



A 5-and a-half-year-experiment shows precipitation thresholds in litter decomposition and nutrient dynamics in arid and semi-arid regions

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Abstract

Precipitation is a key driver of litter decomposition in arid/semiarid regions; where soils are poor in organic matter, and thus re-incorporation of litter is key for soil nutrient accumulation and soil structure. It remains unclear, though, whether litter decomposition responds symmetrically to precipitation variation (e.g., if precipitation surpluses produce a stimulatory effect of a similar magnitude, but opposite direction to inhibitory effects of precipitation deficits), and whether litter decomposition and litter nutrient dynamics in arid and semiarid ecosystems that differ in climate show similar responses to precipitation. We set up a 5-and-a-half-year experiment that manipulated rainfall along a gradient (7 treatments): increases by 20%, 40%, and 60%, background precipitation, and reductions by the same 3 percentages. We applied such experiment in two sites with different patterns of precipitation (Urat: arid; and Naiman: semiarid) in Inner Mongolia to elucidate our questions. Litter mass loss and all nutrients that we measured (carbon, nitrogen, phosphorous, potassium, plus lignin) decomposed faster at the highest level of surplus precipitation, and more slowly in the two largest precipitation reductions. This indicates that these levels of precipitation constitute thresholds (value of precipitation beyond which ecosystem function is critically altered). Litter decomposition in the semiarid site was faster and more complete, but decomposition in the drier Urat was more efficient per unit cumulative rainfall. Thus, site specific effects played an important role in decomposition. Reductions in precipitation decreased the loss of C, N, P, K, and lignin from litter; and clear precipitation thresholds in the dynamic of these nutrients in litter were observed. Overall, this indicated the importance of precipitation limitation at controlling nutrient release. Our study highlights the importance of long-term studies on litter decomposition in environments with slow decomposition rates, and the importance of taking into account mechanistic effects of water availability on decomposition.

Keywords Arid and semiarid regions · litter mass loss · litter nutrients' dynamics; precipitation thresholds · ecosystem functioning · precipitation limitation of decomposition

Introduction

Climate change is causing changes in precipitation in many different parts in the world (Ladwig et al. 2012), and it is predicted that the variability of global precipitation will

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continue to increase in the future (Easterling et al. 2000; Meehl et al. 2007; IPCC 2014). For arid and semiarid ecosystems, such increased variability will translate into higher uncertainty in inter-annual precipitation variation in these ecosystems that are water-limited (Suseela et al. 2018), with subsequent consequences on key functions such as litter decomposition and the dynamics of C, N, and P driven by litter decomposition (Huang et al. 2016). Although our understanding on litter decomposition controls in arid and semiarid areas has improved (Moorhead and Reynolds 1991; Throop and Archer 2009; Gliksman et al. 2017), we still lack a more mechanistic view of the effects of precipitation on this process (Berg and Laskowski 2005). For instance, precipitation gradient studies, manipulative experiments, and vote-counting works have found contradictory evidence on the effects of precipitation on litter decomposition; varying from null (e.g., Kemp et al. 2003; Li et al. 2016) to positive (e.g., Schwinning et al. 2004). In a review involving 200 published studies (20% in arid and semiarid areas), Zhang et al. (2013) even found instances when litter decomposition was negatively correlated to mean annual precipitation in arid areas. They speculated that photodegradation might have a relative more important role as rainfall becomes more limiting.

A number of factors might account for the lack of consistent responses of litter decomposition studies to precipitation in arid and semiarid areas. Firstly, studies using precipitation gradients have multiple confounding factors (e.g., mean annual temperature, soil conditions) which are rarely accounted for, but inherent to the comparison of different geographic locations (Yahdjian and Sala 2006). Such confounding factors limit our capacity to interpret whether effects of precipitation variation on the target ecosystem processes are independent of particular site conditions. Secondly, manipulative experimental approaches usually do not contrast different experimental sites with differences in their environment (Throop and Belnap 2019), and the range of precipitation in the experimental treatments is rather narrow. This latter point is important to identify precipitation thresholds beyond which the litter decomposition can be severely impaired or enhanced. Finally, disparities among studies might result from the fact that most of them are short-term, but since decomposition in arid/semiarid areas is a slow process, the picture we might obtain from short-term studies is rather fragmented.

Here, we report results of a field experiment designed to overcome those above-mentioned limitations in precipitation-decomposition studies presented above. Our results span for almost six years of observations in an experiment that manipulated rainfall amount across a wide range of precipitation treatments (with both reductions and surpluses), and contrasted two experimental sites with differences in long-term precipitation in Northern China. We also followed

litter C, N, P, K, and lignin dynamics as decomposition took place. This latter aspect on litter chemical composition dynamics has been usually neglected in the literature on litter decomposition, particularly in arid and semiarid areas (Spohn and Berg 2023). Our main aim was to explore how variation in precipitation controls litter decomposition and litter nutrient dynamics in our two contrasting study sites. Our first research question is whether there are thresholds when litter decomposition either becomes significantly impaired by precipitation reductions or enhanced by precipitation surpluses, and whether these thresholds differ between sites with different long-term precipitation regimes. Our second research question is whether litter nutrient dynamics response varies across precipitation thresholds and whether such response differs between our experimental sites. Finally, given the range of the precipitation gradient we worked with, we also wonder whether changes in precipitation rendered litter decomposition more difficult to be described by simple models of mass loss.

Material and methods

Site description

The study took place at both the Naiman Desertification Research Station (Naiman Station, 42°55'N, 120°42'E), and the Urat Desert Steppe Research Station (Urat station, 41°25'N, 106°58'E) (Fig. S1). Both stations are affiliated to the Chinese Academy of Sciences. The Naiman study site is located in the Horqin Sandy Land of China with a temperate, semi-arid continental-monsoon climate. Naiman has a mean annual temperature of 6.4 °C, annual average precipitation of 360 mm, annual pan-evaporation of 1935 mm, and average annual wind speed of 3.5 m/s (Qu et al. 2017). Main plant species in Naiman include *Agriophyllum squarrosum*, *Salix gordejewii*, *Caragana microphylla*, *Artemisia halodendron*, *Lespedeza davurica*, *Melissitus ruthenicus*, *Leymus secalinus*, and *Bassia dasyphylla* (Qu et al. 2021). The Urat study site is located on the Urat desert steppe, with a temperate, arid continental monsoon climate (more arid than Naiman). It has an average annual temperature of 5.3 °C, mean annual precipitation of 180 mm, and average annual wind speed of 5 m/s. For Urat the main plant species are *Stipa klemenzii*, *Peganum harmala*, *Achnatherum splendens*, *Caragana microphylla*, *Bassia dasyphylla*, and *Reaumuria songarica* (Zhang et al. 2019). Both sites contain fragile ecosystems and are located around the same latitude, but as it can be seen they differ in their precipitation regimes: Naiman is semiarid, Urat is arid. A well-pooled soil sample produced the following results for soil nutrients (6 replicates): C, 4.52 g kg⁻¹; N, 0.32 g kg⁻¹; P, 9.78 mg kg⁻¹; K, 84.65 mg kg⁻¹; and

C, 6.33 g kg⁻¹; N, 0.56 g kg⁻¹; P, 7.97 mg kg⁻¹; K, 66.98 mg kg⁻¹ for Naiman and Urat, respectively.

