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RESEARCH ARTICLE

# Long-term nitrogen addition consistently decreased litter decomposition rates in an alpine grassland

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**Abstract**
*Aims* Litter decomposition is a crucial component of nutrient recycling. Short-term nitrogen (N) deposition has been shown to influence litter decomposition in temperate steppe with significant variability due to differences in atmospheric N deposition, species identity, and experimental duration. Therefore, the effect of N addition, especially long-term, on litter decomposition in alpine grassland still needs further investigation.

*Methods* To address these knowledge gaps, we examined the influence of long-term N addition on litter decomposition, taking advantage of a field experiment with five N addition levels (0, 10, 30, 90, and 150 kg N ha$^{-1}$ yr$^{-1}$) with a meta-analysis, which has been running for 11 years in an alpine grassland, Northwest China.

*Results* Long-term N addition consistently decreased litter decomposition rates, and N negative effect became stronger with the increasing N addition rates. Reduced litter decomposition rates were related to lower soil enzymes activities. Litter decomposition rates were strongly correlated with litter quality, but weakly correlated with soil quality, but which suggested that litter

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quality and soil quality played important role in regulating litter decomposition. Furthermore, a regional meta-analysis revealed that N addition accelerated litter decomposition when all data were averaged. Although N addition indirectly increased litter decomposition, it had no direct effect on decomposition. However, the direction and degree of the direct effect of N on litter decomposition were regulated by N addition rate, experimental duration and form of N fertilizer.

*Conclusions* Overall, these results demonstrated that long-term N addition decreased litter decomposition and N negative effect increased over time.

**Keywords** Alpine grassland · Litter quality · Litter decomposition rates · Long-term nitrogen addition · Meta-analysis · Soil enzymes activities

## Introduction

Decomposition of plant litter is the primary mechanism by which nutrients are returned to soils, controlling nutrient limitation for primary producers and soil fertility (Gosz et al. 1973; Aber and Melillo 1980; Zhou et al. 2019; Canessa et al. 2020). It is also the major pathway for the return of $CO_2$ fixed during photosynthesis to the atmosphere, and influences terrestrial ecosystem C cycling (Gray and Fierer 2012). Therefore, understanding litter decomposition and the regulating factors of decomposition has significant implications. Litter decomposition rates are influenced by a wide variety of factors, such as litter quality, climate, soil nutrient status and soil organisms (Cornwell et al. 2008; Manning et al. 2008; Garcia-Palacios et al. 2013). Climate plays a vital role in regulating global litter decomposition because the process of microbial decomposition is strongly correlated with soil moisture and temperature (Zhang et al. 2008; Garcia-Palacios et al. 2013). In addition to the external abiotic conditions, litter quality, including Na, Fe, Mn, protein, lignin, and nitrogen (N) contents, is another important determinant of litter decomposition (Canessa et al. 2020). However, at specific regions or sites, litter decomposition rates are determined by litter quality and soil nutrient status (Aber and Melillo 1980; Melillo et al. 1982; García-Palacios et al. 2016; Pichon et al. 2020).

Anthropogenic activities have profoundly altered and accelerated global N cycling, and atmospheric N deposition has enhanced 3–fivefold over the past century (Galloway et al. 2008). China has experienced a 60% increase in reactive N deposition owing to rapid economic progress (Liu et al. 2013). Numerous studies have indicated that litter decomposition is influenced by N deposition, mainly by altering litter quality and soil quality (Liu et al. 2009; Hobbie et al. 2012; Hou et al. 2020). However, variable results have also been reported, with studies demonstrating that N addition increased (Dong et al. 2020; Hou et al. 2020), decreased (Fang et al. 2007; Li et al. 2017), or had no significant effect (Xing et al. 2021) on litter decomposition. Even in a single system, positive, negative, and no effects of N addition have been observed among different litter types (Song et al. 2018, 2019; Yan et al. 2020). These considerable variations in the effects of N on litter decomposition might be owing to the differences in litter quality, experimental duration, and N input rate (Zhang et al. 2018). Therefore, investigation of the response of litter decomposition rate to multiple levels of N addition could help clarify the effect of N-enriched environments on litter decomposition.

Litter quality, such as N and lignin contents in the decomposing grass material, has long been considered to play a determinant role in mediating litter decomposition (Melillo et al. 1982), which may interplay with N addition to influence litter decomposition rate. It has been reported that the effect of N on litter decomposition depended on litter quality and N addition rate (Knorr et al. 2005); N addition not only increased decomposition of smaller lignin concentration litter, but also decreased the decomposition of greater lignin concentration litter (Knorr et al. 2005). Song et al. (2018) found that N addition did not significantly influence high-quality *Eriophorum vaginatum* litter decomposition, but enhanced low-quality *Vaccinium uliginosum* litter decomposition. In contrast, Liu et al. (2006) indicated that N addition enhanced low-quality *Stipa krylovii* litter decomposition, but had no significant effect on high-quality *Allium bidentatum* litter decomposition. These contradictory results might be attributed to litter quality, N addition rates, and experimental duration (Guo et al. 2021). Furthermore, it has been reported that N addition decreased grass litter decomposition, increased legume litter decomposition, and had null effects on forbs litter decomposition (Song et al. 2019), implying that the effect of N addition on litter decomposition rate may vary among different functional groups. To date, knowledge on the effect of long-term N addition on litter decomposition rate with respect to different litter quality and functional groups is still limited.

