Applied Soil Ecology 128 (2018) 35–42

Contents lists available at ScienceDirect

Applied Soil Ecology

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

Responses of litter decomposition and nutrient release to N addition: A meta-analysis of terrestrial ecosystems

Tian'an Zhang[a,b], Yiqi Luo[b], Han Y.H. Chen[c], Honghua Ruan[a,*]

[a] Co-Innovation Center for Sustainable Forestry in Southern China, College of Biology and the Environment, Nanjing Forestry University, Nanjing 210037, PR China
[b] Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ 86011, USA
[c] Faculty of Natural Resources Management, Lakehead University, 955 Oliver Road, Thunder Bay, ON P7B 5E1, Canada

ARTICLE INFO

Keywords:
Litter decomposition
Meta-analysis
Nitrogen deposition
Nutrient release
Plantation
Secondary forest

ABSTRACT

As atmospheric nitrogen (N) concentrations increase, it can wreak havoc on the entire planet, as well as the fragile ecosystems, once it exceeds the demand of ecosystems. Chronically elevated N deposition affects litter decomposition, which is a crucial process that controls nutrient cycling, soil fertility, and primary productivity. Nevertheless, the responses of litter decomposition and nutrient release to N addition remain elusive. Here we conduct a meta-analysis using 3434 paired observations from 55 publications to evaluate these responses. We found that although litter decomposition rate did not change significantly under N addition when averaged across all studies, it decreased with N application rate and experimental duration, showing that it was stimulated at low levels but suppressed at high levels of N application and duration. Phosphorus released more slowly under N enrichment, and this response became greater with longer duration. Moreover, the decomposition of lignin was depressed under N addition, and this effect was more pronounced with the increase of N application rate and experimental duration. Importantly, in terms of different ecosystems, the decomposition of litter was significantly inhibited by N addition in plantations, but was promoted in secondary forests, and there were no significant changes in primary forests, grasslands and wetlands. The responses of litter mass loss, along with the release of nutrients to N fertilization, changed with mean annual temperature and mean annual precipitation of the study sites. Our results provided a synthetic understanding of the effects of N addition on the decomposition of litter and nutrient release under climate change scenarios.

1. Introduction

Anthropogenic activities, such as intensive agriculture, stockbreeding and combustion of fossil fuels, have prominently altered the global nitrogen (N) cycle over the last several decades (Ciais et al., 2013; Kanakidou et al., 2016), which have resulted in increases in the content of nitrogenous compounds in the ambient atmosphere, and increases several fold in N deposition (Galloway et al., 2008; Galloway et al., 2004). Increasing N deposition influences numerous ecosystem processes, including litter decomposition (Frey et al., 2014; Lovett et al., 2013; Zak et al., 2008) and nutrient cycling (Yuan and Chen, 2015). Litter comprises a top layer in soil profiles, and serves as the energy and nutrient source of microbial metabolism (Magill and Aber, 2000). Litter decomposition, as a mechanism of nutrient release, is a key process in the functioning of both managed and natural ecosystems (Bonan et al., 2013; Jonczak, 2013). Thus, the stability of ecosystems is contingent on the long-term balance between plant growth and litter decomposition. However, how elevated N deposition influences litter decomposition and nutrient release, to the best of our knowledge, remains formative and incomplete. A better understanding of litter and nutrient responses to the addition of N is essential to forecasting the impact of elevated N on terrestrial ecosystems.

Lignin and cellulose are both primary components of litter, where their degradation is an essential process for maintaining carbon (C) balance (Berg and Mcclaugherty, 2013). Further, the process and pace of litter decomposition greatly impact how plants and microbes utilize and absorb C, N, phosphorus (P), and other nutrients (Wardle, 2004). Meanwhile, potassium (K), calcium (Ca) and magnesium (Mg) are crucial macronutrients for energy metabolism, photosynthesis, and membrane transport in plants (Hüttl and Schaaf, 1997; Yue et al., 2016). Although Sodium (Na) is not a critical nutrient for all plants, it is important for animals and litter decomposers (Geerling and Loewy, 2008). It is necessary to elucidate nutrient release patterns during decomposition processes as affected by the addition of N, since the release of P from litter may play a critical control of productivity and nutrient release through litter decomposition could lead to improvement in soil

* Corresponding author.
E-mail address: hhruan@njfu.edu.cn (H. Ruan).

https://doi.org/10.1016/j.apsoil.2018.04.004
Received 6 February 2018; Received in revised form 31 March 2018; Accepted 4 April 2018
Available online 09 April 2018
0929-1393/

fertility (Yang et al., 2004).

Exogenous N might have multiple effects on litter decomposition and nutrient release. First, we expected that elevated N would have negative effects on the decomposition of litter and lignin as well as the release of nutrient, which maintain ionic balance. Nitrogen addition has negative effects on microbial biomass and activities in soils (Compton et al., 2004; Treseder, 2008; Zhang et al., 2018). Externally applied N inhibits the growth of white rot fungi that produce lignin, and reduces the activity of cellulolytic enzyme along with lignin-degrading enzyme such as lignin phenol oxidase (Deforest et al., 2004; Edwards et al., 2011; Sun et al., 2016). As N addition promotes the consumption of C, the supply of C becomes unstable and lignin decomposition is reduced (Magill and Aber, 1998), which leads to a reduction in the reserves of C for other heterotrophic microbial metabolic activities. Elevated N may also alter soil microbe community compositions, reduce microbial biodiversity (Allison et al., 2007), and inhibit the activity of soil fauna, which would suppress litter decomposition and nutrient release.

Second, we expected that environmental and experimental factors would interact with N deposition to influence litter decomposition and nutrient release. To be specific, we expected that litter and nutrient responses would scale proportionally with experimental duration and N addition rate, as a previous meta-analysis revealed that the amount of N fertilizer applied at a site was one of the important predictors influencing decomposition rates (Knorr et al., 2005). Climatic factors such as mean annual temperature (MAT) and mean annual precipitation (MAP) would also influence these responses, since litter decomposition is regulated by both biotic and abiotic factors including climatic conditions (Ngao et al., 2009; Zhou et al., 2008).

Third, we expected that responses of litter decomposition and nutrient release to N addition would differ in different terrestrial ecosystems. Primary forests are natural forests without apparent and reported human impacts, whereas secondary forests are naturally developed stands with native species (Don et al., 2011; Guo and Gifford, 2002). They differed from plantations mainly regarding to human activity involved in the stand establishment. Furthermore, secondary and primary forests are highly diverse in vegetation structure and species composition, which is up to their age, topographical location and disturbance history (Barlow et al., 2007; Chazdon, 2003). Wetlands are areas saturated with water whereas grasslands are dominated by herbaceous vegetation. Such differences in land-use types might induce inconsistent litter and nutrient responses to elevated N deposition.