Materials

The *Caragana microphylla* shrub is widely distributed in northern China and plays an important role in windbreak and sand fixation, the decomposition of its litter also improves soil nutrients' status (Yang and Liu 2019; Yang et al. 2021a). Leaf litter material from *C. microphylla* (a species common to the two sites) was collected from both sites (almost in a 1:1 proportion) to prepare litter bags for the experiment. We collected dead leaves of the litter collection year (2015) that had not yet fallen to the ground ("standing litter" cf. Zhang et al. 2014) to be sure they were at the same decomposition phase. Before the start of the experiment, the collected litter was well-mixed, cleaned and oven-dried at 65 °C until a constant weight was reached.

Experimental design

Our long-term experiment used a patented "platform" (National Utility Model Patents of China, patent number: ZL201220126834.3) to manipulate rainfall amount (Fig. S2-1). The platform was designed by the Naiman Station's staff. A detailed description of the platform is given by Zhang et al. (2019). In brief, the receptors on the roof of the system are made of high transparency polycarbonate with transmittance $\geq 95\%$ to limit the blocking of incoming radiation. The receptors collect rainfall and deliver it into a container. The collected rain in the container can then be redistributed if necessary to adjacent plots through redistributing pipes. The area under the roof is a rain-shelter (precipitation reduction zone, 6 × 6 m plot), and the area of redistributed rain (also on a 6 × 6 m plot) corresponds to precipitation surpluses. The central area at each of these zones (4 × 4 m) is the effective experimental area of each plot. The density of receptors is varied to achieve a desired rainfall input amount.

On each station, 18 sets of rainfall manipulation platforms were set up to include the following 7 treatments: 3 precipitation surplus treatments where rain was increased by +20%, +40%, +60% with respect to background precipitation; the background precipitation itself (control); and 3 reduced-rainfall treatments where rain was decreased by -20%, -40%, and -60% with respect to the background. Each platform includes one precipitation surplus treatment and a corresponding reduced-rainfall treatment. A random block design was used, with six blocks, each with 7 precipitation treatments (6 × 7 = 42 plots per site) (Fig. S2-2).

We used a single-cohort litter bag experiment where litter bags with 20g of intact litter of *C. microphylla* were placed on the surface of each plot in May 2015 (each litterbag 15 × 10 cm, mesh size 1 mm, all of these are usual settings

in litterbag experiments in Inner Mongolia, e.g., Liu et al. 2006). Litter bags were retrieved every six months since November 2015 (in May and November every year). The last retrieval took place in November 2020 (11 retrievals in total, spanning around 2000 days for the oldest litter bags). There were 42 plots × 2 sites × 11 retrieval times = 924 litter bags in total, plus other 84 litter bags at t_0 , N= 1008). After retrieval, litter was cleaned by rinsing its surface repeatedly with distilled water to remove impurities such as mud and sand, and it was then oven-dried at 65 °C until constant weight. We used oven drying instead of air-drying to avoid attracting insects that could feed on the litter material, and could alter the results of the experiment.

Lab analysis

Total C and total N of all leaf litter were measured with an elemental analyser (vario MACRO cube; Elementar, Langenselbol, Germany). P contents of leaf litter were determined with a colorimetric method. Briefly, the sample was digested with H₂SO₄-H₂O₂, and the acidity of the resulting solution was adjusted for colorimetric determination. Calculation of P content was carried out as:

$$P(\%) = p \cdot V \cdot F \cdot 10^{-4} \div m$$

where p (μg/mL) is the mass concentration of P in the chromogenic standard solution, V (mL) is the volume of the chromogenic solution, F is the volume of the digestion solution (mL)/volume of absorbed digestion solution (mL), and m is the mass of the dry sample. The K contents of leaf litter were determined with the flame spectrometry method. The sample was digested with H₂SO₄-H₂O₂, distilled water was added to a set volume, and K was measured with a spectrophotometer. K contents were calculated in the same way as for P contents (Bao 2000).

Lignin content of all leaf litter was determined by gravimetry using hot sulfuric acid digestion (Rutigliano et al. 1996). The assay uses concentrated sulfuric acid to hydrolyze the non-lignin part of the litter sample, so that the remaining residue is considered as the lignin fraction. Litter material is triturated in a crucible and weighed to 1g (down to the 0.001 g accuracy). The triturated material is wrapped with a filter paper and placed in a Soxhlet extractor. The material is then extracted with a 2:1 volume ratio of a benzene-ethanol mixture for 6 h. After air drying, 15mL of 75% sulfuric acid is added to the sample into a conical flask with a stopper, then the sample is allowed to react at 25 °C for 2 h for the hydrolysis of fiber components into polysaccharides or monosaccharides to take place. After this, additional hydrolyzation is carried out by diluting the sample extract with water (down to 2% to 10% sulfuric acid), boiling it and refluxing it for 1-5 hours. The sample is let to settle, filtered

and washed until neutral pH. Finally, the residue (together with filter paper) is transferred to a crucible and dried at 105 °C until constant weight to obtain the lignin fraction. A well-mixed batch of the litter collected for the experiment had the following initial values for nutrients and lignin: C%, 48.5; N%, 3.85 (C: N, 12.6); P%, 0.37; K%, 10.2; lignin%, 37.3%, and such values are very similar to those measured in other studies (Yang et al. 2022).

Weather and climate

Soil surface temperature for each site was recorded automatically by HOBO temperature data loggers (Onset Company, MA, USA). The air temperature, and precipitation data were provided by standard weather stations placed in both experimental sites. Rainfall data were corrected for each plot according to its precipitation treatment.

Statistical analysis

We analysed litter decomposition dynamics as the percentage of litter mass remaining, following a similar model to the Olson's first-order negative exponential one (Olson 1963). In its linear form, the model for percentage of mass litter remaining can be expressed as:

$$\ln(M_t) = \ln(M_0) - kt$$

where M_t is the percentage of mass remaining in time t , M_0 is the initial litter mass (100 %), t is time since the beginning of the experiment (in days), and k is the decay rate or decomposition constant (ln of % mass loss day⁻¹). To assess if precipitation changes exerted control on how erratic decomposition rate became, we fitted two kinds of regression to the mass loss data with the above-mentioned negative exponential model. We used (1) a simple linear regression and (2) a piece-wise regression (Lecerf 2021) in R (Muggeo 2008). A brief explanation of the piecewise model approach to fit mass loss data is presented in Fig. S3. A higher erratic decomposition was defined as one where the capacity of simple linear regression was lower to describe the mass loss process than that performed by piece-wise regression (R^2 , RMSE values, and parameter estimates' errors).

