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RESEARCH ARTICLE

Forest soil acidification consistently reduces litter decomposition irrespective of nutrient availability and litter type

Ying Shen[1,2] | Dashuan Tian[1,3] | Jihua Hou[4] | Jinsong Wang[1] | Ruiyang Zhang[1] | Zhaolei Li[1] | Xinli Chen[5] | Xuehong Wei[6] | XinYu Zhang[1] | Yicheng He[1,4] | Shuli Niu[1,3]

[1]Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China

[2]CAS Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Beijing, China

[3]College of Resources and Environment, University of Chinese Academy of Sciences, Beijing, China

[4]Key Laboratory for Forest Resources & Ecosystem Processes of Beijing, Beijing Forestry University, Beijing, China

[5]Faculty of Natural Resources Management, Lakehead University, Thunder Bay, ON, Canada

[6]Resources & Environment College, Tibet Agricultural and Animal Husbandry University, Nyingchi Tibet, China

Correspondence
Dashuan Tian
Email: tiands@igsnrr.ac.cn
Shuli Niu
Email: sniu@igsnrr.ac.cn

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Abstract

1. Nitrogen (N), phosphorus (P) and acid deposition are co-occurring in many ecosystems, likely with complex interactive effects on litter decomposition.
2. Few studies have been conducted to distinguish the interactive effects of these three factors on forest litter decomposition. Thus, we performed a 5-year litter decomposition experiment with N, P, acid addition in a temperate forest of Changbai Mountain in China, including four litter types from *Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis* and their mixtures.
3. Our results showed that acid addition consistently reduced litter decomposition rate, irrespective of nutrient addition or litter types. In contrast, N and P addition had less impact on litter decomposition. Litter decomposition rate linearly reduced with decreasing soil pH, but positively increased with soil N availability. No relationship was found between soil P availability and litter decomposition. Soil enzyme activity played a key role in regulating litter decomposition response, such as acid phosphatase, xylosidase, N-cacetyl-b-D-glucosaminidase and α-1,4 glucosidase. Besides, low-quality litter (i.e. high C concentration, C:N and C:P ratio) amplified the negative effect of soil acidification on litter decomposition.
4. This study suggests that soil acidification consistently decelerates litter decomposition in temperate forests, which is independent of soil nutrient availability and litter types. The intensifying soil acidification with continuous N deposition in the future will greatly reduce litter nutrient return to soil, increasing the risk of multiple soil nutrient limitation.

KEYWORDS
enzyme activities, litter decomposition, nitrogen and phosphorus deposition, soil acidification, temperate forest

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1 | INTRODUCTION

Litter decomposition, a fundamental ecosystem process, plays a key role in driving ecosystem nutrient cycling (Attiwill & Adams, 1993; Prescott, 2010). Atmospheric nitrogen (N), phosphorus (P) and acid deposition are simultaneously occurring among many ecosystems, likely altering soil nutrient availability and causing acidification (Meng et al., 2019; Tian & Niu, 2015; Tian et al., 2016; Zhu et al.,2016). Though litter decomposition may be sensitive to soil nutrient availability, acidification and their interactions (Ferreira et al., 2016; Hobbie & Vitousek, 2000; Makkonen et al., 2012), few experiments have been conducted to systematically distinguish the interaction effects of these three drivers on litter decomposition.

The individual effects of N or P addition on litter decomposition are found to be highly variable, ranging from positive to negative (DeForest, 2019; Hou et al., 2020; Kaspari et al., 2008; Zhang, Chen, et al., 2018). For example, low N input normally stimulates microbial processes (i.e. biomass and enzyme activities) and litter decomposition (Currey et al., 2010; Zhang, Luo, et al., 2018). In contrast, high N enrichment could intensify P limitation and soil acidification, further inhibiting microbial decomposition (Meng et al., 2019; Tian & Niu, 2015; Zhang, Chen, et al., 2018). Furthermore, P addition accelerates litter decomposition in P-limited tropical forests (Kaspari et al., 2008; Sarah & Peter, 2000), but it decelerates litter decomposition in N-limited temperate forests (Daryl & Sinsabaugh, 2006; DeForest, 2019). It seems that initial soil P availability may be a crucial factor to drive variable litter decomposition responses to P input. For soil acidification, it is usually found to suppress microbial processes and litter decomposition (Lv et al., 2014; Meng et al., 2019; Xiao et al., 2020).