Over the last few decades, numerous experiments have been conducted to investigate the responses of litter decomposition and nutrient release to N deposition. In this study, we aimed to: (1) assess the responses to N addition of 11 variables, including percentage of remaining litter, C, N, P, K, Ca, Mg, Na, lignin and cellulose, and decomposition rate; (2) test how these responses change with N addition rate, experimental duration, and variations in MAT and MAP; (3) examine how these responses differ among ecosystems. We collected 3434 paired observations from 55 publications encompassing wetlands, grasslands, plantations, primary forests, and secondary forests (Fig. 1, Supplementary information, Appendix S1). Our meta-data included studies that were conducted with a mean N application rate of 122.8 kg ha^{-1} y^{-1}, ranging from 2.4 to 640 kg ha^{-1} y^{-1}, a mean experimental period of 12.5 months (0.5–108 months), and a mean background N deposition rate of 40.6 kg ha^{-1} y^{-1} (0.5–97.5 kg ha^{-1} y^{-1}). The mean annual temperature ranged from −3 to 26.6 °C, and mean annual precipitation, from 150 to 5100 mm. For each variable, our model simultaneously estimated the average effect of N addition and the responses to N addition rate and experimental duration.

2. Materials and methods

2.1. Data collection

We investigated published peer-reviewed journal articles that evaluated the response of litter decomposition and nutrient release to N addition in terrestrial ecosystems, using the Web of Science and Google Scholar. The search terms were "(nitrogen addition OR nitrogen enrichment OR nitrogen deposition OR nitrogen fertilization OR nitrogen input OR nitrogen application OR elevated nitrogen) AND (litter decomposition OR litter decay OR nutrient release)". To minimize publication bias, only primary studies that satisfied the following criteria were included in this meta-analysis. (1) Nitrogen fertilizers were directly added to terrestrial ecosystems and at least one of the considered variables was measured. (2) The N addition and control plots were established under the same abiotic and biotic conditions. (3) Only the control and N addition treatment data were selected if the experiment included a treatment other than N addition. (4) The N application rate and experimental duration were clearly recorded. (5) The means, standard deviations and sample sizes of the selected variables were available, or could be calculated, from related publications.

All original data were extracted from the text, tables, figures, and appendices of the publications. When data were graphically presented, Engauge software 4.1 was employed to obtain numeric data (http://digitizer.sourceforge.net). Measurements from different ecosystem types, species, and treatment levels within a single study were considered as independent observations. Meanwhile, environmental variables: mean annual temperature (MAT), and mean annual precipitation (MAP) were recorded directly from cited papers, or in the cases where these were not reported, they were extracted from the Global Climate database at http://www.worldclim.org/ using coordinates (e.g., latitude and longitude). Our final dataset included 3434 paired observations from 261 individual studies in 55 published papers with a total of 11 variables related to litter mass loss, nutrient release, and the decomposition rate.

2.2. Meta-analysis

We used the natural log response ratio (ln*RR*) to assess the responses of litter decomposition and nutrient release to N addition to avoid biased effect estimates because the natural logarithm of a ratio has better statistical properties (Hedges et al., 1999). On the one hand, logarithm linearizes the metric (Rodríguez-Barranco et al., 2017), coherently treating deviations in the numerator and those in the denominator, i.e., when the ratio is influenced more by variations in denominator, the log-transformed ratio is influenced equally by variations in either numerator or denominator. On the other hand, the distribution of response ratio (*RR*) is skewed, while the distribution of ln*RR* is symmetric (Koricheva et al., 2013). That is, if X_t and X_c are normally distributed, then ln*RR* is approximately normally distributed (Hedges et al., 1999). Natural log response ratio was calculated as:

$$\ln RR = \ln(X_t/X_c) = \ln(X_t) - \ln(X_c) \tag{1}$$

where X_t and X_c are mean values of the selected variable under N treatment and in control, respectively.

We calculated the weight (w) of each ln*RR* by the inverse of variance (v_i) as:

$$v_i = (1/n_t) \times (S_t/X_t)^2 + (1/n_c) \times (S_c/X_c)^2 \tag{2}$$

where n_t, n_c, S_t, S_c, X_t, X_c were sample sizes, standard deviations, and mean response values in the treatment and control, respectively.

For each variable, we tested whether the overall ln*RR* differed from zero and whether the ln*RR* was affected by N addition rate (N, kg ha^{-1} yr^{-1}) and experimental duration (D, months) using the following model:

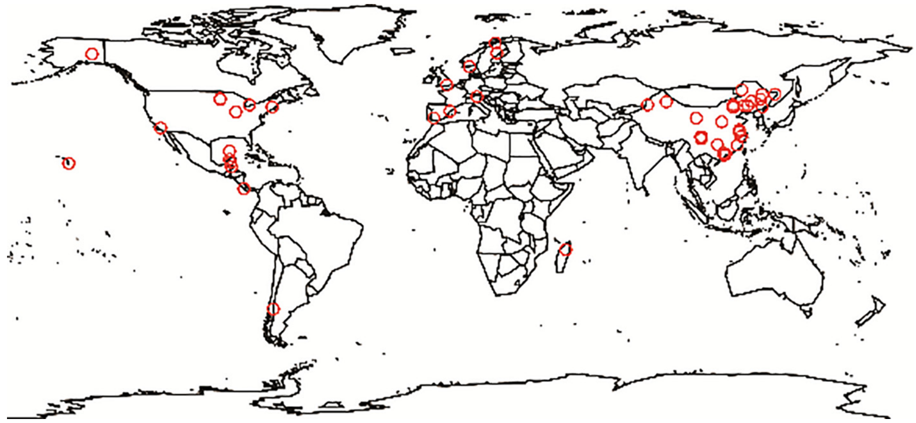

Fig. 1. Global distribution of study sites included in the meta-analysis.

$$\ln RR = \beta_0 + \beta_1 \cdot N + \beta_2 \cdot D + \pi_{study} + \varepsilon \quad (3)$$

where β, π_{study} and ε are coefficient, the random effect factor of "study" and sampling error, respectively. The random effect explicitly accounts for autocorrelation among observations within each "study". We conducted the analysis using maximum likelihood estimation with the lme4 package (Bates et al., 2017). When continuous predictors, i.e., N and D in Eq. (3), are centered or scaled (minus mean and divided by one standard deviation), β_0 is the overall mean ln*RR* at the mean N and D (Cohen et al., 2013). To facilitate the comparison among litter decomposition and nutrient release variables that had variable N and D, we scaled these predictors in our analysis. We also used four other alterative models, and all alternative models resulted in similar or higher Akaike information criterion values (Table A1). For consistency, we analyzed all variables with Eq. (3).

