Forest Ecology and Management 400 (2017) 123–128

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Effects of nutrient additions on litter decomposition regulated by phosphorus-induced changes in litter chemistry in a subtropical forest, China

Zemei Zheng [a,b,*], Meiliban Mamuti [a,c], Heming Liu [a], Yuqin Shu [a], Shuijin Hu [b,d], Xihua Wang [a], Binbin Li [a], Li Lin [a], Xu Li [a]

[a] Tiantong National Forest Ecosystem Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China
[b] Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695, USA
[c] Poskam No.1 Middle School, Kaishi, Xinjiang 844800, China
[d] College of Resources and Environmental Sciences, Nanjing Agricultural University, Nanjing 21009, China

ARTICLE INFO

*Article history:*
Received 15 December 2016
Received in revised form 1 June 2017
Accepted 2 June 2017
Available online 9 June 2017

*Keywords:*
Nutrient availability
P limitation
Litter decay
Fertilization

ABSTRACT

Nutrient additions directly alter exogenous nutrient availability in soil, and then affect endogenous nutrient concentration in litter (i.e., litter chemistry), modifying litter decomposition. However, how nutrient-induced changes in litter chemistry interacting with altered soil nutrients affect litter decomposition remain unclear. In this study, three field experiments with reciprocal transplants using litter bags were conducted in a phosphorous (P) limiting subtropical forest with control, nitrogen addition (+N), P addition (+P), and +NP treatments to examine effects of exogenous and endogenous nutrient availability on litter decomposition. Our results showed that, in Experiment I, decomposition of litter collected from the control plots was significantly inhibited by 16% under both +P and +NP treatments and reversed to become net P accumulation from P release compared to that in the control. In Experiment II, since litter collected from +P and +NP plots had higher litter P, lower C/P and N/P, its decomposition was significantly faster in the control plots by 9% and 26%, respectively, with the faster release of N and P in the litter. The *in situ* Experiment III found that +P and +NP treatments reduced litter decomposition by 6% and 14%, respectively, but +N did not affect it compared to the control. Our results indicate that effects of P addition on litter decomposition were mediated by P-induced changes in litter chemistry, which need to be incorporated into land surface models for predicting effects of nutrient deposition on ecosystem C cycling and assessing the climate-biosphere feedbacks.

*Main finding:* Effects of nutrient additions on litter decomposition were regulated by P-induced changes in litter chemistry.

© 2017 Elsevier B.V. All rights reserved.

## 1. Introduction

Litter decomposition is critical for nutrients cycles in terrestrial ecosystems, which is an important process to return nutrients to soils (Attiwill and Adams, 1993). Nutrient availability is widely considered as a controlling factor for litter decomposition, especially at the early stages (Swift et al., 1979; Hobbie, 2005; van Huysen et al., 2013). During this period, immobilizations of nitrogen (N) and phosphorus (P) in litter had often been observed, suggesting the low nutrient availability relative to carbon (C) in litter for decomposers (Gosz et al., 1973; Staaf and Berg, 1981). Meanwhile, litter decomposition constants are often positively correlated with initial litter nutrient concentration but negatively with C/N or C/P (Aber and Melillo, 1991; Melillo et al., 1982).

Although it has been well documented that nutrient availability impacted litter decomposition, relative effects of endogenous (i.e., litter chemistry) and exogenous (e. g., fertilization) nutrient availability on litter decomposition are not well known (Prescott, 1995; Hobbie, 2005; Craine et al., 2007; van Huysen et al., 2016). Altered nutrient availability in litter may have different effects on litter decomposition compared to that from exogenous nutrient supply (Prescott, 1995; Hobbie and Vitousek, 2000) due to the difference of the inherent mechanisms (Hobbie, 2005; Craine et al., 2007; Cheever et al., 2013). Litter decomposition rates often positively correlated with endogenous nutrient availability within a specific

---

* Corresponding author at: 500 Dongchuan Road, Minhang District, Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China.

*E-mail address:* zmzheng@des.ecnu.edu.cn (Z. Zheng).

http://dx.doi.org/10.1016/j.foreco.2017.06.002
0378-1127/© 2017 Elsevier B.V. All rights reserved.

plant or site (Prescott et al., 1992; Hobbie, 2005; Chen et al., 2015), while increased exogenous nutrient availability through N and P fertilization exhibited diverse responses with negative, positive or neutral effects on litter decomposition (Kozovits et al., 2007; Vivanco and Austin, 2011; Chen et al., 2013). A meta-analysis showed that the effect of exogenous N supply on litter decomposition was dependent on site-specific ambient N-deposition level and the amount of N fertilizers as well as soil background levels of nutrient availability (Knorr et al., 2005). Increased endogenous nutrients in litter are preferentially used by decomposers, but exogenous nutrient additions may lead to changes in soil pH and/or decomposer community (Chen et al., 2013; van Huysen et al., 2016), thereby affecting litter decomposition through depressed N or P mining (Craine et al., 2007; Weedon et al., 2009).