Based on the above reasoning, it is expected that high N enrichment and soil acidification might amplify the negative effects of soil H^+ on microbial processes and litter decomposition (positive interaction; Růžek et al., 2021; Tie et al., 2020). However, the combined N and P input may have less negative effect on microbial decomposition than high N input alone (Chen et al., 2013), because P addition alleviates the intensified P limitation caused by N enrichment (Huang et al., 2018; Yang, 2017). Furthermore, soil acidification likely enhances P availability in alkaline and neutral soil (Andersson et al., 2015; Li et al., 2012), but it reduces P availability in acidic soil (Eghball et al., 1990; Yang et al., 2013). Hence, soil acidification and P availability may have complex interactions on microbial decomposition.

In addition to microbial processes, litter type or quality also plays a vital role in affecting litter decomposition. Generally, litter with lower C but higher N and P concentration has a faster decomposition rate (Aerts, 1997; Sarah & Peter, 2000; Sun et al., 2018). This suggests a widespread co-limitation of litter N and P for microbial decomposition (Ochoa-Hueso et al., 2020). Thus, the combination of N and P input may have a greater positive interaction on decomposition rate with lower litter N and P (Thirukkumaran & Parkinson, 2002). In contrast, the negative effects of high N enrichment, soil acidification and their interactions may be intensified on litter decomposition with lower quality (Růžek et al., 2021). Furthermore, soil water and temperature may also modify litter decomposition response. Normally, high soil water and temperature accelerate litter decomposition (Liu et al., 2017; Suseela & Tharayil, 2018). Recent studies found that stimulated above-ground biomass by nutrient enrichment could reduce soil temperature but enhance soil moisture via the stronger 'shading effect' with increasing plant cover (Chen et al., 2013; Knorr et al., 2005; Wang et al., 2019). This indicates that any change in soil water and temperature caused by nutrient enrichment perhaps mediates litter decomposition response. Therefore, quantifying and comparing the relative importance of these mechanisms will deepen our understanding of litter decomposition dynamic under changing environments.

In a temperate forest of Changbai Mountain in China, we conducted a 5-year experiment of N, P and acid addition, yearly monitoring litter decomposition rate. Through measuring the decomposition dynamics of four types of leaf litters, the associated microbial processes and soil properties over 5 years, we aimed to explore the responses and mechanisms of litter decomposition to experimental addition of N, P, acid and their interactions. The specific questions are as follows: (a) How N, P and acid addition individually and interactively influence litter decomposition? (b) Which mechanisms are important to determine litter decomposition response?

2 | MATERIALS AND METHODS

2.1 | Experiment site

Our experiment was implemented in a temperate forest located in Changbai Mountain of northeast China (42°24′2″N, 128°05′42″E). The experimental area is characterized by temperate continental mountain climate. Mean annual temperature and precipitation are 2.8°C and 731 mm, respectively. The investigated ecosystem is a mixed forest of conifer and broad-leaved species, dominated by *Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis* and *Acer mono*. Initial soil pH is 5.15, and soil total N and P concentration are 3.55 g/kg and 0.86 g/kg, respectively.

2.2 | Experimental design and field sampling

In May 2013, we established an experiment of N, P and acid addition, with a randomized block design. Treatments involved control, N addition (10 g N m^{-2} yr^{-1}), P addition (10 g P m^{-2} yr^{-1}), acid addition (A, 15 ml acid m^{-2} yr^{-1}) and three combined treatments of N+P, N+A and P+A. Totally, there were 28 plots (10 m × 15 m) with 7 treatments × 4 replicates. To be clear, we next used the consistent terms 'acid addition alone' for the single factor treatment, and 'all acid treatments' for those of acid addition, N+A and P+A. N and P fertilizers were NH_4NO_3 and NaH_2PO_4, respectively, and acid was diluted H_2SO_4, which were added by six times from May to October in each year since 2013. In each time, we dissolved the fertilizer or diluted acid solution in 75 L water and then added them to each plot by sprayer, assuring treatment effects as even as possible except control plots.

TABLE 1 Effects (*F* and *p* value) of N, P, acid addition and their interactions on litter decomposition rates among four litter types

		Pinus koraiensis		*Tilia amurensis*		*Quercus mongolica*		All species	
Treatment	***df***	***F* value**	***p* value**	***F* value**	***p* value**	***F* value**	***p* value**	***F* value**	***p* value**
N	1	0.92	0.35	0.01	0.93	0.23	0.64	2.53	0.13
P	1	1.32	0.26	0.21	0.65	0.18	0.68	0.74	0.40
Acid	1	16.20	**0.001**	17.90	**<0.001**	6.21	**0.02**	27.63	**<0.001**
N × P	1	0.36	0.55	0.30	0.59	1.48	0.24	0.54	0.47
N × Acid	1	1.07	0.31	1.38	0.25	1.66	0.21	1.72	0.20
P × Acid	1	2.47	0.13	0.10	0.76	0.02	0.88	0.53	0.47

Bold indicate the significant of *p* values.

