RESEARCH ARTICLE

Mass loss and nutrient dynamics during litter decomposition in response to warming and nitrogen addition in a desert steppe

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Abstract Plant litter decomposition has been studied extensively in the context of both warming and increased atmospheric nitrogen deposition. However, the temporal patterns of mass loss and nutrient release in response to warming and nitrogen addition remain unclear. A 2-year decomposition experiment aimed to examine the effects of warming and nitrogen addition on decomposition rate, and nitrogen and phosphorus dynamics. The effects of warming and nitrogen addition on decomposition of litter of *Stipa breviflora*, a dominant species in a desert steppe of northern China, were studied. Warming and nitrogen addition significantly enhanced litter mass loss by 10% and 16%, respectively, and moreover promoted nitrogen and phosphorus release from the litter in the first year of decomposition, followed by an immobilization period. The interactive effects of warming and nitrogen addition on mass loss, nitrogen and phosphorus concentrations of litter were also found during the decomposition. This study indicates that warming and nitrogen addition increased litter mass loss through altering litter quality. These findings highlight that interactions between climate change and other global change factors could be highly important in driving decomposition responses.

Keywords climate warming, grassland, litter decomposition, nitrogen deposition, nutrient release

1 Introduction

The global mean surface temperature has increased by 0.85°C over the period from 1880 to 2012. At the current levels of CO_2 concentrations it is projected to exceed 3.7°C by the end of the 21st century[1]. As temperature regulates almost all biogeochemistry processes, climate warming will have an effect on ecosystem functions and services, such as C storage[2]. With increasing N deposition caused by increasing use of N fertilizers and combustion of fossil fuels[3], enhanced N supply will influence ecosystem processes, such as plant growth, especially in N-limited ecosystems. Therefore, changes in temperature and available N can profoundly affect ecosystem C and N cycling.

Plant litter decomposition links plant C turnover and nutrient mobilization (e.g., N mineralization)[4]. The decomposition of litter is one of the major processes of the ecosystem C balance and contributes about 70% of the total annual C flux[5]. Litter decomposition is also a fundamental ecological process that provides energy and nutrient sources for microbial metabolism[6]. As litter decomposition rate is influenced by temperature and litter N content[7,8], climate warming and increased N deposition are likely to alter decomposition rate.

Warming effects on decomposition can occur directly through changes to the activity of soil organisms[7], and indirectly as a result of soil moisture decline[9] or via changes to litter quality[10]. Warming was found to increase litter decomposition in a meadow steppe[11] but decrease decomposition in a low-moisture treatment[5]. Nitrogen addition can directly stimulate microbial activity[12] or enhance litter nitrogen content[13], leading to an increase in decomposition. However, negative or no effects of N addition on litter decomposition were also found[14,15]. Therefore, the effects of warming and N addition on litter decomposition remain controversial. Although Gong et al.[11] reported that warming and N addition interactively affected litter quality and consequently promoted decomposition, data on the interaction between warming and N addition are scarce.

Decomposition time scale might have a key role in determining the responses of decomposition to global change. For instance, warming can accelerate C turnover shortly after litter incubation (i.e., over the initial 6 months[16]), while changes in C pool, microbial biomass and C use efficiency can diminish the warming effects over longer time scales (i.e., years[17]). Similarly, N addition enhanced the decomposition of newly senesced litter but slowed the turnover of recalcitrant material that accumulated in the long-term[12,18]. Although interactive effects of warming and N addition on decomposition may also be time-dependent, such temporal variation of litter mass loss and nutrient release is still not well understood.

The temperate steppe of Inner Mongolia in northern China is a dominant vegetation type in Eurasia and is reported to be sensitive to environmental change[19]. With the projected increases in nitrogen deposition and climate warming in this area[1], N addition and warming would presumably impact litter decomposition. In the present study, we selected the dominant species, *Stipa breviflora*, from a desert steppe ecosystem, to examine the progression of litter decomposition and nutrient release responses over 2 years in the context of an established warming and N addition field experiment. Specifically, we aimed to address two fundamental questions: (1) How do warming and N addition affect litter mass loss? (2) What are the impacts of warming and N addition on nutrient release over time during the decomposition?