Human activity (e.g., fossil fuel burning, deforestation, and fertilizer consumption) had doubled reactive N deposition since the industrial and agricultural revolution (Galloway et al., 2008; Gruber and Galloway, 2008). Such N fertilization led to the direct increase in exogenous nutrient availability, which considerably affected litter decomposition (Fang et al., 2007). On the other hand, N addition can also alter litter chemistry through influencing foliar nutrient stoichiometry and resorption (Kozovits et al., 2007). Nutrient-induced changes in litter chemistry might enhance or alleviate effects of nutrient additions on litter decomposition (van Diepen et al., 2015; Zhang et al., 2016). For example, using the reciprocal litter transplant experiment, van Diepen et al. (2015) found that changes in litter quality induced by a 22-year N deposition reinforced the N-induced suppression of litter decomposition in a mixed hardwood forest. Zhang et al. (2016) found that changes in litter quality could mediate N effect on plant litter decomposition in a subtropical forest. However, how nutrient-induced changes in litter chemistry interacting with altered soil nutrients affect litter decomposition remain unclear (Hobbie and Vitousek, 2000; Finn et al., 2015; Zhang et al., 2016).

Previous studies mainly focused on responses of litter decomposition to N availability in N-limited systems (Aerts and de Caluwe, 1997; Vitousek, 1998; Vestgarden, 2001). However, effects of endogenous or exogenous P availability on litter decomposition in P-limited systems are rare (Hobbie and Vitousek, 2000; Chen et al., 2013; van Huysen et al., 2013). Actually, P availability plays a critical role in the nutrient cycles in terrestrial ecosystems (Kozovits et al., 2007; Chen et al., 2016; van Huysen et al., 2016). For example, Chen et al. (2016) indicated that the woody debris decomposition in their P-limited tropical forest was primarily constrained by P availability. Kozovits et al. (2007) found that litter decomposition rates at the first-year decay responded more strongly to the combined addition of N and P than to fertilization with N or P alone on a dystrophic soil. These results suggested that more attention should be paid on the importance of P availability, especially when P is the limiting resource in terrestrial ecosystems.

In this study, we conducted three field decomposition experiments in a P-limited subtropical forest as suggested by the foliar N/P of 18.77 (Yan et al., 2008). Experiment I was designed to examine direct effects of nutrient additions on litter decomposition by putting the litter collected from the unfertilized plots (control) in N addition (+N), P addition (+P) and +NP plots. Experiment II was to quantify effects of nutrient-induced changes in litter chemistry on its decomposition by putting litter collected from +N, +P and +NP plots in the control. Experiment III was to ascertain the combined effects of nutrient additions and nutrient-induced changes in litter chemistry on litter decomposition by *in situ* decomposition of plant litter under their respective plots. We hypothesized: (1) P addition would stimulate litter decomposition due to the additional P supply to satisfy the microbial P requirement in this P-limited forest; (2) nutrient-induced changes in litter chemistry would enforce the positive effect of P addition on litter decomposition.

## 2. Materials and methods

### 2.1. Study site

The study was conducted in Tiantong Forest Ecosystem Observation and Research Station (29°48′N, 121°47′E, 160 m.a.s.l.). This area is characterized by a subtropical monsoon climate, with a mean annual temperature of 16.2 °C and precipitation of 1374 mm. The stand was harvested in the 1960s and has undergone natural reforestation. The soil type is Acrisol, with a medium-heavy loam texture and an organic layer of roughly 5 cm thick (Song and Chen, 2007; Gao et al., 2014).

### 2.2. Fertilization treatments

Nutrient additions with four treatments (Control: 0 kg N $ha^{-1}$ $yr^{-1}$; +N: 100 kg N $ha^{-1}$ $yr^{-1}$, +P: 15 kg P $ha^{-1}$ $yr^{-1}$ and +NP: 100 kg N $ha^{-1}$ $yr^{-1}$ + 15 kg P $ha^{-1}$ $yr^{-1}$) were conducted in twelve 20 m × 20 m plots in an evergreen broadleaved forest. Each treatment was replicated in triplicate and completely randomly designed. Each plot was enclosed with PVC board inserted into soil at 60 cm depths and separated by at least 10 m from each other. Details of vegetation and soil properties for each treatment are given in Table 1. Since January 2011, fertilizer ($NH_4NO_3$ or $NaH_2PO_3$ in 20 L of water) was applied monthly over the litter layer and continued to be applied throughout the whole period in this study. The control plots received 20 L of water to avoid the throughfall differences among different treatments.

### 2.3. Leaf litter decomposition experiment

The dominant species, *Schima superba*, in fertilization plots was chosen for leaf litter decomposition experiment. Our record showed that *S. superba* had the highest diameter at breast height and richness in the studied forest. Litter was collected in May 2012 (16 months after the first fertilizer application). Only fresh leaf litter on the top litter layer in each plot was collected. The collected litter was cleaned with wet cloth to remove the soil and other possible adhering fertilizer outside of the litter, and then pooled within treatments and air-dried for decomposition.

Experiment I: Litter collected from the control plots was put in +N, +P and +NP plots, respectively, to be decomposed. This experiment was conducted to examine direct effects of nutrient additions on litter decomposition.

Experiment II: Litter collected from the +N, +P and +NP plots was put in the control plots. This experiment was conducted to quantify effects of nutrient-induced changes in litter chemistry on its decomposition.

Experiment III: Litter collected from the control, +N, +P and +NP plots was put under their respective plots. This experiment was conducted to ascertain the combined effects of nutrient additions and nutrient-induced changes in litter chemistry on litter decomposition.