In September 2013, fresh leaf litter of *P. koraiensis*, *Q. mongolica* and *T. amurensis* was collected randomly from the place near our experiment site. Furthermore, we evenly mixed the litter of three species to constitute a mixed litter type. Totally, we had four types of leaf litter in our decomposition experiment. Each type of litter was thoroughly mixed and air-dried, and 10 samples in each litter type were randomly taken to measure initial litter quality (C, N and P concentration; Table S1). Before the decomposition experiment, we weighed about 9 g (dry weight) of each litter sample for *P. koraiensis*, *T. amure nsis*, *Q. mongolica* or mixture of all species (equal proportion). Litter samples were then put into litterbags (25 cm × 15 cm), made of polyethylene mesh with the hole sizes of 0.2 mm (below) or 0.5 mm (above). In each plot, 32 litterbags were randomly placed above the ground (4 sampling year × 4 litter types × 2 bags per sampling time), generating a total of 896 litterbags (32 bags × 28 plots).

Every October, we sampled two litterbags of each litter type in each plot. All samples were carefully cleaned by water to remove the impurity, which were then oven-dried for 48 hr at 60°C and weighed. In addition, fresh soil samples were randomly collected at 0–10 cm depth in each plot from 2013 to 2017, and then sieved through 2-mm meshes. One part of soil sample was stored in a freezer, in order to measure soil N availability as well as microbial biomass C and enzymes activities (acid phosphatase, xylosidase, NAG, α-1,4 glucosidase and β-1,4 glucosidase). The other part of air-dried soil was used to measure soil available P and pH. In addition, field soil temperature and moisture were monitored four times during growing season every year.

2.3 | Chemical analyses

Initial litter C and N concentrations were measured by an elemental analyzer (vario E1 III, Elementar Analysensysteme GmbH). Molybdenum stibium anti-reagent colour method was employed to determine litter P concentration (Liu et al., 2016). Additionally, soil available N and P were first extracted by 1.0 M KCl solution and NH_4F–HCl solution, respectively. Then an automatic continuous flow analyzer (AA3, SEAL, Analytical GmbH) and molybdenum antimony spectrophotometer (Bray & Kurtz, 1945) were correspondingly applied to measure soil N and P availability. Microbial biomass C was first extracted by 0.5 M K_2SO_4 after chloroform fumigation (Brookes et al., 1985), and then measured by TOC analyzer (LIQ TOC II/mutiNC3100, Elementar Analysensysteme GmbH). Microbial enzyme activities were assayed spectrophotometrically (Lv et al., 2013). Soil pH was determined by pH meter. The average values of these soil variables during 2013–2017 were used for following analyses.

2.4 | Data analysis

We calculated decomposition rates (*K*) over time by using an exponential decomposition model (Wider & Lang, 1982), *K* is defined as follows:

$$X = e^{-kt},$$

X is the percentage of remaining litter mass versus initial mass at time *t*, and *k* is the constant of decomposition rate against time. Here the decomposition model was set the percentage of initial litter mass to be 100%. Moreover, we found that this traditional model was fitted well by our data across different treatments and litter types (Figure S1).

First, three-way ANOVA was adopted to analyse the main effects of N, P, acid addition and their interactions on the decomposition rate (*K*) among four litter types. Second, *t*-test was used to compare the difference in decomposition rate of combined treatments (N+P, N+A or P+A) versus control treatment. Third, simple linear regression was employed to analyse the relationships of decomposition rate with soil pH, nutrient availability, microbial biomass and enzyme activities, initial litter quality, soil temperature or water content. In addition, all the statistical analyses were performed by the SPSS 21.0 software, and the graphs were made by the Sigmaplot 12.5 software.

3 | RESULTS

3.1 | Effects of N, P and acid addition on litter decomposition

Overall, our results showed that litter decomposition rate was mainly affected by acid addition, rather than nutrient addition

(Table 1). Specifically, acid addition alone consistently reduced the decomposition rates of four litter types. In contrast, N addition only had a close to marginally significant effect ($p = 0.13$) on litter mixture's decomposition, while N+P addition significantly reduced the decomposition of *P. kaiensis* litter. Similar with acid addition alone, treatments with acid (N+A and P+A) also depressed four litter types' decomposition (Figure 1). No significant interaction was found between acid and nutrient addition (Table 1). In addition, we found similar response patterns of different litter types among all treatments (Figure 1).