To examine whether ln*RR* changed geographically, we tested the effect of MAT or MAP or ecosystem type on ln*RR* by adding the term of MAT, MAP or ecosystem type to Eq. (3). For ease of interpretation, ln*RR* and its corresponding confidence intervals were transformed back to the percentage change as $(e^{\ln RR}-1) \times 100\%$. In all analyses, we used $1/v_i$ to weigh for individual observations and studies, as a random effect to account for autocorrelation among observations within each study. If the 95% confidence intervals (CI) of ln*RR* for a variable did not cover zero, the impact of N addition on the variable differed significantly (at $\alpha = 0.05$) between the control and N treated. All statistical analyses were performed in R 3.4.3.

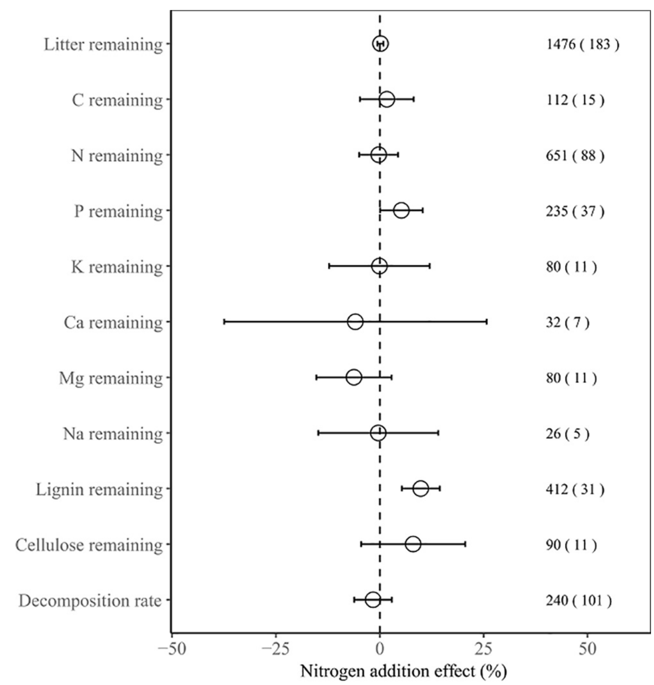

Fig. 2. Natural-log-transformed response ratios (ln*RR*) of studied litter decomposition attributes. Values are mean ± 95% confidence intervals of ln*RR* between the N addition and the control. The number of observations is beside each variable without parentheses, and the number of studies is in parentheses.

3. Results and discussion

3.1. Responses of litter decomposition and nutrient release to N addition

Across all studies, the litter mass remaining did not change significantly ($P = 0.708$) under N fertilization than the control (Fig. 2). The percentages of P and lignin remaining were 5.20% (95% confidence interval, 0.10–10.31%, $P = 0.055$) and 9.86% (5.30–14.41%, $P < 0.001$) higher under elevated N than control experiments respectively (Fig. 2), showing that N enrichment decreased P release and the decomposition of lignin. Moreover, there were no significant changes in the decomposition rate and percentage remaining of C, N, K, Ca, Mg and cellulose between the N addition treatment and the control on average (Fig. 2).

Our first hypothesis is partially confirmed in that lignin decomposition was depressed under N enrichment, which is not surprising as the activity of oxidative enzymes involved in lignin degradation could be suppressed by the addition of N (Carreiro et al., 2000; Zak et al., 2008). In terms of litter decomposition, our result is consistent with Knorr et al. (2005) who found that N addition had no statistically significant effect on litter decay when averaged across all studies. Nitrogen addition delayed the release of P in litter, which may be due to chemical immobilization and microbial assimilation (fungal hyphae can transfer P from decomposing litter and soil) (Hobbie, 2008; Hobbie and Vitousek, 2000). The insignificant responses of litter decomposition and other nutrient release to elevated N could be attributed to various factors including N application rate, experimental duration, substrate litter quality, as well as environmental conditions such as MAT and MAP, which may have an effect on these responses (Ngao et al., 2009; Prescott et al., 2010).

3.2. Influences of N addition rate, experimental duration, MAT and MAP

With the increase of N addition rate and experimental duration, the percentage mass remaining of litter and cellulose showed a decreasing trend while the decomposition rate increased (Figs. 3 and 4), which indicated that the decomposition of litter and cellulose were promoted at low levels but were inhibited at high levels of N addition and duration. The negative effect of N addition on lignin decomposition

