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Yak Dung Deposition Affects Litter Mixing Effects on Mass Loss in Tibetan Alpine Grassland☆

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ABSTRACT

Plant litter and livestock excreta are two important ways of carbon and nutrient input to soil in grassland grazing systems. Grazing livestock often deposit dung on plant litter, which may affect litter decomposition through a changing microenvironment. We assessed effects of yak dung on litter mixing effects on litter decomposition in a Tibetan alpine grassland. Six common species were selected, including low-quality litter species *Kobresia capillifolia*, *Elymus nutans*, and *Ligularia virgaurea* and high-quality litter species *Anemone rivularis*, *Saussurea nigrescens*, and *Thermopsis lanceolata*. Litter bags containing each species alone and all two-species combinations were allowed to decompose with and without experimental dung addition in the field. Mass loss of the leaf litter was measured after 6 and 12 mo. High-quality litter species had significantly greater mass loss than low-quality litter species. Dung significantly accelerated litter mass loss after both 6 and 12 mo for low-quality litter species, but only after 12 mo for high-quality litter species. Litter mixtures containing both high- and low-quality species showed positive nonadditive effects (NAEs) on mass loss after 6 mo but additive effects after 12 mo. Dung increased the strength of NAEs after 6 mo and shifted litter mixing effects from positive to negative NAEs after 12 mo. Our results support previous findings that litter mixing could produce NAEs on litter decomposition and that these NAEs could change with incubation time. Most importantly, we show that dung can modify NAEs, demonstrating that litter mixing effects are dependent on the microenvironment. Our findings also demonstrate that yak dung can influence soil processes by varying both single-species litter decomposition rates and litter interactions within mixtures. Furthermore, the results suggest yak dung is closely related to material and nutrient cycling, so we believe dung should remain and not be substantially removed from this grazing ecosystem.

Introduction

Plant litter decomposition is the most important source of nutrients for plants in terrestrial ecosystems (Swift et al., 1979), controlling both carbon and nutrient cycling (Hättenschwiler et al., 2005). Studies focusing on litter from single species have shown that litter decomposition is primarily influenced by climatic factors (e.g., temperature and moisture) and litter quality such as nitrogen (N) and phosphorus (P) concentrations, C-to-N and lignin-to-N ratios (Cornwell et al., 2008). More recent studies have investigated decomposition processes within multispecies litter mixtures (e.g., Gartner and Cardon, 2004; Vos et al., 2013), showing that decomposition of a given litter type may be influenced by the presence of other litter types.

Deviations from the expected decomposition of litter mixtures (i.e., rates based on the decomposition of each mixture component alone), or nonadditive effects (NAEs of litter mixing are frequently observed (Wardle et al., 1997; Gartner and Cardon, 2004). NAEs can either result from more rapid than expected overall litter decomposition (synergistic effects) or slower than expected results (antagonistic effects) and are likely a consequence of complex litter species–microbial interactions during decomposition. Potential mechanisms of litter mixing effects on decomposition include nutrient transfers between litter of varying quality (Salamanca et al., 1998; Lummer et al., 2012), stimulation or inhibition of particular microbes (Nilsson, 1994; Hättenschwiler and Vitousek, 2000), resource complementarity (Vos et al., 2011, 2013), and improved microenvironmental conditions (Wardle et al., 2003; Makkonen et al., 2013). Such nonadditive litter-mixing effects on decomposition processes often occur idiosyncratically because their direction and magnitude can change with incubation time (Marco et al.,

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2011; Wu et al., 2013; Cuchietti et al., 2014) and decomposition environment or context (Madritch and Cardinale, 2007; Jonsson and Wardle, 2008; Rosemond et al., 2010; Bretherton et al., 2011). It is therefore necessary in highly heterogeneous environments to consider how the environmental context affects litter mixture interactions over time.

