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Review paper

The effects of simulated nitrogen deposition on plant root traits: A meta-analysis

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ABSTRACT

Global atmospheric nitrogen deposition has increased steadily since the 20th century, and has complex effects on terrestrial ecosystems. This work synthesized results from 54 papers and conducted a meta-analysis to evaluate the general response of 15 variables related to plant root traits to simulated nitrogen deposition. Simulated nitrogen deposition resulted in significantly decreasing fine root biomass (<2 mm diameter; −12.8%), while significantly increasing coarse root (≥2 mm diameter; +56.5%) and total root (+20.2%) biomass, but had no remarkable effect on root morphology. This suggests that simulated nitrogen deposition could stimulate carbon accumulation in root biomass. The root: shoot ratio decreased (−10.7%) suggests that aboveground biomass was more sensitive to simulated nitrogen deposition than root biomass. In addition, simulated nitrogen deposition increased the fine root nitrogen content (+17.6%), but did not affect carbon content, and thus decreased the fine root C:N ratio (−13.5%). These changes delayed the decomposition of roots, combined with increasing of the fine root turnover rate (+21.4%), which suggests that simulated nitrogen deposition could increase carbon and nutrient retention in the soil. Simulated nitrogen deposition also strongly affected the functional traits of roots, which increased root respiration (+20.7%), but decreased fungal colonization (−17.0%). The effects of simulated nitrogen deposition on the plant root systems were dependent on ecosystem and climate zone types, because soil nutrient conditions and other biotic and abiotic factors vary widely. Long-term simulated experiments, in which the experimental N-addition levels were less than twofold of the average of atmospheric nitrogen deposition, would better reflect the response of ecosystems under atmospheric nitrogen deposition. These results provide a synthetic understanding of the effects of simulated nitrogen deposition on plant root systems, as well as the mechanisms underlying the effects of simulated nitrogen deposition on plants and the terrestrial ecosystem carbon cycle.

1. Introduction

With the increased use of fossil fuels and artificial fertilizers (Davidson, 2009), atmospheric nitrogen deposition has increased by three-to five-fold over the past century (IPCC, 2007) and even further in some regions (Galloway et al., 2004; Dentener et al., 2006). Global annual nitrogen deposition rates are projected to increase by a factor of 2.5 by the end of the century (Lamarque et al., 2005). Atmospheric nitrogen deposition has many negative effects on terrestrial ecosystems, such as the loss of biodiversity (Vitousek et al., 1997; Maskell et al., 2010; De Schrijver et al., 2011). Excessive nitrogen deposition can also affect terrestrial ecosystems through soil acidification (Hoegberg et al., 2006), loss of base cations, and nitrate leaching (Hoegberg et al., 2006; Dise et al., 2009). However, atmospheric nitrogen deposition can stimulate plant growth, thereby increasing carbon sequestration in plant biomass and soil carbon pools (Pregitzer et al., 2008; Reay et al., 2008; Thomas et al., 2010). Plant root systems play critical roles in terrestrial carbon cycling because they not only take up water and nutrients from soil for plant production, but also release carbon through root respiration and rhizodeposition. Atmospheric nitrogen deposition produces strong impacts on plant root systems by influencing morphology (e.g., root length and diameter), biomass, and functions related to carbon cycling (e.g., root respiration) (Nadelhoffer,

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2000; Rasse, 2002). Therefore, the effects of atmospheric nitrogen deposition on root traits can better explain the underlying mechanisms of nitrogen deposition on ecosystem carbon cycling.

Atmospheric nitrogen deposition influences plant root systems directly by injuring tissues and indirectly by changing soil nitrogen availability (Mcquattie and Schier, 1992; Galloway et al., 2004). Soil nitrogen availability plays an important role in plant root dynamics (Vogt et al., 1995). Many studies have suggested that fine root biomass decreased as the nitrogen availability increased (Nadelhoffer, 2000; Hendricks et al., 2006). When soil nitrogen availability increases, the responses of fine root lifespans are inconsistent, both increases (Vogt et al., 1986) and decreases (Nadelhoffer et al., 1985; Pregitzer et al., 1995) were observed. An increase in soil nitrogen availability also alters the root C: N ratio, thereby influencing carbon accumulation in belowground biomass. In addition, an increase in soil nitrogen availability can lead to other nutrient limitations (e.g., phosphorus) (Güsewell, 2004; Vitousek et al., 2010). Soil acidification caused by atmospheric nitrogen deposition can change the environment surrounding plant roots and root fungi (Majdi and Persson, 1993). Therefore, atmospheric nitrogen deposition integrates various factors, which are difficult to quantify but can be revealed by exploring the effects of simulated nitrogen deposition on plant root traits.

Different ecosystem and climate zone types involving different abiotic and biotic factors have various responses to nitrogen deposition (Vogt et al., 1995). In addition, the responses of root systems are markedly different between short- and long-term simulated nitrogen depositions (Persson and Ahlstrom, 1990; Hendricks et al., 2006). The impacts of different experimental N-addition levels on root systems also significantly differ because of the different degrees of soil nitrogen availability (Nadelhoffer, 2000).