2   Materials and methods

2.1   Study site and experimental design

This experiment was conducted at Siziwang Grassland Research Station in Inner Mongolia, northern China (111°53′ E, 41°46′ N; elevation 1456 m). Annual precipitation averages 280 mm (1961–2010) with 70% falling between June and September. Mean annual temperature is 3.4°C. The soil is classified as brown chestnut according to the Chinese classification, or Haplic Calcisols according to the FAO classification. The background values of organic C and total N in the 0–10 cm mineral soil were 1.93%±0.05% (mean±SE) and 0.13%± 0.01%, respectively. The plant community in the study site is mainly dominated by two perennial grasses, *S. breviflora* and *Cleistogenes songorica,* and one perennial forb, *Artemisia frigida*. The growing season in this temperate grassland runs from early April to late September.

In May 2006, the experiment was established in a homogeneous and flat field as a split-plot design with warming as the main plot and N addition as the subplot. There were six pairs of 3 m × 4 m main plots, in which one plot was assigned for the ambient and the other for warming. Each main plot was divided into two 3 m × 2 m subplots which were randomly assigned to no N addition

and N addition treatment. Thus there were four treatments: control, warming, N addition and warming plus N addition. Each treatment had six replicates. The warming plots were heated continuously using MSR-2420 infrared radiators (Kalglo Electronics Inc. Bethlehem, PA, USA) suspended 2.25 m above the center of each plot. In the control and N addition plots, a dummy heater with the same shape and size was installed to simulate the shading effects of the infrared radiator. The heaters were set at a radiation output of about 2000 W. The surface soil temperature (0 cm) in the warming treatment was 1.3°C higher than the control[20]. Nitrogen (10 g·m^{-2}·yr^{-1}) which was estimated as the community saturation rate of N deposition for temperate grasslands[21], was applied in the form of ammonium nitrate in June each year.

2.2   Litter decomposition and chemical analyses

The selected species in this study, *S. breviflora*, is the dominant species in this desert steppe. In late September 2007, the senescent leaf litter of *S. breviflora* from that year was collected, air-dried, and placed in polyethylene mesh bags (15 cm × 20 cm, 1-mm mesh size at the top of the litterbag and 0.25-mm mesh size at the bottom of the litterbag). Each bag was filled with 10 g litter (refer to as litter bags below). Litter samples were collected from each plot in the experimental site, and then were placed on the original plots where litters were collected. The initial litter weight (10 g air-dried litter) in each bag was used for the duration of the experiment (~2 years), and provided sufficient material for measurement of decomposition rate and chemical analysis.

On October 2, 2007, the litter bags were fixed to the ground using metal pins to prevent movement from wind. The litter bags were retrieved after 182, 243, 357, 612 and 706 d, during the following 2 years. At each collection date, one set of litter bags was randomly collected and taken to the laboratory for further analyses. Living plants and plant tissues were removed, and soil particles were carefully wiped off. Samples were oven-dried for 48 h at 65°C and weighed.

Total C, N and P concentrations in the original non-decomposed samples were measured to determine the initial litter chemistry. Only N and P concentrations were determined for the litter samples harvested during decomposition. All the litter samples were ground using a ball mill (Retsch MM 400; Retsch, Haan, Germany). Total N and C concentrations were analyzed with the Auto-Kjeldahl method (Kjeltec System 1026 distilling unit; Kjeltec Systems, Sweden) and K_2CrO_7–H_2SO_4 oxidation, respectively. Total P concentration was measured with persulfate oxidation followed by colorimetric analysis[22].

2.3   Statistical analyses

The percent remaining mass of the litter (R) during

decomposition was calculated as follows:

$$R(\%) = M_t/M_0 \times 100\%$$

where M_0 is the initial dry mass of the litter before decomposition and M_t is the dry residual mass of litter in the litter bag after a specific time period (t) of decomposition.

Repeated measures ANOVAs were used to examine the temporal variation and effects of warming and N addition on percent mass remaining, litter N and P concentrations. One-way ANOVA with Duncan's multiple range test was used to evaluate the differences between the experimental treatments within each sampling date. Linear regression analyses were employed to determine the relationships between percent mass remaining and litter nutrients concentrations. All statistical analyses were performed using SPSS 16.0 software (SPSS Institute Inc., Chicago, IL, USA).