The effects of precipitation on litter mass remaining and litter chemistry dynamics (on a mass basis) were analysed with mixed linear models (Pinheiro and Bates 2022). We excluded values at t_0 since litter variables' values did not vary. Site, precipitation treatments, time, average air temperature (5 months before sampling + sampling month), and litter mass remaining were considered fixed effects (the last 3 as covariates). We only used air temperature because it was highly correlated with soil temperature (Kendall $\tau = 0.71$, $P < 0.001$). For litter nutrients and lignin, we included

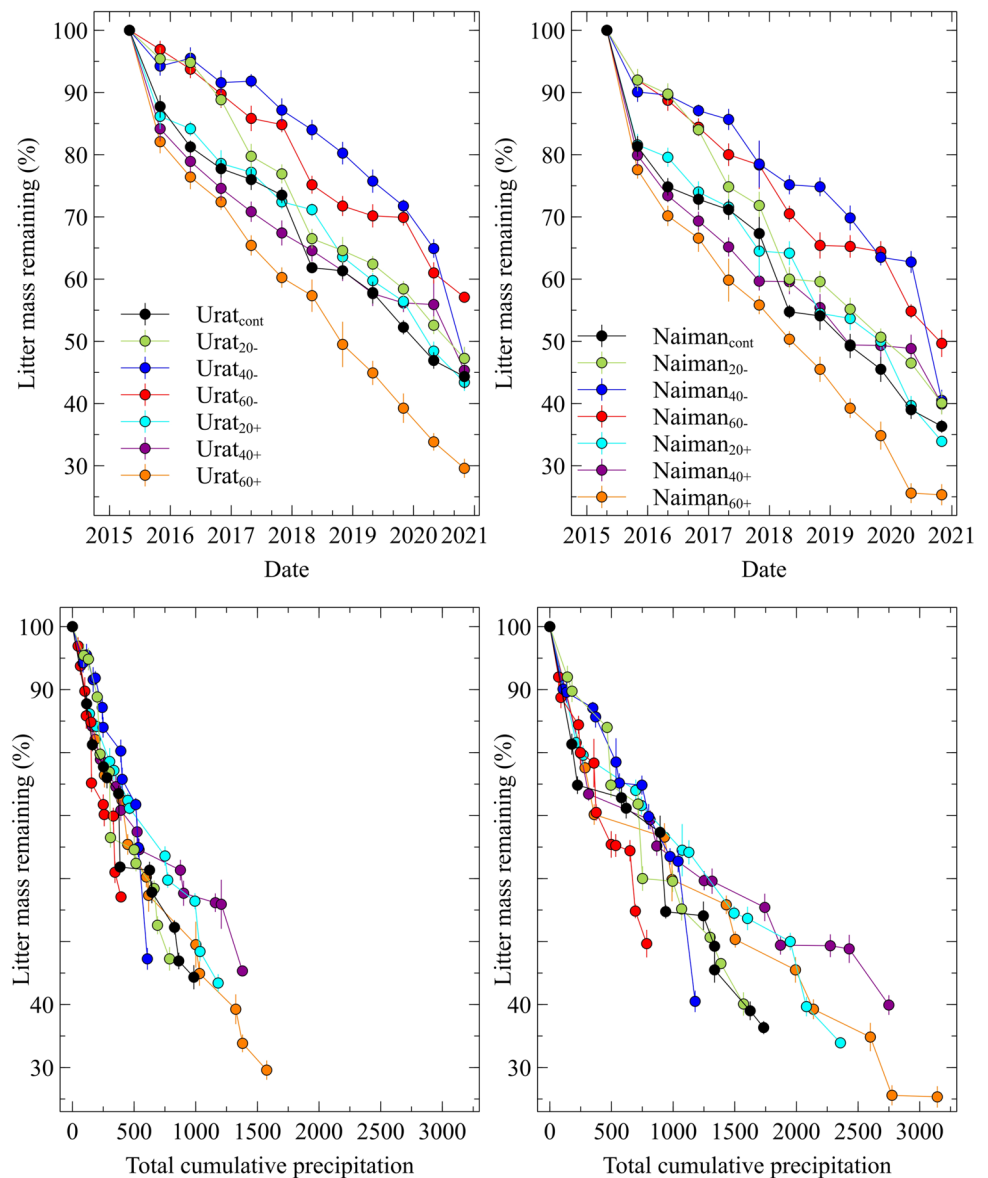
the square of litter mass remaining as a covariate (since the relation between nutrient contents and litter mass remaining was not linear) to isolate the effects of mass loss from those of precipitation treatments. Plot at each sampling time was considered a random effect (equivalent to a repeated times analysis). All data analyses were carried out with R (R Core Team 2022); with transformed data when appropriate, and plots created with Veuzs for Linux (Sanders 2008).

Results

Mass loss

Precipitation had a clear effect on mass loss (Fig. 1, Table 2). Precipitation surpluses, not reductions, rendered the decomposition process more unpredictable in both Naiman and Urat. This was shown by a lower predictive power of simple linear regression in both precipitation treatments in comparison with the control (Table 1, Table S1 for a complete view of model parameters' results). Main reasons for such lower prediction power were a lower observed mass loss than that predicted in precipitation surpluses treatments (i.e., an overestimation, mainly in the first retrieval times), and a higher observed mass loss than that predicted in reduced precipitation treatments (mainly in middle stages of decomposition) (Figs. S4 and S5). Overall, the piece-wise approach outperformed simple linear regression to describe the decomposition process (Table 1, Table S1). Simple linear regression overestimated more often than piece-wise regression the intercept at precipitation decreasing treatments (Figs. S4 and S5), although both underestimated it at precipitation surpluses. The piece-wise approach has the additional advantage that it divided decomposition into two recognisable stages: initial and final stage (Figs. S3, S4, and S5). The final stage had a faster mass loss than the initial stage in all treatments at both sites, except for the 40+ treatment (Table 1, column Δ Speed). When comparing treatments at the initial stage of decomposition, precipitation reductions slowed down such early decomposition at both sites, but more acutely in Urat (0.4 to 0.7 slower than control in Urat, 0.6–0.7 in Naiman, Table 1). When comparing decomposition rates among treatments and the control at the initial stage, an increase was evident at both sites in the 40+ treatment (2.6 and 3.1 times faster than controls in Urat and Naiman respectively), and the 60+ treatment (1.4 times faster than controls at both Urat and Naiman). For the final decomposition stage, mass loss was much faster than that in the control in the 40– treatments at both sites (2.3 and 4.6 times faster in Urat and Naiman respectively), but it was slower in Naiman at the 20– treatment (0.8 times). Final values of mass losses are presented in Table S2.