Five collected samples of each plot were oven-dried for 48 h at 65 °C to identify the coefficient between air-dried and oven-dried weight. Another five collected samples of each plot were oven-dried for 48 h at 80 °C to litter chemistry identification. Litter organic C was determined using the oil bath-$K_2CrO_4$ oxidation method (Nelson and Sommer, 1996). Litter N and P concentrations were determined colorimetrically on the Auto Chemical Analysis Meter (SCHMART, LTC.) after the micro-Kjeldahl digestion.

**Table 1**
Initial litter chemistry of *S. superba* leaf litter collected in different fertilization plots; values are means ± SE ($n = 3$). Treatments mean in which litter was collected. Different letters indicate significant differences among treatments ($P < 0.05$).

| Treatments | C (mg $g^{-1}$) | N (mg $g^{-1}$) | P (mg $g^{-1}$) | C/N | C/P | N/P |
|---|---|---|---|---|---|---|
| Control | 568 ± 8.1a | 8.34 ± 0.11a | 0.28 ± 0.02a | 69 ± 1.2b | 2116 ± 69b | 30 ± 2.7b |
| +N | 582 ± 9.1a | 8.80 ± 0.12ab | 0.27 ± 0.01a | 66 ± 1.6ab | 2197 ± 58b | 34 ± 1.4b |
| +P | 575 ± 9.5a | 8.43 ± 0.26ab | 0.36 ± 0.02b | 68 ± 2.7b | 1694 ± 29a | 23 ± 3.7a |
| +NP | 582 ± 7.99a | 9.14 ± 0.21b | 0.39 ± 0.03b | 61 ± 2.0a | 1678 ± 23a | 21 ± 1.0a |

Approximately 10 g of leaf litter was weighed and inserted into a nylon bag (1 mm; 25 cm × 25 cm) before bags were placed in July 2012. In each plot, 3 places were randomly selected for bag placement. Before bags were placed, the surface litter was pushed aside. Then litter bags were placed and ground litter was put back to cover litter bags. A total of 540 litter bags were placed.

One litter bag at each place was collected (3 bags per plot for each treatment) at 78, 104, 131, 165, 200, 226 and 286 days. Litter from the collected litter bags was cleaned, dried for 48 h and weighed. Then litter was smashed to 150 μm sieve and total N and P were determined colorimetrically on the Auto Chemical Analysis Meter (SCHMART, LTC.) after the micro-Kjeldahl digestion.

### 2.4. Data analysis

Litter mass remaining was calculated with litter oven-dried weight divided by initial litter oven-dried weight. Nutrient remaining was calculated by multiplying litter mass remaining and litter nutrient concentration.

An exponential model (Eq. (1)) was used to analyze the relationship between the mass remaining and decomposition time

$$y = e^{-kt} \tag{1}$$

where $y$ is the mass remaining at a specific time $t$, $k$ is the decomposition rate constant ($yr^{-1}$).

One-way ANOVA was used to determine the difference in initial chemical traits of litter collected from different fertilization plots, and to determine nutrient additions and litter chemistry effects on decomposition rate constants. Correlation analysis was used to determine the relationship between the initial litter chemistry and decomposition rate constant and mean value of N or P remaining during the whole decomposition period. Data were natural-log-transformed when normal distribution and homogeneity of variance assumptions were not met. Above statistics were conducted using SPSS 13.0 (SPSS Inc., Chicago, IL, USA). Linear mixed effects models (LMMs) (R3.2.1, R Core Team 2015) were used to determine effects of nutrient additions and litter chemistry on mass remaining, N remaining and P remaining over the decomposition period. Treatments (Control, +N, +P and +NP) were considered fixed factors, and collection time as a random factor. The "lmer" function of lme4 package was used to perform the LMMs (Bates et al., 2013). In Experiment I, fixed factors referred to treatments in which litter was decomposed. In Experiment II, fixed factors referred to treatments in which litter was collected. In Experiment III, fixed factors referred to treatments in which litter was collected and decomposed.

## 3. Results

### 3.1. Initial litter chemistry

Nutrient additions significantly affected the initial leaf litter chemistry, but these effects differed among fertilization treatments (Table 1). Specifically, N addition treatment had no effect on litter chemistry after 16-month fertilization. Litter in the +P plots had higher P concentration and lower C/P and N/P compared to that in the control. Similarly, litter in the +NP plots had significantly higher N and P concentrations, resulting in lower litter C/N, C/P and N/P.

### 3.2. Litter decomposition rates

Litter mass retained 56–66% of their initial mass after 286 days' decomposition. The mass loss dynamics of litter fitted the exponential model very well for all treatments ($R^2 = 0.77–0.97$). In Experiment I and III, litter decomposition rate constants ($k$-values) did not differ among treatments (Table 2). In Experiment II, litter collected from +P and +NP plots had significantly higher $k$-values (0.72 and 0.83 $yr^{-1}$, respectively) compared to litter collected from the control plots (0.66 $yr^{-1}$). $k$-values were only significantly correlated with the initial litter P concentration in Experiment II, but they did not show a significant relationship with any of the litter chemistry in Experiment III (Table 3).