3.2 | Factors controlling litter decomposition response

Among different treatments, those with all acid treatments or N addition alone caused a significant reduction in soil pH (Figure S2). Moreover, we further found a significant decrease of litter decomposition rates with reduced soil pH (Figure 2). In addition, we revealed a positive relationship of litter decomposition with soil available N ($p = 0.08$), but no relationship with soil available P or N:P ratio as well as soil temperature or water content (Figure 3).

Meanwhile, we found a positive relationship of decomposition rates with microbial biomass C ($R^2 = 0.120$) and most soil enzymes activities, such as N-cacetyl-b-D-glucosaminidase, acid phosphatase, xylosidase and α-1,4 glucosidase ($R^2 = 0.123$–0.183; Figure 4). Only β-1,4 glucosidase activity did not influence litter decomposition (Figure 4f). Initial litter quality exerted a significant effect on its decomposition rate as well (Figure 5). Litter decomposition was negatively affected by its higher C concentration, but accelerated by greater N and P concentration. With increasing litter C:N, C:P or N:P ratio, its decomposition rate reduced significantly.

4 | DISCUSSION

This study has some distinct points in comparison with traditional studies (Hou et al., 2020; Knorr et al., 2005; Song et al., 2018; Sun et al., 2018). First, our experiment is the first to fully distinguish the main effects of N, P and acid addition as well as their interactions on litter decomposition. Second, our results revealed the dominant role of soil acidification in inhibiting litter decomposition, which was independent of soil N, P availability and litter type. Third, soil enzyme activity and litter quality were main mechanisms to govern litter decomposition in response to the combined effects of soil nutrient and acidification. Overall, our study indicates that soil acidification will be more important in determining litter decomposition than soil nutrient availability under the context of rapid soil acidification (Meng et al., 2019; Tian & Niu, 2015; Yang et al., 2012), which may potentially weaken forest ecosystem nutrient cycling (Lv et al., 2014).

4.1 | Effects of N, P and acid addition on litter decomposition

Our results demonstrated that all acid treatments consistently suppressed litter decomposition in the temperate forests of Changbai Mountain. Moreover, the linear decrease of litter decomposition rate with soil acidification indicates that litter decomposition in this forest is quite susceptible to soil acidification caused by N or acid deposition, both of which keep increasing in the past decades (Duan et al., 2016; Gao et al., 2018; Zhang et al., 2010; Zhu et al., 2016). This result is partly supported by a recent global meta-analysis study revealing the negative impact of soil acidification on microbial processes (Meng et al., 2019). Considering widespread soil acidification caused by N enrichment (Tian & Niu, 2015) and the continuous accumulation of future N deposition in many terrestrial ecosystems

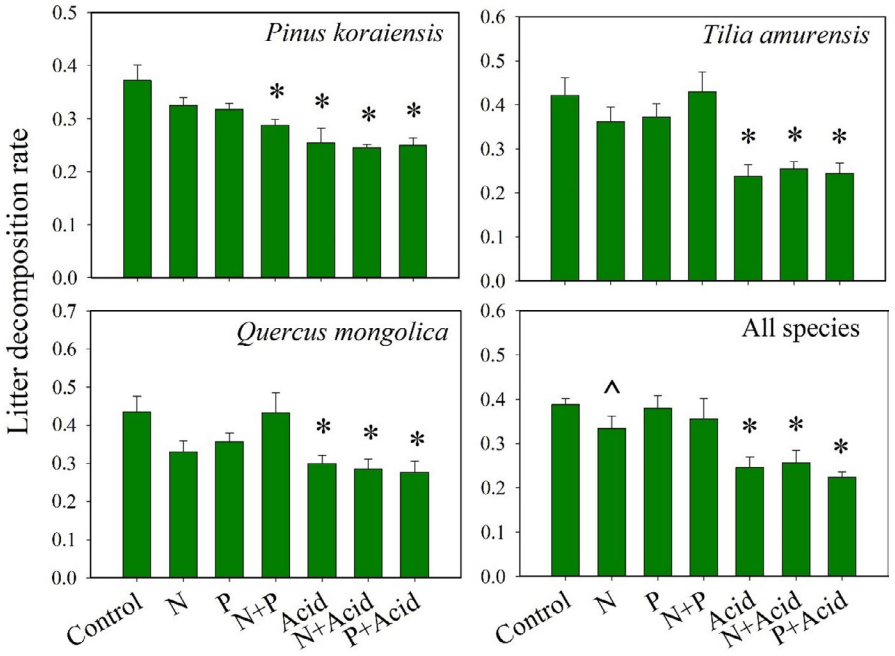


FIGURE 1 Effects of N, P, acid addition and their combined treatments on the decomposition rates of four litter types (*Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis*, mixture of all species). Bar height indicates decomposition rates (*K* value, Equation 1) with standard error. '*' and '^', respectively, mean significant and marginally significant difference of treatments versus control