Fig. 1 Top: Mass loss across 5-and-a-half years from a litterbag experiment under precipitation manipulation at two experimental sites (Urat and Naiman) in Inner Mongolia, China. Urat is more arid than Naiman. Precipitation treatments include precipitation background (cont), –20%, –40%, and –60% decreases; and percentages of increase as +20%, +40%, and +60%. Lines are not best fit lines, but only a help to identify the treatments. Bottom: Mass loss dynamics as a function of cumulative precipitation. Labels as for the top figure. Lines are not best fit lines, but they only help to link the treatments. Symbols are mean values \pm standard deviation for each treatment in each experimental site per date ($n = 6$)



Additionally, the overall dynamics of mass loss during the time of our study (Fig. 1), and the significant differences in mass loss at the late observation points (Fig. 1, Table S2), clearly determine precipitation surpluses or deficits values that define precipitation thresholds, mainly for treatments 60+, and 40-, and 60- at both sites. These thresholds are values of precipitation treatments for which mass loss showed a different dynamic and different final values to those in the controls and other treatments. When analysed in terms of total cumulative precipitation (Fig. 1), the precipitation threshold values on decomposition for the 60+, and 40-, and 60- treatments became also apparent. In Urat, the cumulative wet threshold was around 1200 mm total cumulative precipitation, this is the value when the 60+ treatment diverged from the others resulting in a more complete decomposition. In Naiman, the similar threshold

value occurred until 2500 mm. The dry threshold cumulative value (i.e., when decomposition was severely impaired with respect to controls and other treatments) occurred at around 400 and 800 mm in Urat and Naiman respectively (represented mainly by 60- treatments at both sites). Using cumulative precipitation also allowed us to compare our two sites at similar total cumulative precipitation values, where we observed a non-additive response of decomposition to precipitation as a consequence of precipitation thresholds. In this way, Urat 20- and Naiman 60- had similar total cumulative rainfall at about 800 mm, but the final mass loss was slightly lower in Urat (Table S2). Thus, litter decomposition in Urat was slightly more efficient per unit cumulative rainfall when Naiman experienced its driest conditions (dry threshold in Naiman). For the 60+ treatment in Urat (around 1600 mm, wet threshold in Urat), litter

Table 1 Parameter estimation (intercept = M_0 , slopes = k) of mass loss (%) as a function of day since the beginning of the experiment. Parameters were derived either from simple linear regressions or from one-break piecewise regressions (where subscripts are used to identify the k 's). Note changes in decomposition rates within each treatment for different stages of decomposition derived from the piecewise regressions: “ Δ Speed” (k_2/k_1). Acceleration Δ Speed > 1, slowing down Δ Speed < 1. Also note comparisons for the piecewise regression results among precipitation treatments and the control (last two columns)

Site	Treatment	Simple linear regression		Piecewise regression (one break)				Piecewise k 's comparisons		
		M_0^\dagger	k^\ddagger	M_0^\dagger	k_1^\ddagger	Break ‡	k_2^\ddagger	Δ Speed	k_{1s}/k_{1cont}	k_{2s}/k_{2cont}
Urat	cont	97.5	0.140	96.5	0.13	1461	0.178	1.4	1	1
	20–	104.6	0.137	99.5	0.055	366	0.147	2.7	0.4	0.8
	40–	107.8	0.105	100.5	0.064	1628	0.416	6.6	0.5	2.3
	60–	103.5	0.100	101.5	0.09	1645	0.179	2	0.7	1
	20+	98.5	0.134	95.6	0.113	1584	0.261	2.3	0.9	1.5
	40+	91.8	0.116	100.5	0.342	196	0.105	0.3	2.6	0.6
Naiman	60+	98.5	0.205	94.6	0.18	1376	0.279	1.6	1.4	1.6
	Cont	94.6	0.169	91.8	0.145	915	0.188	1.3	1	1
	20–	103.5	0.162	102.5	0.155	1801	0.296	1.9	1.1	1.6
	40–	103.5	0.12	98.5	0.088	1823	0.869	9.8	0.6	4.6
	60–	100.5	0.116	98.5	0.103	1645	0.224	2.2	0.7	1.2
	20+	97.5	0.168	93.7	0.142	1645	0.383	2.7	1	2
	40+	88.2	0.137	100.5	0.445	208	0.121	0.3	3.1	0.6
	60+	95.6	0.235	90.9	0.201	1350	0.324	1.6	1.4	1.7

† Mass percentage (back-transformed)

‡ year⁻¹ (adjusted from daily-based rates)

‡ Days

Table 2 ANOVA results (main effects, interactions and covariates) of mixed models for litter mass remaining and litter nutrients+lignin. F values for factor with similar degrees of freedom provide an estimate of the goodness of fit of that treatment to the model (i.e., importance). Non-significant values in bold

Factor	Site (S)	Precipitation (Pr)	Time (t)	S × Pr	S × t	Pr × t	S × Pr × t	Mass loss	Air temp
<i>F</i> values	$F_{1,830}$	$F_{6,830}$	$F_{1,59}$	$F_{6,830}$	$F_{6,830}$	$F_{6,830}$	$F_{6,830}$	$F_{1,830}$	$F_{1,830}$
Variables									
Litter mass	1115***	1129***	10392***	0.9	13**	56***	0.84	NA	1.9
Litter C mass	1741***	3797***	10532***	4.5**	51***	116***	1.8	5945***	1.08
Litter N mass	5956***	10879***	10463***	67***	22***	156***	6.3***	3559***	36***
Litter P mass	2306***	4133***	10318***	21***	0.98	47***	6.9***	1571***	19***
Litter K mass	1501***	14008***	48443***	370***	338***	63***	34***	9083***	1.7
Litter lignin mass	790***	2159***	69978***	6.7***	94***	11***	2.5***	3437***	123***

**0.001

***0.0001

NA not applicable

decomposition became much more efficient per unit rainfall than in Naiman (Naiman 20–). Our mixed model showed that the main control (apart from time) on mass loss was precipitation, whereas average temperature did not have a significant effect on it (Table 2).

Litter nutrient and lignin dynamics and their controls

Results for the effects of precipitation treatments on litter nutrient and lignin concentration dynamics can be found in Fig. S6. In general, we observed 3 kinds of responses: (1)

C, N, and P % responded proportionally to precipitation independent of site effects (increased precipitation treatments reduced these nutrient contents in litter with respect to controls at both sites); (2) lignin % was unresponsive to precipitation treatments; and (3) K % response to precipitation depended strongly on site effects. In this way, the reduction in K litter % in response to increased precipitation was particularly evident in Urat, but not in Naiman (Fig. S6). When expressed on a per mass basis, all litter nutrients and lignin showed significant three-way (except C) and two-way interactions (Table 2). For C, N, P, and lignin, the *Site* × *Precipitation* interaction showed that their response to the

precipitation treatments did not remain constant at the two sites (i.e., higher decompositions in Naiman could be more pronounced in one precipitation treatment than in other with respect to Urat); and that such non constant response also differed at different times (significant 3-way interaction). Yet, precipitation had a consistent effect on these nutrients, with the 40- and 60- treatments showing consistently higher nutrient masses (e.g., slower decomposition) than the control at both sites for most of dates (Figs. 2, 3, and 4). On the other hand, 20- showed slower decomposition (more moderately than for 40- and 60-) with respect to the control only for N and P at both sites. The 60+ treatment showed consistently a higher decomposition for C, N, P, and lignin at both sites for most of sampling dates (Figs. 2, 3, and 4). On the other hand, 40+ showed higher decomposition only for litter N, and P in Naiman for most sampling dates (although they converged with the 20+ treatment at the end of the experiment). The 20+ treatment in Urat also showed the lowest masses for this site (after 60+) for litter C, N, P, and lignin.