In Experiment I, effects of exogenous nutrient additions on litter mass loss differed among fertilization treatments (Fig. 1a). The +P and +NP treatments significantly inhibited litter decomposition (both $P < 0.001$), but the +N treatment had no effect on litter decomposition ($P = 0.057$). In Experiment II, effect of endogenous nutrient supply on litter mass loss was opposite relative to exogenous nutrient additions (Fig. 1b). Litter collected from the +NP plots decomposed significantly faster ($P < 0.001$) compared to the control. In Experiment III, litter under nutrient additions decomposed significantly slower than that in the control plots (all $P < 0.001$) (Fig. 1c).

### 3.3. Dynamics of litter nutrients

In Experiment I, although litter mostly exhibited net N release over the whole decomposition period under all treatments, exogenous N addition or with P addition together inhibited N release in litter (Fig. 2a, $P < 0.001$ and =0.013 for +N and +NP treatments, respectively). In Experiment II, litter collected from +NP plots (with higher N) released N faster compared to that from the control plots ($P = 0.049$, Fig. 2b). In Experiment III, N release in litter did not show significant difference among treatments (Fig. 1c).

Litter in the control plots mostly exhibited a slow net release of P over the whole decomposition period and litter P remaining was more responsive to nutrient supply than litter N remaining (Fig. 3). In Experiment I, +P and +NP treatments exhibited a net P accumu-

**Table 2**
Decomposition rate constants ($k$-values) of litter at different treatments; values are means ± SE ($n = 3$); Treatments mean in which litter was decomposed for Experiment I, collected for Experiment II, collected and decomposed for Experiment III. Different letters indicate significant differences among treatments ($P < 0.05$).

| Treatment | Experiments | | |
|---|---|---|---|
| | I | II | III |
| Control | 0.66 ± 0.02 a | 0.66 ± 0.02 a | 0.66 ± 0.02 a |
| +N | 0.60 ± 0.04 a | 0.66 ± 0.02 a | 0.57 ± 0.03 a |
| +P | 0.57 ± 0.06 a | 0.72 ± 0.04 b | 0.62 ± 0.15 a |
| +NP | 0.57 ± 0.06 a | 0.83 ± 0.01 c | 0.58 ± 0.02 a |

**Table 3**
Pearson correlation coefficients ($r$) between initial litter chemistry and litter decomposition rate constant ($k$-value), N remaining and P remaining in Experiment II and Experiment III ($n = 4$).

| Litter chemistry | Experiment II | | | Experiment III | | |
|---|---|---|---|---|---|---|
| | *k*-value | N remaining | P remaining | *k*-value | N remaining | P remaining |
| C | 0.464 | −0.401 | −0.405 | −0.993** | 0.055 | 0.469 |
| N | 0.711 | −0.789 | −0.633 | −0.816 | 0.110 | 0.284 |
| P | 0.928* | −0.427 | −0.965* | 0.261 | −0.791 | 0.769 |
| C/N | −0.848 | 0.809 | 0.789 | 0.747 | −0.087 | −0.409 |
| C/P | −0.840 | 0.257 | 0.899* | 0.157 | 0.892 | −0.813 |
| N/P | −0.883 | 0.393 | 0.931** | 0.061 | 0.818 | −0.682 |

* $P < 0.05$.
** $P < 0.001$.

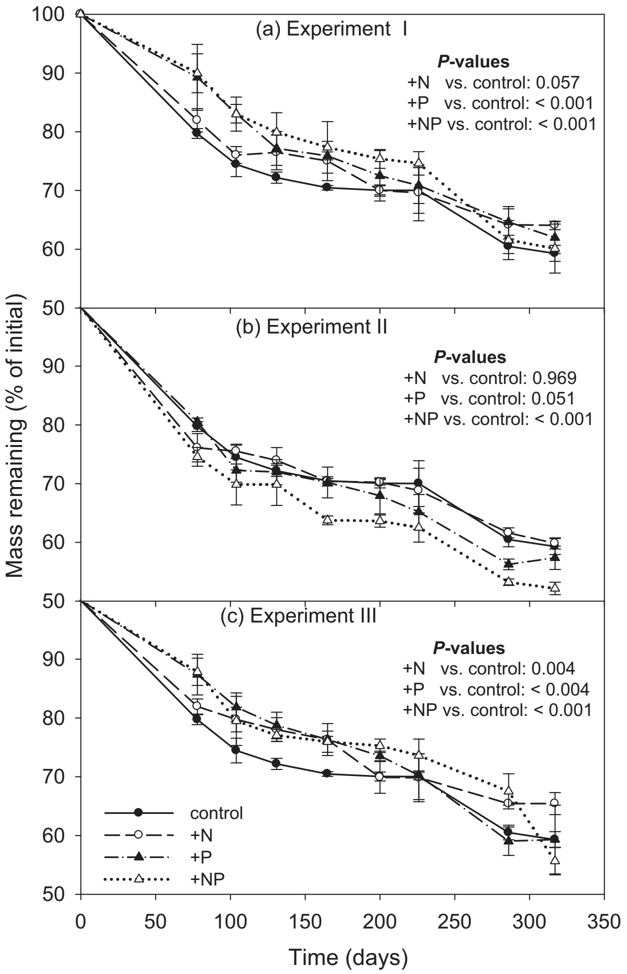

**Fig. 1.** Litter mass remaining over the decomposition period. (a) Litter collected from control plots but decomposed in control, +N, +P and +NP plots. (b) Litter collected from control, +N, +P and +NP plots but decomposed in control plots. (c) *In situ* decomposition of plant litter under their respective fields. Error bars are ±SE of means for $n = 3$. *P*-values for treatment effects based on linear mixed effects model are given.