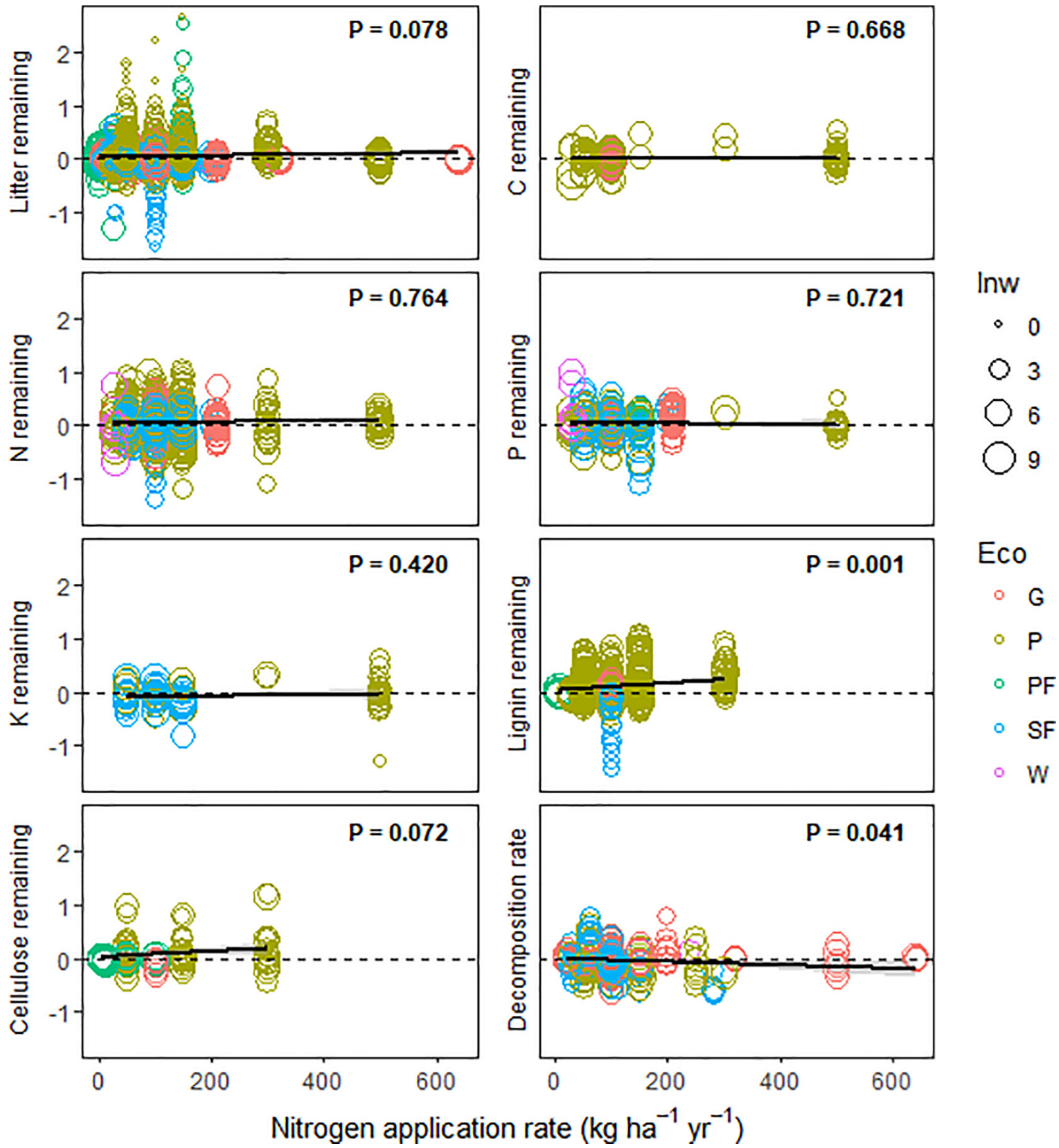

Fig. 3. Natural-log-transformed response ratios (ln*RR*) as a function of N application rates on litter decomposition attributes. Fitted regressions and corresponding levels of significance (P) are presented. The sizes of circles represent the natural logarithm of relative weights (ln*w*) for corresponding observations. G, P, PF, SF and W represent grassland, plantation, primary forest, secondary forest and wetland, respectively.

increased significantly with both N application rate and experimental duration (Figs. 3 and 4). Additionally, the percentage remaining of C, N and P increased with longer duration (Fig. 4), showing that the release of these nutrients were suppressed at higher levels of experimental period.

This is partially consistent with Knorr et al. (2005) who found that the mass loss of litter decomposing for less than 2 years was promoted, while litters that had been decomposing for more than 2 years exhibited suppression. The litter decomposition process is generally divided into early and later stages, as the decomposition rate is dominated by different organic chemical components (De Santo et al., 2009). Soluble components decay, or are rapidly leached away in the early stages of decomposition (Berg, 2000). As decomposition proceeds, N addition influences the chemical processes involved in litter decomposition; excess N might be combined with lignin or polyphenol, which produces recalcitrant compounds (Aerts et al., 2006) and increases lignin concentration (Manning et al., 2008), where their degradation dominates litter decomposition (Berg et al., 1993). Furthermore, increasing N addition rate might increase the concentration of N in the soil, which would hamper lignin degradation due to repression of the formation of ligninase in lignin-degrading microbe populations (Berg and Mcclaugherty, 2013), or by favoring the formation of new recalcitrant compounds.

Variations in MAT and MAP of the study sites had certain impacts on the responses of litter decomposition and nutrient release to N fertilization (Table 1). On the one hand, the decomposition of litter and cellulose, along with the release of N and Mg were increased under N enrichment in cold climates but were inhibited in warm climates (Fig. A1). On the other hand, litter and cellulose decomposition, and the release of K and Mg were promoted in dry regions while depressed in wet regions (Fig. A2). The Ca release showed a completely different trend with increased MAT and MAP, which may indicate decreased microbial activity and litter decomposition, since litter Ca is related to increased microbial activity, fungal and earthworm abundance and diversity (Aponte et al., 2010; Reich et al., 2005).

Our findings that N addition would inhibit litter decomposition in warmer climates and wetter regions are inconsistent with Knorr et al. (2005) who found that MAT and MAP did not appear to be significant factors regulating the effect of N addition on litter decomposition. However, it is plausible since increasing temperature and moisture

