Postprint of Meta-analysis on Response of Terrestrial Plant Biomass Allocation to Simulated Nitrogen Deposition

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Abstract

This study analyzed the response of biomass allocation in aboveground and belowground tissues of terrestrial plants to nitrogen deposition, providing a reference for research and practice related to carbon and nitrogen cycling processes in terrestrial ecosystems, plant biomass allocation, timber harvesting, and targeted cultivation under the background of atmospheric nitrogen deposition. A total of 63 original datasets from published studies both domestically and internationally were collected and compiled for Meta-analysis to quantitatively evaluate the effects of nitrogen deposition on plant biomass allocation, with subgroup analyses further conducted to explore the influences of different ecosystem types, plant species, nitrogen fertilizer forms, nitrogen application levels, and duration on biomass allocation. The results showed that, overall, nitrogen application significantly promoted aboveground biomass allocation, with both leaf biomass and stem biomass increasing significantly under nitrogen addition; however, the stimulatory effect on belowground biomass was lower than that on aboveground parts, as evidenced by no significant changes in fine root biomass and coarse root biomass under nitrogen input; plant root-to-shoot ratio decreased significantly under nitrogen deposition; leaf mass ratio, stem mass ratio, and root mass ratio showed no significant changes under nitrogen deposition. Furthermore, subgroup analysis results indicated that ecosystem type and plant type significantly affected the response of total plant biomass and root-to-shoot ratio to nitrogen deposition, with herbaceous plants showing significantly better biomass accumulation than woody plants under nitrogen deposition, suggesting that short-term nitrogen deposition may increase the coverage area of herbaceous plants; fertilizer form exhibited distinct effects on root-to-shoot ratio, with ammonium nitrate having a more significant effect on plant root-to-shoot ratio compared to urea; different nitrogen application levels significantly affected aboveground biomass allocation, with medium nitrogen levels (60-120 kg hm-2 a-1 in this study) exhibiting the strongest enhancement, while the

stimulatory effect at high nitrogen levels (120 kg hm-2 a-1 in this study) was significantly weakened, which was consistent with the changes in total biomass, indicating that excessive nitrogen deposition would inhibit plant growth; the duration of nitrogen deposition treatment also showed significant differences in its effects on aboveground biomass, with the promotion effect of nitrogen deposition on aboveground biomass almost diminishing when the nitrogen application duration exceeded 3 years. In summary, short-term nitrogen deposition causes plants to allocate more biomass to aboveground parts, and the effect of nitrogen deposition on biomass accumulation in herbaceous plants is significantly better than that in woody plants. These findings can provide a scientific basis for future research on aboveground and belowground carbon storage, plant community structure, vegetation dynamics, and related topics under the background of atmospheric nitrogen deposition.

Full Text

A Meta-Analysis of the Response of Terrestrial Plant Biomass Allocation to Simulated Nitrogen Deposition

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Abstract: This study aimed to reveal how terrestrial plant biomass allocation between aboveground and belowground tissues responds to nitrogen (N) deposition and to provide a foundation for research on carbon (C) and N cycles, stand harvests, directed cultivation, and related practices regarding plant biomass allocation in different ecosystems. By synthesizing data from 63 peer-reviewed publications, we quantified the response of plant biomass allocation to N deposition through meta-analysis and assessed the influences of different ecosystem types, plant species, N forms, and N levels on plant biomass allocation. This study found that N deposition significantly increased plant aboveground biomass, with both leaf biomass and stem biomass showing increasing trends under N application. However, although belowground biomass also increased under N deposition, the increase was less than that of aboveground biomass. Fine root biomass and coarse root biomass did not change significantly under N deposition. The root:shoot ratio decreased significantly under N application. Leaf weight ratio, stem weight ratio, and root weight ratio did not change significantly under N deposition. In addition, subgroup analysis showed that there were differences in the response of the root:shoot ratio and total biomass to N deposition for both ecosystem type and plant species. Herbaceous plant biomass accumulation increased significantly more than that of woody plants, which meant N deposition could increase the coverage of herbaceous plants. Nitrogen forms significantly affected the response of the root:shoot ratio to N application, with ammonium nitrate having a more significant effect on the root:shoot ratio than urea. The response of aboveground biomass to N application was significantly affected by the level of N application. Aboveground biomass was promoted the most at a medium N level (60-120 kg hm ^{2}), and at a high N level (120 kg hm ^{2}), there was less of an effect, which was consistent with the change in total biomass. This result indicates that excessive N deposition inhibits plant growth. In addition, there were temporal differences in the effects of N application on plant aboveground biomass. In this study, when the N application time was longer than 3 years, the effect of N application on aboveground biomass was negligible. In conclusion, short-term N application will allow most terrestrial plants to allocate more biomass to aboveground parts, and the biomass accumulation of herbaceous plants is better than that of woody plants. These conclusions will provide a reasonable scientific basis for future correlative studies on plant carbon storage, community structure, tree species diversity, and vegetation dynamics under N deposition.