Litter K was different because whereas its decomposition was slightly higher in Naiman for most of precipitation treatments (Fig. 4), the highest decomposition occurred actually in Urat on 60+, (*Site × Precipitation* interaction). Litter K was significantly higher than the control in 60-. Air temperature had a positive significant effect on decomposition only for N and P; and it was particularly important for lignin (Table 2).

Weather and climate

The dynamics of monthly rainfall, average monthly air temperature, and average monthly soil temperature can be seen in Fig. S7. Annual average rainfall since the year the experiment started (2015) was higher in Naiman than in Urat ($335 \text{ mm year}^{-1}/3712$ vs $169.0 \text{ mm year}^{-1}/2456$, respectively -mean/variance, $N = 6$). The values for the long-term records are $295 \text{ mm year}^{-1}/3684$, $N = 21$; and $168 \text{ mm year}^{-1}/2126$, $N = 11$; for Naiman and Urat, respectively. In several occasions during the study, monthly rainfall in Naiman far exceeded the long-term records (e.g., 2015, 2016, 2017, and 2019), mainly during the growing season (the largest occurring in August 2017, 175% above the long-term record). An exception was 2021, when precipitation was below average during the growing season. For Urat, above-average observations occurred also in 2019 and 2020, but a particularly wet year was recorded in 2018 (with monthly precipitations in July and August exceeding by 230 and 330% the long-term averages).

Average monthly air temperatures during the hottest months were slightly higher in Naiman than in Urat (except for August where they were $10 \text{ }^\circ\text{C}$ higher in Naiman, Table S3). Average monthly air temperatures were much lower in Urat during the coldest months in January and February though (Table S3). Similar patterns in both sites were observed for soil temperatures (Fig. S7).

Fig. 2 Litter C dynamics for two experimental areas in Inner Mongolia China (Urat and Naiman) from a litterbag experiment under a precipitation manipulation experiment. Urat is more arid than Naiman. Labels as for the top figure in Fig. 1. Lines are not best fit lines, but only a help to identify the treatments. Symbols are mean values \pm standard deviation for each treatment in each experimental site per date ($n = 6$)

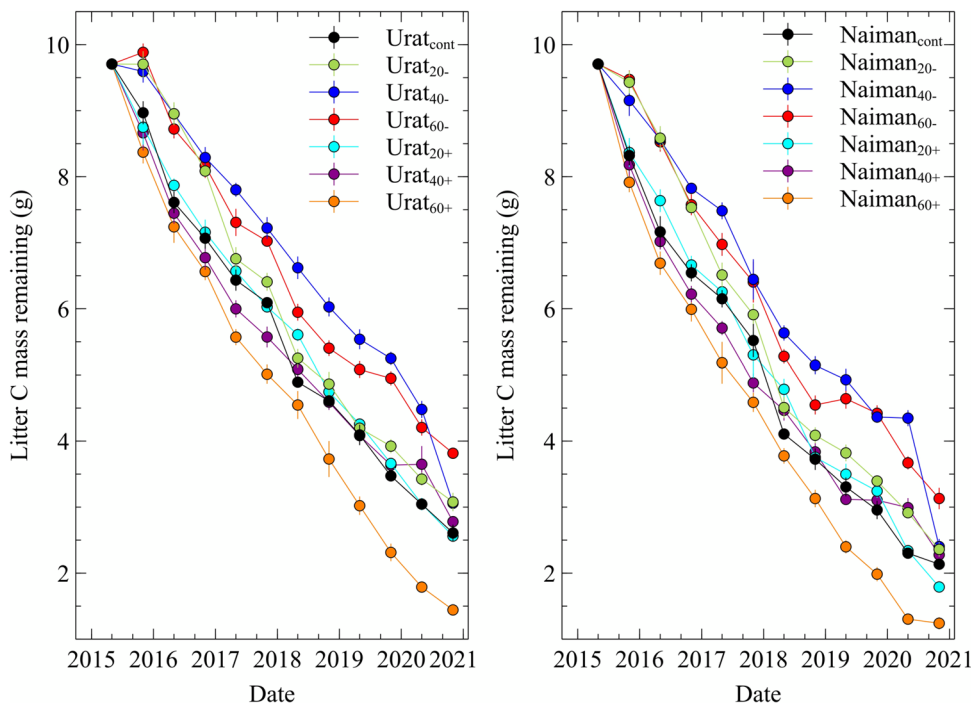
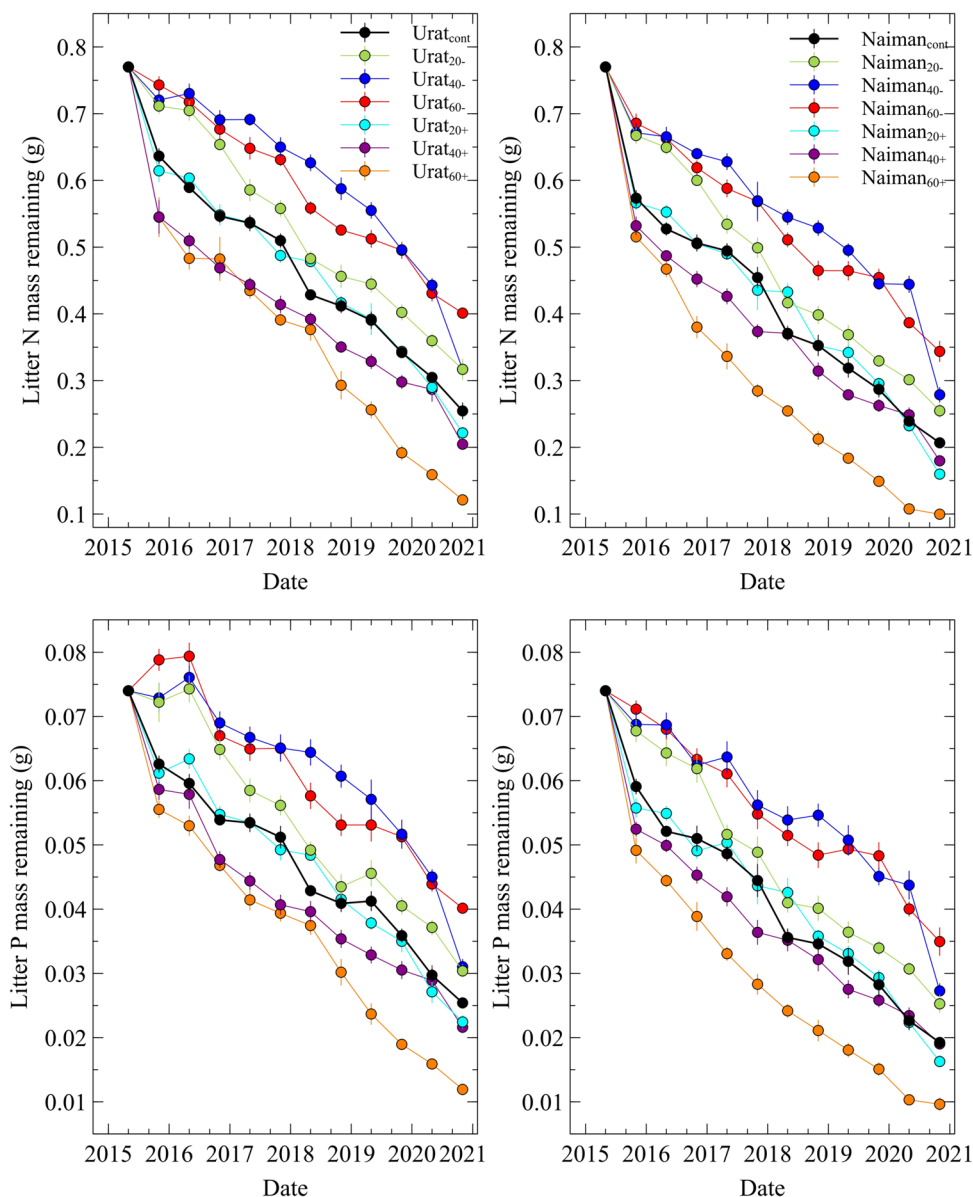