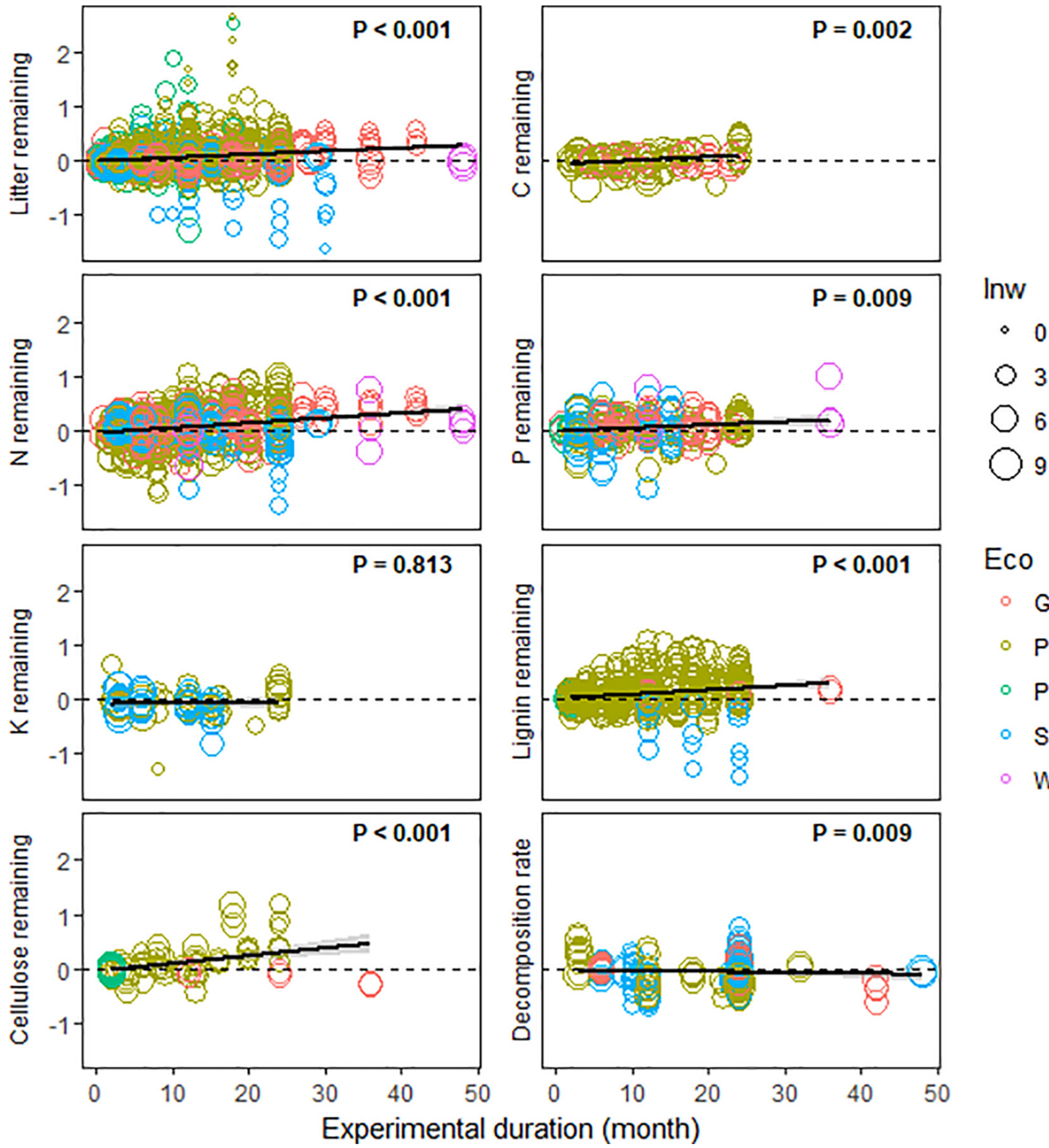

Fig. 4. Natural-log-transformed response ratios (ln*RR*) as a function of experimental duration on litter decomposition attributes. Fitted regressions and corresponding levels of significance (P) are presented. The sizes of circles represent the natural logarithm of relative weights (ln*w*) for corresponding observations. G, P, PF, SF and W represent grassland, plantation, primary forest, secondary forest and wetland, respectively.

Table 1
The effect (P values) of mean annual temperature (MAT), mean annual precipitation (MAP) and ecosystem type on natural log response ratios of studied litter decomposition attributes.

Attribute	MAT		MAP		Ecosystem	
	df	P	df	P	df	P
Litter remaining	1, 124	**< 0.001**	1, 289	**0.005**	4, 137	**< 0.001**
C remaining	1, 9	0.991	1, 8	0.880	1, 8	0.796
N remaining	1, 95	**0.012**	1, 92	0.667	3, 92	**0.003**
P remaining	1, 29	0.233	1, 21	0.367	4, 19	0.356
K remaining	1, 15	0.068	1, 16	**0.022**	1, 8	0.181
Ca remaining	1, 6	**0.010**	1, 9	**0.001**	*NA*	
Mg remaining	1, 32	**0.036**	1, 27	**0.020**	1, 7	0.529
Na remaining	1, 23	0.770	1, 24	0.769	*NA*	
Lignin remaining	1, 23	0.901	1, 84	0.756	3, 42	**0.008**
Cellulose remaining	1, 43	**< 0.001**	1, 67	**< 0.001**	2, 21	**< 0.001**
Decomposition rate	1, 75	**< 0.001**	1, 63	0.051	3, 104	0.491

Linear mixed effect models used Satterthwaite approximation for degrees of freedom (df). NA means not applicable as there was only one ecosystem type of experiments.

would cause the leaching of NO_3^-, which can take away a mass of base cations like Ca^{2+}, causing decreased soil pH (Tian and Niu, 2015). Thus, greater soil acidification would inhibit the activity of microbes involved in litter decomposition, which lowers the decomposition rate (Mo et al., 2004). Given the global climate warming as well as increasing N deposition rate and longer duration worldwide (Galloway et al., 2008; IPCC, 2013; Ren et al., 2017), our findings indicate that litter decomposition and nutrient release would suffer progressive inhibition and continue to decrease at a global scale.

3.3. Different responses among ecosystem types

Most importantly, when categorized by ecosystem types, we found that N treatment increased the percentage remaining of litter, lignin and cellulose by 3.45% (1.59–5.31%, $P < 0.001$), 14.88% (11.86–17.91%, $P < 0.001$) and 15.25% (7.09–23.42%, $P < 0.001$) in plantations, respectively (Fig. 5). Nevertheless, N addition reduced the percentage remaining of litter and lignin by 2.00% (1.29–2.72%, $P < 0.001$) and 31.62% (20.84–42.40%, $P < 0.001$) in secondary forests, respectively (Fig. 5). Percentage of N remaining was 10.29%