Keywords: terrestrial plant; meta-analysis; N deposition; plant biomass allocation; root:shoot ratio; root weight ratio

Introduction

Since the Industrial Revolution, atmospheric nitrogen deposition has increased significantly due to fossil fuel combustion and fertilizer use. Global average nitrogen deposition is projected to reach approximately 200 Tg N a ^{1} by the mid-21st century, about double current levels [1]. Nitrogen deposition has serious impacts on terrestrial ecosystems [2-3], and simulation studies of nitrogen deposition have become a hot area in global climate change research. Increased nitrogen deposition enhances nitrogen availability, alters soil nutrient status, and affects the quantity and allocation of photosynthetic products in various plant tissues [4-5]. Some studies have shown that plants in nutrient-poor habitats allocate more biomass to roots, while aboveground biomass is greater when nutrients are abundant, consistent with the functional equilibrium hypothesis [6]. Plants adapt to environmental changes by altering biomass allocation patterns [7-9]. Although there are many studies on plant biomass allocation under nitrogen deposition [10-11], the specific effects of nitrogen deposition on biomass allocation among plant tissues remain unclear, necessitating further research in this area.

Leaves, stems, and roots all play crucial roles in plant life history, jointly regulating plant survival, growth, and reproduction [12]. The allocation strategy of terrestrial plant biomass between aboveground and belowground parts is an important measure for adapting to different environments. Biomass allocation patterns are the result of long-term adaptation to natural selection, and the root:shoot ratio can reflect the evolutionary history of reproductive isolation for certain plants in terrestrial environments [13-14]. Quantitative understanding of plant biomass allocation patterns is of great significance to ecological research. In recent years, many studies have explored the responses of aboveground and belowground biomass and root:shoot ratio to environmental changes [15-18], but conclusions from different studies have not been consistent. To derive general patterns of plant biomass allocation, it is necessary to conduct an integrated analysis of experimental data from relevant studies worldwide. This study collected field simulation experimental data from domestic and international sources on the effects of atmospheric nitrogen deposition on plant biomass allocation, quantitatively assessed the impacts of nitrogen deposition treatments on plant biomass allocation, and through subgroup analysis clarified the effects of different ecosystem types, nitrogen application levels, and durations on aboveground and belowground biomass, root:shoot ratio, and total biomass. We explored the patterns of nitrogen deposition effects on plant biomass allocation to provide a reference basis for future research on plant biomass allocation under scenarios of increasing atmospheric nitrogen deposition.

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1. Data Collection and Inclusion Criteria

This study utilized keyword searches in databases including Web of Science and China National Knowledge Infrastructure (CNKI). Keywords included nitrogen fertilizer and biomass allocation, among others. A total of 63 peer-reviewed papers [15,19-80] with 1,164 observations were used for meta-analysis. Collected papers had to meet the following criteria: (1) each paper had to contain at least one selected indicator for analyzing plant biomass allocation, with clear descriptions of experimental duration, species, climate type, and ecosystem type; (2) only field simulation experiments of nitrogen deposition were considered to assess the effects of climate conditions and ecosystem type on biomass allocation under nitrogen application, while indoor experiments were excluded; (3) experimental and control areas in each independent study had to be under the same climate conditions; (4) means and standard deviations of each indicator had to be reported in the articles or be extractable from figures using Engauge Digitizer software (Free Software Foundation, Inc., Boston, MA, USA) or calculable; (5) for studies with interactions, only simulated nitrogen deposition experimental groups and control groups were extracted.

To avoid publication bias, Egger's linear regression method was used to test each dataset for more reliable data sources. In the database, indicators were divided into aboveground biomass (AGB), belowground biomass (BGB), root:shoot ratio (R/S), total biomass (TB), leaf biomass (LB), stem biomass (SB), fine root biomass (FRB), coarse root biomass (CRB), stem weight ratio (SWR), root weight ratio (RWR), and leaf weight ratio (LWR) to illustrate plant biomass allocation under nitrogen deposition. Different subgroups were used to further explore the relative effects of different factors on nitrogen deposition-induced biomass allocation changes. Specific groupings were as follows: ecosystem type was divided into forest, grassland, and others; plant type was divided into herbaceous (grass), broadleaf, conifer, and shrub; nitrogen addition form was divided into ammonium nitrate (NH NO), urea (CO(NH)), and others; nitrogen addition level was equally divided into high nitrogen (HN, 120 kg hm ²), medium nitrogen (MN, 60–120 kg hm ²), and low nitrogen (LN, 60 kg hm ²); study duration was divided into 3 years and >3 years.