Together with litter decomposition, spatially localized patches of excreta (dung) from grazing animals may alter both nutrient distributions in grasslands in general and the decomposition microenvironment immediately below dung pats (Augustine and Frank, 2001; White et al., 2001; Auerswald et al., 2010; Cai et al., 2014). While the effects of inorganic N addition to litter have been extensively studied (Craine et al., 2007), dung addition involves changes in both nitrogen and carbon availability to decomposers, as well as moisture and other microclimate changes (Aarons et al., 2009; Cai et al., 2014; Liu et al., 2017). The impact of dung addition on litter decomposition is generally poorly studied (Bloor, 2015; Liang et al., 2018), and its influences on the NAEs of mixed litter decomposition have never been assessed. Evaluating the effect of dung on litter decomposition definitely improves understanding of the role of dung in maintaining ecosystem function in a grazing grassland system.

Grazing is the main land use on Tibetan grasslands, where the open grazing of more than 13.3 million domestic yaks, 20 000 wild yaks, and 50 million sheep is practiced (Yao et al., 2006). The average individual mature yak excretes between five and seven dung pats each day in Tibetan alpine meadows (Li et al., 2012; Liang et al., 2018). No studies, however, have examined the impact of this dung on litter mixture dynamics. In this study we conducted a field incubation experiment to examine how yak dung impacted the decomposition of litter mixtures from six common Tibetan alpine meadow plant species that differed in their quality.

Materials and Methods

Study Site

The study was conducted at the Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University at 3 550 m elevation (33°40′N, 101°52′E), on the eastern Tibetan Plateau, China. Mean annual precipitation is 620 mm, occurring mainly during the short, cool summer. The average temperature is 1.2°C, ranging from −10°C in January to 11.7°C in July. Soils are classified as alpine meadow soils (Institute of Soil Science, 1986). Vegetation is dominated by the perennial sedge *Kobresia capillifolia* and perennial grass *Elymus nutans*. Other common species include *Anemone rivularis, Saussurea nigrescens,* and *Thermopsis lanceolata*. Aboveground litter production averaged 505 g m^{-2} yr^{-1} (DW) and comprised ≈78% leaves, 16% stems, and 6% reproductive parts. The study area is moderately grazed by yak (ca. 3 head per ha) in winter (from late October to late March).

Litter and Dung Collection

We selected six common species with contrasting litter quality including the low-quality litter species *K. capillifolia* (Kc), *E. nutans* (En), and *Ligularia virgaurea* (Lv) (characterized by low N concentration, and high C-to-N and lignin-to-N ratios) and high-quality litter species *A. rivularis* (Ar), *S. nigrescens* (Sn), and *T. lanceolata* (Tl) (high N concentration, low C-to-N and lignin-to-N ratios; see Table S1 available online at https://doi.org/10.1016/j.rama.2018.11.004). During late October 2013, we collected freshly fallen leaves and air dried them at room temperature.

Litter bags (15 × 15 cm) were made from nylon fabric of 2-mm mesh size (this mesh size minimized fragmentation but allowed free access by a large proportion of the soil fauna). Each bag was filled with about 10 g air-dried leaf litter of either a single species or a 50:50 mixture of each of the 15 possible two-species combinations.

Fresh yak dung (30.8 ± 1.2 mg/g N, 2.9 ± 0.2 mg/g P, C/N 11.0 ± 0.5 based on elemental analysis of a dried, ground dung subsample, $n = 8$) was collected from a yak shed and mixed thoroughly to ensure homogeneity. Dung was from animals that had grazed natural grasslands and had not been supplemented with other fodder. Simulated dung patches (20-cm diameter, depth 5 cm) were similar to those excreted by mature yaks in the field and had a fresh weight of ≈1 500 g per patch.

Experimental Design

The field experiment was conducted in a factorial experiment on the basis of randomized complete block design with seven replications in October 2013. Litter species treatments included each single species and all possible 50:50 two-species combinations. The yak dung treatment was the presence or absence of a dung pat covering the litter bag. Litter bags were retrieved from the field after 6 and 12 mo of incubation. We chose to test all possible two-species mixtures to avoid richness or diversity effects, as we were primarily interested in whether the litter mixing effect had occurred or not. A 1-ha area of native grassland was fenced to protect against yaks destroying litter bags. Within the fenced area, seven blocks (8 × 8 m) were established with between-block distances of at least 10 m. All naturally occurring aboveground litter within each block was removed. Litter bags were placed on the soil surface in a randomized arrangement within each block and held in place by metal pins. Subsamples of litter from each species were retained for the determination of initial chemical composition of the litter, as well as determination of air-dry to oven-dry weight ratio.