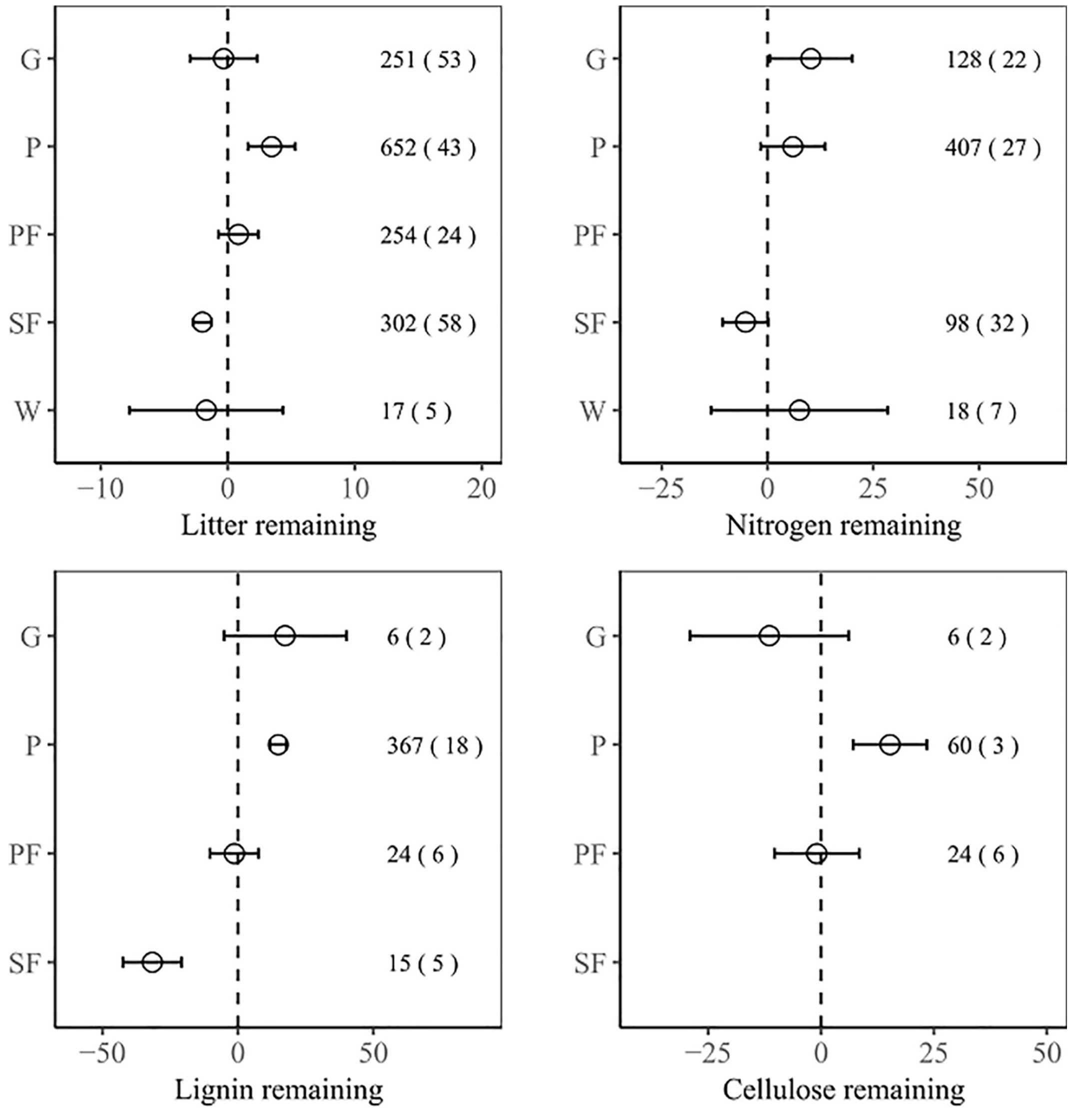

Fig. 5. Natural-log-transformed response ratios (ln*RR*) of litter decomposition attributes in response to N addition when data were grouped by different ecosystem types. Values are mean ± 95% confidence intervals of ln*RR* between N addition and the control. The number of observations is beside each variable without parentheses and the number of studies is in parentheses. G, P, PF, SF and W represent grassland, plantation, primary forest, secondary forest and wetland, respectively.

(0.55–20.03%, $P = 0.050$) higher under N addition in grasslands, but was decreased by 5.22% marginally ($P = 0.068$) in secondary forests. Results in secondary forests showed a dramatic opposite response (Figs. 3, 4, A1 and A2), so we compared the mean value of environmental and experimental parameters of the observations for each ecosystem type to see whether this pattern was mainly affected by geographical variation or experimental factors (Table A2). On average, the latitude, longitude, MAT, MAP, ambient N deposition, N application rate and experimental duration of observations in secondary forests were neither the highest nor the lowest. Thus, these factors would not be the dominating factor concerning the various responses of different ecosystem types.

It is one of our most crucial findings that N addition decreased the decomposition of litter, lignin and cellulose in plantations, but increased litter and lignin decomposition in secondary forests. Scientists have suggested that litter decomposition rates are mainly controlled by initial litter quality (Loranger et al., 2002; Wieder et al., 2009; Zhang et al., 2008). In general, high-quality litter with low lignin:N and low C:N ratios is decomposed with almost all decomposers and can improve nutrient availability in the soil (Mukhopadhyay and Joy, 2010). Litter decomposition rate is positively related to its N concentration, which has been regarded as a rate-accelerating factor for decomposition (Berg, 2000; Hobbie et al., 2012). The negative effect of lignin content on decomposition has been found in different ecosystems (Fioretto et al., 2005; Ngao et al., 2009). The C:N ratio is also one of the best prediction indexes for decomposition rates, in that it reflects the ratio of carbohydrates to proteins in litter, which is an essential property of the litter substrate (Talbot and Treseder, 2012). As is recognized, the higher the C:N ratio, the lower the decomposition rate is, as soil microbes require external N to meet growth demands (Cornwell et al., 2008; Hobbie, 2005).

Substrate quality of litter are reported to depend on plant diversity and successional stage at the stand level (Berg and Laskowski, 2006; Deng and Janssens, 2006). Plant richness and diversity have been suggested to primarily explain the variations in litter decomposition in that decomposition rate in less diverse forests was lower than that in diverse forests (Pérez et al., 1998). Therefore, the increased decomposition rate in secondary forests under N addition is likely explained by its plant diversity and high litter quality (low C:N ratio and high N content) (Li et al., 2005; Yu et al., 2014), while the decreased decomposition rate in plantations can be attributed to the high lignin content and high C:N ratio in litter (Cizungu et al., 2014). Litter quality in wetlands differed from site to site, and the site effect is stronger than the effect of litter quality (Rejmánková and Houdková, 2006). The overall insignificant effects for wetlands could be attributed to waterlogging, as Song et al. (2011) found that the accelerated litter decomposition under N addition was suppressed in waterlogging condition. However, factors influencing decomposition rate are complex and there exist few paired data to validate this relationship.

4. Conclusions

The direction and degree of responses to N deposition of litter decomposition and nutrient release are regulated by increasing rate and duration of N application. Climatic warming and precipitation have interactive effects on these responses. Importantly, litter decomposition is inhibited in plantations but promoted in secondary forests, which is likely attributed to the difference in litter quality and plant diversity. This meta-analysis provides a synthetic understanding of the effects of N addition on litter decomposition and nutrient release, which will deepen our understanding of the mechanisms underlying the effects of N deposition on biogeochemical cycles under climate change scenarios.

Conflict of interest

The authors declare no conflict of interest.

Acknowledgements

We thank the authors whose work is included in the meta-analyses. Funding was provided by the National Key Research and Development Program of China (No. 2016YFD0600204) and the Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD) supported this research. The senior author acknowledges the Doctorate Fellowship Foundation of Nanjing Forestry University, Postgraduate Research & Practice Innovation Program of Jiangsu Province, and the Chinese Government Scholarship.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2018.04.004.