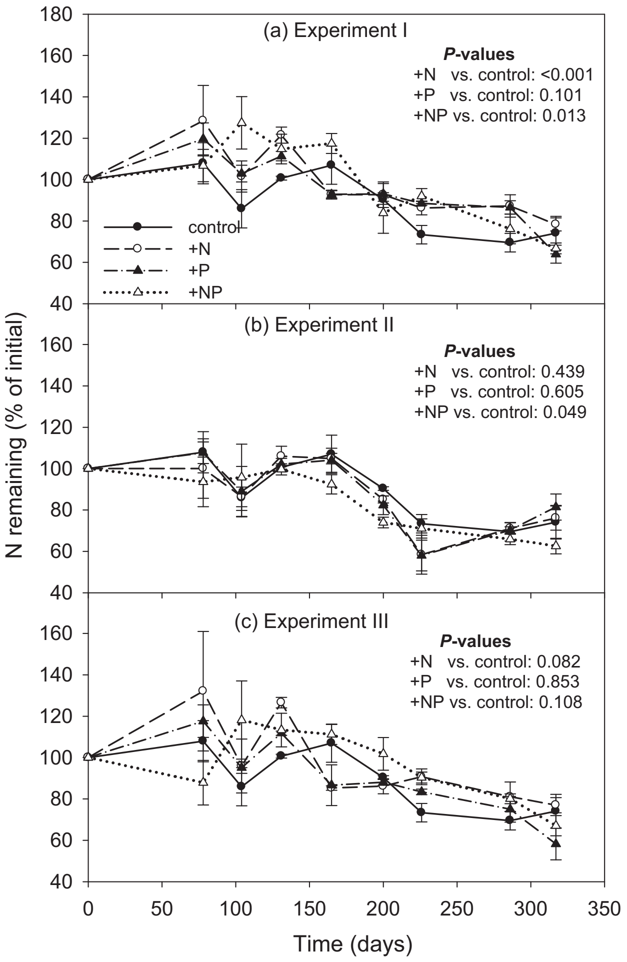

**Fig. 2.** Litter N remaining over the whole decomposition period. (a) Litter collected from control plots but decomposed in control, +N, +P and +NP plots. (b) Litter collected from control, +N, +P and +NP plots but decomposed in control plots. (c) *In situ* decomposition of plant litter under their respective fields. Error bars are ±SE of means for $n = 3$. *P*-values for treatment effects based on linear mixed effects model are given.

lation in litter (Fig. 3a, both $P < 0.001$). In Experiment II, endogenous nutrient supply did not lead to different pattern of dynamics in litter P remaining (Fig. 3b), but the litter P remaining was negatively correlated with P and positively correlated with C/P and N/P (Table 3). Yet, in Experiment III, litter in +P and +NP treatments showed a significant increase in P accumulation over the whole decomposition period (Fig. 3c, both $P < 0.001$).

## 4. Discussions

### 4.1. Different effects of N and P additions on litter mass loss

Diverse effects of N additions on litter mass loss have been observed in forest ecosystems, which were dependent on fertilizer type and site-specific soil nutrient availability (Mo et al., 2006; Jacobson et al., 2011; Chen et al., 2013). Our results showed that +N treatment had no effect on litter mass remaining (Fig. 1a),

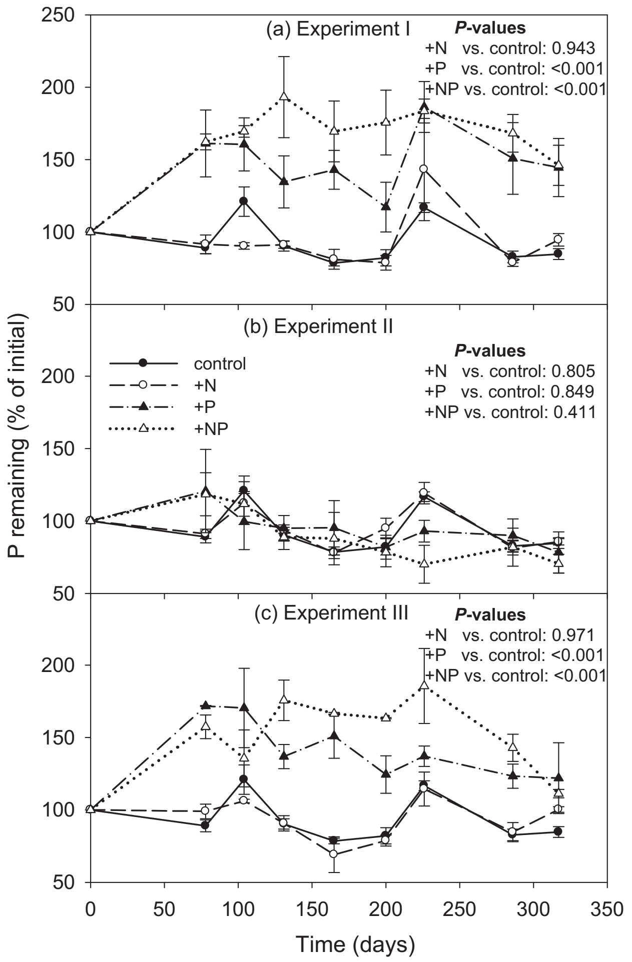

**Fig. 3.** Litter P remaining over the decomposition period. (a) Litter collected from control plots but decomposed in control, +N, +P and +NP plots. (b) Litter collected from control, +N, +P and +NP plots but decomposed in control plots. (c) *In situ* decomposition of plant litter under their respective fields. Error bars are ±SE of means for $n = 3$. *P*-values for treatment effects based on linear mixed effects model are given.

