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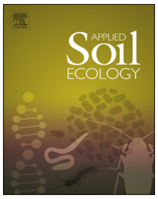

Responses of litter decomposition and nutrient release to N addition: A meta-analysis of terrestrial ecosystems

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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

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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: