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Asymmetric responses of litter decomposition to altered precipitation: Double evidence from field experiments and global synthesis

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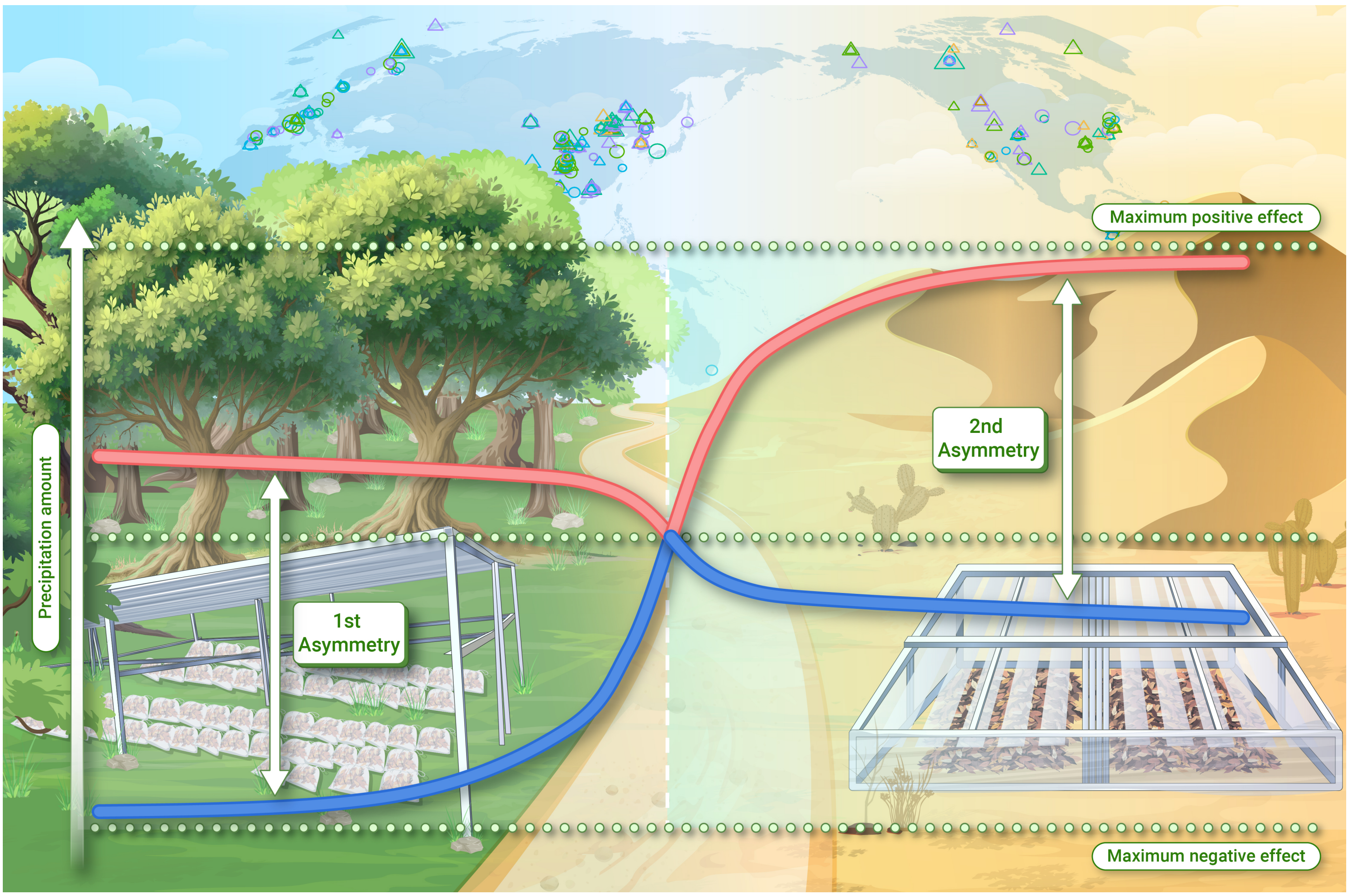
GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- Increasing precipitation (WET) speeds up litter decomposition, while decreasing precipitation (DRY) slows it down.
- In arid regions litter decomposition is more sensitive to WET, while in humid regions it's more sensitive to DRY.
- A double asymmetric model best explains the litter decomposition-altered precipitation relationships.
- Meta-analyses confirm that this asymmetrical effect between humid and arid regions is true globally.

Asymmetric responses of litter decomposition to altered precipitation: Double evidence from field experiments and global synthesis

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Altered precipitation regimes as a result of global climate change have significant implications for ecosystem processes, such as the decomposition of litter, a vital process in carbon (C) and nutrient cycling in terrestrial ecosystems. However, the effects of altered precipitation regimes on litter decomposition across humid and arid biomes remain unresolved. To address this knowledge gap, we conducted a comparative analysis using data from a geographically replicated precipitation–manipulation field experiment that studied litter decomposition and a global meta-analysis of 778 paired observations from 207 peer-reviewed articles. Our findings indicated that the litter decomposition constant (*k*) was 7.7–31.3% greater under increased precipitation and 10.0–41.0% lower under decreased precipitation than under the control treatments. Litter decomposition, soil moisture, microbial biomass, and enzymatic activity had stronger responses to increased precipitation in the arid region and to decreased precipitation in the humid region, which was consistent with the double asymmetric model. A global meta-analysis also confirmed the asymmetrical effects of altered precipitation regimes on litter decomposition between humid and arid regions. Our results highlight the potential asymmetry in the effects of altered precipitation regimes on C and nutrient cycling between humid and arid terrestrial ecosystems.

INTRODUCTION

Precipitation is an important factor that governs energy flow and hydrological cycling, which in turn affects the structure and function of terrestrial ecosystems.[1] Alterations in atmospheric circulation and hydrologic processes intensified by elevated atmospheric CO_2, warming and other global climate change factors have raised concerns about changes in precipitation regimes.[2] Mounting evidence from current climatic data and models has confirmed that precipitation regimes are being altered at the global and regional scales, such as in Europe and the USA.[3-5] However, changes in the precipitation regime are uneven, and while some regions experience increased precipitation,[6] others may also face decreased precipitation, thereby leading to severe drought.[7] These contrasting changes in the precipitation regime can affect surface evaporation, transpiration and soil moisture, which in turn influence ecosystem structure and function across broad spatial scales.[8] The multiple effects of altered precipitation regimes on ecosystem function at regional and global scales, however, remain largely unexplored.