Previous studies have indicated that short-term N addition did not notably influence soil microbial activity, whereas long-term N addition considerably decreased soil microbial activity (Treseder 2008; Jian et al. 2016), thus resulting in significant differences in litter decomposition rate between short- and long-term N addition. A study on alpine grassland has demonstrated that reductions in the litter decomposition rates along N addition levels were correlated with N-induced changes in the soil bacterial diversity (Wei et al. 2022). A recent investigation has also revealed that the changes in soil enzymes activities and pH induced by long-term N addition significantly influenced litter decomposition (Shen et al. 2021). In contrast, Mo et al. (2006) showed that short-term N addition produced no positive and even some negative effects on leaf decomposition in mature forest, but enhanced leaf decomposition in both pine and pine-broadleaf mixed forests. However, Fang et al. (2007) observed that 2 years of N addition significantly inhibited litter decomposition in pine and mature forest, but had no significant effect on litter decomposition in pine-broadleaf mixed forest. These results suggested that N addition had a cumulative effect on litter decay, and that litter decay in response to N addition depended on the initial soil N status. Although the effects of N addition on litter decomposition varied with the experimental duration, knowledge on the influence of short- and long-term N addition on litter decomposition rate in grassland ecosystem is still limited. Berg et al. (1982) reported that the decay rate of high-quality litter was initially faster than that of nutrient-poor litter; however, after 3 years, the accumulated mass loss was noted to be similar for the two kinds of litter. Therefore, the effect of short-term N addition on plant litter decomposition might be different from that of long-term N addition. Moreover, atmospheric N deposition has also been found to regulate the impact of N addition on litter decomposition (Knorr et al. 2005), with positive effects noted under low atmospheric N deposition ($<5$ g N ha$^{-1}$ yr$^{-1}$), negative effects detected under medium atmospheric N deposition (5–10 g N ha$^{-1}$ yr$^{-1}$), and a null effect observed under high atmospheric N deposition ($>10$ g N ha$^{-1}$ yr$^{-1}$). Therefore, the influence of N addition on litter decomposition in alpine grasslands with lower N deposition ($<10$ g N ha$^{-1}$ yr$^{-1}$) may be different from that in temperate grasslands (Dong et al. 2019; Liu et al. 2006; Gong et al. 2020; Hou et al. 2020). To date, our knowledge about the effects of long-term N addition on litter decomposition in alpine grasslands, especially under multilevel N addition, remains scarce. Given the vast carbon stocks in grassland litter (20 Tg C) (Tang et al. 2018), even small changes in litter decomposition can have considerable effects on regional atmospheric $CO_2$ concentration (Gray and Fierer 2012). Therefore, research to better understand the impact of long-term N addition on litter decay in alpine grasslands is necessary.

In China, grasslands are mainly distributed in arid and semi-arid areas, and are very sensitive to environmental changes (Bai et al. 2004). In the recent 30 years, the trend and interannual variations of global terrestrial C sink have mainly been detected in arid and semi-arid ecosystems (Poulter et al. 2014). Therefore, there is a need to investigate the impact of N addition on litter decay owing to its importance in litter-mediated C fluxes. Anthropogenic disturbance has caused a rapid increase in reactive N concentrations in the Bayinbuluk alpine grassland (Li et al. 2021). A previous study on this alpine grassland found that N addition decreased soil microbial biomass N and soil pH, but enhanced soil N availability (Su et al. 2021), suggesting that these changes induced by long-term N addition may influence litter decomposition. The present work aimed to answer the following questions: (1) How does long-term N addition influence decomposition of various litter (*Festuca ovina*, *Potentilla anserina*, and *Astragalus propinuus schischkin*) representing different functional groups? (2) What factors (litter quality vs. soil quality) play crucial roles in regulating litter decomposition in response to N addition? (3) Does the effect of N addition on litter decomposition increase with the experimental duration (long-term vs. short-term) in the grassland ecosystem? To address these questions, an in-situ decomposition experiment was conducted from September 2019 to September 2021 to examine the response of litter decomposition to long-term N addition and the factors regulating the effects of N on litter decomposition. In addition, a meta-analysis was employed to perform N addition experimental studies and assess the effects of N on litter decomposition rate in Chinese grasslands.

## Materials and methods

### Study site

This study was conducted in Bayinbuluk Grassland Ecosystem Research Station, located in the Tianshan Mountains of Northwest China (83°42.5′E, 42°53.1′N). The annual average temperature and precipitation in the study area from 1980 to 2012 were −4.8 °C and 282.3 mm, respectively (Li et al. 2012). While the dominant species in this ecosystem is *Festuca ovina*, the subdominant species, *Potentilla anserina* and *Astragalus mongholicus Bunge,* are widely distributed as a result of heavy grazing or grassland degradation, accounting for 70–85% of the total aboveground biomass. In addition, this alpine grassland has received approximately 8.0 kg N $ha^{-1}$ $yr^{-1}$ from atmospheric deposition owing to human activity (Li et al. 2015). More information about this alpine grassland can be found in the study by Li et al. (2012).

### Experimental design

At the end of May 2009, we established multiple-level N addition experiment in the selected alpine grassland, which is ongoing till date. The experiment included a randomized block design with four blocks and five N input levels (0, 10, 30, 90, and 150 kg N $ha^{-1}$ $yr^{-1}$, abbreviated as N0, N1, N3, N9, and N15, respectively). Thus, the experiment comprised 20 plots (5 N levels × 4 blocks), with 5 plots (4 m × 8 m) within a block. The distance between the blocks was a 1-m buffer strip and the plots within a block were divided by a 1-m buffer strip. The N fertilizer ($NH_4NO_3$) was applied two times in late May and June each year. At each time of N addition, $NH_4NO_3$ was dissolved in 8 L of water and then sprayed evenly onto each plot. Simultaneously, the same amount of water without N was added to the control plots (Li et al. 2015).

Three types of litter representing three functional groups (grass: *F. ovina*; forbs: *P. anserina*; legume: *A. mongholicus Bunge*) were selected to examine the impact of long-term N addition on litter decomposition rate. In our study, plant litter was collected from no-N receiving plots, and incubated in N receiving plots. In the late August 2019, freshly senesced litter in a natural alpine grassland without N addition was collected within a 20 m × 20 m plot using scissors, and dried for 48 h at 65 °C to a constant weight. Then, 4.00 g of dried litter were transferred into 20 cm × 25 cm nylon litterbags (0.5-mm mesh) and placed in the N addition experimental plots. A 0.5-mm mesh was adequately large for the decomposition of grassland litter, and could avoid the loss of *F. ovina* and small litter fragments (Milcu and Manning 2011; Baker and Allison 2015; Wei et al. 2022).

We chose three types of litter representing three functional groups (grass: *Festuca ovina*; forbs: *Potentilla anserina*; legume: *Astragalus mongholicus Bunge*) to examine the effect of long-term N addition on litter decomposition rate and placed them back in the corresponding N treatment plots (four replicates). Litterbags were manually fixed to soil surface with small nails in each plot (3kinds of litter × 6 six sampling dates = 18 litterbags), to ensure that the litterbags were in contact with the soil surface throughout the experimental period. Due to frequent strong winds in this alpine grassland, we were worried that the litter bags would be blow away and affected our experiment, so we put an extra litterbag in all corresponding N treatment plots for each species for standby application.