At each sampling time (April and October 2014), litter bags were cleaned to remove dung, soil, and other contamination. Mixtures were sorted to separate the component species to assess individual litter species mass loss in mixtures. Litter bag contents were then dried at 65°C for 48 h before being weighed to determine the mass remaining.

Dung and Litter Chemical Analysis

Litter chemical composition was determined for each treatment combination at the start of the experiment and after litter bag retrieval. Total C was determined using the H_2SO_4-$K_2Cr_2O_7$ oxidation method (Nelson and Sommers, 1996). Total N and P were determined with a continuous flow auto analyzer (Bran and Luebbe GmbH, Norderstedt, Germany) after litter samples were digested with H_2SO_4 and catalyst. Lignin was estimated in litter subsamples following Rowland and Roberts (1994).

Data Analysis

Litter mass loss was calculated as:

$$\text{Litter mass loss }(\%) = \left(\frac{\mathrm{M_0} - \mathrm{M_t}}{\mathrm{M_0}}\right) \times 100\% \tag{1}$$

where M_0 was the initial dry mass and M_t was the dry mass at retrieval time t (mo).

To detect mixture effects on leaf litter mass loss at each harvest, the NAE was calculated for each mixture using the following formula:

$$\text{NAE }(\%) = \left(\frac{\text{Observed ML} - \text{Expected ML}}{\text{Expected ML}}\right) \times 100\% \tag{2}$$

where *Observed ML* was the observed mass loss of the litter mixture and *Expected ML* was calculated from the mean mass loss of the component litter species in isolation. Expected ML values were calculated separately for each block. Deviations from zero indicate nonadditive mixture effects with positive and negative values referring to as synergistic and

Table 1
Results of three-way of analysis of variance testing effects of litter species, dung, and incubation time on litter mass loss at the Alpine Meadow and Wetland Ecosystems Research Station on the Tibetan Plateau, China in 2013−2014.

Source of variance	*df*	*F*	*P*
Block	6	1.27	0.27
Dung	1	421.98	< 0.001
Incubation time	1	6144.52	< 0.001
Litter species	5	810.85	< 0.001
Dung × species	5	5.66	< 0.001
Dung × incubation time	1	48.61	< 0.001
Litter species × incubation time	5	14.04	< 0.001
Dung × incubation time × litter species	5	10.77	< 0.001

antagonistic effects, respectively. In addition, to explore the mechanisms underlying NAE in mixtures, we compared the mass loss of individual component species in mixtures to the average mass loss of that species in isolation in the corresponding dung treatment at each harvest using the individual performance (IP) as follows:

$$\mathrm{IP}(\%) = \left(\frac{\mathrm{ML_{mix}} - \mathrm{ML_{iso}}}{\mathrm{ML_{iso}}}\right) \times 100\% \qquad (3)$$

Where ML_{mix} was the mass loss of individual litter species in mixtures and ML_{iso} was mass loss of the same litter species in isolation (Butenschoen et al., 2014).

One-way analysis of variance (ANOVA) followed by Student-Newman-Keuls (S-N-K) multiple comparisons were used to test for differences in initial litter chemical properties. Three-way ANOVA was used to test for the effects of litter species, dung, and incubation time on single-species litter decomposition, followed by S-N-K multiple comparisons among litter species within dung treatment and between dung treatments after 6 and 12 mo, respectively. At a given sampling time, we used one-sample Student's *t*-tests to test 1) whether NAEs were

