ensuing litter decomposition after the standing-dead become litter on the soil surface.

Microbes living in the soil and in the phyllosphere both play a role in litter decomposition (Lindow and Brandl 2003; Zhan et al. 2021). Microbes attached to standing litter may experience a drier microclimate, greater temperature fluctuations, and more nutrient limitation than those in the soil, thus they are less active and affects litter decomposition rates (Lin and King 2014; Wang et al. 2017). Several studies suggest that the decomposition of standing litter is not primarily related to soil microbe decomposers, but is influenced by abiotic processes such as leaching of soluble organic matter (Michalzik et al. 2001), physical fragmentation of plant remnant, and photochemical degradation of organic compounds like lignin (Rahman et al. 2013; Yanni et al. 2015; Austin et al. 2016; Wang et al. 2017). These processes aid in increasing the reduction in litter mass and serve as a pretreatment for biotic decomposition. During the dry season, solar radiation is considered the most significant factor that modifies the litter (Gliksman et al. 2018). Recent studies have shown that photodegradation, caused by solar radiation, can break the refractory lignin structure, making it more accessible to microorganisms for decomposition (Lin et al. 2015; Austin et al. 2016; Mendez et al. 2022). This process is known as photopriming, and has been demonstrated to enhance microbial activity and litter degradation (King et al. 2012; Austin et al. 2016; Mendez et al. 2022). The amount of solar irradiation that reaches the surface of the litter layer can greatly affect the photodegradation process. In areas where the litter is shaded from sunlight, microbiological degradation is the primary mode of decomposition, while photodegradation is less significant (Lin and King 2014). This phenomenon is observed in both woodland and grassland ecosystems. For example, in forest gaps, the rate of litter loss is approximately 40% higher than in the forest understory (Wang et al. 2021a). Similarly, in the semi-arid grassland, suspended litter decomposes faster than litter on the soil surface (Lin and King 2014; Wang et al. 2017). In addition, in alpine meadows located in the Qinghai-Tibet Plateau, where solar radiation is intense, even soil-dissolved organic matter can undergo significant photodegradation (Wang et al. 2021b). Although photodegradation is not the sole cause of increased decomposition of suspended litter, its importance as an abiotic process cannot be ignored.

The natural steppe grasslands in Northern China cover an extensive area of 2.82 million km^2, play a pivotal role in supporting pastoral activities and ensuring ecological security in the region (Li et al. 2019). The typical steppes are the most important and representative steppes in the region, with *Leymus chinensis* and *Stipa grandis* as the most dominant species (Giese et al. 2009; Peng et al. 2014). These species have tall and erect stems and remain standing for an extended period after senescence in autumn. Grazing, mowing and fencing are the main types of land use in the region, with grazing being the most common management method, including rotational and continuous grazing (Li 1989; Baoyin et al. 2014; Zhang et al. 2020). Animal grazing and trampling during the non-growing season can accelerate the lodging of plant litter, shortening the standing-dead period (Mor-Mussery et al. 2021). Thus, the dead plants at the end of the growing season may detach from the plants and become litter on the soil surface without undergoing a standing dead stage on the grazing grassland, whereas the dead plants on the grassland without animal grazing, may retain standing over the long winter period, and fall to the soil surface during animal grazing in the coming spring and summer. These facts underscore the significance of trampling in dryland litter decomposition, as it promotes the formation of soil-litter films through the burial of litter (Liu et al. 2018; Wei et al. 2021). The effects of the standing stage of plant litter are often

overlooked, as trampling by livestock removes its importance to some extent. Further investigation is needed to comprehend fully the role of standing-dead stage in nutrient cycling in different land use systems such as grazing in different seasons.

We conducted a two-year experiment in Central Inner Mongolia to compare the decomposition process of the litters detached in autumn versus that detached in spring of the two dominant steppe species *L. chinensis* and *S. grandis.* We hypothesized that (1) If the senesced plants experience a standing-dead stage, their decomposition rate would be lower during this period than those becoming the litter on the soil surface immediately after senescence; (2) plant residues experienced the standing stage exhibit a greater degradability and quicker decomposition rate than those freshly fallen counterparts owing to changes in their lignin content. As grazing is the major factor affecting the status of senescent plant materials, this study would provide insights into the ecological consequences of maintaining standing dead biomass from a perspective of nutrient cycling.

2. Material and methods

2.1 Site description

The research was carried out at the Grassland Ecosystem Research Station of Inner Mongolia University, situated in 60 km northeast to Xilinhot City, Inner Mongolia Autonomous Region, China (116°31' E, 44°15' N; 1146m). The area features a temperate semi-arid climate characterized by an mean annual temperature (MAT) of 2.8℃ and mean annual precipitation (MAP) between 280 and 350 mm. The annual rainfall varies considerably from year to year, with approximately 80% of it occurring in the growing period between May to September (Figure S1 and S2). The native steppe is primarily characterized by *L. chinensis* and *S. grandis* as dominant plant species, with major species include *Carex duriuscula* (Trin) Keng and *Cleistogenes squarrosa* Kom. The soil is classified as a calcic-orthic aridisol soil in the US soil taxonomy classification system.

2.2 Field experimental design

The experiment was executed in a 50 m×50 m grassland paddock that had been used as pasture land but had not been grazed for six years prior to the 2018 experiment. We assessed the litter decomposition using litterbags over a two-year period. In November 2017, we collected the standing dead material of the two dominant plants, *L. chinensis* and *S. grandis*, from the given grassland plot. The collected dead material was air dried at room temperature and divided into exactly 10.00 g samples and then placed in 15 cm×20 cm litter bags made of 1 mm size nylon mesh. This mesh size was selected to avoid loss of smaller litter fragments throughout the field incubation period, while still allowing access to the litter by soil micro- and mesofauna, but restricting access to macrofauna (Vossbrinck et al., 1979; Uselman et al., 2011; Nichols et al., 2008). All litterbags were set up in two parts to mimic the decomposition process of autumn and spring litter. The first part, known as "surface litter", was consisted of litter material placed directly on the soil to simulate the autumn litter that began to decompose after lodging. The second part, known as "standing litter", was initially suspended vertically 0.1 m above the ground for 7 months of