The litterbags were collected after 8, 9, 10, 12, 20, and 25 months. The remaining litter mass was oven-dried for 48 h at 65 °C to a constant weight and weighed after carefully removing the soil particles with a brush and fresh plants by hand. Litter mass loss and decay rate constant (k, $yr^{-1}$) were calculated according to Eqs. (1) and (2) (Olson 1963) as follows:

$$\mathrm{Mass\ loss}(\%) = (m_0 - m_t)/m_0 \times 100 \tag{1}$$

$$m_t/m_0 = ae^{-kt} \tag{2}$$

where $m_0$ is the initial litter mass (g), $m_t$ is the remaining dry mass (g), k is the decay constant ($yr^{-1}$), and t is the time of litter incubation (months).

### Field sampling and chemical analysis

The fresh leaves (n = 20) of three kinds of species were weighed before being scanned to measure leaf area using ImageJ software (Schneider et al. 2012); the leaves were then dried at 70 °C for 48 h hand weighed using a Sartorius balance with an accuracy of $10^{-4}$ g (Zhou et al. 2018). Specific leaf area (SLA) and leaf dry matter content (LDMC) were calculated as follows:

SLA = leaf area ($cm.^2$)/leaf mass (g)
LDMC = dried leaf weight (mg)/saturated fresh leaf weight (mg).

Surface soil (0–10 cm) was randomly sampled in each plot in October 2018 and May and August 2019, and sieved with a 2-mm mesh. Fresh soil was used to determine soil enzymes activities (β-1,4-glucosidase, cellobiohydrolase, β-1,4-xylosidase, leucyl aminopeptidase, β-N-acetyl glucosaminidase and alkaline phosphatase; hereafter, are abbreviated as βG, CBH, βX, LAP, NAG and AKP, respectively) according to the methods described by Sinsabaugh et al. (2008). Soil pH was assessed with air-dried soil using a pH meter. To calculate the soil available N (AN) content, 5.0 g of air-dried soil were extracted with 50 mL of 2 M KCl, and the filtered extract was assayed using a FIAstar 5000 instrument (Denmark).

The initial litter C and N contents were analyzed using TOC analyzer (Analytik Jena, Germany), the initial litter P content was determined by an AA3 Continuous Flow Analyzer (Seal Analytical, Germany), and the contents of lignin, hemicellulose, and cellulose in the litters were evaluated according to the Van Soest method (Van Soest and Wine 1968).

## Statistical analysis

The single-exponential litter decomposition model was used to calculate the litter decomposition rate (Olson 1963). The mean values determined in October 2018 and May and August 2019 were used to present the soil enzymes activities. The effects of N addition on soil enzymes activities, soil pH, soil AN content, and litter nutrients contents (such as cellulose, hemicellulose, and lignin contents) were analyzed via one-way analysis of variance ($P < 0.05$). The relationship between the litter decomposition rates and N addition, soil pH, soil AN content, soil enzymes activities, and litter initial chemical traits (C, N, P, cellulose, hemicellulose, and lignin, and their stoichiometric ratio) was also analyzed by linear or nonlinear regression analysis. To assess the impacts of long-term N addition on the decomposition of litter with different quality, univariate covariance analysis was applied to compare the slope of equations for litter decomposition rates and N addition rates. Variance analysis was performed using SPSS software (version 23.0), and all graphs were created using Origin (version 9.0).

## Meta-analysis

Studies on litter decomposition rates after N addition in northern Chinese grasslands over the period of 2000–2021 were collected from Web of Science and China Knowledge Resource Integrated databases using a combination of keywords (such as "N addition or N enrichment or N deposition," "litter decomposition or litter decay or litter decomposition rates," "China or Chinese," and "grassland or steppe"), focusing only on the litter decomposition rate constant (k) reported in these papers. Finally, 252 data sets from 20 publications were included in this study. All the data were obtained using Engauge Digitizer (Free Software Foundation, Inc., Boston, MA, USA). The analyses of the N effects were grouped into the following categories:

Categories of N effect (Liu et al. 2009): (1) N effect on litter decomposition by soil (direct effect), (2) N effect on litter decomposition by litter quality (indirect effect), and (3) N effect on litter decomposition by soil and litter quality (overall effect).

The N addition rate (kg N $ha^{-1}$ $yr^{-1}$): (1) ≤ 50, (2) 50–150, and (3) > 150.
N addition experimental duration (yr): (1) ≤ 3, (2) > 3.
Form of N fertilizer: (1) $CO(NH_2)_2$, (2) $NH_4NO_3$, and (3) mixed N (organic and inorganic N added together).

The response ratio was used to assess the effect of N on litter decomposition rates, and the effect size (ln(R)) was calculated as follows:

$$\ln R = \ln\left(\frac{X_t}{X_c}\right)$$

where $X_t$ indicates the mean value for N addition plots and $X_c$ denotes the control value for no N addition plots.

The variance (v) was determined as follows:

$$v = \frac{1}{n_t} \times \left(\frac{S_t}{X_t}\right)^2 + \frac{1}{n_c} \times \left(\frac{S_c}{X_c}\right)^2$$

where $n_t$ and $n_c$ indicate the replications from N treatment and no N treatment groups, respectively, and $S_t$ and $S_c$ are the standard deviations for N treatment and no N treatment groups, respectively. The effect size was weighted based on the number of variances. Weighted mean effect size was expressed as percent relative change as follows:

$$\text{Relative change}(\%) = ((e^{\ln(R)} - 1) \times 100)$$

A random-effect model was used to calculate the mean effect size of N addition effect, and the bootstrapping procedure with 4999 iterations was used to produce 95% confidence interval (CI) (Rosenberg et al. 2000). A categorical random-effect model was applied to calculate the mean effect size of different groups, including N addition rates, N addition experimental duration, and form of N fertilizer. All the calculations were conducted using MetaWin 2.1. Each group was identified to have notable impacts on the object variable when the 95% CI did not intersect with the zero line. Two groups were considered to show significant differences when 95% CI did not overlap with one another. A positive weighted mean effect size revealed that N addition accelerated decomposition, whereas negative values indicated that N addition slowed decomposition.

## Results

### Initial chemical traits of the experimental litter

There was significant difference in the initial litter chemistry among the experimental litter species (Fig. 1). In particular, legume litter (*A. mongholicus Bunge*) showed the highest N, P, and lignin contents, but a lower lignin:N ratio and LDMC. Grass litter (*F. ovina*) had lower N and P contents and SLA, but higher LDMC, cellulose, hemicellulose, and lignin:N ratios. Forbs litter (*P. anserina*) presented the lowest cellulose and hemicellulose contents and N:P ratio.