Fig. 3 Top: Litter N, bottom: litter P dynamics for two experimental areas in Inner Mongolia China (Urat and Naiman) from a litterbag experiment under a precipitation manipulation experiment. Urat is more arid than Naiman. Labels as for the top figure in Fig. 1. Lines are not best fit lines, but only a help to identify the treatments. Symbols are mean values \pm standard deviation for each treatment in each experimental site per date ($n = 6$)



Discussion

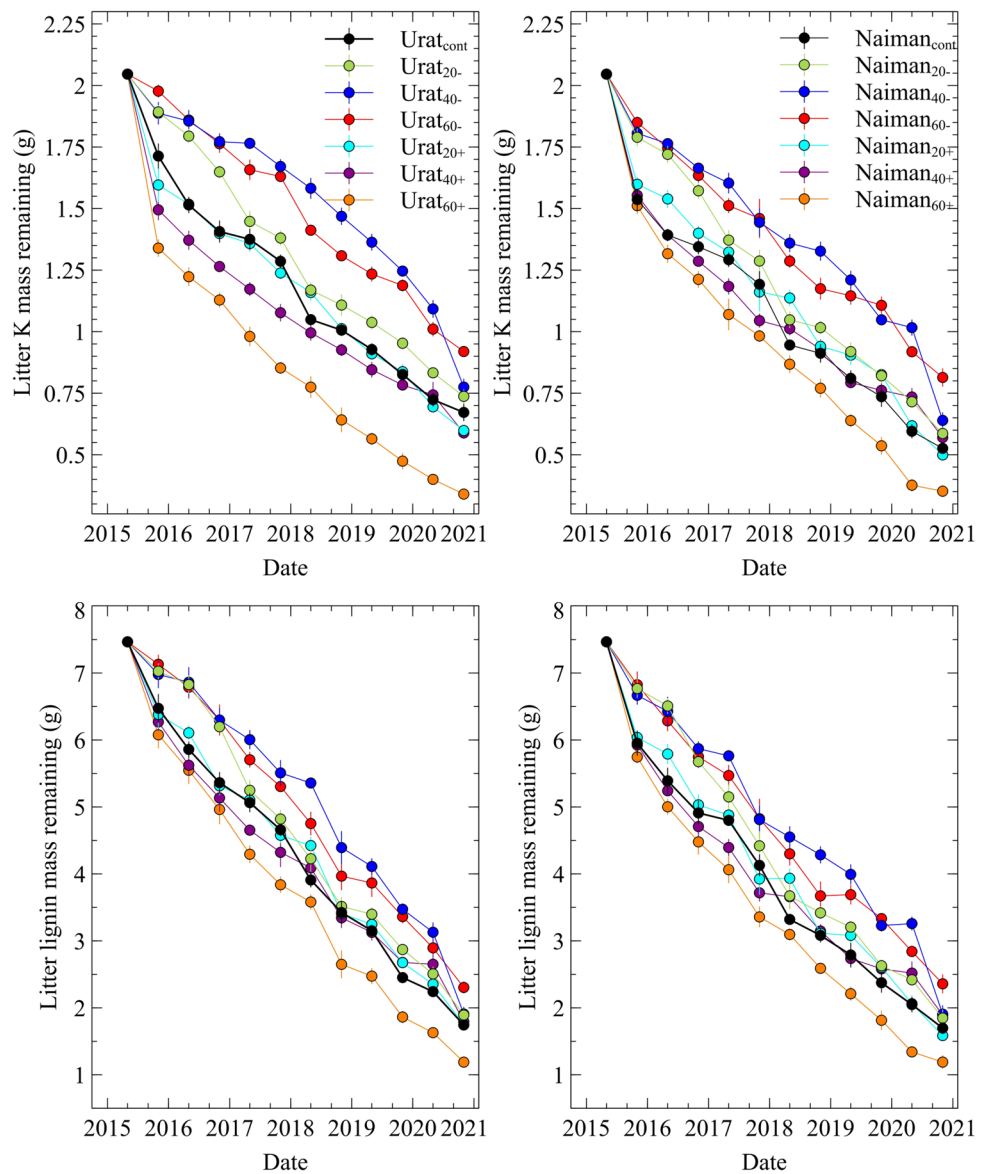
We set to answer 3 main questions regarding the effects of precipitation on litter decomposition and litter nutrient dynamics using our experimental approach.