Table 1 shows the abbreviations, definitions, and units used in this article.

The natural logarithm of the response ratio was used as the effect size to measure the impact of nitrogen deposition on plant biomass allocation. The calculation process was performed through MetaWin 2.1 (Sinauer Associates Inc., Sunderland, MA, USA) and Stata 12 (Stata Corp., College Station, TX, USA). In the formulas, X and X represent the means of experimental and control groups, respectively; S and S represent the standard deviations of experimental and control groups; n and n represent the sample sizes of experimental and control groups. Weight w was calculated by formula (5). Since the number of observations in some studies was greater than 1, the weight was adjusted to the total number of observations in each study. The overall effect size was estimated through total weight w (6,7). n is the total number of observations in each study. w and lnRR are the weight and effect size corresponding to the kth observation.

This study adopted a random effects model for meta-analysis. When the 95% confidence interval of the mean effect size of an indicator did not cross zero, it was considered that nitrogen deposition had a significant effect on that indicator, meaning the effect was statistically significant. When the effect size was greater than 0, it indicated a positive effect of nitrogen deposition on the indicator; otherwise, it indicated a negative effect.

Total heterogeneity Q was divided into between-group heterogeneity Q and within-group heterogeneity Q . Between-group heterogeneity Q was used to test differences among ecosystem types, nitrogen application levels, and durations. The process is shown in formula (8), where m represents the number of groups in a classification. When the 95% confidence interval of the effect size of an indicator did not cross zero and the significance was $P < 0.05$, it indicated that the effect size was significantly different.

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2. Effects of Nitrogen Deposition on Biomass Allocation

External nitrogen application can effectively promote plant biomass accumulation. Plant total biomass increased significantly under nitrogen application, with a mean effect size of 0.266 (95% CI: 0.155–0.378). Among the 11 selected indicators, 7 showed significant responses to external nitrogen application. External nitrogen application significantly increased plant aboveground biomass allocation, but the promotion effect on belowground biomass was lower than that on aboveground parts, resulting in a significant reduction in plant root:shoot ratio under nitrogen application (mean effect size = -0.055; 95% CI: -0.106 to

-0.004). This indicates that plant aboveground parts are more sensitive to nitrogen deposition.

For plant aboveground parts, both stem biomass and leaf biomass increased significantly under nitrogen application. For plant belowground parts, although nitrogen application had promotion effects on both fine root and coarse root biomass, they were not significant (mean effect size = 0.060; 95% CI: -0.036 to 0.155). Stem weight ratio and leaf weight ratio showed increasing trends under nitrogen deposition, but not significantly. Root weight ratio showed a decreasing trend under nitrogen application, but this was not significant.

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3. Response of Plant Biomass Allocation to Simulated Nitrogen Deposition in Different Ecosystem Types

Ecosystem types were divided into forest, grassland, and others. The response of plant root:shoot ratio to simulated nitrogen deposition differed significantly among ecosystem types ($Q = 20.952$, $P < 0.001$). Nitrogen application significantly reduced the root:shoot ratio of plants in forest ecosystems (mean effect size = -0.186; 95% CI: -0.426 to 0.054), but in grasslands, nitrogen input had no significant effect on plant root:shoot ratio (mean effect size = 0.024; 95% CI: -0.070 to 0.119). The response of plant total biomass to simulated nitrogen deposition also differed significantly among ecosystem types ($Q = 13.730$, $P = 0.001$), with significant increases in all ecosystems (forest: mean effect size = 0.553; 95% CI: 0.303–0.802; grassland: mean effect size = 0.354; 95% CI: 0.161–0.547). Unlike root:shoot ratio and total biomass, the association between ecosystem type and nitrogen deposition effects on plant aboveground and belowground biomass allocation was weak, meaning ecosystem type had no significant effect on aboveground and belowground biomass.