winter before being placed on the soil to mimic the decomposition of spring litter that underwent standing stage before lodging. This setup allowed for the comparison of the decomposition processes of the autumn litter versus spring litter in a controlled environment. A method for mimicking standing litter through the use of a specific construction. This involves the use of two 40 cm long iron-bars, with a diameter of 4 mm, placed vertically in the soil, 15 cm apart and 10 cm deep. To complete the construction, each corner of the litterbag is then tied to the iron bars using thin iron wire, with a diameter of 0.45 mm (Fig. 1). This method was used to place both autumn and spring litter from all studied species in five replications, using a complete random design. This resulted in a total of two plant litter species (*L. chinensis vs. S. grandis*) × 2 litter types (spring litter *vs.* autumn litter) × 4 sampling measurements × 5 replications = 80 litterbags.

2.3. Litter sampling and analysis

At 7, 12, 19, and 24 months since the deployment, litterbags samples from each treatment were analyzed four times in the laboratory. Ultimately, five types of litter were analyzed: the initial litter; the spring litter at the 7th months after deployment (7M spring litter), i.e., after the decomposition over the seven months (Nov. 2018 Jun. 2019) as standing litter, and at the end of 2-year decomposition period (2Y spring litter) after another 17 months decomposition as litter on the soil surface; and the autumn litter at the 7th months (7M autumn litter) and at the end of decomposition period (2Y autumn litter) on the soil surface for the whole period. After being extracted from the sampled bags, the materials were thoroughly cleansed using tap water, dried at 60°C for 48 hours, and then meticulously weighed with an accuracy of 0.1 mg. Subsequently, the litter samples were finely ground to a particle size of ≤ 0.2 mm to facilitate chemical analysis.

The concentrations of carbon (C%) and nitrogen (N%) were quantified using an elemental analyzer (Vario MACRO cube, Elementar, Germany). Neutral detergent fiber content (NDF%) and acid detergent fiber content (ADF%) were measured using an ANKOM 2000 Automated Fiber Analyzer (A2000i, Fiber Analyzer, American). The digestion of acid detergent lignin (ADL%) in 72% H_2SO_4 solution, obtained by the lignin sulfate method, was used to analyze the lignin content of ADF fractions (Trofymow et al. 2002).

2.4 Calculation and statistics

The remaining mass (R_M) and the quality indicators, carbon (C) and nitrogen (N) content, were evaluated throughout the litter decay process. R_M was defined in Eq. (1), where X_0 denotes the initial litter mass, and X_t represents the litter mass at a specific time *t* within the experimental duration. The decay rate constant, denoted as "*k*" (yr^{-1}) was calculated through positional integration using a single exponential decay model (Eq. (2); Olson, 1963).

The relative alterations in litter quality indicators, including total carbon, total nitrogen, hemicellulose, cellulose and lignin contents (R_{Ct}) within a specific timeframe from 0 to *t*, were computed using Eq. (3),

where the variables X_0, C_0 and X_t, C_t respectively denote the dry weight and chemical content of litter at an initial time point (t = 0) and a designated time point (t), respectively.

$$R_M = X_t / X_0 \times 100\%$$

1

$$X_t / X_o = e^{-kt}$$

2

$$R_{Ct} = \frac{(X_t \times C_t)}{(X_0 \times C_0)} \times 100\%$$

3

We used one-way ANOVA with Tukey's HSD as a *posthoc* test to test the differences in litter characteristics (e.g., C, N, hemicellulose, cellulose, and lignin contents and C/N, and lignin/N ratios), and the R_M and quality indicators of each plant litter species were compared across different treatments. We used three-way repeated measures ANOVA with decomposition time, litter types, plant species, and their interactions to test the treatment effects on litter decomposition. Pearson correlation coefficients were used to elucidate the relationship between litter quality and litter decomposition rate. We used SPSS 22.0 (IBM SPSS Statistics Inc., USA) to conduct all statistical analyses, and OriginPro 2022 (OriginLab Inc., USA) to visualize the results.

3. Results

3.1 Changes in plant litter mass

The litter remaining mass (R_M) was significantly influenced by the decomposition time (F = 3381.61, P< 0.001), litter types (F = 92.63, P< 0.001), plant species (F = 14.29, P< 0.01) and their interactions (T*P: F = 6.92, P< 0.01; T*L: F = 24.58, P< 0.001; T*P*S: F = 9.08, P< 0.001) (Table 1).

Table 1

P-values of three-way repeated measures ANOVA on the effects of decomposition time (T), litter types (L) and plant species (P) and their interactions on the mass remaining (R_M), nitrogen content (N), carbon content (C), lignin content, carbon to nitrogen ratio (C/N), and lignin to nitrogen ratio (Lignin/N) of plant litter.

	Term	df	F	*P*
R_M	Time	1.89	3381.61	**< 0.001**
	Plant species	1	14.29	**< 0.01**
	Litter types	1	92.63	**< 0.001**
	T*P	1.89	6.92	**< 0.01**
	T*L	1.89	24.58	**< 0.001**
	P*L	1	0.58	0.46
	T*P*L	1.89	9.08	**< 0.001**
N	Time	3	135.58	**< 0.001**
	Plant species	1	71.00	**< 0.001**
	Litter types	1	0.36	0.56
	T*P	3	2.56	0.07
	T*L	3	63.85	**< 0.001**
	P*L	1	27.56	**< 0.001**
	T*P*L	3	3.89	**< 0.05**
C	Time	1.95	51.35	**< 0.001**
	Plant species	1	60.84	**< 0.001**
	Litter types	1	94.23	**< 0.001**
	T*P	1.95	0.06	0.98
	T*L	1.95	23.99	**< 0.001**
	P*L	1	51.12	**< 0.001**
	T*P*L	1.95	6.02	**< 0.01**
Lignin	Time	3	8.64	**< 0.001**
	Plant species	1	0.70	0.42
	Litter types	1	433.20	**< 0.001**