Mass loss

Our first research question was whether there are precipitation thresholds when decomposition and nutrient dynamics either become significantly impaired or enhanced. For this question, we found that indeed, the arid and semiarid sites we studied display thresholds above/below which litter mass loss is largely enhanced/impaired, but such thresholds were not a simple additive function of

amount of precipitation when comparing both study sites. In this way, the 60+ treatments in both sites clearly diverged from all the rest, with a more complete decomposition in all variables we measured by the end of the experiment (Figs. 1, 2, 3, 4). However, the dry threshold differed from the wet threshold when it came to mass loss (Fig. 1, Table 2). Thus, the 40- and 60- treatments had similar litter mass trajectories at both sites for most of the experiment (except for the last sampling date when the 40- converged with controls, Fig. 1). Therefore, a surplus in precipitation from a 40 to 60% did not have the same size effect on litter mass loss as a reduction from 40 to 60% for most of the experiment, but until the last sampling date! The asymmetry between the wet and dry thresholds might be a result of the relative importance of mechanisms and feedbacks

Fig. 4 Top: Litter K, bottom: litter lignin dynamics for two experimental areas in Inner Mongolia China (Urat and Naiman) from a litterbag experiment under a precipitation manipulation experiment. Urat is more arid than Naiman. Labels as for the top figure in Fig. 1. Lines are not best fit lines, but only a help to identify the treatments. Symbols are mean values \pm standard deviation for each treatment in each experimental site per date ($n = 6$)



during the litter decomposition process (e.g., synergistic action of leaching and microbial activity only beyond a wet threshold). Li et al. (2016) observed no effect on litter decomposition (either of a low C: N forb or two high C: N grasses) to an addition of around 30% of precipitation (with respect to background) in experimental units close to Naiman after 3 years. They concluded that water did not have a strong role in controlling litter decomposition, and that soil saprophytes high metabolic resistance to dry conditions might have been able to compensate for litter decomposition (in comparison to their wet treatment). Our results are partially in accordance with those from Li et al. (2016). On one side, we did observe a neutral effect of surplus precipitation on litter mass loss for similar levels of increased precipitation as them. This suggests indeed that in these levels of additional precipitation, soil saprophytes

metabolism is not enhanced. We also corroborated Li et al. (2016) conclusion of certain level of metabolic resistance in soil saprophytes, but such level was mainly restricted to the -20% treatment. However, unlike Li et al. (2016), we clearly showed that precipitation was the main control of litter decomposition in both of our experimental sites (*ceteris paribus*, given the fact that our litter was of low C:N ratio and high lignin content), despite site differences in climate and soil. Such control of precipitation in semiarid and arid areas has been observed in several studies (Liu et al. 2006; Brandt et al. 2007; Huang and Li 2017; Wang et al. 2015, 2017; Yang et al. 2021b), although values of precipitation thresholds vary, and there seems to be differences depending on initial plant litter chemistry. Li et al. (2022) also observed that small water additions (15% of background) increased slightly decomposition of

leaf litter, and they correlated such higher decomposition to an increase in the soil bacteria to fungal ratio. Overall, lack of response of litter decomposition to water addition in several studies might be related to the amount of water added. The non-additivity of the precipitation thresholds was also apparent when mass loss was compared in terms of cumulative precipitation between sites. Thus, Naiman litter decomposition underperformed that in Urat for a similar level of precipitation (i.e., Naiman reached its dry threshold, Fig. 2). However, litter decomposition in Urat outperformed by far that in Naiman for a similar level of precipitation when Urat was in its wet-threshold (Fig. 2). Yahdjian and Sala (2006) have pointed out how few studies are able to disentangle site differences in their response to altered precipitation (what they called direct —e.g., leaching, fragmentation, microbial activity-, vs indirect effects of precipitation —e.g., differences in species composition or other site effects). Our sites differed only slightly in summer and winter mean temperatures (Urat being slightly cooler), but were quite different in terms of precipitation (Urat has a rainfall of around 56% of that in Naiman) and soil nutrients. Thus, our results showed that although the direct effects of precipitation on litter mass loss were similar between Urat and Naiman, there were still some site differences (i.e., differences in decomposition efficiency). Such site differences might be driven by differences in the soil microbial communities and the background level of soil nutrients between the two sites rather than by the direct effect of site differences in precipitation. In a study across a precipitation gradient in Inner Mongolia, Wang et al. (2021) found a higher diversity of soil microbial communities in wet sites, which they attributed mainly to a higher soil C:N ratio in wet sites in comparison to dry ones. They concluded that such differences could be interpreted as adaptations that soil microbes have developed to cope with the conditions in their respective habitats. Thus, the site differences we observed suggest that microbial communities in Urat are more efficient in decomposing litter as a result of long-term adaptation to living in a more arid area. It has been shown that changes in precipitation can affect directly decomposers' metabolic activity (Salamanca et al. 2003), but the influence of differences in climate on the soil environment (e.g., including differences in soil microbial community composition) and how such differences affect decomposition is less understood. Respiratory losses from *Caragana mycophylla* litter have been observed under optimal moisture and temperature conditions at the first stage of decomposition, so that nutrients' leaching and microbial decomposition are likely to account for our observations at the first decomposition stage (Yang et al. 2022). Significant higher mass loss in the precipitation threshold (60+) in the long term though, it is likely to result of the effects of higher soil moisture availability on

soil biogeochemistry. Higher moisture availability in arid and semiarid areas is associated with higher N availability and plant available N flushes (Medina-Roldán et al. 2013) that could have maintained higher microbial activity to decompose litter. Recently, Wen et al. (2022) found that frequent precipitation events increased the amount of N taken up by both plant and microorganisms in a semiarid steppe in Inner Mongolia, which supports our view that higher mass loss in the long-run in the highest precipitation treatment might be mediated by changes to soil nutrients that increase microbial activity.

Mass loss dynamics

We also enquired whether surpluses or reductions in precipitation affect the capacity of simple decomposition models (e.g., Olson's exponential decay based on linear regression) to describe litter decomposition (i.e., if it becomes more complicated to be described). Our results suggest that this was again the case, although this varied with the experimental site. This was shown by the lower efficiency (in terms of goodness of fit, error of predictions, and size of errors in the parameter estimates) of the simple model to predict litter mass loss in comparison to one that allowed the decomposition constant to vary (piece-wise-based models) (Table S1; Figs. S4 and S5). Although there is not a perfect model to describe litter decomposition (with both explanatory and predictive capacities, Adair et al. 2008), and the simple models performed reasonably well (Table S1); our results are of interest for some reasons. First, deviations of observations from simple models' predictions were overall larger in our driest site in the modified precipitation treatments (Table S1). Such deviations from predictions were rather high in some sampling dates (Figs. S4, S5). Therefore, attention needs to be given when using decomposition constants derived from simple decomposition models. This is particularly true when doing studies in arid environments that incorporate effects of precipitation variation in the short- to mid-term scales (Hoover et al. (2018) found that most of them lasted between one and four years). Our study highlights the importance of long-term studies on litter decomposition in environments with slow decomposition rates. This was clear since many of the responses we observed developed only until certain time since the beginning of the experiment elapsed. Secondly, our results also indicate that simple models miss out some aspects the decomposition dynamics. We observed that mass loss was quicker at later stages in decomposition, but only in the precipitation reduction treatments. Such behaviour has been observed in other decomposition studies (e.g., Du et al. 2020), and it was correctly modelled by the piece-wise regression, which contrasts with the view that decomposition becomes slower

as decomposition proceeds (Couteaux et al. 1995; Joseph and Henry 2008). Our piece-wise approach did not capture well the dynamic of decomposition in precipitation surplus treatments though (particularly in Naiman, the wetter site), where a large mass loss occurred just at the first litterbag (Figs. 1, S4, and S5) retrieval. However, this was a matter of our decision to use models with a single break for ease of comparison, as more complicated dynamics can be included as well (data not shown).