References

Aerts, R., Van Logtestijn, R., Karlsson, P., 2006. Nitrogen supply differentially affects litter decomposition rates and nitrogen dynamics of sub-arctic bog species. Oecologia 146, 652.
Allison, S.D., Hanson, C.A., Treseder, K.K., 2007. Nitrogen fertilization reduces diversity and alters community structure of active fungi in boreal ecosystems. Soil Biol. Biochem. 39, 1878–1887.
Aponte, C., García, L.V., Marañón, T., Gardes, M., 2010. Indirect host effect on ectomycorrhizal fungi: leaf fall and litter quality explain changes in fungal communities on the roots of co-occurring Mediterranean oaks. Soil Biol. Biochem. 42, 788–796.
Barlow, J., Gardner, T.A., Ferreira, L.V., Peres, C.A., 2007. Litter fall and decomposition in primary, secondary and plantation forests in the Brazilian Amazon. Forest Ecol. Manage. 247, 91–97.
Bates, D., Martin Maechler, Ben Bolker, Steven Walker, Rune Haubo Bojesen Christensen, Henrik Singmann, Bin Dai, Gabor Grothendieck, Green, P., 2017. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-13.
Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. Forest Ecol. Manage. 133, 13–22.
Berg, B., Laskowski, R., 2006. Litter decomposition: a guide to carbon and nutrient turnover, pp. 1–421.
Berg, B., Mcclaugherty, C., 2013. Plant litter. Decomposition, humus formation, carbon sequestration.
Berg, B., Mcclaugherty, C., Johansson, M.B., 1993. Litter mass-loss rates in late stages of decomposition at some climatically and nutritionally different pine sites. Long-term decomposition in a Scots pine forest VIII. Can. J. Bot. 71, 680–692.
Bonan, G.B., Hartman, M.D., Parton, W.J., Wieder, W.R., 2013. Evaluating litter decomposition in earth system models with long-term litterbag experiments: an example using the Community Land Model version 4 (CLM4). Glob. Change Biol. 19, 957.
Carreiro, M.M., Sinsabaugh, R.L., Repert, D.A., Parkhurst, D.F., 2000. Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. Ecology 81, 2359–2365.
Chazdon, R.L., 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspect. Plant Ecol. 6, 51–71.
Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Al., E., House, J.I., 2013. Carbon and other biogeochemical cycles: Climate change 2013: The physical science basis. Contribution of working group i to the fifth assessment report of the intergovernmental panel on climate change.
Cizungu, L., Staelens, J., Huygens, D., Walangululu, J., Muhindo, D., Cleemput, O.V., Boeckx, P., 2014. Litterfall and leaf litter decomposition in a central African tropical mountain forest and Eucalyptus plantation. Forest Ecol. Manage. 326, 109–116.
Cohen, J., Cohen, P., West, S.G., Aiken, L.S., 2013. Applied Multiple Regression/Correlation Analysis for the Behavioral Sciences. Routledge.
Compton, J.E., Watrud, L.S., Porteous, L.A., Degrood, S., 2004. Response of soil microbial biomass and community composition to chronic nitrogen additions at Harvard forest. Forest Ecol. Manage. 196, 143–158.
Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol. Lett. 11, 1065–1071.
De Santo, A.V., De Marco, A., Fierro, A., Berg, B., Rutigliano, F.A., 2009. Factors regulating litter mass loss and lignin degradation in late decomposition stages. Plant Soil 318, 217–228.
Deforest, J.L., Zak, D.R., Pregitzer, K.S., Burton, A.J., 2004. Atmospheric nitrate deposition and the microbial degradation of cellobiose and vanillin in a northern hardwood forest. Soil Biol. Biochem. 36, 965–971.
Deng, Z., Janssens, M.J.J., 2006. Litter fall production in west-african forests and plantations, Conference on International Agricultural Research for Development. University of Bonn, pp. 1–5.
Don, A., Schumacher, J., Freibauer, A., 2011. Impact of tropical land-use change on soil organic carbon stocks – a meta-analysis. Glob. Change Biol. 17, 1658–1670.
Edwards, I.P., Zak, D.R., Kellner, H., Eisenlord, S.D., Pregitzer, K.S., 2011. Simulated atmospheric n deposition alters fungal community composition and suppresses ligninolytic gene expression in a northern hardwood forest. PloS One 6, e20421.
Fioretto, A., Di Nardo, C., Papa, S., Fuggi, A., 2005. Lignin and cellulose degradation and nitrogen dynamics during decomposition of three leaf litter species in a Mediterranean ecosystem. Soil Biol. Biochem. 37, 1083–1091.
Frey, S.D., Ollinger, S., Nadelhoffer, K., Bowden, R., Brzostek, E., Burton, A., Caldwell, B.A., Crow, S., Goodale, C.L., Grandy, A.S., Finzi, A., Kramer, M.G., Lajtha, K., LeMoine, J., Martin, M., McDowell, W.H., Minocha, R., Sadowsky, J.J., Templer, P.H., Wickings, K., 2014. Chronic nitrogen additions suppress decomposition and sequester soil carbon in temperate forests. Biogeochemistry 121, 305–316.
Galloway, J., Townsend, A., Erisman, J., Bekunda, M., Cai, Z., Freney, J., Martinelli, L., Seitzinger, S., Sutton, M., 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. Science 320, 889.
Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S. P., Asner, G.P., Cleveland, C.C., Green, P.A., Holland, E.A., 2004. Nitrogen cycles: Past, present, and future. Royal Horticultural Society.
Geerling, J.C., Loewy, A.D., 2008. Central regulation of sodium appetite. Exp. Physiol. 93, 177–209.
Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis. Glob. Change Biol. 8, 345–360.
Hüttl, R.F., Schaaf, W., 1997. Magnesium Deficiency in Forest Ecosystems. Springer, Netherlands.
Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156.
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., 2008. Nitrogen effects on decomposition: a five-year experiment in eight temperate sites. Ecology 89, 2633–2644.
Hobbie, S.E., Eddy, W.C., Buyarski, C.R., Adair, E.C., Ogdahl, M.L., Weisenhorn, P., 2012. Response of decomposing litter and its microbial community to multiple forms of nitrogen enrichment. Ecol. Monogr. 82, 389–405.
Hobbie, S.E., Vitousek, P.M., 2000. Nutrient limitation of decomposition in Hawaiian forests. Ecology 81, 1867–1877.
IPCC, 2013. Climate change 2013: the physical science basis. Contrib. Working 43, 866–871.
Jonczak, J., 2013. Dynamics, structure and properties of plant Litterfall in a 120-year old beech stand in Middle Pomerania between 2007–2010. Soil Sci. Annual 64, 8–13.
Kanakidou, M., Myriokefalitakis, S., Daskalakis, N., Fanourgakis, G., Nenes, A., Baker, A.R., Tsigaridis, K., Mihalopoulos, N., 2016. Past, present and future atmospheric nitrogen deposition. J. Atoms Sci. 73, 2039–2047.
Knorr, M., Frey, S.D., Curtis, P.S., 2005. Nitrogen additions and litter decomposition: a meta-analysis. Ecology 86, 3252–3257.
Koricheva, J., Gurevitch, J., Mengersen, K., 2013. Handbook of Meta-analysis in Ecology and Evolution.
Li, Y., Xu, M., Zou, X., Shi, P., Zhang, Y., 2005. Comparing soil organic carbon dynamics in plantation and secondary forest in wet tropics in Puerto Rico. Glob. Change Biol. 11, 239–248.
Loranger, G., Ponge, J.F., Imbert, D., Lavelle, P., 2002. Leaf decomposition in two semi-evergreen tropical forests: influence of litter quality. Biol. Fert. Soils 35, 247–252.
Lovett, G.M., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D., Templer, P.H., 2013. Nitrogen addition increases carbon storage in soils, but not in trees, in an eastern U.S. deciduous forest. Ecosystems 16, 980–1001.