Numerous individual studies have been conducted to investigate the effects of simulated nitrogen deposition on root systems, but data synthesis is still unavailable. The present study compiled 15 variables related to plant root traits from 54 experimental studies. A meta-analysis was conducted to identify the general patterns of the responses of plant root traits to simulated nitrogen deposition, investigate the differences among different settings of simulated nitrogen deposition experiments (e.g., ecosystem types, climate zone types, treatment durations, and experimental N-addition levels), and evaluate the response of root traits to increased atmospheric nitrogen deposition under the global change scenario.

2. Materials and methods

2.1. Data collection

In this meta-analysis, data were collected from 54 peer-reviewed journal articles (Supporting Information, Appendix S1) published since 1990 using the Web of Science resource. The search terms were "nitrogen deposition" and "root" or "fertilization" and "root". A total of 15 variables (Appendix S2 and S3) related to plant root traits were compiled from experiments in the control and simulated nitrogen deposition treatments. The following criteria were applied to select proper observations: (1) Only field simulated nitrogen deposition studies were selected and laboratory incubation studies were not included; (2) The control and treatment plots were established to have the same abiotic and biotic conditions; (3) At least one of the selected variables was measured and values calculated by models were excluded; (4) For multifactorial studies, only the control and simulated nitrogen deposition treatment data were selected and the interacting effects were excluded; (5) In N-fertilization experiments, the fertilizers only contained nitrogen and no other nutrients (e.g. K, P, Ca, and Mg); (6) The means, standard errors (SE) or standard deviations (SD) and sample sizes (n) were reported.

Considering the complexity of the dataset, the selected variables were categorized into four groups as follows: (1) Root morphology and biomass (i.e., fine root diameter, fine root length, specific root length, fine root biomass, fine root density, coarse root biomass, total root biomass, and the root: shoot ratio); (2) Root carbon and nitrogen contents (i.e., fine root nitrogen, fine root carbon, and the fine root C:N ratio); (3) Root turnover (i.e., fine root production, fine root turnover rate, and fine root respiration); (4) Fungal colonization. These four groups' plant root traits can well describe the status of roots and their ability to exchange carbon, water, and other nutrients between roots and soil; thus, these traits play critical roles in determining carbon accumulation in plant and soil carbon pools (Brunner and Godbold, 2007). Data were compiled directly from Tables and extracted by Engauge software (4.1) from Figures in the published articles.

To avoid confounding the responses of variables to experimental treatments, the variables of each study were categorized according to the environmental and simulated factors into the following four groups: climate zone types (tropical, subtropical, temperate, and boreal climate zones), ecosystem types (forest and grassland), experimental N-addition levels [N-addition levels ranged from 10 kg N ha^{-1} yr^{-1} to 560 kg N ha^{-1} yr^{-1}, which were divided into low (<100 kg N ha^{-1} yr^{-1}), medium ($\geq$100 and <200 kg N ha^{-1} yr^{-1}), and high levels ($\geq$200 kg N ha^{-1} yr^{-1})], and treatment durations [experimental N-addition treatment durations ranged from 0.2 years to 13.6 years, which were divided into short (<three years), medium ($\geq$three and < ten years), and long terms ($\geq$ten years)]. In addition, experiment location, ambient nitrogen deposition, mean annual temperature (Ta), and mean annual precipitation (P) were also obtained (Appendix S2).

2.2. Meta-analysis

We used the natural log-transformed response ratio (*RR*), defined as the "effect size," as an index to weigh the response of root traits to simulated nitrogen deposition (Hedges et al., 1999). The *RR* was calculated as the ratio of its value in the N fertilization treatment group ($\overline{X}_t$) to that in the control group ($\overline{X}_c$) (Equation (1)). The logarithm of *RR* was carried out to improve its statistical behavior in meta-analyses (Hedges et al., 1999):

$$\ln RR = \ln\left(\overline{X}_t / \overline{X}_c\right) = \ln\overline{X}_t - \ln\overline{X}_c \tag{1}$$

The variance (v) of logarithmic effect size was calculated by:

$$v = \frac{S_t^2}{n_t \overline{X}_t^2} + \frac{S_c^2}{n_c \overline{X}_c^2} \tag{2}$$

where S_t and S_c are the standard deviations ($SD = SE\sqrt{n}$) for the N-addition treatment and control groups, respectively, and n_t and n_c are the sample sizes for the N-addition treatment and control groups, respectively.

The weighting factor(w) of each observation was calculated as the inverse of the variance (Eq. (3)). Because some study cases contain two or more observations, we adjusted the weights by total number of observations per study (Bai et al., 2013), and used the total weighting factor($w\prime$) to estimate the mean effect size (RR_{++}) (Eqs. (4)–(6)):

$$w = \frac{1}{v} \tag{3}$$