	Term	df	F	*P*
	T*P	3	1.72	0.18
	T*L	3	1.90	0.14
	P*L	1	0.31	0.58
	T*P*L	3	1.25	0.30
C/N	Time	3	117.52	**< 0.001**
	Plant species	1	69.46	**< 0.001**
	Litter types	1	14.68	**< 0.001**
	T*P	3	2.96	**< 0.05**
	T*L	3	44.25	**< 0.001**
	P*L	1	88.24	**< 0.001**
	T*P*L	3	8.93	**< 0.001**
Lignin/N	Time	1.79	54.79	**< 0.001**
	Plant species	1	24.27	**< 0.001**
	Litter types	1	161.08	**< 0.001**
	T*P	1.79	0.44	0.63
	T*L	1.79	15.10	**< 0.001**
	P*L	1	10.14	**< 0.01**
	T*P*L	1.79	4.31	**< 0.05**

Both spring litter and autumn litter exhibited a significant decrease in litter mass during decomposition for both litter species (*L. chinensis* and *S. grandis*). For *L. chinensis*, the mass remaining of spring litter (89.12%) was significantly higher than that of autumn litter in the first seven months (87.20%) ($P < 0.05$), while there was no significant difference between the spring litter (87.28%) and autumn litter (89.56%) ($P > 0.05$) for *S. grandis*. By the 12th months, the R_M of spring litter (75.72%) for *L. chinensis* was significantly lower than that of autumn litter (78.68%), while there was still no significant difference between the spring litter (77.89%) and autumn litter (80.74%) ($P > 0.05$) for *S. grandis*. By the 19th months, the R_M of spring litter on the soil surface (*L. chinensis*: 53.18%; *S. grandis*: 56.55%) was generally lower than that of autumn litter (*L. chinensis*: 60.26%; *S. grandis*: 62.86%) ($P < 0.05$). These patterns persisted also at the 24th months, with significant lower R_M of spring litter (*L. chinensis*: 42.30%; *S. grandis*: 43.83%) than autumn litter (*L. chinensis*: 47.46%; *S. grandis*: 52.42%) ($P < 0.05$) (Fig. 2).

3.2 Changes in litter quality

Both the decomposition time (C: F = 51.35, $P < 0.001$; N: F = 135.58, $P < 0.001$), and plant species (C: F = 60.84, $P < 0.001$; N: F = 71.00, $P < 0.001$) had significant effects on litter C and N content, while their interactions had no significant effect on either litter C (F = 0.06, $P = 0.98$) or N content (F = 2.56, $P = 0.07$). Litter types had a significant effect on litter C content (F = 94.23, $P < 0.001$), but not N content (F = 0.36, $P = 0.56$). The interaction of litter types with both plant species (C: F = 51.12, $P < 0.001$; N: F = 27.56, $P < 0.001$) and decomposition time (C: F = 23.99, $P < 0.001$; N: F = 63.85, $P < 0.001$) had significant effects on litter C and N contents (Table 1).

The C content in the autumn litter of *L. chinensis* and *S. grandis* remained stable during the first seven months. Similarly, the C content of the standing dead of *L. chinensis* (spring litter) also showed no a significant change at the end of the first seven months ($P > 0.05$), while that of the standing dead of *S. grandis* declined significantly ($P < 0.05$). Over the two-year period, the C content of both autumn and spring litter of both plant species significantly decreased ($P < 0.05$) (Table 2).

Table 2

The C, N, hemicellulose, cellulose and lignin contents, and C/N and lignin/N ratios in *Leymus chinensis* and *Stipa grandis* during the decomposition. Initial - in the initial stage; 7M and 2Y respectively represents at the 7th months and the end of two-year decomposition period. spring and autumn denote the spring litter and autumn litter. Values are the means ± s.e. Different lower case letters indicate significant differences among decomposition stages in the same litter specie at $P < 0.05$.

	C	N	C/N	Hemicellulose	Cellulose	Lignin	Lignin/N
L. chinensis							
Initial	44.23 ± 0.05a	1.16 ± 0.01c	38.0 ± 0.3b	31.5 ± 1.5b	30.2 ± 1.4a	7.64 ± 0.26b	6.56 ± 0.19a
7M spring	43.98 ± 0.08a	1.00 ± 0.02d	44.1 ± 1.1a	34.7 ± 0.5a	29.4 ± 0.4a	5.26 ± 0.31c	5.29 ± 0.40b
7M autumn	43.88 ± 0.05a	1.19 ± 0.01c	36.9 ± 0.3b	29.7 ± 0.5b	30.6 ± 0.5a	8.53 ± 0.22a	7.18 ± 0.21a
2Y spring	40.38 ± 0.48b	1.89 ± 0.01a	21.5 ± 1.0d	21.0 ± 0.5c	19.1 ± 0.5b	4.26 ± 0.18d	2.40 ± 0.11c
2Y autumn	40.73 ± 0.58b	1.44 ± 0.04b	30.0 ± 0.8c	20.3 ± 0.9c	20.9 ± 0.6b	7.59 ± 0.09ab	5.28 ± 0.19b
S. grandis							
Initial	44.99 ± 0.21a	1.05 ± 0.02c	42.8 ± 0.9b	33.7 ± 0.7a	28.6 ± 0.7a	8.42 ± 0.27a	8.01 ± 0.41a
7M spring	42.52 ± 1.04b	0.72 ± 0.06d	59.4 ± 4.3a	32.6 ± 1.0a	24.6 ± 1.5bc	5.49 ± 0.36b	7.63 ± 0.56a
7M autumn	45.31 ± 0.22a	1.17 ± 0.04bc	38.8 ± 1.5b	29.0 ± 0.3b	27.0 ± 0.9ab	8.44 ± 0.37a	7.20 ± 0.30ab
2Y spring	40.32 ± 0.49c	1.69 ± 0.06a	24.0 ± 1.1d	22.0 ± 0.6c	19.6 ± 1.6d	4.46 ± 0.36c	2.65 ± 0.13c
2Y autumn	40.73 ± 0.58c	1.27 ± 0.04b	32.1 ± 1.0c	20.8 ± 0.7c	22.1 ± 0.8cd	7.97 ± 0.14a	6.30 ± 0.30b

The N content in the spring litter of *L. chinensis* and *S. grandis* decreased significantly within the first 7 months (as standing dead materials), while that of the autumn litter of *L. chinensis* showed no significant change over the same seven-month period (as litter on soil surface). The N content increased significantly in all the litters over the 2-year period, and the increase was significantly higher in spring litter than autumn litter ($P < 0.05$) (Table 2).