which was possibly related to the early or medium stage of this N-saturated forest in subtropical regions (Wang et al., 2015). In addition, +N treatment did not influence litter chemistry in the studied forest (Table 1), although P was limited as suggested by the foliar N:P (Yan et al., 2008). However, the results were inconsistent with the negative or positive responses of litter mass loss to N addition in previous studies (Hobbie, 2000; Mo et al., 2006; Chen et al., 2013; van Diepen et al., 2015) due to different site-specific soil nutrient availability. Litter decomposition was always inhibited in forests with N oversaturation (Chen et al., 2013; van Diepen et al., 2015) and was stimulated with N limitation (Hobbie, 2000).

It is commonly considered that external nutrient additions would stimulate litter decomposition if fertilizer is a limited nutrient for decomposers (Hobbie and Vitousek, 2000). Thus, the increase in litter decomposition under extra exogenous P supply would be expected as our first hypothesis. However, litter mass loss were significantly inhibited in +P and +NP additions (Fig. 1a) in Experiment I, which was consistent with the results in Chen et al. (2013) but inconsistent with the positive and neutral responses of litter mass loss in Hobbie and Vitousek (2000) and Barantal et al. (2012), respectively. The negative response of litter mass loss to P addition in our P-limiting forest may be related to the suppression of microbial P mining as suggested by Craine et al. (2007), because some microbes used labile C to decompose recalcitrant organic matter in order to acquire P. Instead of spending energy on P acquisition at high C cost (Weedon et al., 2009), decomposers with high P-requirement would prefer to use the exogenous supply of P directly, resulting in the lower rate of litter decomposition in +P and +NP treatments (Fig. 1a).

### 4.2. Litter nutrient dynamics under fertilization

Litter nutrient dynamics can represent the nutrient availability for the decomposer community (Hobbie, 2005). Due to the high N or P relative to C in decomposers, litter always contains insufficient N or P for the decomposers, resulting in the nutrient accumulation in litter during the early decomposition stage (Gosz et al., 1973). Our results showed that +P and +NP treatments stimulated the P accumulation in litter (Fig. 3a), which were also observed in other studies (Chen et al., 2013). The increase in P accumulation under P fertilization might be ascribed to several reasons. Firstly, P fertilization would lead to a more redundant P in soil relative to litter, resulting in the suppression of P mining from litter. Besides, decomposers may also forage P (such as available P under P fertilization) and import into the poor-P litter relative to microbes (Gosz et al., 1973). The suppression of microbial P mining from litter and foraging P to litter from soil microbes together may lead to the P accumulation in litter under +P and +NP treatment in Experiment I (Fig. 3a).

### 4.3. Litter chemistry effect on litter decomposition

Litter chemistry often has a critical control on litter decomposition (Melillo et al., 1982; Berg, 2014; Marklein et al., 2016), as litter decomposition constants are positively correlated with initial litter nutrient concentration and/or the inverse of C/N or C/P ratio (Hobbie, 2005; van Huysen et al., 2013). Our results showed that litter with higher P (lower C/P and N/P) decomposed faster than that in the control (Table 2) and had a significant correlation between litter P concentration and decomposition rate constants or P remaining (Table 3). Other studies with P-fertilized litter also exhibited that litter decomposition were strongly related to initial litter chemistry (van Huysen et al., 2016). The control of litter N or P on litter decomposition may link with decomposer activities (Cheever et al., 2013). Higher nutrient supply in litter means the increase in substrate quantity (more metabolic forms) and quality (easily to be mineralized through leaching), which would satisfy the P acquirement of decomposers in this P-limited forest. This would enhance soil microbial activities (Cheever et al., 2013), and thus litter mass loss was stimulated (Fig. 1b). Our results suggest that the limiting nutrient in litter may function as the primary driver that regulates the litter decomposition.