### Impacts of long-term N addition on soil pH, nutrients, and enzymes activities

Long-term N addition significantly decreased soil pH, but consistently enhanced soil AN and AN: available P (AP) ratio, exhibiting a significant positive correlation with N addition rates (Fig. 2). Furthermore, long-term N addition notably decreased most of the soil enzymes activities related to soil C, N, and P cycling. However, soil NAG and CBH enzyme activity showed a hump-shaped relationship with N addition rates, and peaked at the intermediate level of N addition (Fig. 2).

### Impacts of long-term N addition on accumulated litter mass loss

After 2 years of field incubation, the mass loss of all the three litter species significantly varied with different N addition rates, and the experimental data well fitted the single-exponential decay model across N addition treatments and experimental litters (Fig. S1). In the control plots, legume litter presented the fastest mass loss. The litter decomposition rates were negatively correlated with N addition rates (Fig. 3), revealing that long-term N addition consistently decreased litter decomposition rates. Univariate covariance analysis indicated that the degrees of long-term N addition effect on litter decomposition (slope) were not significantly different, and the response of decomposition rates of litter with different quality to long-term N addition was similar.

### Factors mediating litter decomposition in response to long-term N addition

Litter initial traits produced significant impacts on litter decomposition rates (Fig. 4). In particular, significant positive relationships were noted between the litter decay rate and litter N, P, SLA, lignin, and cellulose contents and the N:P ratio. However, significant negative relationships were observed between the litter decay rate and the litter C:N, C:P, and lignin:N ratios and LDMC. In addition, the litter decomposition rates showed a hump-shaped relationship with litter initial hemicellulose content, and peaked at the intermediate level of hemicellulose content (Fig. 4).

The soil pH, AN content, and enzymes activities significantly affected the litter decomposition rates (Fig. 5). The litter decomposition rate was positively correlated with soil pH, but a negative correlation with soil AN content and the soil AN:AP ratio. Furthermore, the litter decomposition rates were

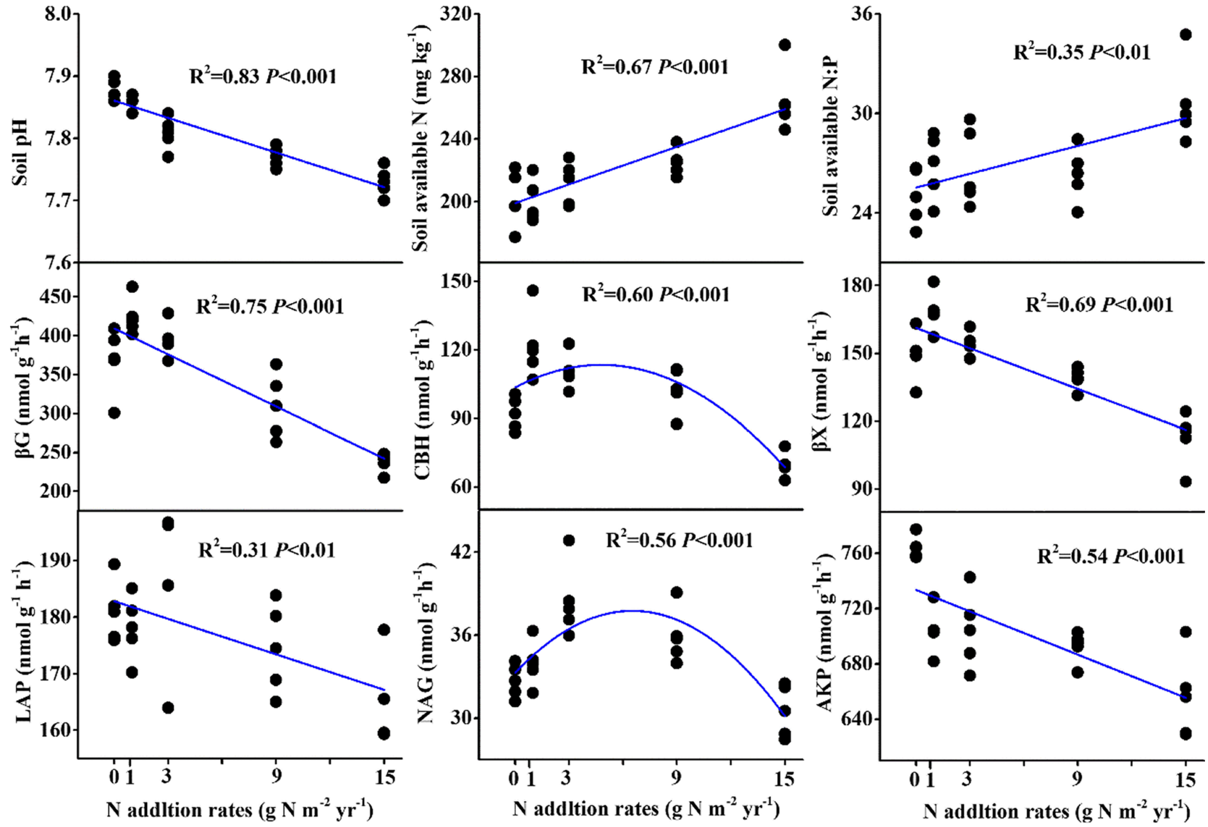


**Fig. 1** Initial chemical traits of the experimental litter from no-N receiving plots. Solid and dashed lines in the box, lower and upper edges, bars and dots in or outside the boxes represent median and mean values, 25th and 75th, 5th and 95th, and,5th and .95th percentiles of all data, respectively. Different lowercase letters indicate significant differences among species. *Astragalus mongholicus Bunge* (A.M.B), *Potentilla anserina* (A.P), *Festuca ovina* (F.O)

positively correlated with most of the soil enzymes activities (Fig. 5).

Examination of the influence of N addition on litter decomposition rate in northern Chinese grasslands by meta-analysis

Across all the data, N addition significantly enhanced litter decomposition rate in the northern Chinese grasslands (Fig. 6). The litter decomposition rates were increased by N overall and indirect effects, but were not affected by N direct effect. Furthermore, N addition produced significant effects on litter decomposition, with low and high N addition presenting inhibitory effects, whereas medium N addition exerting stimulative effect. Besides, the degree of negative effect of N addition on litter decomposition increased with the N addition experimental duration (Fig. 6). While short-term N addition accelerated litter decomposition within 3 years after N addition, long-term N addition notably decreased litter decomposition. Moreover, litter decomposition in response to N addition depended on the form of N fertilizer (Fig. 6), with $NH_4NO_3$ and $CO(NH_2)_2$ addition decreasing litter decomposition, whereas mixed N addition significantly accelerating litter decomposition.