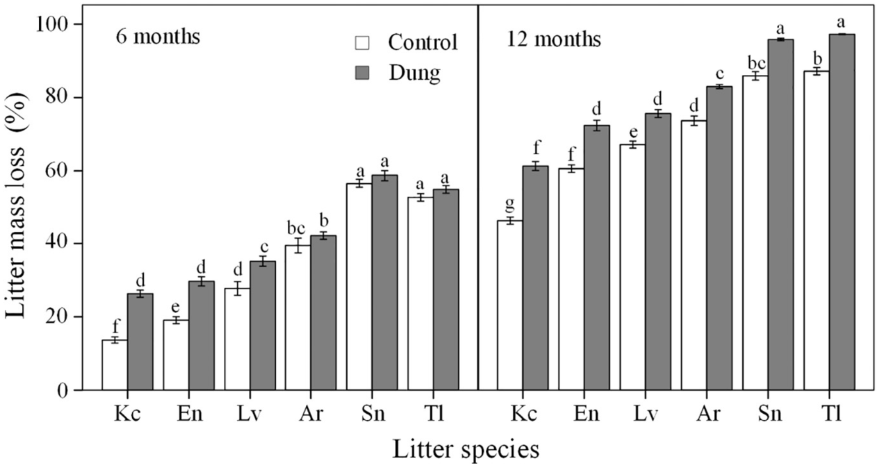

Figure 1. Percent mass loss in single litter species in dung treatments after 6 and 12 mo, respectively, at the Alpine Meadow and Wetland Ecosystems Research Station on the Tibetan Plateau, China in 2013−2014. Significant differences ($P < 0.05$) are indicated by different lowercase letters. Values are means ± SE ($n = 7$). Kc, *Kobresia capillifolia;* En, *Elymus nutans;* Lv, *Ligularia virgaurea;* Ar, *Anemone rivularis*; Sn, *Saussurea nigrescens;* Tl, *Thermopsis lanceolata*.

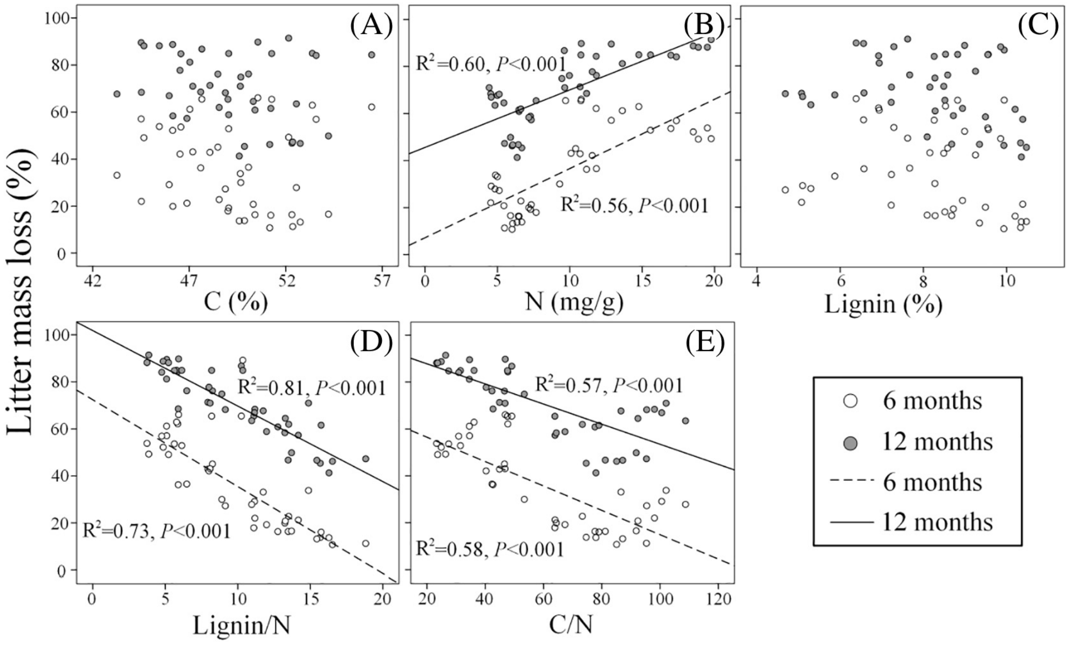

Figure 2. Relationships between the initial litter C (**A**), N (**B**), Lignin (**C**), Lignin/N (**D**) and C/N (**E**) values and the mass loss of single litter after 6 *(open circles)* and 12 *(gray circles)* mo, respectively, at the Alpine Meadow and Wetland Ecosystems Research Station on the Tibetan Plateau, China in 2013−2014.