The C remaining (R_C) of all litters declined significantly over the time (Fig. 3). The N remaining (R_N) decreased first during the first 7 months (Nov. 2018 Jun. 2019), then increased during the following 5 months (Jun. Nov. 2019), then decreased again for spring litters; while the R_N declined continuously for

autumn litters (Fig. 3). At the beginning of decomposition period, *L. chinensis* and *S. grandis* had a similar C/N ratio. After 7 months of the decomposition, the C/N ratio of the spring litters increased significantly, while no change occurred in the autumn litters. Over the two-year decomposition period, the C/N ratio of both spring and autumn litters reduced significantly ($P < 0.05$) (Table 2).

The hemicellulose and cellulose contents in both spring and autumn litters declined significantly over the two-year period ($P < 0.05$) (Table 2), and both the hemicellulose remaining and the cellulose remaining of all litters declined significantly through time ($P < 0.05$) (Fig. 4).

The lignin content in the spring litter of both *L. chinensis* and *S. grandis* decreased significantly during both the first 7 months as standing dead and the rest of experimental period as the litter on ground surface ($P < 0.05$). In contrast, the lignin content in the autumn litter showed no a significant change during the first 7 months, nor over the whole decomposition period. The lignin content was significantly lower in spring litter than in autumn litter throughout the experimental period ($P < 0.05$) (Table 2).

The spring litter lignin/N ratio of *L. chinensis* was significantly decreased during the first 7 months ($P < 0.05$) (Table 2), while its autumn litter showed no a significant change ($P > 0.05$). The lignin/N ratio significantly decreased over the two-year decomposition period for all the litters ($P < 0.05$), with a significant larger decrease for spring litter than autumn litter ($P < 0.05$). The lignin/N ratio of *S. grandis* showed no a significant change over the first 7 months of decomposition, regardless of the litter type (spring or autumn), while the ratio significantly decreased at the end of two-year decomposition period. The lignin/N ratio of *S. grandis* was significantly lower in spring litter than in autumn litter ($P < 0.05$) (Table 2, Fig. 3).

3.3 Relationships of litter decomposition rate with litter quality

Decomposition time, litter types, plant species and their interactions all influenced litter quality significantly ($P < 0.05$, Table 1). Remaining mass was significantly and negatively related with the N content of the litter (r_{Spring}=-0.797, $P < 0.001$; r_{Autumn}=-0.646; $P < 0.001$), but positively related with C/N ratio (r_{Spring}=0.803, $P < 0.001$; r_{Autumn}=0.645; $P < 0.001$), lignin content (r_{Spring}=0.570, $P < 0.001$; r_{Autumn}=0.404; $P < 0.01$), and lignin/N ratio (r_{Spring}=0.755, $P < 0.001$; r_{Autumn}=0.618; $P < 0.001$). These linear relations were significant in both the spring litter and the autumn litter (Fig. 5).

4. Discussion

Litter decomposition rates vary greatly among ecosystems and are influenced by litter quality, decomposer organisms and environment (Bradford et al. 2016). Many studies have shown the effects of litter N and lignin content on litter decomposition rates (e.g., Liao et al. 2022). According to our results, the rate of litter decomposition is correlates positively with the litter N content, but negatively correlated with the lignin content, C/N ratio or Lignin/N ratio (Fig. 5), which is in consistent with the findings of previous studies (Duan et al. 2018; Wang et al. 2022). Our findings also indicate that *L. chinensis* litter appears to

be of better quality (i.e., a higher N content, lower C/N ratio or lignin/N ratio), thus a faster decomposition rate, than *S. grandis* litter (Table 2, Fig. 2). Our results further demonstrate that the autumn litter of *L. chinensis*, which is always in contact with soil, decomposes faster than the spring litter, which is standing upright during the first seven months. In contrast, the decomposition rate of the *S. grandis* litter is similar between the spring litter and autumn litter. The better initial quality of *L. chinensis* than *S. grandis* may explain the different between these two species of litters. That is, the high initial N content in *L. chinensis* could meet the requirements of microbial metabolism during the initial period of the autumn litter decomposition, but not of the spring litter that has no direct contact with soil during the first seven months. Most of the litter mass loss during this period is driven by soil microorganisms, including fungi rapidly invading leaves through openings and less mobile bacteria, while most phyllosphere microorganisms are not involved in decomposition, except for pathogens (Berg 2014). In contrast, *S. grandis* litter has relatively lower quality, thus a slower decomposition rate and has no significant difference between spring litter and autumn litter.