### 4.4. Interactive effect of litter chemistry with fertilization on litter decomposition

Nutrient-induced changes in litter chemistry could interact with altered soil nutrients by nutrient additions, reinforcing or alleviating the effect of nutrient additions on litter decomposition (Hobbie, 2005; van Diepen et al., 2015; Zhang et al., 2016). Our results showed that the effect of P-induced changes in litter chemistry on litter decomposition was opposite to the direct effect of nutrient additions on litter chemistry and their combined effects (Figs. 1 and 2). These results indicated that effects of nutrient additions on litter decomposition were regulated by P-induced changes in litter chemistry in our forest. The mediation effect of litter chemistry with nutrient additions on litter decomposition was also observed by Hobbie (2005) and Zhang et al. (2016). The inconsistent effects of exogenous nutrient additions and endogenous nutrient supply on litter decomposition (Figs. 1 and 2) were probably due to the decomposer nutrient use strategy and controlling mechanisms of endogenous nutrient availability on litter decomposition. In this P-limited forest, decomposers with high P-requirement prefer to use the exogenous nutrient with lower energy cost instead of mining the organic N or P in litter (Weedon et al., 2009), resulting in the reduction of litter mass loss and P accumulation in litter (Figs. 1a and 3a). However, the P increase in litter chemistry would increase microbial activities (Cheever et al., 2013) and thus stimulated the decomposition of organic matter in litter (Fig. 1b). The direct effects of nutrient additions on litter decomposition and their controlling mechanisms were different from effects of nutrient-induced changes in litter chemistry (Prescott, 1995; Hobbie and Vitousek, 2000; van Diepen et al., 2015; Zhang et al., 2016), which should be incorporated into regional and even global models to predict effects of nutrient deposition on ecosystem C cycling.

## 5. Conclusions

Nutrient-induced changes in litter chemistry will interact with altered soil nutrient under fertilization to influence litter decomposition. By assessing effects of exogenous N and P additions, endogenous N and P availability, and their interaction on litter decomposition, we found that the inhibition of litter decomposition and P accumulation under nutrient additions were modified by the effects of P increase in litter. Effects of nutrient additions on litter decomposition were regulated by P-induced changes in litter chemistry in this P-limited forest, suggesting that microbial need for the limiting nutrient in litter may function as the primary driver that regulates the litter decomposition. However, the microbial community composition and activities in nutrient additions or exogenous nutrient supply need to be further studied and microbial P mining of litter organic P should be paid more attention.

## Acknowledgments

We thank for Jiang Lu, Dandan Li and Yan Lv for help with the field and laboratory work. We would also like to thank Dr. Xuhui Zhou and Hunter Whittington for assistance in editing the manuscript. This study was supported financially by the National Natural Science Foundation of China (31000231). The authors declare no competing financial interests.

## References

Aber, J.D., Melillo, J.M., 1991. Terrestrial Ecosystems. Saunder College Publishing, Orlando, Florida, USA.

Aerts, R., de Caluwe, H., 1997. Nutritional and plant-mediated controls on leaf litter decomposition of Carex species. Ecology 78, 244–260.

Attiwill, P.M., Adams, M.A., 1993. Nutrient cycling in forests. New Phytol. 124, 561–582.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2013. lme4: linear mixed-effects models using Eigen and S4. R package version 3.2.1.

Berg, B., 2014. Decomposition patterns for foliar litter – a theory for influencing factors. Soil Biol. Biochem. 78, 222–232.

Barantal, S., Schimann, H., Fromin, N., Hättenschwiler, S., 2012. Nutrient and carbon limitation on decomposition in an Amazonian moist forest. Ecosystems 15, 1039–1052.

Cheever, B.M., Webster, J.R., Bilger, E.E., Thomas, S.A., 2013. The relative importance of exogenous and substrate-derived nitrogen for microbial growth during leaf decomposition. Ecology 94, 1614–1625.

Chen, H., Dong, S.F., Liu, L., Ma, C., Zhang, T., Zhu, X.M., Mo, J.M., 2013. Effects of experimental nitrogen and phosphorus addition on litter decomposition in an old-growth tropical forest. PLoS ONE 8, e84101. doi: 84110.81371/journal.pone.0084101.

Chen, Y., Sayer, E.J., Li, Z., Mo, Q., Li, Y., Ding, Y., Wang, J., Lu, X., Tang, J., Wang, F., 2016. Nutrient limitation of woody debris decomposition in a tropical forest: contrasting effects of N and P addition. Funct. Ecol. 30, 295–304.

Chen, Y.C., Sun, J., Xie, F.T., Wang, X.D., Cheng, G.W., Lu, X.Y., 2015. Litter chemical structure is more important than species richness in affecting soil carbon and nitrogen dynamics including gas emissions from an alpine soil. Biol. Fertil. Soils 51, 791–800.

Craine, J.M., Morrow, C., Fierer, N., 2007. Microbial nitrogen limitation increases decomposition. Ecology 88, 2105–2113.

Fang, H., Mo, J., Peng, S., Li, Z., Wang, H., 2007. Cumulative effects of nitrogen additions on litter decomposition in three tropical forests in southern China. Plant Soil 297, 233–242.

Finn, D., Page, K., Catton, K., Strounina, E., Kienzle, M., Robertson, F., Armstrong, R., Dalal, R., 2015. Effect of added nitrogen on plant litter decomposition depends on initial soil carbon and nitrogen stoichiometry. Soil Biol. Biochem. 91, 160–168.

Galloway, J.N., Townsend, A.R., Erisman, J.W., 2008. Transformation of the nitrogen cycle: recent trends, questions and potential solution. Science 320, 889–892.

Gao, Q., Hasselquist, N.J., Palmroth, S., Zheng, Z., You, W., 2014. Short-term response of soil respiration to nitrogen fertilization in a subtropical evergreen forest. Soil Biol. Biochem. 76, 297–300.

Gosz, J.R., Likens, G.E., Bormann, F.H., 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook forest, New Hampshire. Ecol. Monogr. 43, 173–191.