Table 2
Results of mixed linear model with species combination, dung, and incubation time as fixed factors and block as a random factor testing for nonadditive effects of litter mixing effect on mass loss at the Alpine Meadow and Wetland Ecosystems Research Station on the Tibetan Plateau, China in 2013−2014.

Source of variance	*df*	*F*	*P*
Block	6	1.25	0.280
Species combination	14	4.42	< 0.001
Dung	1	0.45	0.503
Incubation time	1	282.66	< 0.001
Species combination × dung	14	0.36	0.984
Species combination × incubation time	14	9.37	< 0.001
Dung × incubation time	1	74.74	< 0.001
Species combination × dung × incubation time	14	1.05	0.401

significantly different from zero within each treatment and 2) whether IPs were significantly different from zero for component species in mixtures. Student's *t*-tests were used to test the differences in both NAE in each species combination and the IP of a given component species between control and dung, respectively, at a given harvest time. The NAEs of litter mixtures were analyzed using linear mixed effects models with species combination, dung, and incubation time treated as fixed factors and block as a random factor. If there was a significant incubation time by dung interaction, we analyzed the effects of species combination and dung on NAE for both incubation times separately. All statistical analyses were conducted using SPSS 20.0.

Results and Discussion

Effect of Dung on Mass Loss of Single Litter Types

Litter species, dung, and incubation time had significant effects on litter decomposition, and there were significant interactions among litter species, dung, and incubation period (Table 1). In the absence of dung, we found that the high-quality litter species *A. rivularis*, *S. nigrescens*, and *T. lanceolata* had significantly greater mass loss than the low-quality litter species *K. capillifolia*, *E. nutans*, and *L. virgaurea*, after 6 and 12 mo, respectively (Fig. 1). Litter mass loss was higher for species with higher initial N concentrations and lower for species with higher C-to-N and lignin-to-N ratios (Fig. 2). Strong control of decomposition rates by initial litter quality as observed here is common in many grassland ecosystems (Cornwell et al., 2008).

Dung significantly accelerated litter mass loss for low-quality litter species during both incubation periods but only during the 12-mo period for high-quality litter species (see Fig. 1). An explanation for the greater impacts of dung on low-quality litter may be that there is a priming effect from either the available carbon or nitrogen in the dung. Dung can supply exogenous carbon sources that can alleviate energy limitations for decomposers using low-quality litter species, facilitating more decomposer activity (Kuzyakov et al., 2000). Conversely, there is also limited evidence that exogenous nitrogen additions to litter may increase decomposition rates (Craine et al., 2007).

Effect of Dung NAE on Mass Loss of Litter Mixtures

We found that species combination and incubation time significantly affected NAE, and there were significant interactions among incubation time, dung, and species combinations (Table 2). In the absence of dung, the mean NAE on mass loss was + 4.91% and differed significantly from zero (t = 5.84, $P < 0.001$). Litter combination significantly affected NAE after 6 mo (Fig. 3A); however, after 12 mo the NAE of litter mixtures was not significantly different from zero (t = −0.56, $P = 0.57$) (Fig. 3B). The results showed that NAE varied depending on decomposition time, in line with recent findings (Lecerf et al., 2011; Wu et al., 2013; Chen et al., 2013). Only high-low quality litter combinations showed positive NAEs after 6 mo (Fig. 3A), supporting the notion that the chemical heterogeneity of mixtures is an important driver of decomposition rates of litter mixtures (Wardle et al., 1997; Pérez