Litter decomposition rate is not only affected by soil microbial communities, but also by solar radiation (Wang et al. 2021a; Jiang et al. 2022). Previous studies have proved that litter decomposition can be directly accelerated by solar radiation via photochemical mineralization, and indirectly via the encouraging process of biotic degradtion, known as photofacilitation, in many terrestrial ecosystems (Lee et al. 2012; Austin et al. 2016). Our findings reveal that the mass loss of spring litter is greater than that of autumn litter for both *L. chinensis* and *S. grandis*, regardless of at the 12th or 17th months of decomposition following the 7-month exposure as standing dead of litter on ground. The decomposition rate of the spring litter (that has undergone the standing-dead stage) is faster than that of the autumn litter (that has not undergone the standing-dead stage). This result is consistent with previous studies, which show that the retention of plant standing-dead biomass promotes subsequent decomposition in the soil surface (Day et al. 2015; Angst et al. 2017). The faster decomposition of spring litter than autumn litter after the 7-month winter period is most likely related with the photodegradation during the winter period. Lignin is the primary target of photodegradation in litter by absorbing sunlight radiation, such as ultraviolet and blue-green light (King et al, 2012; Austin et al. 2016). Meanwhile, lignin, as a key component of plant tissue cell walls that serves as a protective structure, is notoriously difficult to biodegrade in the litter (Huang et al. 2022). However, solar radiation can break down lignin during the standing-dead stage, thus facilitate subsequent microbial decomposition (King et al. 2012; Mendez et al. 2022). Our data shows that, after the 7 months of exposure, the lignin concentration in the *L. chinensis* spring litter (as standing dead for the first 7-months) decreased by 31.15%, while that of the *L. chinensis* autumn litter increased by 11.65%. The similar trend is observed in the decomposition of *S. grandis* litters. The extensive destruction of lignin unblocks the subsequent microbial decomposition, resulting in faster decomposition of spring litter than autumn litter over the rest 17-month decomposition period under identical environmental conditions. Our results show that the hemicellulose concentration in the spring litter of both *L. chinensis* and *S. grandis* decreases by 36% in average over the 17 months, compared to a 30% decrease in the autumn litter. This may be a consequence of the interplay between hemicellulose photo-oxidation and the legacy effects of lignin photodegradation. Lin et al. (2015) proposed that the

photo-oxidation of hemicellulose acetylated xylan might be one of important mechanisms of photodegradation enhancing litter degradability.

It has been demonstrated that standing litter experiences greater temperature and humidity fluctuations compared to litter on the ground (Lin and King 2014; Wang et al. 2017), these fluctuations create conditions that promote the breakdown of litter and the formation of small organic compounds (Uselman et al. 2011). Our monitored data on air temperature, relative humidity, and soil temperature and water content for the 0–5 cm soil layer (Figs. S1 and S2) indicate larger fluctuation in air temperature and humidity than the soil. These findings are consistent with previous experiments (Lin and King 2014; Wang et al. 2017), demonstrating that standing litter experiences different microclimates than soil surface litter, making it more susceptible to environmental factors and ultimately resulting in greater mass loss. Furthermore, the harsher environment of standing litter may result in lower microbial biomass attached to the litter, leading to reduced consumption of dissolved organic carbon (DOC) in the litter (Almagro et al. 2015). As a result, soluble organic carbon accumulates and provides high-quality, unstable carbon sources for new microorganisms during the growing season, which further promotes spring litter decomposition (Kuzyakov et al. 2000; Uselman et al. 2011).

Litter decomposition releases nutrients in conjunction with litter mass loss, which varies with nutrient types and decomposition processes (Wang et al. 2020). In our study, the litter remaining C declined in a pattern consistent with litter mass remaining, which makes sense because the mass of litter is predominantly composed of carbon (Fig. 2, Fig. 3). Our data also suggest that among the structural carbohydrates of plant litter, the loss of hemicellulose is the fastest, while that of lignin is the slowest (Fig. 4). this is reasonable as lignin is a complex and recalcitrant molecule, and decompose slowly; while hemicellulose and cellulose are relatively simple structures consisting of monosaccharides and can be broken by the cellulolytic enzymes during the early decomposition stage (Berg and Mcclaugherty 2020; Ristok et al. 2019).

The N concentration in autumn litter consistently increases during decomposition (Table 2), which is in consistent with the results in previous studies (Wang et al. 2020, Xu et al. 2020; Pastorelli et al. 2021). A possible reason for this is microbial transformation of external nitrogen into biomass (N immobilization) after litter is in contact with the soil (Frey et al. 2004). It is worth noting that the N concentration of spring litter decreases during the first seven months as standing dead, then increases after being placed on soil surface (Table 2, Fig. 3). Lignin may act as a structural barrier, limiting enzyme access to the bulk of senescent plant tissue compounds (Pauly and Keegstra 2008; Berg and McClaugherty 2020). Therefore, photodegradation of spring litter during the standing period would release C from lignin and enhance degradation of many other compounds, which increases the likelihood of N releases (Manzoni et al. 2008); combined with precipitation leaching, these factors could ultimately lead to a decline in N concentration (Berg and Staaf 1981; Guggenberger 1994; Du et al. 2021). This explanation also applies to the potential changing of the C:N ratio of the spring litter (Fig. 3). Meanwhile, the consistent decrease in C:N ratio of autumn litter is possibly associated with the leaching of readily decomposable low molecular

weight substances (dissolved carbon), the swift C respiration, and N immobilization by microorganisms throughout the decomposition process (Yang et al. 2019).

5. Conclusion

Our study shows that spring litters undergoing the standing-dead stage experience more lignin loss than autumn litters that lie on soil surface, and the more lignin loss facilitates the litter decomposition during the subsequent stages. The more photodegradation of refractory structures in the standing than the lying litters is most likely the reason for the facilitation of the standing-dead stage to overall decomposition. Our findings highlight the importance of considering litter status (standing dead or lying on soil surface) and the factors that alter the litter status such as animal grazing when calculating or modeling the litter decomposition in semi-arid grassland ecosystems.

Declarations

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Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Not applicable.

Consent for publication Not applicable.

Consent to participate Not applicable.