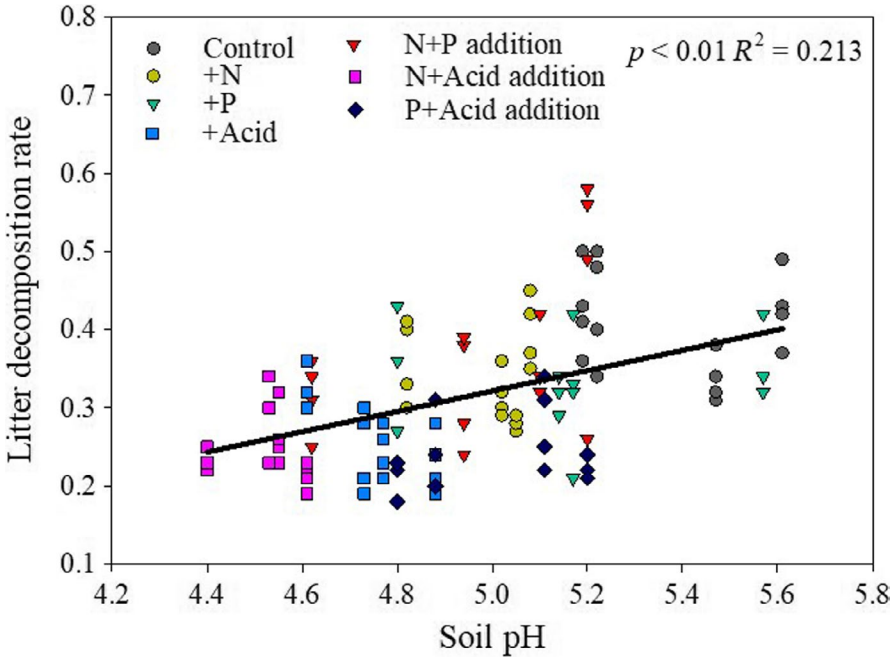


FIGURE 2 The relationship of litter decomposition rate with soil pH. Different colours represent different treatments