## Discussion

The findings of the present study are not consistent with those reported in previous studies (Song et al. 2018, 2019; Hou et al. 2020; Xing et al. 2021). The present study found that long-term N addition consistently decreased litter decomposition, and the results of regional meta-analysis also demonstrated

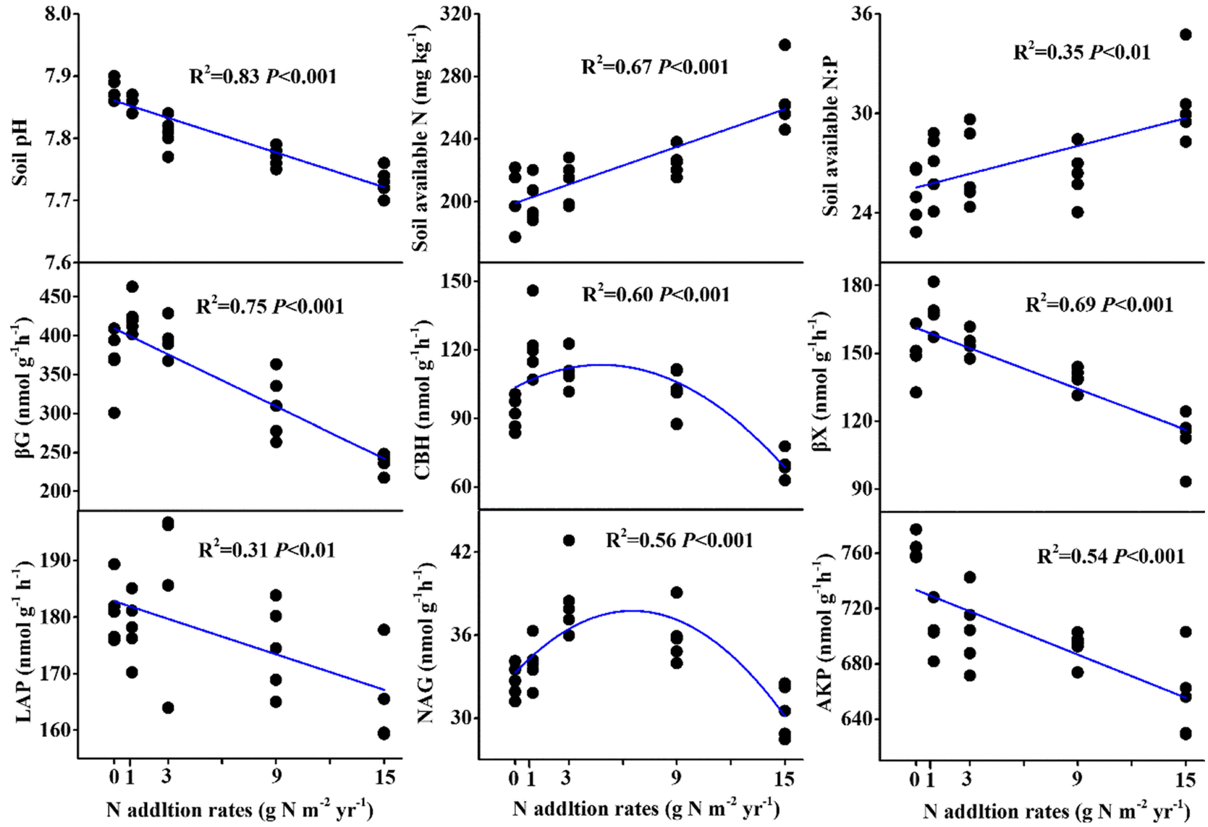


**Fig. 2** Effect of long-term N addition on soil pH, available N and C-N-P cycling related enzymes activity

that the influence of N addition on litter decomposition is related to the experimental duration. On the one hand, litter quality was observed to play more dominant roles than soil enzymes activities in regulating litter decomposition. On the other hand, soil acidification induced by long-term N addition was found to produce notable effects on litter decomposition. In addition, litter lignin content alone could not better predict litter decomposition in the studied alpine grassland. Overall, the results obtained indicated that litter chemical characteristics could have stronger effects on the litter decomposition rate; however, the changes in soil nutrients and enzymes activities induced by long-term N addition could also significantly decrease the litter decomposition rate, thus implying that litter-mediated nutrient cycling in alpine grassland ecosystem could weaken with increasing atmospheric N deposition (Wei et al. 2022).

## Effects of litter traits on litter decomposition

Numerous studies have proved that the litter decomposition rate is often correlated with initial litter chemical traits, such N content, lignin content, and the C:N and lignin:N ratios (Aber and Melillo 1980; Melillo et al. 1982; Zhou et al. 2019; Knorr et al. 2005). The results of the present study also support most of these previous observations; i.e., high-quality litter, such as litter with a greater N concentration and smaller lignin:N ratio, usually decomposed faster. However, a significant positive relationship was noted in the present study between litter lignin content and litter decomposition rate, suggesting that lignin content alone could not predict litter decomposition in the studied alpine grassland. It has been reported that the lignin content or lignin:N ratio had different effects on litter decomposition among various study sites (Aber