Litter decomposition is a critical process in organic matter transformation and C and nutrient cycling in terrestrial ecosystems,[9] it is driven by multiple physical, chemical and biological processes, including litter fragmentation, leaching, microbial decomposition through the release of extracellular enzymes, and the feeding activity of various soil invertebrates, which are strongly affected by soil hydrological properties. Therefore, altered precipitation regimes may directly and indirectly alter litter decomposition. Increased precipitation can accelerate decomposition by improving litter chemical traits,[10] promoting leaching, enhancing microbial activity or improving nutrient immobilization due to better moisture availability.[6] In contrast, decreased precipitation has the opposite effect, increasing the intensity and duration of drought.[11] While the influence of altered precipitation regimes on litter decomposition has been widely studied, a clear global understanding is still lacking, as positive, negative, and neutral effects of increased/decreased precipitation on litter decomposition have been reported.[12-17]

The inconsistent responses of litter decomposition to altered precipitation regimes can be explained by the following two mechanisms: on the one hand, most studies have been conducted at a single site, and the results reflect the site-specific nature of the treatment effects due to differences in physical, chemical and biological characteristics and their effects on ecological processes among sites.[18] However, the excessive attention given to homogenized studies at different sites has ignored potential contrasting responses. Most studies have used identical altered precipitation regimes, although the resistance or sensitivity to these regimes may vary with the regional conditions of an ecosystem, including energy flow, hydrological conditions, or species composition at a specific site.[19] A more comprehensive understanding of the responses of litter decomposition to altered precipitation regimes is therefore essential to project the cycling of terrestrial material under scenarios of future global climate change.[20]

A double asymmetric model is used to understand the relationships between aboveground net primary productivity (ANPP) and altered precipitation regimes,[21] which predicts positive and negative asymmetric responses of ANPP to altered precipitation regimes. Specifically, positive asymmetry represents a greater sensitivity of ANPP change in response to increased precipitation, and negative asymmetry has the opposite pattern. This double asymmetric model can also be used to account for the widely observed differential effects of altered precipitation regimes on ecological processes between humid and arid regions.[22] For example, increasing evidence suggests that soil respiration,[23] the microbial community and nitrogen cycling are more sensitive to increased precipitation in arid regions but more sensitive to decreased precipitation in humid regions.[24,25] However, these results confirm the two limitations mentioned earlier, which may hinder our understanding of the global responses of litter decomposition to altered precipitation regimes. A broader-scale analysis of litter decomposition under conditions of increased or decreased precipitation in both humid and arid regions is urgently needed, as this information is imperative for assessing the importance of altered precipitation regimes on terrestrial material cycling under ongoing and future global climate change scenarios. To address this challenge, we compared data from a manipulative field experiment using litterbags with a global meta-analysis of peer-reviewed articles. The geographically replicated precipitation–manipulation field experiment was conducted simultaneously in both humid and arid regions to investigate the responses of litter decomposition and associated factors (soil moisture, microbial biomass, and enzymatic activity) to both increased and decreased precipitation. We also performed a meta-analysis using 778 pairwise observations from 207 peer-reviewed articles to assess the generalizability of the field experiment results on a global scale. Our study tested the following hypotheses: (1) Increased and decreased precipitation would enhance and retard litter decomposition, respectively, irrespective of the regional climate (humid or arid); (2) the effects of altered precipitation regimes on litter decomposition would differ substantially between humid and arid regions, with humid ecosystems being more sensitive to decreased precipitation and arid ecosystems being more sensitive to increased precipitation; and (3) the responses of litter decomposition and associated factors to altered precipitation regimes, such as soil moisture, microbial biomass or enzymatic activity, would be (double or double-double-) asymmetric at the global scale.

MATERIALS AND METHODS

Regional field experiments

This study was part of a larger project to evaluate the potential differential effects of ongoing altered precipitation regimes (Table S1) on plants and soils in humid *vs.* arid terrestrial ecosystems. Field experiments simulating increased and decreased precipitation were set up in 2019 at two sites representing typical humid and arid terrestrial ecosystems in China (Figures S1 & S2), which explored the responses of ecosystems to altered precipitation regimes in arid versus humid regions.

Study site description. The first site was at the Tianmushan Forest Ecosystem Research Station in Zhejiang, China (30.30°N, 119.38°E and 330 m *a.s.l.* (Figure S1)), which has a humid subtropical monsoon climate. The mean annual precipitation (MAP) and mean annual temperature (MAT) were 1630 mm and 14.9°C, respectively. The soil was classified as an Alisol based on the International Union of Soil Science (IUSS). The detailed basic characteristics of the surface soil are presented in Table S2. The vegetation naturally regenerated following large-scale industrial logging and represented a typical community of secondary forest succession in southeast China.

The second site, at the Fukang Desert Ecosystem Observation and Experiment Station, was near the southeastern fringe of the Gurbantunggut Desert, Xinjiang, China (44.28°N, 87.93°E and 475 m *a.s.l.* (Figure S1)). This region has an arid temperate continental climate, with MAP and MAT of 160 mm and 6.6 °C, respectively. The soil was classified as a Calcisol with a high pH and low nutrient availability (Table S2).

Experimental design. A randomized complete split-plot block design was established at each site with three treatments: decreased precipitation (DRY), increased precipitation (WET), and the control (CK). Three 50 × 50 m replicate blocks were randomly set up in August 2019, with a 10-m buffer zone between adjacent blocks. Each block consisted of three 5 × 5 m plots at 3-4 m intervals, representing the three treatments (a total of nine plots per site). We intercepted 50% of the annual precipitation in DRY to simulate possible extreme drought, considering the fluctuations in interannual precipitation (Table S1). The water intercepted in the DRY plot was added to a WET plot to simulate a 50% increase in precipitation, which is predicted to be the amount of increase in precipitation in some areas in China over the next century.[26] Each CK plot was left undisturbed or under ambient conditions (Figure S2, Appendix S1). The precipitation-manipulation experiments were carried out from September 2019 to October 2021, for a total of 726 days.