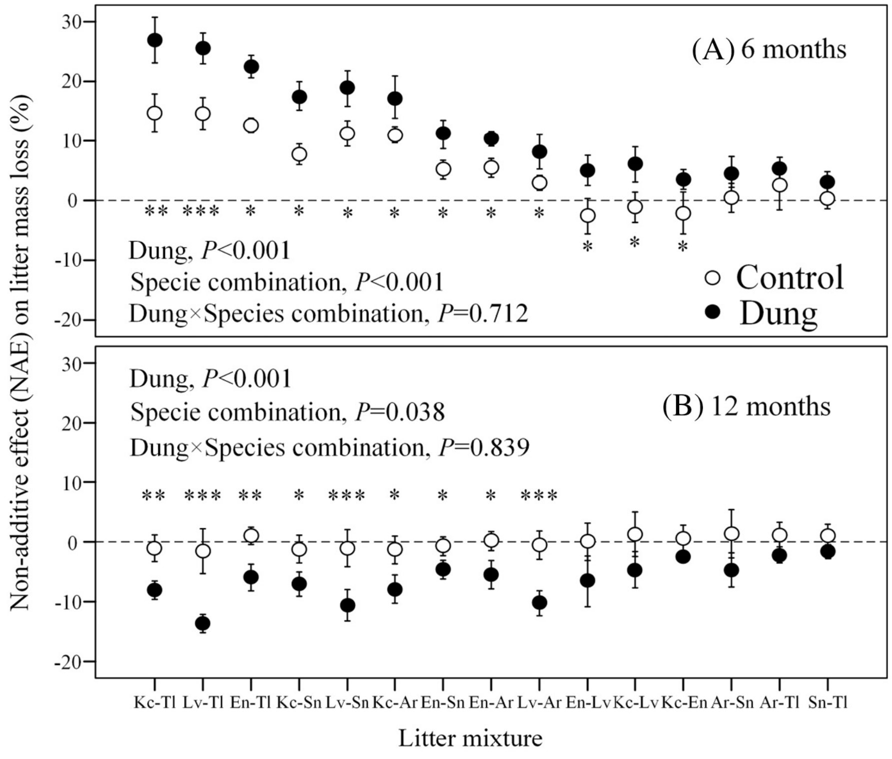

Figure 3. Nonadditive effects (NAEs) on litter mass loss (mean ± SE) for 15 different litter mixtures (species combination) under control *(open circles)* and dung *(closed circles)* treatments after 6 (**A**) and 12 (**B**) mo at the Alpine Meadow and Wetland Ecosystems Research Station on the Tibetan Plateau, China in 2013−2014. Positive deviations from zero indicated synergistic effects, and negative deviations indicated antagonistic effects. *Asterisks* denote significant differences in NAE on the mass loss of litter mixtures between control and dung (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Kc, *Kobresia capillifolia;* En, *Elymus nutans;* Lv, *Ligularia virgaurea;* Ar, *Anemone rivularis*; Sn, *Saussurea nigrescens;* Tl, *Thermopsis lanceolate.*

Harguindeguy et al., 2008; Cuchietti et al., 2014). As decomposition proceeded, the effect of differences in litter quality decreased (Fig. S1, available online at https://doi.org/10.1016/j.rama.2018.11.004) and appeared to be largely additive effects after 12 mo. Changing NAE through time may result from variation of litter quality over the decomposition processes. NAE changes for a given litter mixture with time are likely due to the complex nature of the decomposition process (Wardle et al., 1997), and the mechanisms behind NAEs are lively debated (Makkonen et al., 2013).

Dung addition significantly affected the NAEs on mass loss, with strong positive NAEs after 6 mo (mean = 10.94%, t = 11.08, $P < 0.001$) shifting to negative NAEs after 12 mo (mean = −5.9%, t = −10.90, $P < 0.001$) (Fig. 3A and B). The positive NAEs after 6 mo likely resulted from more mass loss from low-quality litter species in mixtures in the presence of dung (Fig. 4), suggesting that dung addition can stimulate complementary effects for low-quality litter species (Makkonen et al., 2013). The negative NAEs in the presence of dung after 12 mo resulted from less mass loss from high-quality litter in litter mixtures compared with the absence of dung (see Fig. 4). Dung deposition may suppress lignin decomposition by shielding the litter from sunlight (Wu et al., 2015). Further, at later decomposition stages the high lignin levels in low-quality litter may lead to increased formation of recalcitrant lignin-N protein complexes, which can slow down the mass loss in high-quality litter in mixtures by suppressing decomposer activity (Marco et al., 2011). Our study confirms that yak dung can alter NAE in this ecosystem, providing evidence that litter mixing effects on decomposition are dependent on the context (Madritch and Cardinale, 2007; Jonsson and Wardle, 2008; Rosemond et al., 2010).