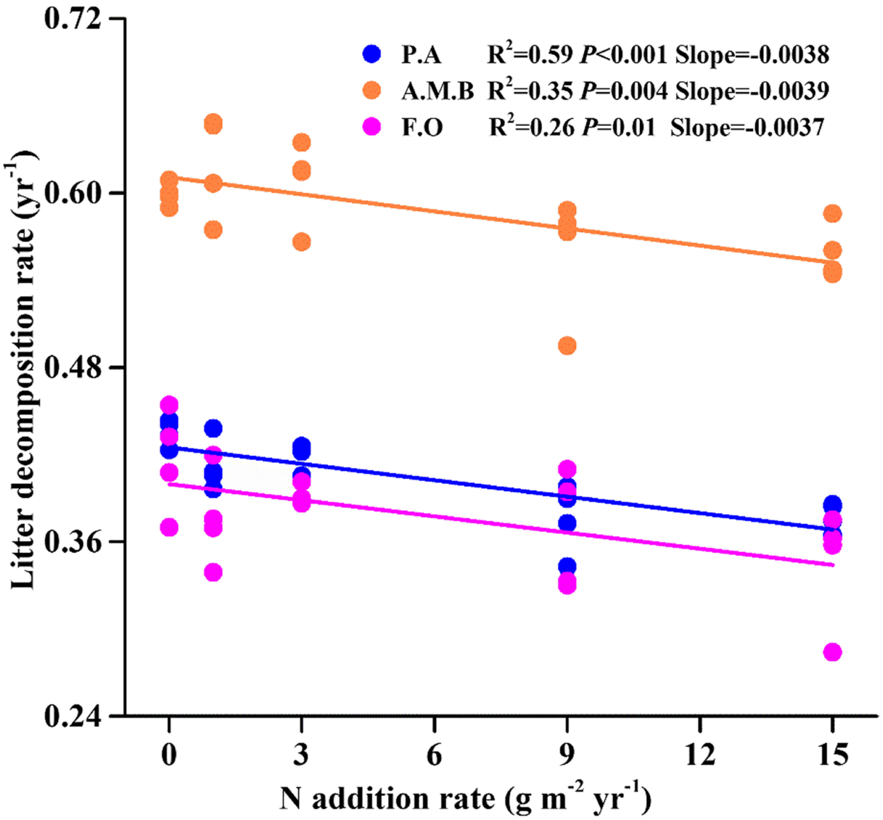


**Fig. 3** The relationship of between litter decomposition rates and N addition rates, *Astragalus mongholicus Bunge* (A.M.B), *Potentilla anserina* (A.P), *Festuca ovina* (F.O)