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Figures

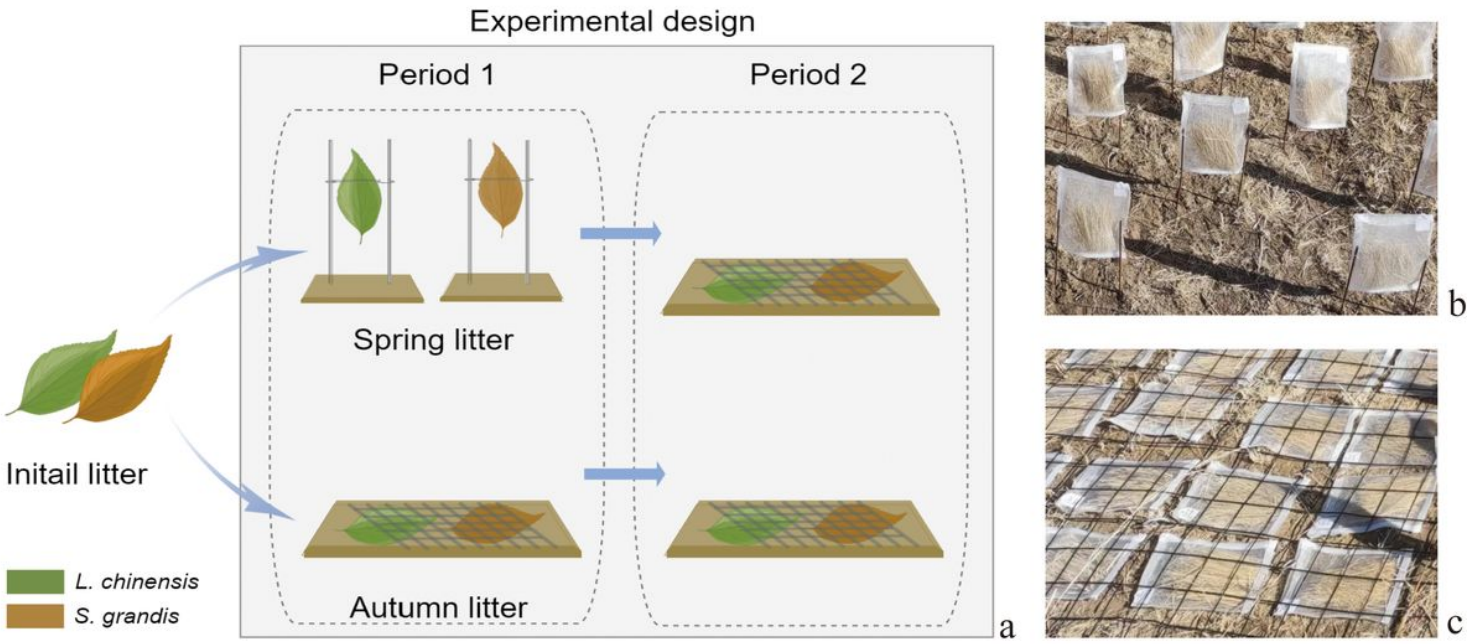

Figure 1

Design of the experiment: (**a**) the spring litter was suspended as standing dead for the first 7 months (of winter, period 1) before being placed on the soil surface for the rest of two-year period (period 2), while the autumn litter was directly placed on the soil surface for the whole decomposition period; photographs (**b**) and (**c**) represent the treatments of standing dead and litter placed on the soil surface, respectively.

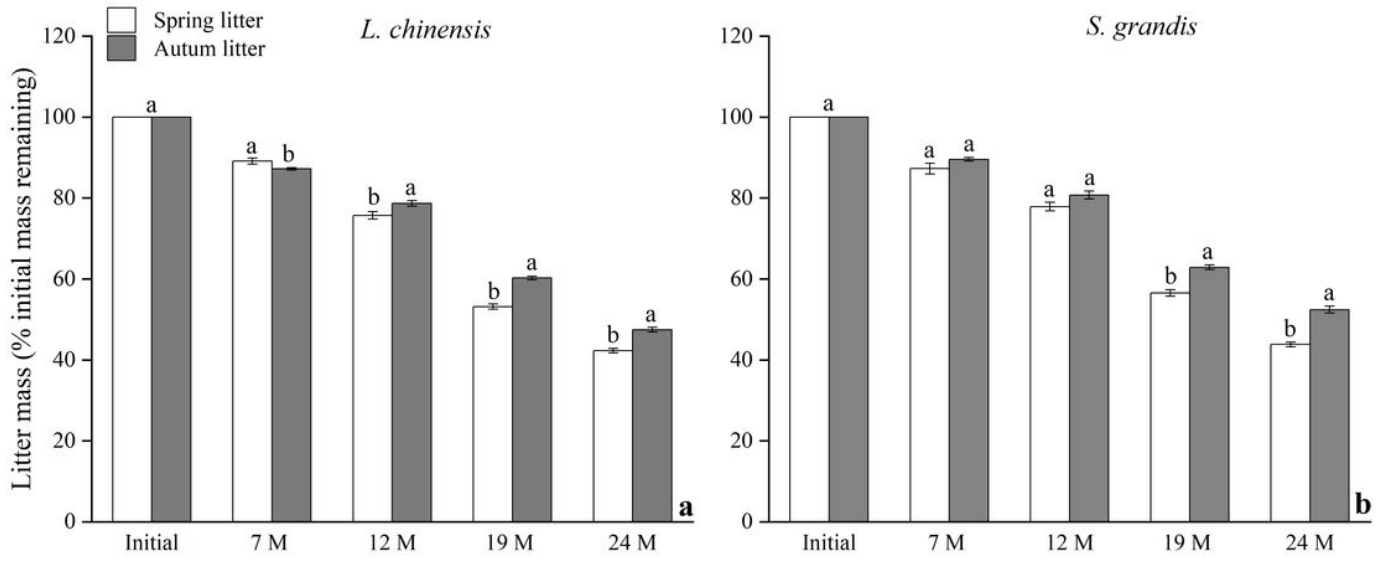

Figure 2

Litter mass remaining (R_M) of *Leymus chinensis* (**a**) and *Stipa grandis* (**b**) during the two-year experimental period. Columns represent means and error bars denote standard error. The spring litter was suspended as standing dead for the first 7 months (of winter) at ambient conditions (7M) before being placed on the soil surface for the rest of two-year period, while the autumn litter was directly placed on

the soil surface for the whole decomposition period. Different lower case letters indicate significant differences between spring litter and autumn litter in the same period at $P < 0.05$.