Gruber, N., Galloway, J.N., 2008. An Earth-system perspective of the global nitrogen cycle. Nature 451, 293–296.

Hobbie, S.E., 2000. Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in a Hawaiian Montane forest. Ecosystems 3, 484–494.

Hobbie, S.E., 2005. Contrasting effects of substrate and fertilizer nitrogen on the early stages of litter decomposition. Ecosystems 8, 644–656.

Hobbie, S.E., Vitousek, P.M., 2000. Nutrient limitation decomposition in Hawaiian forests. Ecology 81, 1867–1877.

Jacobson, T.K.B., Bustamante, M.M.C., Kozovits, A.R., 2011. Diversity of shrub tree layer, leaf litter decomposition and N release in a Brazilian Cerrado under N, P and N plus P additions. Environ. Pollut. 159, 2236–2242.

Knorr, M., Frey, S.D., Curtis, P.S., 2005. Nitrogen additions and litter decomposition: a meta-analysis. Ecology 86, 3252–3257.

Kozovits, A.R., Bustamante, M.M.C., Garofalo, C.R., Bucci, S., Franco, A.C., Goldstein, G., Meinzer, F.C., 2007. Nutrient resorption and patterns of litter production and decomposition in a Neotropical Savanna. Funct. Ecol. 21, 1034–1043.

Marklein, A.R., Winbourne, J.B., Enders, S.K., Gonzalez, D.J.X., 2016. Mineralization ratios of nitrogen and phosphorus from decomposing litter in temperate versus tropical forests. Glob. Ecol. Biogeogarphy 25. 355–346.

Melillo, J.M., Aber, J.D., Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63, 621–626.

Mo, J., Brown, S., Xue, J., Fang, Y., Li, Z., 2006. Response of Litter decomposition to simulated N deposition in disturbed, rehabilitated and mature forests in subtropical China. Plant Soil 282, 135–151.

Nelson, D.W., Sommer, L.E., 1996. Total carbon, organic carbon, and organic matter. In: Sparks, D.L. (Ed.), Methods of Soil Analysis. Part 3. Chemical Methods, Madison, WI.

Prescott, C.E., 1995. Does nitrogen availability control rates of litter decomposition in forests? Plant Soil 168–169, 83–88.

Prescott, C.E., Corbin, J.P., Parkinson, D., 1992. Immobilization and availability of N and P in the forest floors of fertilized Rocky Mountain coniferous forests. Plant Soil 143, 1–10.

Song, Y., Chen, X., 2007. Degradation Mechanism and Ecological Restoration of Evergreen Broad-Leaved Forest Ecosystem in East China. Science Press, Beijing.

Staaf, H., Berg, B., 1981. Accumulation and release of plant nutrients in decomposing Scots pine needle litter. Long-term decomposition in a Scots pine forest II. Can. J. Bot. 60, 1561–1568.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystem. Blackwell Scientific, Oxford, UK.

van Diepen, L.T.A., Frey, S.D., Sthultz, C.M., Morrison, E.W., Minocha, R., Pringle, A., 2015. Changes in litter quality caused by stimulated nitrogen deposition reinforce the N-induced suppression of litter decay. Ecosphere 6, 205.

van Huysen, T.L., Harmon, M.E., Perakis, S.S., Chen, H., 2013. Decomposition and nitrogen dynamics of $^{15}$N-label leaf, root and twig litter in temperate coniferous forests. Oecologia 173, 1563–1573.

Van Huysen, T.L., Perakis, S.S., Harmon, M.E., 2016. Decomposition drives convergence of forest litter nutrient stoichiometry following phosphorus addition. Plant Soil, 1–14.

Vestgarden, L.S., 2001. Carbon and nitrogen turnover in the early stage of Scots pine (Pinussylvestris L.) needle litter decomposition: effects of internal and external nitrogen. Soil Biol. Biochem. 33, 465–474.

Vitousek, M.P., 1998. Foliar and litter nutrients, nutrient resorption, and decomposition in Hawaiian *Metrosideros polymorpha*. Ecosystems 1, 401–407.

Vivanco, L., Austin, A.T., 2011. Nitrogen addition stimulates forest litter decomposition and disrupts species interactions in Patagonia, Argentina. Glob. Change Biol. 17, 1963–1974.

Wang, Y., Cheng, S., Fang, H., Yu, G., Xu, X., Xu, M., Wang, L., Li, X., Si, G., Geng, J., He, S., 2015. Contrasting effects of ammonium and nitrate inputs on soil $CO_2$ emission in a subtropical coniferous plantation of southern China. Biol. Fertil. Soils 51, 815–825.

Weedon, J.T., Cornwell, W.K., Cornelissen, J.H.C., Zanne, A.E., Wirth, C., Coomes, D.A., 2009. Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? Ecol. Lett. 12, 45–56.

Yan, E., Wang, X., Zhou, W., 2008. N:P stoichiometry in secondary succession in evergreen broad-leaved forest, Tiantong, East China. J. Plant Ecol. (Chinese Version) 32, 13–22.

Zhang, W., Chao, L., Yang, Q., Wang, Q., Fang, Y., Wang, S., 2016. Litter quality mediated nitrogen effect on plant litter decomposition regardless of soil fauna presence. Ecology 97, 2834–2843.