3 Results

3.1 Treatment effects on litter mass loss

After 706 d, the litter mass loss was 22% in the control compared to 25% with warming, showing a significant increase of 10% during the entire period of the experiment ($P < 0.0001$, Table 1; Table S1; Fig. 1). N addition significantly enhanced mass loss by 16% compared to the control ($P < 0.0001$, Table 1; Table S1; Fig. 1). Combined warming and N addition produced a greater increase of 27% (Fig. 1). There were significant interactions between warming and time ($P = 0.005$, Table 1) and between N and time ($P = 0.01$, Table 1), which were explained by significant enhancements in mass loss with either warming or N addition over the entire experimental period (Fig. 1). There was an interactive effect of warming and N addition on mass loss ($P = 0.049$, Table 1). After 706 d, warming enhanced mass loss by 10% at both ambient N and increased N supply. N addition increased mass loss by 16% and 15% in the unwarmed and warmed treatments, respectively.
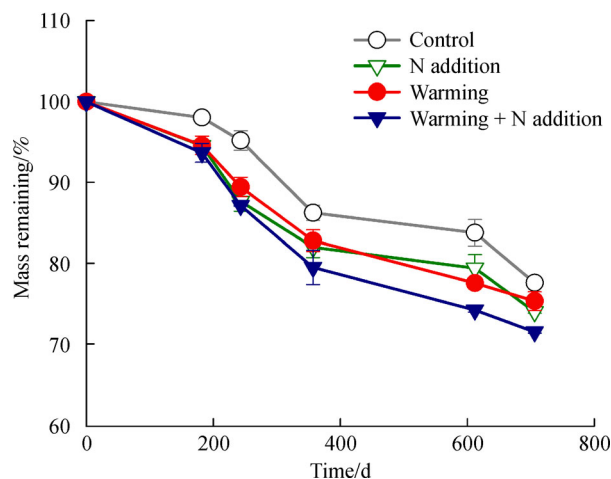

Fig. 1 Effects of warming and N addition on litter mass remaining (% of initial mass) during decomposition of *S. breviflora* over time. Data are means±SE.

3.2 Treatment effects on nutrient release patterns of litter

Compared to the control, initial litter N concentrations showed significant enhancements of 18%, 25% and 29% in response to warming, N addition and combined warming and N addition, respectively (Fig. 2a; Table 1; Table S2). After 706 d, both warming and N addition significantly increased litter N concentration relative to the control (all $P < 0.0001$, Table 1). However, litter N concentration exhibited large fluctuations over time, which was indicated by a significant decrease over the first year but an increase over the second year during the decomposition period (Fig. 2a). Also, there was a significant interaction between warming and N addition on litter N during the decomposition ($P < 0.0001$, Table 1). N addition increased litter N by 25% and 8% under unwarmed and warmed treatments across all sampling dates, respectively. Warming enhanced litter N concentration by 17% and 1% at ambient N and increased N supply, respectively.

There were significant increases of 17%, 14% and 27% in initial litter P concentrations, under warming, N addition and combined warming and N addition, respectively,

Table 1 Repeated-Measures ANOVA of warming and N addition effects on litter mass, and N and P concentrations for the dominant species, *S. breviflora*