Field sampling. We used foliar litter from two common tree species per site, *Pinus massoniana* and *Quercus glauca* at Tianmushan and *Haloxylon ammodendron* and *Tamarix chinensis* at Fukang, at each site. We also used foliar litter of *Quercus mongolica* from the Maoershan Forest Ecosystem Research Station in Heilongjiang, China (45.33°N, 127.50°E and 400 m *a.s.l.*), as a reference because this species is not present at either site and does not have a potential "home-field advantage" effect. Fresh foliar litter from all five species was collected throughout the peak litterfall period via litter traps and was air-dried at room temperature for 3–4 weeks. Fifteen samples per species were oven dried at 70°C for 48 h to determine the water content and chemical traits (Table S3). Ten grams of air-dried litter was placed in 1 mm mesh litterbags (15 × 20 cm) and sealed. The litterbags were then placed on the soil surface in each plot center in October 2019 at 2 cm intervals. Three litterbags per species were randomly collected from each plot after 180, 360, 540 and 720 days of field incubation. We thus sampled a total of 648 litterbags (3 blocks × 3 treatments × 3 species × 4 sampling times × 3 sampling replicates × 2 sites).

Laboratory analysis. Each litterbag sample was divided into two parts after the arthropods and roots were removed. One part was oven-dried at 70°C for 48 h to a constant weight to determine the moisture content, and the other part was stored at 4 °C for determining the microbial biomass (microbial biomass carbon, MBC and microbial biomass nitrogen, MBN) and enzymatic activities (C-, N- and P-acquiring enzymes: β-glucosidase, BG; β-N-acetyl-glucosaminidase, NAG and acid phosphatase, ACP). The detailed descriptions of the laboratory analysis can be found in Appendix S1.

Data analysis. The rate of litter decomposition (ML_t), the decomposition constant (k) and the time to 95% decomposition ($t_{0.95}$) were calculated as described in Appendix S1. An independent sample t test was used to identify differences in the basic characteristics of the surface soil between the two study sites (α = 0.05). A negative exponential decay model was used to determine k and $t_{0.95}$. A repeated-measures ANOVA was used to test the effects of the precipitation manipulation treatments on soil moisture over the field incubation period. One-way ANOVA (with Bonferroni correction) was used to assess the differences in the initial chemical traits of the foliar litter among the species, the moisture content of the surface soil, $t_{0.95}$, the microbial biomass and the enzymatic activities of the litter among the treatments. The mean sizes of the treatment effects (standardized mean difference, Cohen's d) were calculated to facilitate comparisons if both WET and DRY had significant effects.[27] A stepwise regression analysis was implemented to identify the factors in each treatment that significantly influenced the decomposition rate in the humid and arid regions. All the statistical analyses were performed via SPSS 23.0 for Windows (SPSS Inc., Chicago, USA).

Global meta-analysis

Data collection and compilation. Peer-reviewed articles published before September 2022 were searched in the Web of Science, Scopus, China Knowledge Resource Integrated Database (CNKI) and Google Scholar databases via the search term in Appendix S1. The articles had to meet the criteria to be included in our database.

We originally planned to collect data on litter moisture content, MBC and MBN concentrations and BG, NAG and ACP activities from precipitation-manipulation experiments to identify the mechanism of altered precipitation regimes affecting litter decomposition, but we had to collect data for the surface soil (0-5 cm) instead because few studies focused on these aspects in the litter in precipitation–manipulation experiments. We also recorded site characteristics (latitude, longitude and MAP) and experimental information (ecosystem type, climatic zone, experimental duration and magnitude of altered precipitation). The site characteristics were extracted directly from the articles or retrieved from WorldClim (https://www.worldclim.org).

A total of 778 observations (177 for litter decomposition, 149 for soil moisture, 352 for soil microbial biomass and 100 for soil enzymatic activity) were derived from 207 peer-reviewed articles (Figure S3, Appendix S2, Data S1). We selected the climatic zone as the main moderator variable to determine the effects of altered precipitation regimes on litter decomposition between humid and arid ecosystems (Table S4).

Statistical and sensitivity analyses. The effect sizes of the altered precipitation regimes (lnRR), the variance of lnRR ($V_{\ln RR}$), and the weighted mean effect size (lnRR_{++}) were calculated (for more details, please see Appendix S1). The effects of the moderator variable on the magnitudes and directions of the responses of litter decomposition, soil moisture, microbial biomass and enzymatic activity to the altered precipitation regimes were evaluated based on the moderator type and the sample size. The total heterogeneity (Q_{Total}) among the levels of the moderator variable was divided into between-group heterogeneity (Q_{Between}) and within-group heterogeneity (Q_{Within}). We used a categorical random effects model to compare Q_{Between} with Q_{Within} to evaluate the significance of each moderator variable. A continuous random effects model was used to test the relationships between lnRR_{++} of the decomposition rate and MAP. The statistical results are reported as the total heterogeneity of lnRR_{++} among studies (Q_{Total}), the difference among group-cumulative lnRR_{++} (Q_{Among}) and the residual error (Q_{Error}). All meta-analyses and lnRR_{++} calculations were conducted via MetaWin 2.1.

Table 1. Models of litter decomposition from various species in the humid and arid regions.

Climatic zone	Species	Treatment	Model	k	R^2	$t_{0.95}$ (y)
Humid	*P. massoniana*	WET	$y = 100.66e^{-0.028t}$	0.028	0.983	8.94Ab
		CK	$y = 100.69e^{-0.026t}$	0.026	0.981	9.62Ab
		DRY	$y = 100.80e^{-0.019t}$	0.019	0.974	13.17Aa
	Q. mongolica	WET	$y = 101.43e^{-0.043t}$	0.043	0.987	5.83Bb
		CK	$y = 100.98e^{-0.039t}$	0.039	0.983	6.42Bb
		DRY	$y = 100.17e^{-0.023t}$	0.023	0.976	10.86Ba
	Q. glauca	WET	$y = 101.92e^{-0.056t}$	0.056	0.988	4.49Cb
		CK	$y = 101.53e^{-0.052t}$	0.052	0.988	4.83Cb
		DRY	$y = 100.20e^{-0.033t}$	0.033	0.987	7.57Ca
Arid	*Q. mongolica*	WET	$y = 100.30e^{-0.021t}$	0.021	0.981	11.90Ab
		CK	$y = 100.60e^{-0.016t}$	0.016	0.971	15.63Aa
		DRY	$y = 100.08e^{-0.014t}$	0.014	0.961	17.84Aa
	H. ammodendron	WET	$y = 100.27e^{-0.023t}$	0.023	0.982	10.86Bb
		CK	$y = 100.41e^{-0.018t}$	0.018	0.977	13.89Ba
		DRY	$y = 100.34e^{-0.016t}$	0.016	0.976	15.62Ba
	T. chinensis	WET	$y = 100.91e^{-0.026t}$	0.026	0.980	9.63Cb
		CK	$y = 100.29e^{-0.020t}$	0.020	0.975	12.49Ca
		DRY	$y = 100.19e^{-0.018t}$	0.018	0.976	13.88Ca