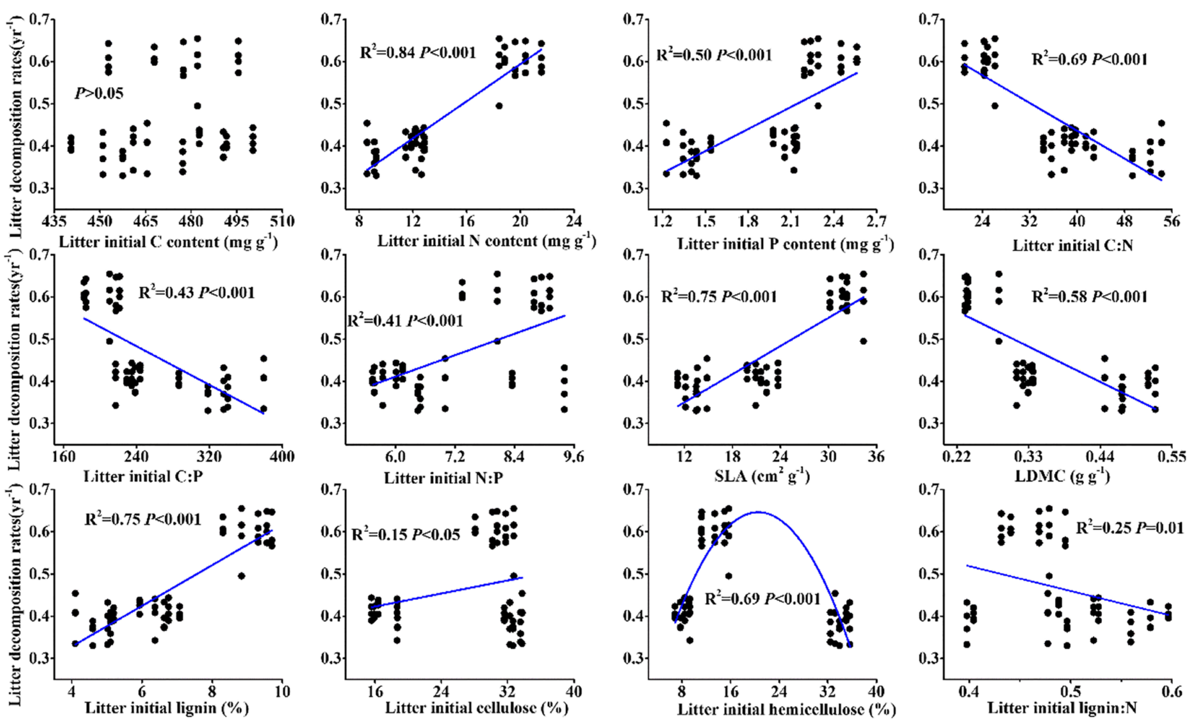


**Fig. 4** Relationship of litter decomposition rates with litter initial traits across all experimental treatments

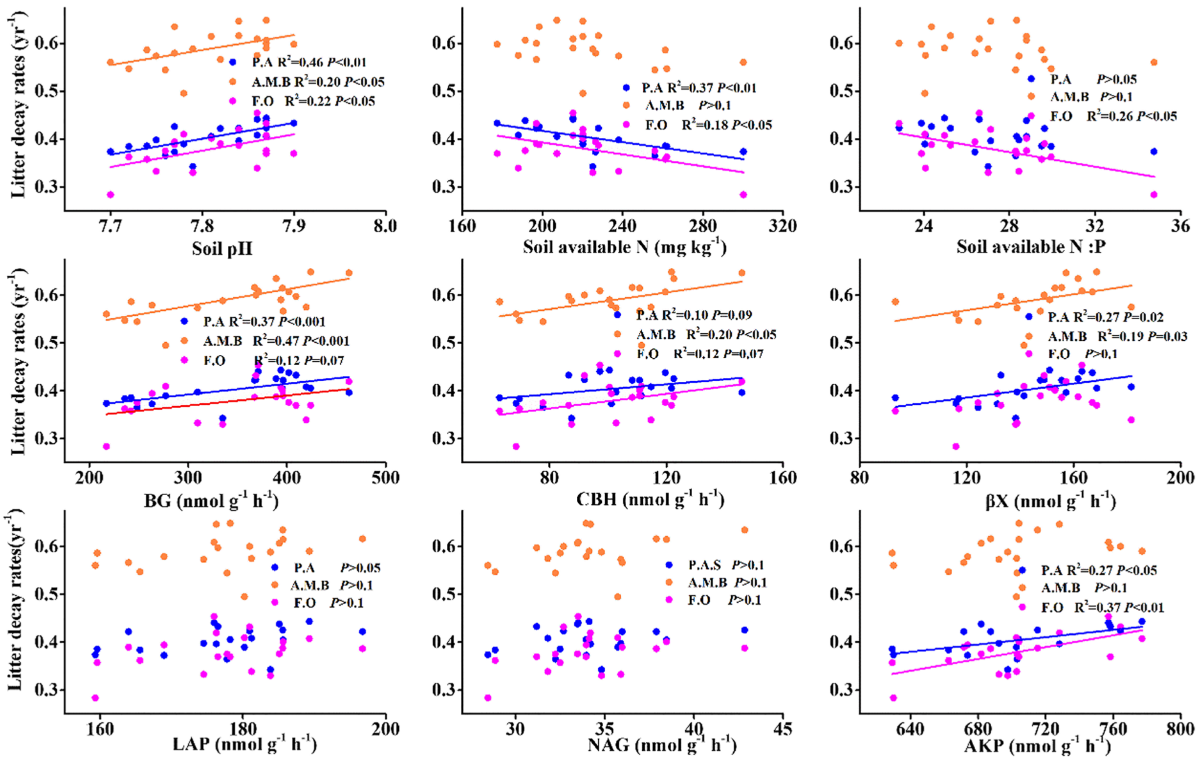


**Fig. 5** Relationship of litter decomposition rates with soil pH, available N, AN: AP and soil enzymes activity across all experimental treatments, *Astragalus mongholicus Bunge* (A.M.B), *Potentilla anserina* (A.P), *Festuca ovina* (F.O)

and Melillo 1980; Melillo et al. 1982; Zhang et al. 2016), and that these differences were significantly correlated with the initial soil N status. However, the results of the present study found that litter P content and their stoichiometric ratio considerably varied and showed significant effects on litter decomposition, which are consistent with the previous reports indicating that litter decomposition is inversely related to the C:P ratio (Manzoni et al. 2010; Chen et al. 2016; Shen et al. 2021). Furthermore, the SLA and LDMC were also observed to be important determinants of litter decomposition rates, which support the results of some previous studies (Bakker et al. 2011; Zhang et al. 2016; De la Riva et al. 2019) that indicated that litter decomposition rates exhibited positive and negative correlation with SLA and LDMC, respectively; in other words, litter with greater SLA and smaller LDMC could decompose faster (Veen et al. 2015).

## Effects of long-term N addition on litter decomposition

The results of the present study indicated that long-term N addition consistently decreased litter decomposition during the 25-month incubation period, and the negative effect of N addition enhanced with the increasing N addition rates and experimental duration. Similar findings have also been observed in semiarid typical steppe ecosystem by Liu et al. (2009) and Li et al. (2017). In addition, these results are also supported by a regional meta-analysis study that revealed that the negative effect of N addition increased with increasing N input when the N addition rates were less than 20 times of atmospheric N deposition (Knorr et al. 2005). Furthermore, the present study noted that the decrease in litter decomposition was strongly correlated with the changes in the decreased soil enzymes activities and soil

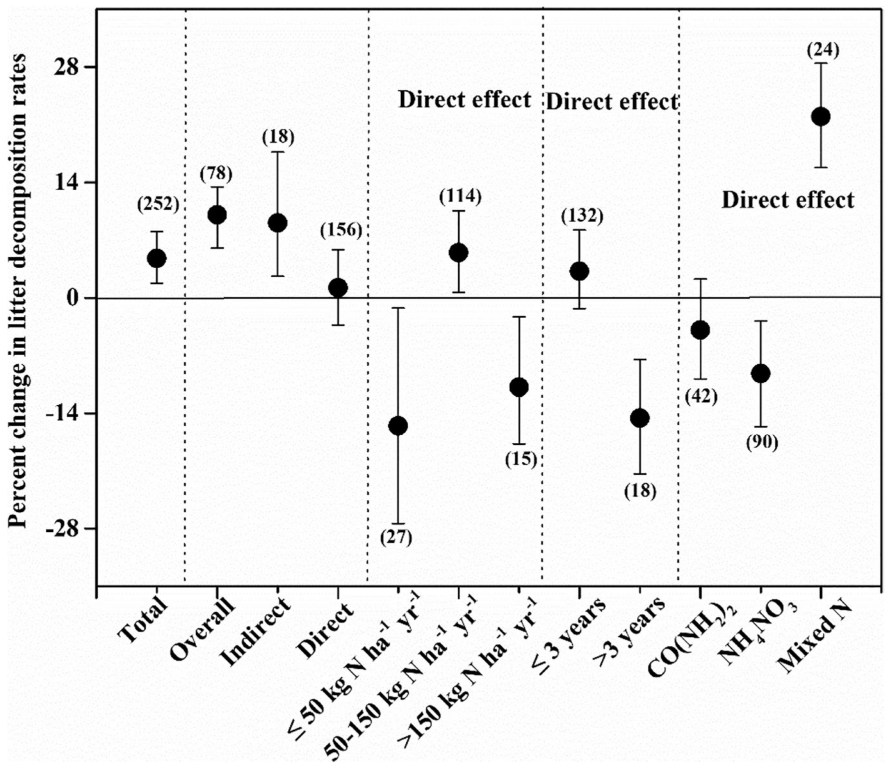


**Fig. 6** Effects of N addition on litter decomposition rates for all studies, categories of N effect (direct, indirect and overall), Nitrogen addition rates, Nitrogen addition experimental duration and form of N fertilizer. The dots with error bars were the mean effect size with the 95% CI and the numbers inside parentheses were the number of observations

acidification. Recent studies have also demonstrated that acid addition significantly inhibited litter decomposition in temperate forest (Shen et al. 2021). The added N can react with lignin and form lignin-derivative complexes that are more resistant to decomposition (Melillo et al. 1982). It has been reported that N addition significantly inhibited soil oxidative enzyme activity (Jian et al. 2016), which is a crucial mechanism by which N addition inhibits litter decomposition (Carreiro et al. 2000). In addition, long-term N addition has been found to markedly promote plant growth and increase plant height (Zhou et al. 2018; Zhao et al. 2018), decrease UV radiation reaching the litterbag (Ma et al. 2021), and thus inhibit litter decomposition (Wei et al. 2022). Similarly, Hao et al. (2020) also found that 11 years of N addition notably decreased the dominance of bacteria in the Bayinbuluk alpine grassland, leading to slower litter decomposition (Hao et al. 2020).