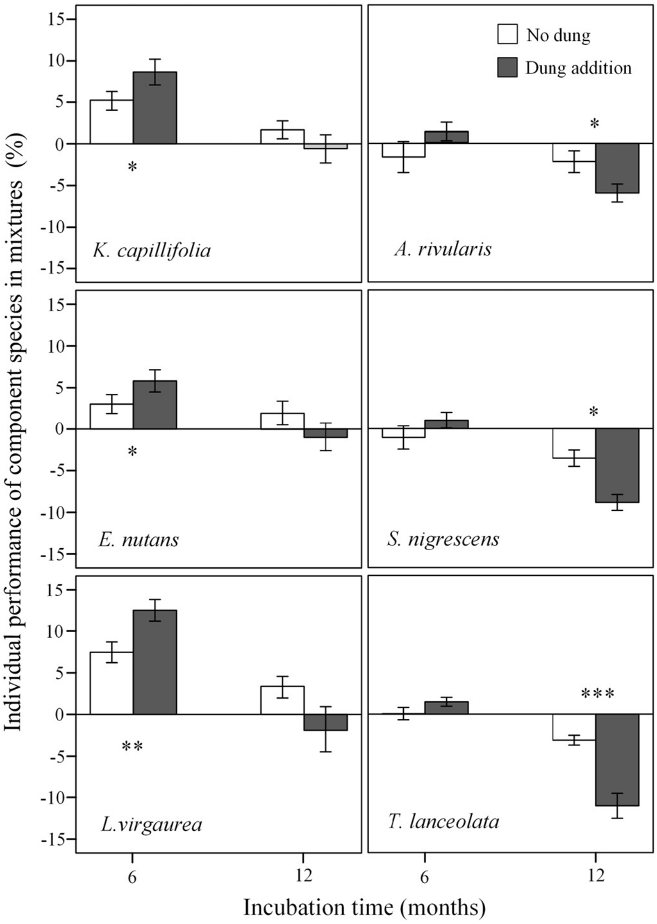

Figure 4. Individual performance (mean ± SE) of component litter species in litter mixtures from control *(white bars)* and dung *(gray bars)* after 6 and 12 mo, respectively, at the Alpine Meadow and Wetland Ecosystems Research Station on the Tibetan Plateau, China in 2013−2014. *Asterisks* denote significant differences between with/without dung addition (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

Implications for Yak Dung Management

Yak dung has long been used as a source of fuel by local farmers because other fuels such as wood and coal are scarce (Rhode et al., 2007), and in recent decades, a great deal of yak dung has been sold to the outside of the pastoral areas as bioenergy or fertilizer (He et al., 2009). The present study demonstrates litter decomposition, a major determinant of ecosystem functioning, is strongly influenced by yak dung deposition in this grazing system. Our results suggest that dung can affect soil process through affecting litter decomposition except through inputting nutrients and organic matter to soil. These findings, taken together with previous studies (He et al., 2009; Yu et al., 2013), have important implications for yak dung management. Yak dung has been substantially removed from this ecosystem over a long period of time, which may result in ecological risk of disorders of material recycling and energy transformation of grassland ecosystem. Further testing needs to be done to determine if yak dung removal is affecting ecosystem processes and ultimately grassland productivity on a larger scale.

Conclusion

In conclusion, our results showed yak dung can affect both single litter decomposition and NAE on litter decomposition and highlight the importance of yak dung in maintaining the Tibetan alpine grassland ecosystem function. Our results suggest that localized dung deposition driven by grazing animal movement patterns can affect soil processes by influencing litter decomposition, improving our understanding of the role of yak dung in driving biogeochemical cycling in this grazing ecosystem.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2018.11.004.

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