WET, increased precipitation; CK, control; DRY, decreased precipitation; y, mass remaining (%); $t_{0.95}$, time to 95% decomposition (means, n = 3). Different uppercase letters indicate significant differences among the species in the same treatment in the humid and arid regions, respectively ($P < 0.05$, Bonferroni correction), and different lowercase letters indicate significant differences among the treatments for the same species in the humid and arid regions, respectively ($P < 0.05$, Bonferroni correction). $P \le 0.035$ for all models in this table.

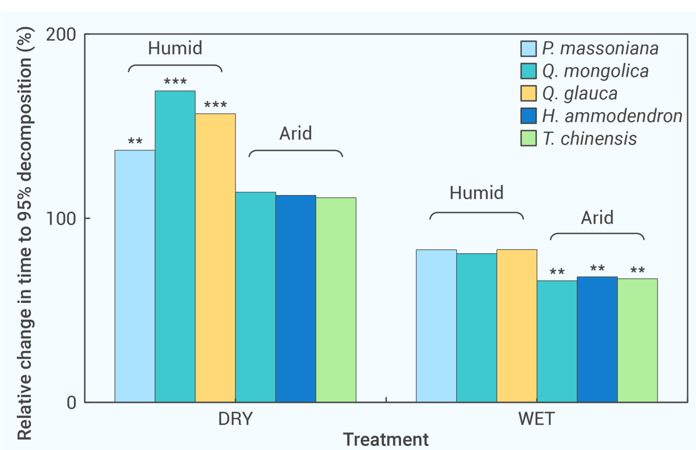

Figure 1. Time to 95% decomposition in WET and DRY relative to CK (mean, n = 3) Asterisks indicate significant differences between CK and DRY or WET. **, $P < 0.01$; ***, $P < 0.001$; WET, increased precipitation; DRY, decreased precipitation.

RESULTS

Effects of altered precipitation regimes in the regional field experiments

The $t_{0.95}$ for all species was ~0.5–4 years shorter in WET than in DRY in both the humid and arid regions ($P \le 0.035$, $R^2 \ge 0.96$) but was significantly shorter only in the arid region (Table 1 & Figure 1). Conversely, the $t_{0.95}$ for all the species was greater in DRY than in WET but was significantly greater only in the humid region. Compared with CK, DRY significantly decreased soil moisture by 1.6-fold in the humid region (P = 0.025 (Figure 2A)) but did not affect it in the arid region (P = 0.061 (Figure 2B)). WET increased soil moisture by ~120% in the arid region (P = 0.004 (Figure 2B)) but did not affect it in the humid region (P = 0.057 (Figure 2A)).

Similarly, the litter microbial biomass and enzymatic activities both decreased in the order WET–CK–DRY, regardless of the species or climatic zone (Figures 3-4). The effects of WET on litter microbial biomass and enzymatic activity were more significant in arid regions than in humid regions, but the effects of DRY were more significant in humid regions (Figures 3-4). The associated effect sizes in WET were accordingly more significant or markedly larger in arid regions than in humid regions (e.g., ACP' d for *H. ammodendron* in arid regions, WET 10.5 ± 4.4 *vs.* DRY 3.2 ± 1.5 (Figure 4C)), and the effect sizes in DRY were opposite between humid and arid regions (e.g., MBC' d for *Q. glauca* in humid regions, WET 3.0 ± 1.5 *vs.* DRY 14.3 ± 5.9 (Figure 3A)). The correlation between the decomposition rate and soil moisture induced in DRY was significantly positive only in the humid region (Adj. R^2 = 0.73, P = 0.023 (Table S5)), and the correlation induced in WET was significantly positive only in the arid region (Adj. R^2 = 0.80, $P < 0.001$ (Table S5)). The decomposition rate, soil moisture, microbial biomass and enzymatic activities thus all responded more strongly to WET in the arid region but more strongly to DRY in the humid region, suggesting that the responses of litter decomposition and associated factors to the altered precipitation regimes were doubly asymmetric (Figure S4).

Effects of altered precipitation regimes in the global meta-analysis

The decomposition rate, soil moisture, MBC, MBN and enzymatic activity increased by 12.1, 15.4, 18.6, 15.0 and 21.3% (Figure 5A), respectively. The positive effects of WET on these parameters were significant only in the arid region (+19.9, +16.9, +23.2, +16.4 and +28.4%, respectively), and the MBC ($Q_{Between}$ = 4.10, P = 0.043) and enzymatic activity ($Q_{Between}$ = 8.27, P = 0.004) differed significantly between the humid and arid regions (Figure 5A). DRY had opposite effects on the decomposition rate, soil moisture, MBC, MBN and enzymatic activity in WET, with values of -11.7, -23.9, -15.9, -23.2 and -20.1%, respectively (Figure 5B). These response variables in DRY were significantly lower only in the humid region, by 12.1, 26.6, 18.3, 26.7 and 25.8%, but not in