However, contrasting results have also been reported with respect to N effect on litter decomposition rate, with a positive effect noted in N-limited grassland ecosystem (Hou et al. 2020) and neutral effect observed in N-limited temperate shrubland and boreal forest (Zhang et al. 2021; Xing et al. 2021). Even within a single ecosystem, positive and neutral effects of N addition have been observed on litter decomposition among different species (Song et al. 2018), while positive, negative, and neutral effects of N addition have been detected on litter decomposition at species and community levels (Song et al. 2019). These results suggested that the effect of N addition on litter decomposition showed large variability, which could be attributed to the following reasons. First, some of these discrepancies might be related to the lack of separation between direct and indirect impacts of N addition on litter decomposition (Liu et al. 2009; Li et al. 2017), with improved litter quality induced by indirect effect accelerating litter decomposition, whereas weakened microbial activity induced by direct effect slowing litter decomposition. The meta-analysis results of the present study also indicated that the effect of N addition on litter decomposition should be considered with respect to direct, indirect, and overall effects, which could help to better understand the factors regulating N effect on litter decomposition. Second, field N deposition could play a crucial role in regulating the effect of N addition on litter decomposition, with different atmospheric N deposition levels exerting stimulation, inhibition, and neutral effects (Knorr et al. 2005). Third, the impacts of N addition on litter decomposition rate may be closely related to soil nutrients status and hydrothermal conditions (Hobbie 2008). The regional meta-analysis results obtained in the present study also demonstrated that the effect of N addition on litter decomposition was strongly correlated with the experimental duration, form of N fertilizer, and N addition rates. Numerous studies on Chinese grasslands have reported that short-term N addition had a nonsignificant positive effect on litter decomposition, because short-term N addition did not notably influence the soil microbial activity (Treseder 2008; Jian et al. 2016). The findings of the present study emphasized that long-term N addition directly decreased litter decomposition from site to region owing to changes in the decreasing soil enzymes activities.

To examine the impact of N addition on the decomposition rates of different litter types, the slope of the relationship was compared based on regression models. The results indicated that the slope of litter decomposition rates and N addition rates did not significantly differ among the three litter species, suggesting that the effect of N addition on litter decomposition did not notably vary with different plant litter quality with three functional groups in the studied alpine steppe. However, this result is not consistent with the findings of Zhang et al. (2016), who revealed that the N negative effect on the decomposition of higher quality litter was stronger than that on the decomposition of lower quality litter. The data obtained in the present study showed that the initial N concentration in the litter was highly correlated with the litter decomposition rate ($R^2 = 0.84$), which might imply that the soil microorganisms involved in litter decomposition largely depended on the initial N concentrations in the experimental litter.

## Factors regulating the effects of N addition on litter decomposition

Soil enzymes activities also play a vital role in predicting the biology of plant litter decomposition (Hobbie et al. 2012; Song et al. 2018; Wu et al. 2019; Shen et al. 2021). In the present study, the litter decomposition rates were strongly related to most of the soil enzymes activities, but their correlations were relatively weak ($R^2 < 0.20$), indicating that N addition might affect microorganisms-related processes. However, the present study only investigated the effect of long-term N addition on the topsoil enzymes activities, considering that there could be a spatial disconnection between the variables in the topsoil and the corresponding properties in litter. Previous studies have also shown that N addition consistently decreased the soil microbial activities, further inhibiting litter decomposition (Fang et al. 2007; Liu et al. 2009; Lv et al. 2013). These findings indicated that soil enzymes activities could be an important factor regulating litter decomposition in the context of increased atmospheric N deposition.

Plant litter quality also plays a crucial role in regulating the litter decomposition rate in response to N addition (Knorr et al. 2005; Zhang et al. 2016). In the present study, the litter decomposition rate was positively correlated with litter N:P ratio, but negatively correlated with litter C:P ratio, suggesting that the initial litter P concentration played an important role in regulating litter decomposition depending on the relative changes in litter P concentration. This finding is partly consistent with the results of Shen et al. (2021), who observed that the litter decomposition rates were negatively correlated with the litter C:P and N:P ratios in temperate forest. Similarly, another study also reported that a higher litter C:P ratio usually resulted in slower litter decomposition in tropical forest (Chen et al. 2016). These findings suggested that litter decomposition could be limited by P availability. Moreover, our previous study in the same sites showed that long-term N addition could significantly increase dominant plant P resorption efficiency and intensify P limitation (Su et al. 2021).

In the present study, the correlation between litter decomposition rates and soil factors (soil pH, AN, and enzymes activities) was weak, with $R^2$ ranging from 0.09 to 0.47. However, most of the initial litter traits were highly correlated with the litter decomposition rate. These results suggested that litter quality had stronger effects on litter decomposition than soil factors. Similarly, previous studies have also indicated that litter species traits, such as litter N and P content, were the predominant factors affecting litter decomposition rate (Cornwell et al. 2008; Mahaney 2009; Hu et al. 2018). Thus, the results of the present study revealed that litter quality and the changes in N-induced soil factors played an important role in controlling litter decomposition, and that the current study indicated that long-term N addition significantly slowed litter decomposition rate in Chinese grassland.

Implication for understanding N effect on ecosystem functioning

Our findings have important implications for understanding the impact of N addition on ecosystem structure and functioning of semiarid grasslands. First, long-term N addition consistently slowed litter decomposition in semi-arid grassland in China, which meant that long-term N addition contribute to nutrients retained in litter, intensify nutrient unbalance, and would weaken litter-mediated nutrient cycling (Wei et al. 2022). Second, previous studies examined the effect of short-term N addition on litter decomposition (Liu et al. 2006; Liu et al. 2009), and our study indicated that N negative effect on litter decomposition increased over time. This suggests that long-term N deposition affecting litter decomposition may be underestimated. In addition, the response of a critical threshold value of litter decomposition rate to N addition is 50–150 kg N ha$^{-1}$ year$^{-1}$, at which range with a shift from negative to positive impacts, which improved our understanding about N enrichment on litter decomposition and nutrient turnover.

## Conclusions

This study examined the impact of N addition on litter decomposition rate by combining field experimental observations with regional meta-analysis. The results indicated that long-term N addition consistently decreased litter decomposition, and the N negative effect became stronger with the increasing N addition rates. Among several factors, initial litter quality and soil enzymes activities were notably crucial to the regulation of litter decomposition rate in response to long-term N addition, with initial litter quality being a more important determinant. The meta-analysis results showed short-term N addition had a nonsignificant positive effect on litter decomposition, whereas long-term N addition inhibited litter decomposition. The effects of N addition on litter decomposition depended on the form of N fertilizer, experimental duration, and N addition rate. Overall, our results demonstrated that long-term N addition consistently slowed litter decomposition, with the N negative effect on litter decomposition increasing with the experimental duration. This meant that long-term N addition contributes to nutrients retained in litter and would weaken litter-mediated nutrient cycling.

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**Data availability** All data are available from the corresponding author on reasonable request.

**Declarations**

**Competing interests** We declare no conflict of interests and all the authors have approved the manuscript.

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