Magill, A.H., Aber, J.D., 1998. Long-term effects of experimental nitrogen additions on foliar litter decay and humus formation in forest ecosystems. Plant Soil 203, 301–311.
Magill, A.H., Aber, J.D., 2000. Dissolved organic carbon and nitrogen relationships in forest litter as affected by nitrogen deposition. Soil Biol. Biochem. 32, 603–613.
Manning, P., Saunders, M., Bardgett, R.D., Bonkowski, M., Bradford, M.A., Ellis, R.J., Kandeler, E., Marhan, S., Tscherko, D., 2008. Direct and indirect effects of nitrogen deposition on litter decomposition. Soil Biol. Biochem. 40, 688–698.
Mo, J., Xue, J., Fang, Y., 2004. Litter decomposition and its responses to simulated N deposition for the major plants of Dinghushan forests in subtropical China. Acta Ecol. Sin. 24, 1413–1420.
Mukhopadhyay, S., Joy, V.C., 2010. Influence of leaf litter types on microbial functions and nutrient status of soil: ecological suitability of forest trees for afforestation in tropical laterite wastelands. Soil Biol. Biochem. 42, 2306–2315.
Ngao, J., Bernhard-Reversat, F., Loumeto, J.-J., 2009. Changes in eucalypt litter quality during the first three months of field decomposition in a Congolese plantation. Appl. Soil Ecol. 42, 191–199.
Pérez, C.A., Hedin, L.O., Armesto, J.J., 1998. Nitrogen mineralization in two unpolluted old-growth forests of contrasting biodiversity and dynamics. Ecosystems 1, 361–373.
Prescott, C.E., Johnson, D., Vile, M., Wieder, K., 2010. Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? Biogeochemistry 101, 133–149.
Reich, P.B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M., Chorover, J., Chadwick, O.A., Hale, C.M., Tjoelker, M.G., 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecol. Lett. 8, 811–818.
Rejmánková, E., Houdková, K., 2006. Wetland plant decomposition under different nutrient conditions: what is more important, litter quality or site quality? Biogeochemistry 80, 245–262.
Ren, H.J., Chen, Y.C., Wang, X.T., Wong, G.T.F., Cohen, A.L., DeCarlo, T.M., Weigand, M.A., Mii, H.S., Sigman, D.M., 2017. 21st-century rise in anthropogenic nitrogen deposition on a remote coral reef. Science 356, 749–752.
Rodríguez-Barranco, M., Tobías, A., Redondo, D., Molina-Portillo, E., Sánchez, M.J., 2017. Standardizing effect size from linear regression models with log-transformed variables for meta-analysis. BMC Med. Res. Method 17, 44.
Song, C., Liu, D., Yang, G., Song, Y., Mao, R., 2011. Effect of nitrogen addition on decomposition of Calamagrostis angustifolia litters from freshwater marshes of Northeast China. Ecol. Eng. 37, 1578–1582.
Sun, T., Dong, L., Wang, Z., Lü, X., Mao, Z., 2016. Effects of long-term nitrogen deposition on fine root decomposition and its extracellular enzyme activities in temperate forests. Soil Biol. Biochem. 93, 50–59.
Talbot, J.M., Treseder, K.K., 2012. Interactions among lignin, cellulose, and nitrogen drive litter chemistry-decay relationships. Ecology 93, 345.
Tian, D., Niu, S., 2015. A global analysis of soil acidification caused by nitrogen addition. Environ. Res. Lett. 10.
Treseder, K., 2008. Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies. Ecol. Lett. 11, 1111–1120.
Wardle, D.A., 2004. Communities and ecosystems: linking the aboveground and belowground components. Austral Ecol. 29, 358–359.
Wieder, W.R., Cleveland, C.C., Townsend, A.R., 2009. Controls over leaf litter decomposition in wet tropical forests. Ecology 90, 3333–3341.
Yang, Y.S., Guo, J.F., Chen, G.S., Xie, J.S., Cai, L.P., Lin, P., 2004. Litterfall, nutrient return, and leaf-litter decomposition in four plantations compared with a natural forest in subtropical China. Ann. For. Sci. 61, 465–476.
Yu, Y.F., Peng, W.X., Song, T.Q., Zeng, F.P., Wang, K.L., Wen, L., Fan, F.J., 2014. Stoichiometric characteristics of plant and soil C, N and P in different forest types in depressions between karst hills, southwest China. Chin. J. Appl. Ecol. 25, 947–954.
Yuan, Z.Y., Chen, H.Y.H., 2015. Decoupling of nitrogen and phosphorus in terrestrial plants associated with global changes. Nat. Clim. Change 5, 465–469.
Yue, K., Yang, W., Peng, Y., Zhang, C., Huang, C., Xu, Z., Tan, B., Wu, F., 2016. Dynamics of multiple metallic elements during foliar litter decomposition in an alpine forest river. Ann. Forest Sci. 73, 1–11.
Zak, D.R., Holmes, W.E., Burton, A.J., Pregitzer, K.S., Talhelm, A.F., 2008. Simulated atmospheric NO_3^- deposition increases soil organic matter by slowing decomposition. Ecol. Appl. 18, 2016–2027.
Zhang, D., Hui, D., Luo, Y., Zhou, G., 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. J. Plant Ecol. 1, 85–93.
Zhang, T.A., Chen, H.Y.H., Ruan, H., 2018. Global negative effects of nitrogen deposition on soil microbes. ISME J.
Zhou, G., Guan, L., Wei, X., Tang, X., Liu, S., Liu, J., Zhang, D., Yan, J., 2008. Factors influencing leaf litter decomposition: an intersite decomposition experiment across China. Plant Soil 311, 61.