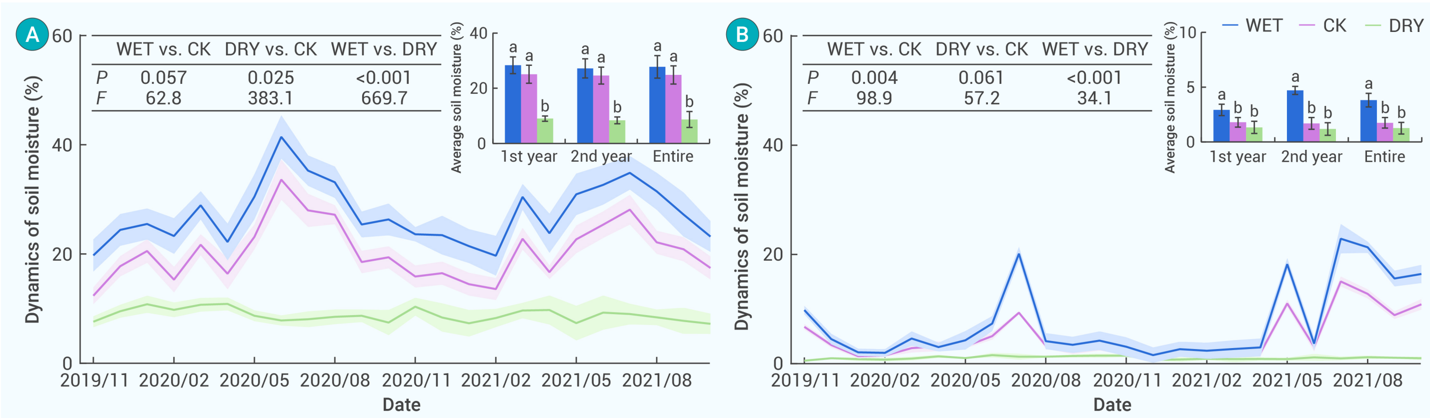

Figure 2. Dynamics and average moisture content of the surface soil (0-5 cm) in the treatments in A, the humid region and B, the arid region (mean or mean ± *SD*, *n* = 3) WET, increased precipitation; CK, control; DRY, decreased precipitation. Different letters indicate significant differences among the treatments within each sampling time ($P <$ 0.05, Bonferroni correction). The gray shading indicates the 95% confidence interval. Table in the figure indicates the results of repeated measure ANOVA.

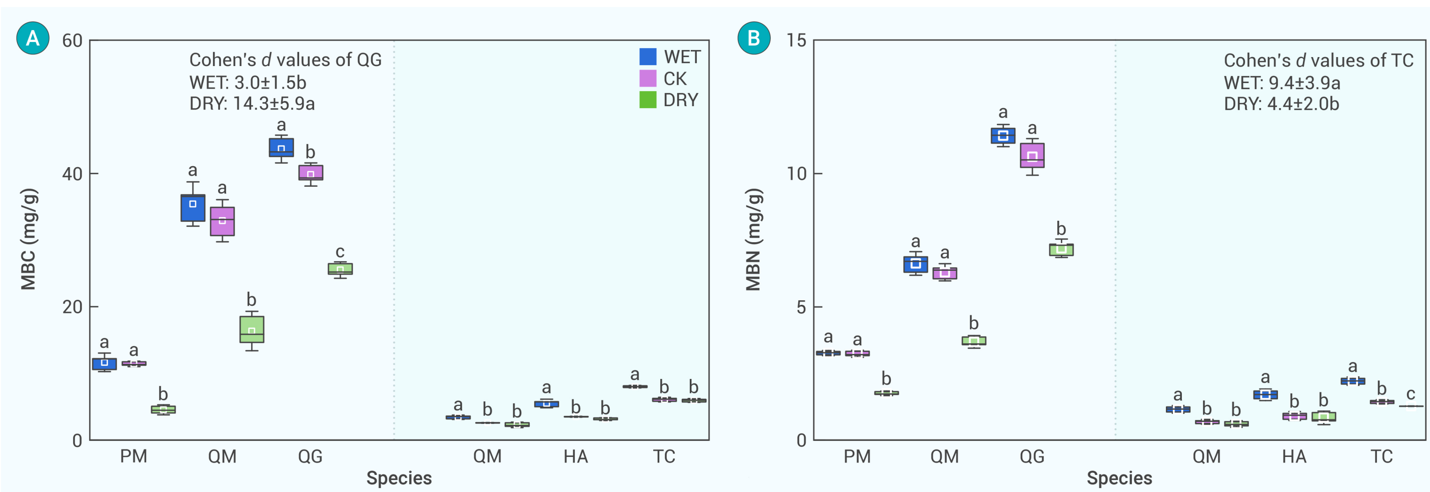

Figure 3. Litter microbial biomass carbon (MBC, A) and nitrogen (MBN, B) concentrations in the treatments after two years of decomposition (mean ± 1.5 *SD*, *n* = 3) WET, increased precipitation; CK, control; DRY, decreased precipitation; PM, *P. massoniana*; QM, *Q. mongolica* (a common species in the humid and arid regions); QG, *Q. glauca*; HA, *H. ammodendron*; TC, *T. chinensis*. The bars represent medians with 25 and 75% quartiles. Different letters indicate significant differences ($P <$ 0.05, Bonferroni correction or *t* test). The light background indicates the humid region, and the dark background indicates the arid region. The values in the figures represent the mean effects sizes of WET and DRY (standardized mean difference ± *SD*, Cohen's *d*), which were calculated to facilitate comparisons when there were significant differences among WET, CK and DRY.

the arid region (except for MBN), although the negative effects of DRY did not strongly depend on the climatic zone (Figure 5B).

The meta-analysis also indicated that the effect sizes of the altered precipitation regimes on the decomposition rate, soil moisture, MBC, MBN and enzymatic activity varied among ecosystem types, experimental durations and magnitude of altered precipitation. The effects of WET were more significantly positive in medium-term and moderate-sized studies, especially in desert regions. The negative effects of DRY were more significant in long-term and large-size studies, particularly in forested regions (Figures S5-S9). The continuous random effects model indicated that MAP was significantly negatively correlated with the effect size of increased precipitation on the decomposition rate (slope = -0.0002, P = 0.004 (Table S6)) but positively correlated with the effect size of decreased precipitation on the decomposition rate (slope = 0.0002, $P <$ 0.001 (Table S6)). Finally, the removal of correlative observations from the complete database did not alter the trends or interpretations of the decomposition rate, soil moisture, MBC, MBN or enzymatic activity (Tables S7-S15), indicating the absence of publication bias.