Nutrient and lignin dynamics

Previous studies have mainly focused on how precipitation affects mass loss during decomposition, and less is known about precipitation impacts on nutrients' dynamics (Bloor and Bardgett 2012; Liu et al. 2014). Thus, our last question focused on the impact of precipitation variation on litter nutrient dynamics. Litter nutrients' dynamics are usually interpreted as a result of metabolic limitations on biologically driven litter decomposition (e.g., decomposers need to incorporate certain amount of a nutrient to maintain a stoichiometric balance, e.g., Bosatta, and Ågren, 1985; Manzoni et al. 2010), and/or as a result of nutrient leaching from litter (other abiotic process such as UV-driven nutrient dynamics are less-well known). In this way, a reduction of a specific nutrient in litter regarding its original mass ("release") is associated to non-limiting conditions of that nutrient/leaching; and vice versa ("export" or "immobilization"). Litter nutrients lost was very high at the first litterbag retrieval time for all nutrients, and it was faster in the precipitation surplus treatments with respect to controls at both sites (C and P dynamic in Urat showed signs of limitation at this early stage, Figs. 2, 3, and 4). We observed a similar litter nutrient flush for both highly soluble and mobile nutrients (e.g., K and N), and also for less mobile and structurally constitutive ones (P and lignin). This indicates that water availability limited nutrient release (Table 2), and that the flush of nutrients such as N and P, which are easily transported through the soil profile by precipitation, seems to be a key driver at early stages of decomposition when precipitation is not limiting (Qu et al. 2020). As mentioned above, respiratory losses from decomposing litter observed under optimal moisture and temperature conditions suggest that nutrient flushes at early stages of decomposition contribute to the flush of nutrients at early stages of decomposition. For nutrients like K, our results are similar to other studies, where nutrient mass (or percentage from initial mass) shows a monotonic decrease with time (e.g., Liu et al. 2009); and a quick flush at the very beginning of the decomposition process with litters rich in K (Osono and Takeda 2004; Mahmood et al. 2009; Wang et al. 2017). This is not the case for N and P, where most studies have observed fluctuations between immobilisations and releases with time (Liu et al.

2009; Gong et al. 2020, 2022; Li et al. 2022). Unlike such studies, we observed a monotonic decrease in all nutrients. Such differences in the nutrient dynamic are likely driven by the C: N ratios (or other stoichiometric ratio) of the litter used in the different experiments (we used a low C: N litter), with litter of high C: N, C: P ratios usually showing cycles of immobilisation-release in N and P (and therefore, temporal variation in conditions of nutrient limitation for decomposers). For P and C, we observed that a reduction in precipitation was associated to immobilizations at early stages of decomposition though, thus suggesting that water availability interacts with other factors in the nutrient limitation process of these nutrients. Lignin also showed a monotonic decrease in all treatments, and it was responsive to the extreme precipitation treatments (Fig. 4), corroborating that water availability also played a role in its decomposition (it also had the stronger response to monthly temperatures, suggesting that the process was microbially driven). This result contrast with that from Huang and Li (2017), since they did not observe a decrease in lignin decomposition when they subtracted the equivalent of a 50% annual precipitation to litters from 5 different species in an arid site (similar in precipitation to Urat) in NW China, even if precipitation did increase litter mass loss. Such different results to ours might be due to site differences in factors such as annual sunshine exposure (Huang and Li 2017); and the fact that abiotic main controls on litter decomposition might vary on a regional basis, but this is something that needs to be further explored. Overall, our results coincide with previous studies that found that frequent heavy rainfall events which keep the soil moist for longer than average conditions will also increase decomposition and nutrient release (Anaya et al. 2012; Jin et al. 2013).

Implications given climate patterns

Our study is a long-term research, and the likelihood of similar conditions (e.g., 60% above/below average precipitation for over 5 consecutive years) seems unlikely. Since we used cumulative precipitation, we were interested in knowing whether similar values had been found in our weather data (given that our dataset is rather recent, we used yearly data and assumed that those values could be extrapolated to the duration of our study). The long-term average accumulated precipitations in the dataset for a similar duration to our study (almost 6 years) were 932 and 1638 mm in Urat and Naiman respectively. These values are similar to those in the controls (984 and 1964 mm in Urat and Naiman respectively). Our most extreme experimental dry conditions (Urat_{.60%} = 394 mm, Naiman_{.60%} = 785 mm cumulative precipitation) were not observed at any of our sites, extrapolating the driest years in our long-term datasets. However, the next dry experimental extremes

(Urat_{-40%} = 590 mm, Naiman_{-40%} = 1178 mm) were similar to extrapolating some individual dry years (Urat = 619 mm, Naiman = 785 mm). For our wet threshold, the wettest years in our long-term dataset were similar to those used between the 20+ and the 40+ treatments in Urat, and to the 20+ treatment in Naiman. From these results, if such most likely long-lasting conditions would occur, the main effects will be on a slower nutrient cycling, although that would depend on inter-annual variation in precipitation. The occurrence of long-lasting precipitation dry conditions though will likely have very strong consequence on soil nutrient dynamics and accrual, and therefore potentially on soil structure and stability. Regarding thresholds, we could see that most nutrients were mainly sensitive to the extreme values of our treatments (on both the dry and wet ends, but mainly to precipitation addition). Changes in global precipitation therefore have the potential to greatly affect the N and P cycle in arid and semiarid areas, as soil moisture can control their availability, through several processes, including mineralisation, and P requirements for plant growth, and microbial activity (Sardans et al. 2007). For instance, in areas of increased drought, plant growth is largely limited by P due to impaired soil phosphatase activity and reduced P supply (Sardans and Penuelas 2005).

Conclusion

Our study demonstrates that precipitation is the main limiting factor (*Ceteris paribus* as we used a low C: N ratio litter) for litter decomposition in the arid and semiarid areas where we set up our experiment. It also shows three important aspects with relevance for litter decomposition experiments using climate change treatments such as precipitation: (1) long-term studies in environments with a slow decomposition rate are key, since significant responses to treatments might develop only until a considerable time has elapsed, (2) a gradient approach such as the one we used —with both reductions and surpluses— allows to identify thresholds in ecosystem functioning, and (3) including different sites with different climates can help to disentangle direct from indirect effects of a treatments. At the levels of precipitation we used, what ultimately seemed to control litter decomposition and litter nutrient dynamics was water availability. Overall, litter decomposition becomes more difficult to describe with simple models in response to variation in precipitation, if this effect occurs only in arid areas is something worth of further research. In summary, our results highlight how reductions in precipitation in arid and semiarid areas will impact negatively on litter decomposition and eventually on soil nutrient accrual, soil structure development and stability in these fragile areas.

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Declarations

Conflict of interest The authors declare no competing interests.

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