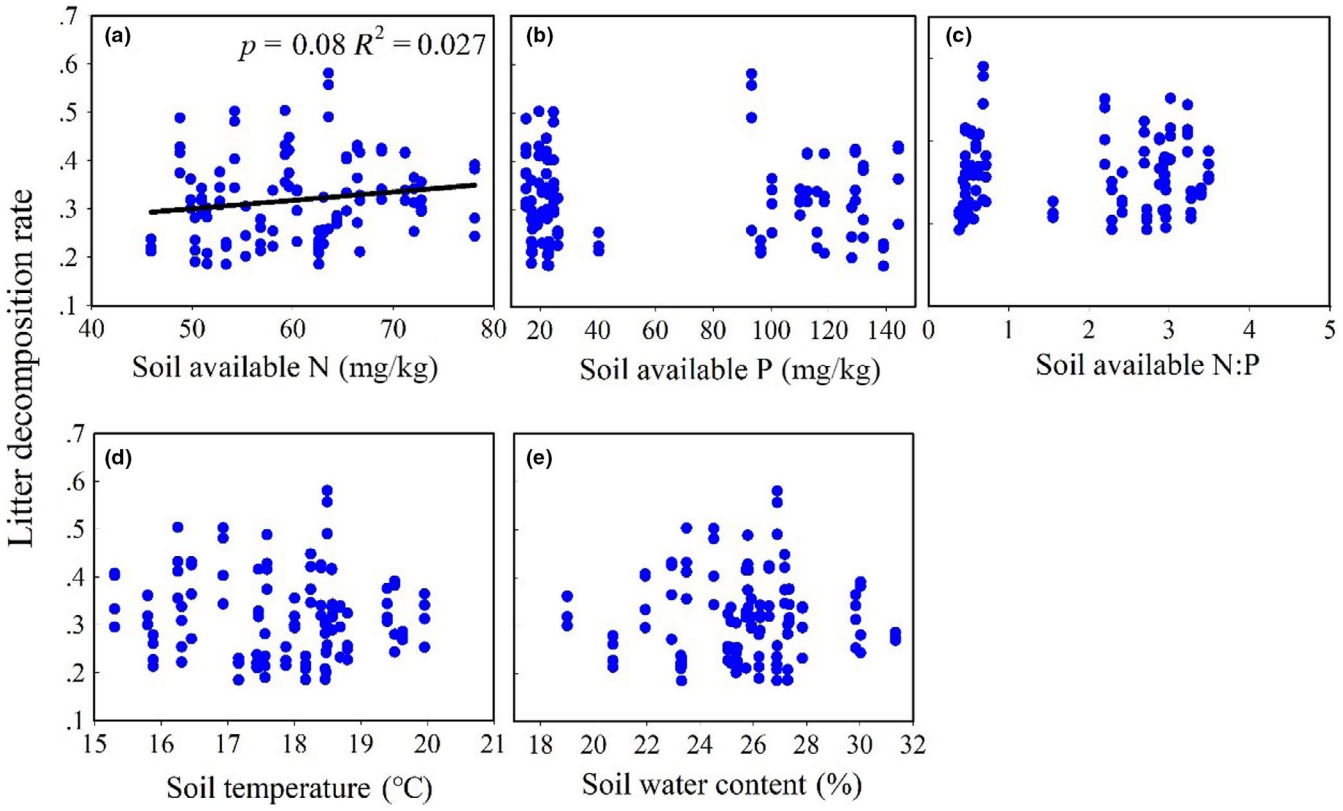


FIGURE 3 Relationships of litter decomposition rates with soil nutrient availability (a–c: soil available N, available P and N:P ratio) or with soil temperature (d) and water content (e) across all treatments

(Zhu et al., 2016), soil acidification will play an increasingly important role in weakening ecosystem nutrient cycling (Lv et al., 2014; Meng et al., 2019). However, we did not find any interactive effect of acid addition alone versus N or P addition, which indicates that the negative impact of soil acidification on litter decomposition does not amplify or fade with soil nutrient availability. In addition, similar patterns were found among four litter types in response to all acid treatments, denoting that the acidification impact of litter decomposition is hardly changed among different litter types.

Inconsistent results were found in previous studies for N effects on litter decomposition, with a positive effect in N-limited condition but negative effect in high-N condition (Chen et al., 2013; Knorr