DISCUSSION

Effects of altered precipitation regimes on the moisture content of surface soils

Litter decomposition is governed by environmental conditions such as climate, soil chemistry, litter quality, and the community composition of decomposers and enzymes produced by bacteria and fungi.[9] Altered precipitation regimes have widely been demonstrated to affect surface soil moisture availability and strongly affect the above conditions,[11] thus possibly affecting litter decomposition. Our field experiment and meta-analysis both revealed that increased precipitation increased surface soil moisture in arid regions, whereas decreased precipitation decreased surface moisture in humid regions, which is supported by the double asymmetry model. Soils in arid regions are sensitive to increased precipitation because they are limited by moisture availability and are close to climatic thresholds; thus, soils are resistant to decreased precipitation because they are adapted to long-term drought due to their ecological resilience.[28] The effects of altered precipitation regimes on soil moisture therefore depend strongly on ecosystem types, such as the forest and desert ecosystems in our study ($Q_{Between} \geq 13.47$, $P \leq$ 0.004, $n \geq 72$ (Figure S6)), as reported in several field experiments and a global synthesis.[23]

In summary, the effects of altered precipitation regimes on soil moisture are clearly constrained by site-specific moisture patterns, indicating that regional climate (humid or arid) is an important factor affecting the impact of altered precipitation regimes on litter decomposition.[29] These findings not only support the unbalanced ecological responses to altered precipitation regimes between humid and arid regions but also suggest that future studies should pay more attention to the influences of changes in soil moisture on litter decomposition under altered precipitation regimes, which may not effectively alter soil moisture.[25,30]

Effects of altered precipitation regimes on microbial biomass

Soil moisture strongly regulates microbial activity and litter decomposition

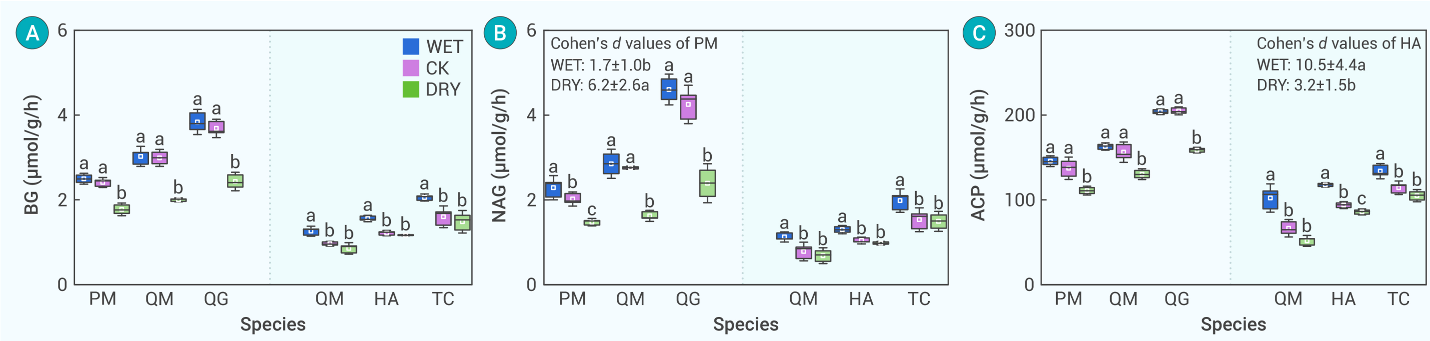

Figure 4. Litter enzymatic activity (β-glucosidase, A; β-N-acetyl-glucosaminnidase, B and acid phosphatase, C) in the treatments after two years of decomposition (mean ± 1.5 *SD*, *n* = 3) WET, increased precipitation; CK, control; DRY, decreased precipitation; BG, β-glucosidase; NAG, β-N-acetyl-glucosaminnidase; ACP, acid phosphatase; PM, *P. massoniana*; QM, *Q. mongolica* (a common species in the humid and arid regions); QG, *Q. glauca*; HA, *H. ammodendron*; TC, *T. chinensis*. The bars represent medians with 25 and 75% quartiles. Different letters indicate significant differences ($P < 0.05$, Bonferroni correction or *t* test). The light background indicates the humid region, and the dark background indicates the arid region. The values in the figures represent the mean effects sizes of WET and DRY (standardized mean difference ± *SD*, Cohen's *d*), which were calculated to facilitate comparisons when there were significant differences among WET, CK and DRY.

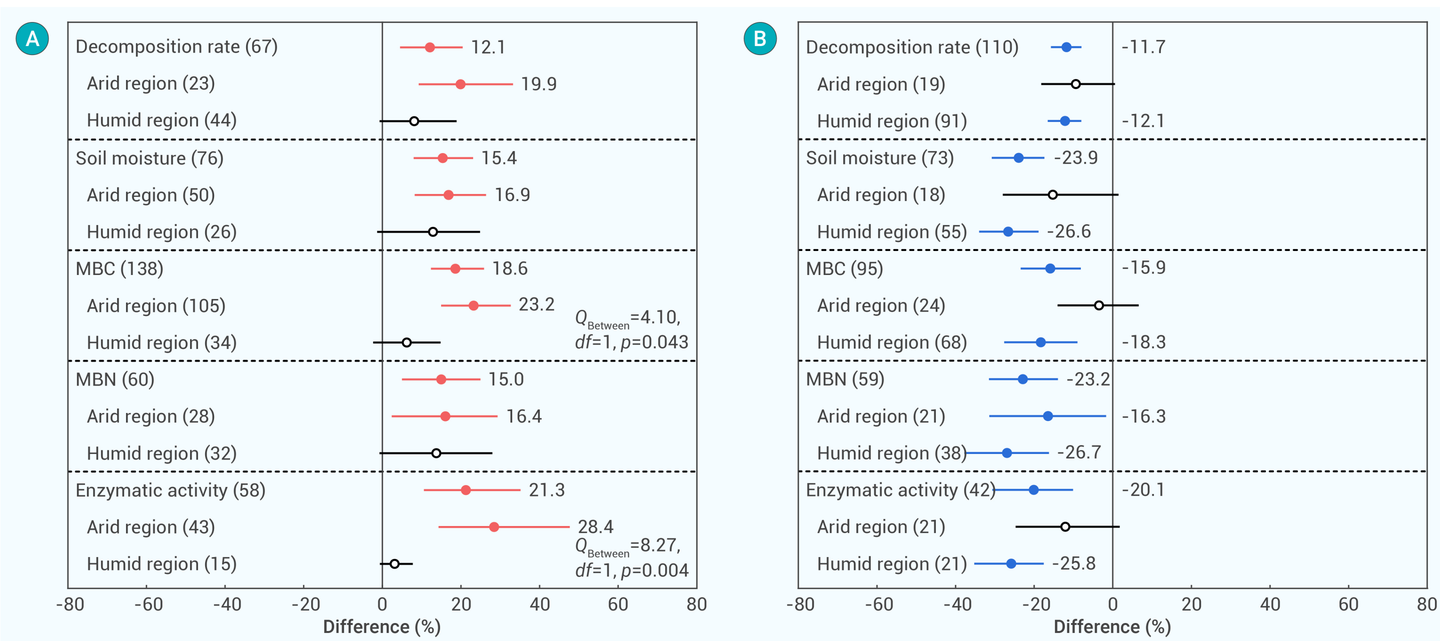

Figure 5. Responses of the rate of litter decomposition, soil moisture content, microbial biomass and enzymatic activity to the effect of increased (A) and decreased (B) precipitation as a percentage relative to the control from the meta-analysis The effect of increased or decreased precipitation is significant when the 95% confidence interval does not overlap with 0. The red dot indicates significant positive effect, the blue dot indicates significant negative effect and the line indicates the 95% confidence interval. Value next to the colored line indicates the mean, and the number of observations is shown in bracket. MBC, microbial biomass carbon concentration; MBN, microbial biomass nitrogen concentration; Enzymatic activity = β-glucosidase + β-N-acetyl-glucosaminnidase + acid phosphatase.