| Effector	DF	Mass		N		P	
		F ratio	*P*	*F* ratio	*P* > *F*	*F* ratio	*P*
Warming	1	197.58	< 0.0001	235.06	< 0.0001	9.72	0.0260
N addition	1	59.60	< 0.0001	237.13	< 0.0001	10.16	0.0020
Time	5	407.12	< 0.0001	132.82	< 0.0001	109.94	< 0.0001
Warming × N addition	1	3.98	0.0490	47.22	< 0.0001	6.28	0.0140
Warming × Time	5	3.55	0.0050	0.47	0.7980	0.22	0.9560
N addition × Time	5	3.17	0.0100	0.26	0.9330	0.40	0.8460
Warming × N addition × Time	5	1.09	0.3700	1.80	0.1190	0.10	0.9930
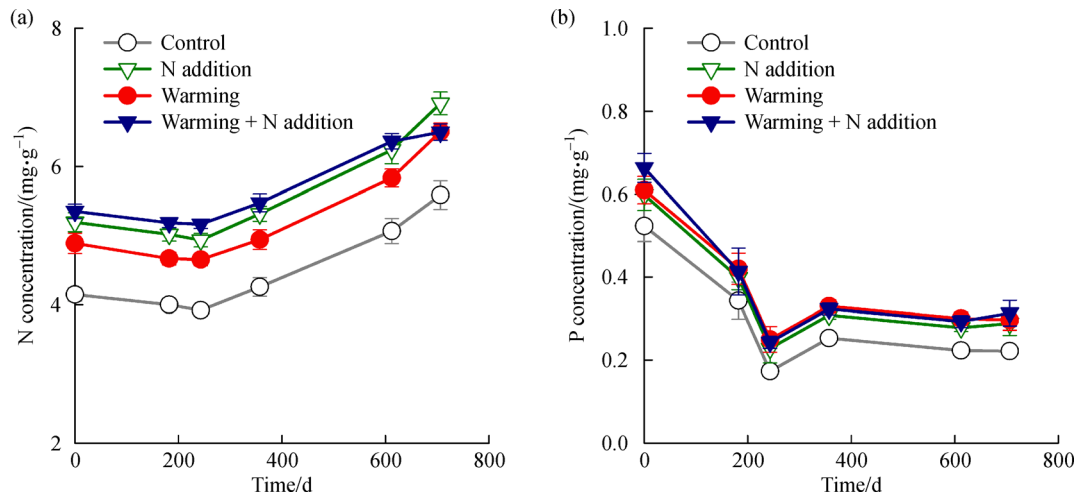
Fig. 2 Effects of warming and N addition on N (a) and P (b) concentrations in litter of *S. breviflora* over time. Data are means±SE.

compared to the control (Fig. 2b; Table 1; Table S3). Litter P concentrations showed an overall decreasing trend during the entire decomposition period, although there was small fluctuation with time. Litter P concentration decreased to the lowest value after 243 d, increased after 357 d and showed no noteworthy fluctuations thereafter (Fig. 2b). Litter P concentration was also affected by the interaction between warming and N addition during the decomposition ($P = 0.014$, Table 1). Warming increased litter P concentration by 21% without N addition and 2% with N addition across all sampling dates. N addition enhanced litter P by 27% and 7% under unwarmed and warmed treatments, respectively.

To examine the potential determinants of litter decomposition, litter mass loss was regressed against litter quality. Litter mass loss after 706 d was positively correlated with initial litter N concentration ($r^2 = 0.41$, $P < 0.001$; Fig. 3a) and P concentration ($r^2 = 0.24$, $P = 0.016$; Fig. 3b). However, litter mass loss was negatively related to initial litter C concentration ($r^2 = 0.53$, $P < 0.001$; Fig. 3c) and C/N ratio ($r^2 = 0.45$, $P < 0.001$; Fig. 3d).

4 Discussion

4.1 Responses of litter mass loss to warming and N addition over time

Our results show that litter mass loss of the dominant species in this desert steppe, *S. breviflora*, was enhanced by both warming and N addition during two hydrologically contrasting growing seasons in 2008 (wet with total precipitation 33% above the long-term mean of 280 mm) and 2009 (dry with total precipitation 32% below the long-term mean). These effects interacted with time. There was a greater increase in litter mass loss in the first year than in

the second year (Fig. 1). Warming and N addition also had an interactive effect on litter mass loss, suggesting that interactions between climate change and other global change factors can be important in driving decomposition responses.

The effect of increased temperature on litter decomposition has been extensively studied[23–26]. However, consistent results have not been obtained. For instance, Gong et al.[11] reported that warming enhanced litter decomposition in a temperate meadow ecosystem. Moise and Henry[25] found that warming increased mass loss for one type of grass litter in an old field. These findings are consistent with our results from the 2-year decomposition experiment. In contrast to our findings, warming was found to decrease litter decomposition in low moisture treatment in a microcosm experiment[5] or have no significant effect on mass loss when moisture limitation occurred in a field experiment[26]. We suspect the differences between the results of that field study[26] and ours can be partly explained by the fact that long-term mean annual precipitation is much lower in our grassland (280 mm) than in that mesic old field (818 mm). When water availability becomes limited, the relatively wet ecosystem would be more sensitive than our arid grassland. The different response patterns between our desert steppe and the mesic old field highlight the fact that the differences in litter mass loss responses to warming may be ecosystem-dependent and suggest that warming may be more influential in litter decomposition in arid regions than in less arid regions.