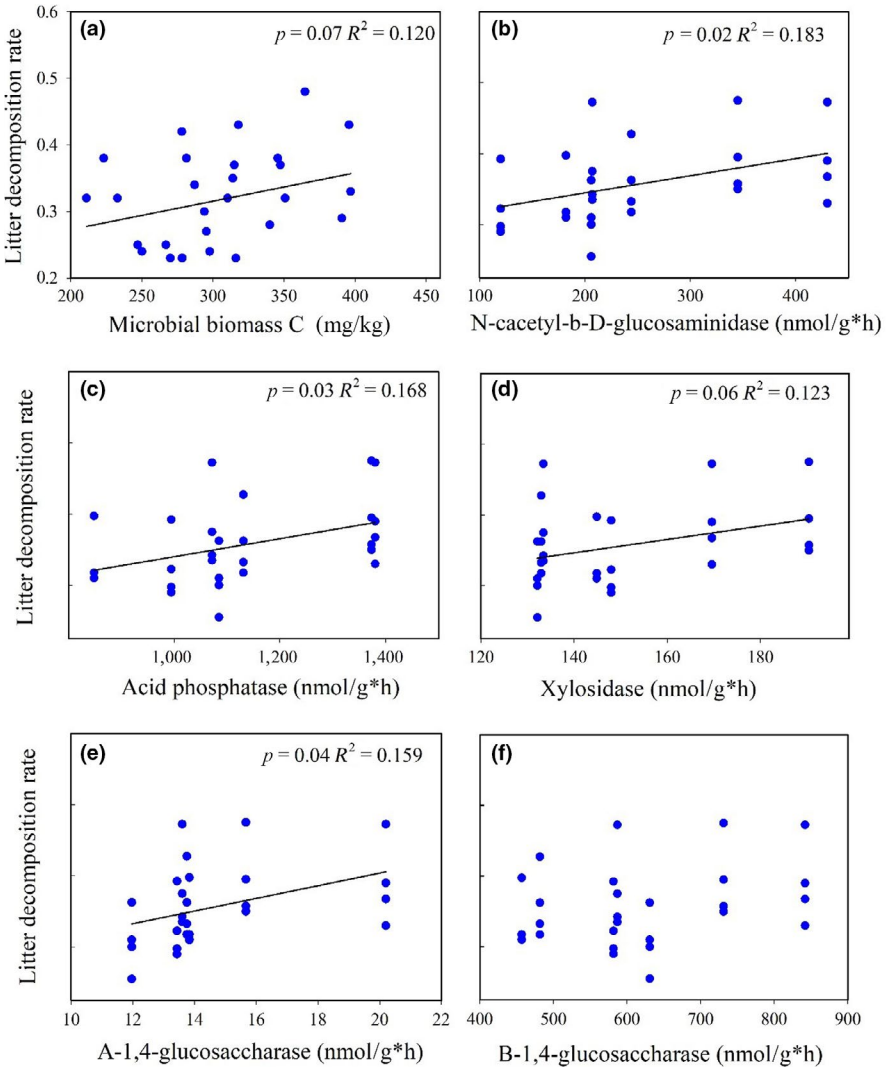


FIGURE 4 Relationships of litter decomposition rates with microbial biomass C and soil enzymes activities (N-cacetyl-b-D-glucosaminidase, acid phosphatase, xylosidase, α-1,4 glucosidase and β-1,4 glucosidase) across all treatments

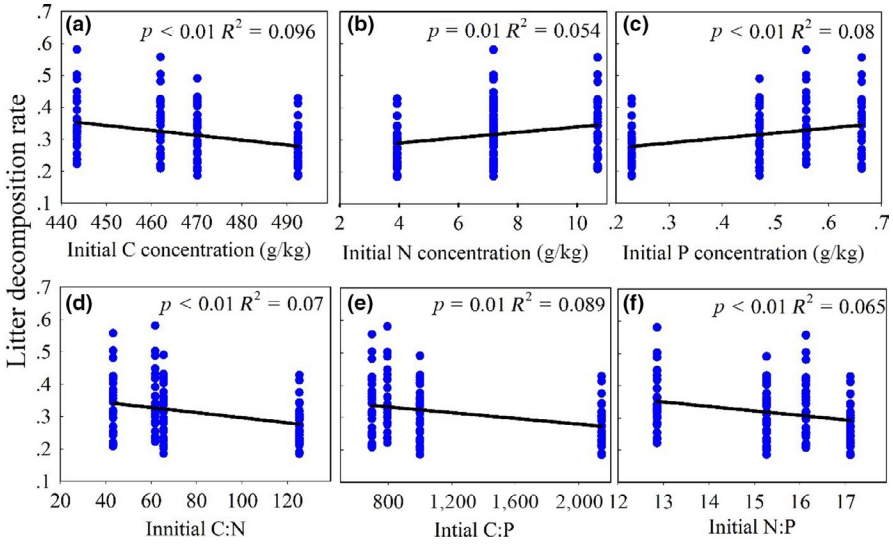


FIGURE 5 Relationships of litter decomposition rates with its initial quality (a–c: C, N and P concentration, and d–f: C:N, C:P and N:P ratio) across all treatments

et al., 2005). Our results revealed that N addition had a minor impact on litter decomposition rates in temperate forest. This may be due to the balanced effect of directly increasing soil N availability (positive effect) and indirectly decreasing soil pH (negative effect) under N enrichment. Though this temperate forest is originally N limited (Shen et al., 2019), the continuous and high N deposition in recent decades has largely lessened ecosystem N limitation, further accelerating soil acidification (Li et al., 2018; Zhu et al., 2016).

Indeed, we found a significant pH decrease of 0.38 after 5 years of N addition, and a positive relationship of litter decomposition with soil N availability. These indicate that high N-induced positive effect of increasing soil N availability may be reversed by soil acidification impact on litter decomposition in this temperate forest. Moreover, a recent global meta-analysis revealed that continuous N enrichment has intensified soil acidification (Tian & Niu, 2015). This signifies that future N deposition may universally inhibit litter decomposition in temperate forests.

Among four litter types, we only found a significantly negative effect of N+P addition on *P. koraiensis*'s litter decomposition, which is partly supported by another litter decomposition study in temperate forest (DeForest, 2019). This negative response of litter decomposition to N+P addition may be due to the combined effects of soil acidification caused by N addition and decreasing 'microbial P mining' effect induced by P addition (Daryl & Sinsabaugh, 2006). The 'microbial P mining' mechanism proposes that microbial P mineralization could be stimulated by P limitation to alleviate ecosystem P stress (Daryl & Sinsabaugh, 2006; DeForest, 2019). Conversely, P addition depresses this mining effect, further decelerating microbial decomposition rate. These differently potential mechanisms underlying litter decomposition responses to N versus P addition require future efforts to test and address them in detail. Altogether, these indicate that soil acidification may become dominant in inhibiting litter decomposition with future continuous N deposition.