by regulating microbial biomass growth,[31] but the magnitude of this effect varies with regional climate (humid or arid). We found that the sensitivity of microbial biomass in litter and surface soils to increased precipitation was greater in arid regions than in humid regions, but the sensitivity to decreased precipitation was greater in humid regions than in arid regions. A recent meta-analysis also revealed that increased precipitation significantly increased topsoil microbial biomass in arid regions (by 21.4%), but decreased precipitation did not affect surface-soil microbial biomass.[32] In contrast, low precipitation significantly decreased microbial biomass by 15.4% in humid regions, but increased precipitation had no significant effect.[32]

The lower microbial growth and microbial biomass under decreased precipitation were a result of the low pore connectivity in dry soils, which limits microbes from migrating toward available substrates.[33] Increased precipitation increases microbial biomass and activity by alleviating moisture-induced substrate restrictions, such as nutrient availability and osmotic stress. We further suggest that arid regions tend to have microbial communities, such as fungi or filamentous bacteria (mycelia or filamentous structures can search for water sources), that are typically more resistant to arid conditions and have a higher water-use efficiency than communities in humid regions,[28] and increased precipitation allows microbial populations to grow rapidly in arid regions.[33,34] In contrast, decreased precipitation has opposite effects because it can limit the growth of microbes in humid regions that have adapted to humid environments. However, increased precipitation may also lead to a waterlogged microenvironment and reduce the oxygen level for microbes in humid regions,[35] hence decreasing microbial growth and biomass.[34] Therefore, altered precipitation regimes can differentially change hydrologically dependent responses such as ANPP and the inputs of plant litter between humid and arid regions and indirectly affect microbial biomass by changing substrate availability.[21,36]

Interestingly, the surface-soil microbial biomass in the desert region was more sensitive to increased precipitation (positive effect ≥ 22.3% (Figures S7 & S8)) and that in the forested region was more sensitive to decreased precipitation (negative effect ≥ 20.6% (Figures S7 & S8)). The negative effects of decreased precipitation on surface-soil microbial biomass were most significant in the long-term and large-size studies, and this trend was opposite to that observed for increased precipitation (Figures S7 & S8). This result was most likely due to the ability of microbes to cope with drought, so only long-term and severe drought stress had a significant negative effect on the microbes. In contrast, only moderate durations and levels of increased precipitation had significant positive impacts on microbes, highlighting the critical ecological roles of the duration and intensity of precipitation.[37] Our results suggest that the double asymmetric model is also applicable for accounting for the differential responses of microbial biomass to altered precipitation regimes between humid and arid regions, regardless of litter or surface soil, but that the regional climate (humid or arid) at the site and the duration and intensity of precipitation should be further considered.

Effects of altered precipitation regimes on enzyme activities

The increased precipitation in our study significantly increased litter and surface-soil enzymatic activities (BG, NAG and ACP) only in the region with a low MAP, whereas decreased precipitation significantly suppressed enzymatic activities, particularly in humid regions (Figure 4). Enzymatic activity is highly sensitive to the dynamics of soil moisture,[38] so altered moisture availability in both litter and surface soils induced by altered precipitation regimes can regulate enzymatic activity through affecting water limitation for microbial activity and substrate diffusion.[39] The greater sensitivity of enzyme activity to increased and decreased precipitation in humid and arid regions was likely due to the corresponding differential responses of microbial biomass, as discussed above, as enzymes are released mainly by microbes.[40]

Altered precipitation regimes affecting belowground net primary productivity (BNPP) may be another important factor contributing to the differential responses of enzymatic activity because plant roots are also important sources of enzymes.[40] Plants in arid regions tend to allocate more biomass to roots to improve the acquisition of belowground resources, so the negative impacts of decreased precipitation on BNPP, as well as those on enzymatic activity, are relatively small.[41] In contrast, decreased precipitation in humid regions can increase root mortality and inhibit the production of enzymes.

In contrast to previous studies, our meta-analysis did not identify different responses of activity to increased or decreased precipitation among BG, NAG and ACP (Figure S9), so we grouped the enzymes for further analysis.[42] The effects on enzymatic activity were statistically significant in croplands, regardless of whether precipitation increased or decreased, perhaps because croplands are highly dependent on anthropogenic water management. The sample sizes for the duration and magnitude of altered precipitation conditions were small (e.g., n = 2 for large-term studies and increased precipitation, and n = 6 for medium-term studies and decreased precipitation (Figure S9)), but enzymatic activity still played critical ecological roles in the duration and intensity of precipitation and was similar to the response of microbial biomass. These results therefore suggest that the effects of altered precipitation regimes on enzymatic activities vary with regional climate (humid or arid) at different sites.