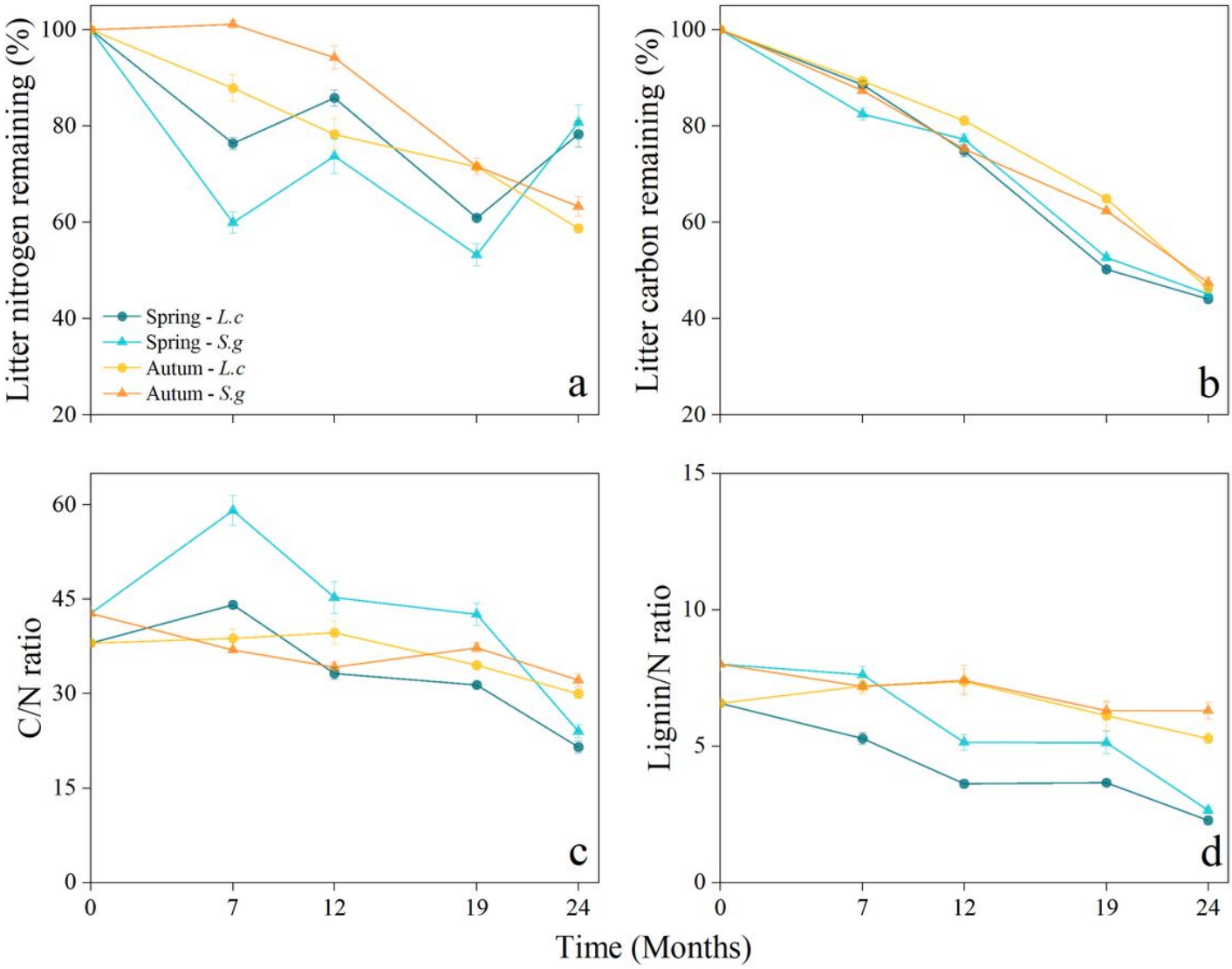

Figure 3

Litter nitrogen remaining (**a**), carbon remaining (**b**), carbon to nitrogen ratio (**c**) and lignin to nitrogen ratio (**d**) of the spring litter and autumn litter of *Leymus chinensis* and *Stipa grandis*. Error bars denote standard error.