4.2 | Mechanisms underlying litter decomposition response

Microbial biomass and soil enzyme activities are directly biologic predictors for litter decomposition (Bastias et al., 2017; Mora-Gómez et al., 2018; Rietl & Jackson, 2012; Wu et al., 2019). In this study, we found that most soil enzyme activities (i.e. xylosidase, N-cacetyl-b-D-glucosaminidase, α-1,4glucosidase, acid phosphatase) and microbial biomass C had positive relationships with litter decomposition. This suggests the vulnerability of these microbial-related functions to soil acidification under N and acid addition. Similarly, previous studies also found that soil acidification generally reduces microbial biomass and enzyme activities related to C and N cycling, further suppressing litter decomposition (Lv et al., 2014; Meng et al., 2019). These suggest that microbial biomass and enzyme activities are likely main mechanisms underlying litter decomposition in face of nutrient enrichment and soil acidification.

Initial litter quality also played an important role in regulating litter decomposition response to nutrient enrichment and soil acidification. Consistent with previous studies (Aerts, 1997; Sarah & Peter, 2000; Sun et al., 2018), we found a decrease in litter decomposition rates with low litter quality (i.e. high C concentration, C:N, C:P ratio), but an increased response with high litter quality (i.e. high N and P concentration). It is because low-quality litter generally contains more difficultly decayed substances, resistant to microbial decomposition (Ferreira et al., 2016). However, we found a negative relationship of litter decomposition with its initial N:P ratio, which indicates a stronger controlling effect of litter P than N concentration. Increasing litter N:P ratio may intensify P limitation for microbial decomposition (Güsewell & Verhoeven, 2006). These together likely suggest a stronger P limitation for decomposition with increasing litter N:P ratio. This result is also partly supported by previous studies revealing that long-term N enrichment has intensified ecosystem P limitation in our experiment region (Li et al., 2018; Shen et al., 2019; Zhu et al., 2016). It seems interesting and deserves future efforts to quantify 'critical litter N:P ratios' for decomposition, indicating the switch of different nutrient limitation (Güsewell & Verhoeven, 2006). Furthermore, these results above imply that the negative effect of N or acid-induced soil acidification may be greater on low-quality than high-quality litter decomposition. It calls our attention to the potential inhibition of litter decomposition by soil acidification under high N or acid deposition, especially those ecosystems with low-quality litter. This inhibition of litter decomposition will substantially decelerate ecosystem nutrient cycling, thus hampering ecosystem functions.

In addition, we did not find any regulation impact of soil water or temperature, different from previous studies revealing the positive effect of soil water and temperature on litter decomposition (Liu et al., 2017; Suseela & Tharayil, 2018). This may be largely due to a small spatial variation of soil water (24.3–27.3%) and temperature (16.9–19.1°C) across our experimental treatments plus a relative high ambient precipitation (731 mm) and wide ambient temperature range. On the whole, all these results indicate that soil enzyme activities and litter quality are important determinants in governing litter decomposition responses to nutrient enrichment and soil acidification.

5 | CONCLUSIONS

Our study fully distinguishes the main and interaction effects of N, P and acid addition on leaf litter decomposition in a temperate forest. We found the vital role of soil acidification in inhibiting litter decomposition, which was less likely affected by soil N, P availability or litter type. Among several mechanisms, soil enzyme activities and initial litter quality were important to determine litter decomposition response. All these results suggest that soil acidification will become more important in inhibiting litter decomposition in the context of N, P and acid deposition. This negative impact of soil acidification likely reverses the positive impact of increasing N availability on litter decomposition under N enrichment scenario, further decelerating ecosystem nutrient cycling and thus functions. Furthermore, these complex effects of soil nutrient and acidification revealed in this study should be fully considered in earth models.

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CONFLICT OF INTEREST

The authors declare no conflicting interests. Shuli Niu is an Associate Editor of Functional Ecology, but took no part in the peer review and decision-making processes for this paper.

AUTHORS' CONTRIBUTIONS

D.T. and S.N. conceived the ideas; Y.S. and D.T. performed the experiments and led the writing, and all authors contributed to the writing and the revision of the manuscript.

DATA AVAILABILITY STATEMENT

Data are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.08kprr51j (Shen et al., 2020).

ORCID

Ying Shen https://orcid.org/0000-0002-6874-3500
Dashuan Tian https://orcid.org/0000-0001-8023-1180
Jinsong Wang https://orcid.org/0000-0002-3425-7387
Xinli Chen https://orcid.org/0000-0003-0542-5959
XinYu Zhang https://orcid.org/0000-0001-8135-2144
Shuli Niu https://orcid.org/0000-0002-2394-2864

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