Other potential mechanisms by which altered precipitation regimes affect litter decomposition

Several potential additional mechanisms could also contribute to the dual asymmetric responses of litter decomposition to altered precipitation regimes between humid and arid regions. First, a double asymmetric relationship for ANPP between altered precipitation regimes and two different climatic regions, as reported in Knapp et al. (2017), could support the doubly asymmetric responses of litter decomposition.[21] More specifically, the percent change in ANPP was greater in response to increased precipitation than in response to decreased precipitation in arid regions, and the negative impacts of decreased precipitation on ANPP were much greater in humid regions, providing additional evidence that litter production supported the doubly asymmetric responses of litter decomposition to altered precipitation regimes. As the relationship between litter production and decomposition is complex, more studies are needed to evaluate it in the future.[9]

The responses of microbes to altered precipitation regimes are represented by both biomass and community structure, and these responses vary significantly among species or functional groups.[43] The filamentous structure of fungi protects their metabolism more effectively than single bacterial cells do because of the strong ability of fungi to accumulate osmoprotectants and thus increase resistance to drought and desiccation.[28,43] The different resistances of microbes to moisture may accordingly lead to shifts in the microbial community structure under altered precipitation regimes.[44] The contributions of microbes to decomposition vary among species or functional types, so shifts in the microbial community structure potentially affect litter decomposition.[45] For example, a long-term precipitation–manipulation experiment conducted in an arid region (MAP = 281 mm) revealed that increased precipitation significantly increased the fungi: bacteria ratio but that decreased precipitation decreased this ratio,[46,47] however, decreased precipitation did not affect the fungi: bacteria ratio in a humid region (MAP = 835 mm). The responses of the microbial community structure to altered precipitation regimes may thus be inconsistent between humid and arid regions, which may also cause different responses of litter decomposition. Future studies should focus more on the influence of microbial community structure on decomposition under altered precipitation regimes, especially the potential differences between humid and arid regions.

Finally, litter is also decomposed by soil fauna, which can influence decomposition directly by fragmentation and feeding and indirectly by modifying the soil environment and interacting with the microbial community.[48] Altered precipitation regimes may have a large impact on soil fauna because moisture regulates the activity, metabolism and community structure of soil organisms,[49] whereas increased and decreased precipitation usually have opposite effects.[50] For example, Peng et al. (2022) reported that increased and decreased precipitation significantly increased and decreased soil faunal density by 24.9% and 27.4%, respectively.[51] The soil fauna in humid and arid regions, however, have already adapted to the environmental climatic conditions, so their responses to increased and decreased precipitation may not necessarily be symmetrical.[52] Two mechanisms can potentially account for the doubly asymmetric responses of soil fauna to altered precipitation regimes: (1) the sensitivity of different soil fauna to drought can vary greatly,[53] and (2) observations at different study sites can vary because the responses of soil fauna to increased precipitation also depend on the local climatic conditions.[54] Our comparative results thus indicate that local climatic conditions, especially regional climates (humid or arid), should not be ignored in studies of the impacts of altered precipitation regimes on soil fauna.

Limitations and future perspectives for research

The complete effects of altered precipitation regimes should be considered, including not only the amount of precipitation but also its frequency, amplitude, seasonality, and intensity.[1] Current field precipitation manipulation experiments can effectively simulate altered amounts of precipitation, but possible alterations in frequency, intensity and seasonal distribution have not yet been simulated naturally. More data from specialized precipitation experiments with a comprehensive design are therefore needed to draw more robust conclusions.

The large dataset we compiled was obtained from studies in Europe, North America and eastern Asia (in particular, humid regions (Figure S3)), and the lack of data from regions such as Central Asia, South America, Africa and Australia reduced our ability to identify general patterns in the responses of litter decomposition to altered precipitation regimes at the global scale. Therefore, we suggest that future research should be conducted in these abovementioned geographical regions.

Wide ranges of long-term field experiments have been conducted to simulate future altered precipitation regimes, which provide a more general understanding of the responses of ecosystems to altered precipitation regimes. Several independent syntheses based on the results of these field experiments have produced databases for specific objectives.[23,25,30,42] Such decentralized and independent efforts may increase the risk of producing redundant collections of data and lead to differential results without clarifying the underlying reasons for divergence. These problems could be solved by creating a publicly available, updatable and curated dataset.

The effects of global climate change on ecosystems, such as altered precipitation regimes, warming and elevated CO_2 levels, are collective rather than individual. Our study quantified the independent effects of altered precipitation regimes on litter decomposition and associated factors. However, few field experiments have focused concurrently on multiple factors of global climate change, which limits our understanding of the combined effects of these factors.[29] This limitation prevents us from assessing whether the combined effects on litter decomposition are additive, synergistic or antagonistic and hampers our ability to draw robust and general conclusions on the effects of global climate change.

Finally, studies focusing on the effects of altered precipitation regimes on specific factors regulating litter decomposition are still rare, limiting our ability to interpret the results of global analysis. For example, initial litter quality is a critical factor governing decomposition, but less research has focused on the dynamics of initial litter quality under altered precipitation regimes. Similarly, few studies have focused on litter moisture content, microbial biomass and enzymatic activity in precipitation–manipulation experiments; the corresponding surface soil data were collected instead, which likely reduced the accuracy of our analysis. We recommend that future studies pay more attention to the complete decomposition of litter and collect as many detailed relevant factors as possible. We therefore believe that well-designed field experiments testing various forms of altered precipitation regimes and other factors related to global climate change are urgently needed and could be combined with a publicly available, updatable and curated dataset to improve our knowledge and predictive ability of the responses of litter decomposition to ongoing and future global climate change.

CONCLUSIONS

Although implications and uncertainties remain due to the limitations in the designs of field experiments and the datasets available for global syntheses, our results clearly showed that (1) increased precipitation had significantly positive effects on the decomposition rate, soil moisture, microbial biomass and enzymatic activity, whereas decreased precipitation produced the opposite results; (2) the decomposition rate and associated factors were more sensitive to increased precipitation in arid regions but more sensitive to decreased precipitation in humid regions; and (3) the double asymmetric model could account for the responses of litter decomposition and associated factors to the altered precipitation regimes; more importantly, the regional climate (humid or arid) at the site was critical. Our findings are beneficial for understanding the relationship between litter decomposition and altered precipitation regimes, which should be considered when predicting the responses of the ecosystem-scale cycling of terrestrial material, as well as other ecological processes, to global climate change.

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AUTHOR CONTRIBUTIONS

Y.L. conceived the research question and designed the experiments; H.Z., Y.J., and N.M. performed the experiments; Q.W. and Y.P. performed all data analyses; Q.W., K.Y. and Z.Z. wrote the first draft of the manuscript. All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

Josep Peñuelas is an Editorial Board member of The Innovation Geoscience and was blinded from reviewing or making final decisions on the manuscript. Peer review was handled independently of this member and their research group. The other authors declare no conflicts of interest.

DATA AND CODE AVAILABILITY

The data that support the findings of this study are openly available in the Supplemental Information.

SUPPLEMENTAL INFORMATION

It can be found online at https://doi.org/10.59717/j.xinn-geo.2024.100117