There are several mechanisms that could explain the observed changes in litter mass loss in response to warming over time. First, warming can increase litter decomposition directly by affecting microbial activity and extracellular enzyme activity[27]. For example, increased temperature has been shown to stimulate microbial activity and enhance decomposition in a Central European
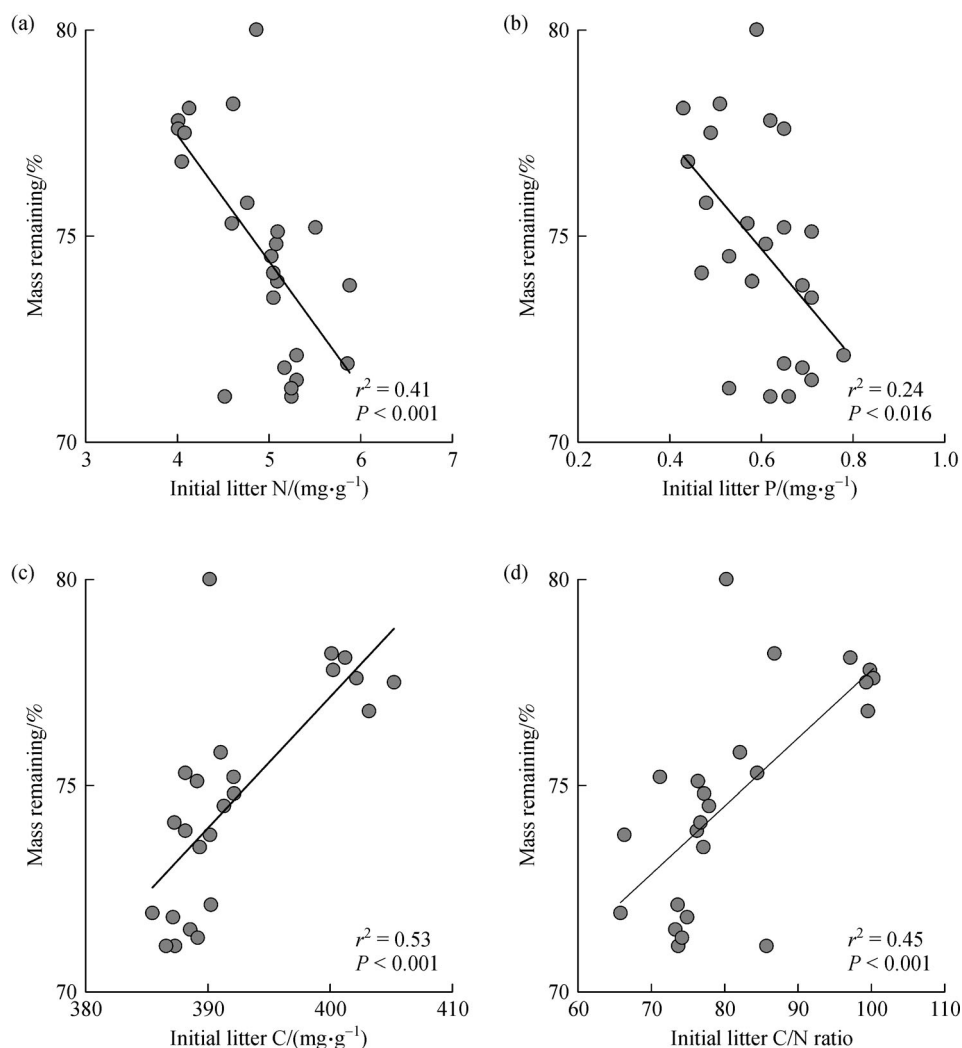
Fig. 3   Relationships between litter mass remaining (% of initial mass) and initial litter N concentration (a), P concentration (b), C concentration (c) and C/N ratio (d) for *S. breviflora*.

mesophilic grassland in the absence of drought[27]. Secondly, warming effects on decomposition can occur indirectly as a result of soil drying[9]. Almost all studies performed in relatively mesic ecosystems indicate that warming reduced soil water availability[7]. Finally, warming can result in changes in plant tissue quality that consequently affect litter decomposition. After 3 years of warming, initial litter N and P concentrations increased and litter lignin content decreased in a meadow steppe[11].