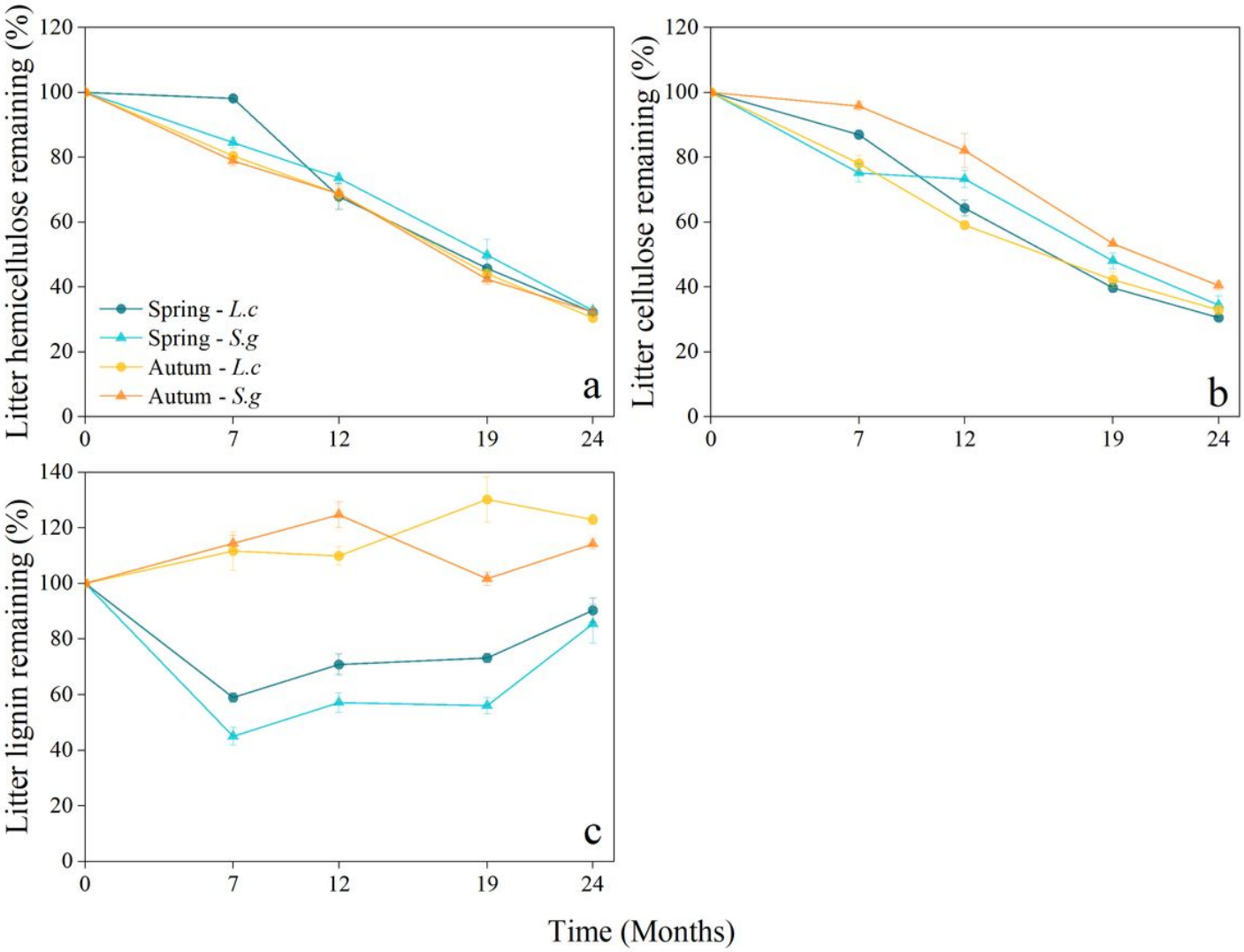

Figure 4

Litter hemicellulose remaining (**a**), cellulose remaining (**b**) and lignin remaining (**c**) of the spring litter and autumn litter of *Leymus chinensis*and *Stipa grandis*. Error bars denote standard error.

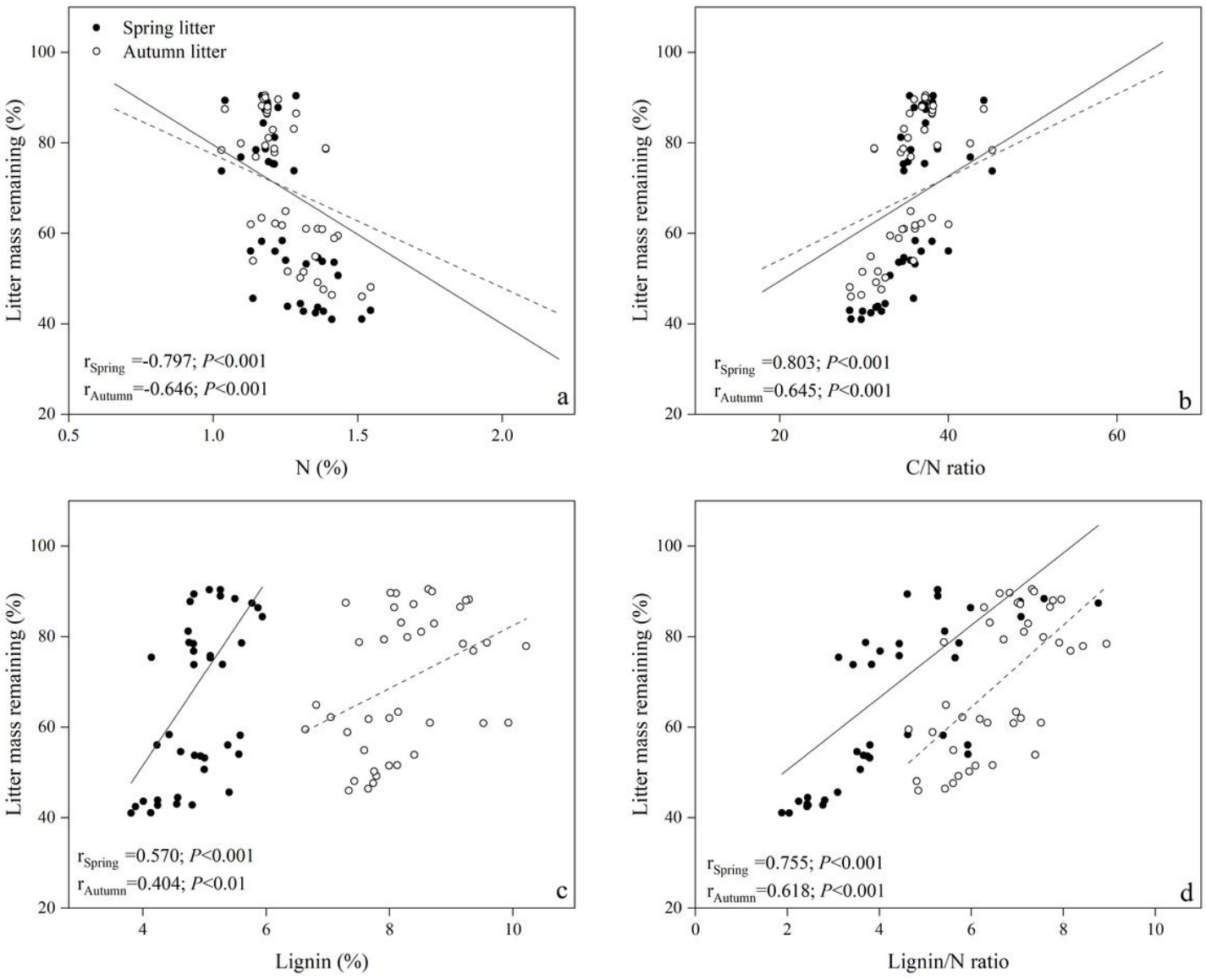

Figure 5

Pearson correlations of spring litter mass remaining (n=40, solid line and full circles) and autumn litter mass remaining (n=40, dashed line and open circles) with the litter nitrogen content (**a**), C/N ratio (**b**), Lignin content (**c**) and Lignin/N ratio (**d**) during the litter decomposition. r_{Spring} and r_{Autumn} represent r values of the linear regression for spring litter and autumn litter, respectively.

Supplementary Files

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