From the present study, we suggest that a third mechanism, changes in litter quality, is the most likely factor responsible for the observed pattern of litter mass loss following warming treatment. After two years of warming, initial litter N and P concentrations increased (Fig. 2). During the decomposition, warming continuously increased litter quality either in a relatively wet year or in a dry year, which may be attributed to N and P immobilization induced by warming[28,29]. The positive correlations between litter mass loss and N and P concentrations, and

the negative correlations between mass loss and C concentration and C/N ratio, further suggest that litter with high quality (enhanced N and P concentration and reduced C/N ratio) induced by warming could accelerate decomposition in the study region.

With respect to N addition, litter mass loss increased with the added N during the 2-year decomposition, which is consistent with previous studies[11,13,26]. However, N addition was found to have no significant effect on decomposition[15] or even reduce litter mass loss[14,30]. The different response patterns of litter decomposition to N addition may be attributed to the differences in fertilizer types and fertilization rates[31]. Nitrogen addition can directly alter microbial activity[12], or may impact litter chemistry, consequently altering decomposition[32]. In our study, initial litter N and P concentrations were enhanced with N addition and exhibited positive correlations with litter mass loss, while initial litter C concentration was negatively associated with mass loss of litter. Nitrogen

addition continuously increased litter mass loss during two hydrological contrasting years. These results suggest that the added N enhanced litter quality, leading to increased litter decomposition.

In addition, litter mass loss was stimulated by the interaction between warming and N addition (Table 1). Significant interactive effects of warming and N have also been found in litter N and P concentrations over the 2-year decomposition period. Similar interaction was observed in another warming and N addition experiment conducted in a meadow steppe[11]. Therefore, interactions between warming and N addition could be important in driving decomposition responses.

4.2   Nutrient dynamics during litter decomposition

During litter decomposition, the N dynamics may be divided into three different phases which include leaching, accumulation and release. However, not all three phases are always present and may not always be clearly distinguished in practical experiments[33]. There are three possible cases of N dynamics. In the first case, a leaching phase is followed by an accumulation and a release phase. In the second case, there may be an accumulation followed by a net release. In the third case, only a release is observed. For instance, the accumulation phase may be absent in litter with high N concentration under nutrient-rich condition.

In the present study, the litter for *S. breviflora* under all treatments released N at the early stage of decomposition, followed by an immobilization period when litter N concentration increased during the decomposition (Fig. 2a), which indicates a rapid release of initially leachable N in litter followed by an accumulation. This result is consistent with the first 2 years of results from Tan et al.[29]. That study found that litter N concentration for *Stipa krylovii* declined in the first year, increased in the second year followed by a decline again in the third year during decomposition in a typical steppe. Increases in litter N concentration during decomposition were widely observed in other studies[28,29], which has generally been attributed to microbial immobilization. Warming and N addition promoted N release during the early period but enhanced N immobilization during the later period of the decomposition, compared to the control.

Few studies report P dynamics during litter decomposition, as most focus on N release. Our study found that P concentration of the remaining litter decreased to the lowest value after decomposition for 243 d, then increased after 357 d and subsequently remained stable (Fig. 2b). Such a pattern of P release over time during the litter decomposition occurred under all four treatments. The slight increase in litter P concentration during decomposition may result from microbial immobilization, particularly when P availability is high due to fertilization[34]. Although litter P concentration was higher after 357 d

than after 243 d, the increased P concentration was not higher than the initial P concentration. In addition, warming and N addition promoted P release during the entire period of the decomposition relative to controls.

5   Conclusions

Future changes in temperature and atmospheric N deposition in a desert steppe and similar terrestrial ecosystems may significantly alter litter decomposition and nutrient release patterns. Litter quality could have a central role in controlling litter decomposition, which would be affected by interactions between warming and increased N deposition. Further work is required to disentangle the contributions of the direct and indirect effects of warming on litter decomposition across various ecosystems along a precipitation gradient.

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