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4. Response of Different Plant Species' Biomass Allocation to Nitrogen Deposition

Plants were divided into herbaceous, broadleaf, conifer, shrub, and others. The response of root:shoot ratio to simulated nitrogen deposition differed significantly among plant types ($Q = 12.460$, $P = 0.002$). The root:shoot ratio of broadleaf tree species decreased significantly under nitrogen input (mean effect size = -0.155; 95% CI: -0.223 to -0.086), but the root:shoot ratios of coniferous species, shrubs, and herbaceous plants did not change significantly under nitrogen input. The response of total biomass to nitrogen deposition also differed significantly among plant types ($Q = 18.924$, $P < 0.001$), with herbaceous plants (mean effect size = 0.371; 95% CI: 0.186–0.556) and broadleaf species (mean effect size = 0.265; 95% CI: 0.098–0.433) showing significant increases under nitrogen deposition. The effect of nitrogen deposition on total biomass of coniferous species was not significant. There were no significant differences in aboveground and belowground biomass among different plant types.

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5. Response of Plant Biomass Allocation to Simulated Nitrogen Deposition Under Different Nitrogen Forms

Many nitrogen deposition simulation studies have used ammonium nitrate (NH NO), urea (CO(NH)), and other forms. In this study, nitrogen forms were divided into ammonium nitrate, urea, and others. Nitrogen form significantly affected plant root:shoot ratio (Q = 6.380, P = 0.041). Under ammonium nitrate, plant root:shoot ratio decreased significantly (mean effect size = -0.102; 95% CI: -0.162 to -0.041), while other nitrogen forms had no significant effect on root:shoot ratio. Nitrogen form had no significant effect on aboveground, belowground, and total biomass.

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6. Response of Plant Biomass Allocation to Simulated Nitrogen Deposition Under Different Nitrogen Levels

This study included three nitrogen levels: high nitrogen (HN, 120 kg hm ^{2}), medium nitrogen (MN, 60-120 kg hm ^{2}), and low nitrogen (LN, 60 kg hm ^{2}). Different nitrogen levels had significant effects on plant aboveground biomass and total biomass (Q = 11.683, P = 0.003 for aboveground biomass; Q = 6.915, P = 0.032 for total biomass). Both aboveground biomass and total biomass increased significantly under different nitrogen levels, with the medium nitrogen level (60–120 kg hm ^{2}) showing the strongest promotion effect (aboveground biomass mean effect size = 0.475; 95% CI: 0.270–0.680; total biomass mean effect size = 0.334; 95% CI: 0.225–0.443). The increases in aboveground biomass at high and low nitrogen levels were similar (high nitrogen mean effect size = 0.176; 95% CI: 0.058–0.294; low nitrogen mean effect size = 0.155; 95% CI: 0.085–0.225). The increase in total biomass at high nitrogen level was lower than at low nitrogen level (high nitrogen mean effect size = 0.163; 95% CI: 0.022–0.304; low nitrogen mean effect size = 0.230; 95% CI: 0.055–0.405). Different nitrogen levels had no significant effect on belowground biomass.

Figure 1 [**Figure 1: see original paper**] shows the effects of external nitrogen input on various plant biomass allocation indicators.

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7. Response of Plant Biomass Allocation to Simulated Nitrogen Deposition Under Different Durations of Nitrogen Application

The duration of nitrogen application was divided into 3 years and >3 years. Different durations had highly significant effects on plant aboveground and belowground biomass (Q = 8.179, P = 0.017 for aboveground biomass; Q = 3.073, P = 0.215 for belowground biomass). Application for 3 years significantly increased plant aboveground biomass allocation (mean effect size = 0.337; 95% CI: 0.176–0.498), but this promotion effect became insignificant when application lasted >3 years. Plant belowground biomass allocation increased significantly when application lasted >3 years (mean effect size = 0.230; 95% CI: 0.055–0.405), but showed no significant change when application lasted 3 years. Plant root:shoot ratio generally decreased under different nitrogen application durations, but the effect of duration on root:shoot ratio and total biomass was not significant (Q = 3.050, P = 0.218 for root:shoot ratio; Q = 1.173, P = 0.744 for total biomass). Although total biomass generally increased, extending the duration of nitrogen application reduced the promotion effect.

Figure 2 [**Figure 2: see original paper**] shows the effects of elevated nitrogen on biomass allocation across different ecological types, vegetation types, N form, N level, and duration.

Table 2 shows the between-group heterogeneity (Q) for nitrogen deposition effect size across different categorical variables of biomass allocation.

Discussion

Meta-analysis studies by Fu et al. [82] showed that nitrogen deposition has a significant promotion effect on plant aboveground biomass, consistent with our results. The significant increase in aboveground biomass under nitrogen deposition may be caused by increased soil available nitrogen, with sufficient soil nutrients leading plants to allocate more biomass to aboveground tissues [83-84]. This study found that stem biomass showed a significant increasing trend under nitrogen input, consistent with the analysis results of Lu et al. [85]. The study also found that as nitrogen application time extended, the promotion effect of nitrogen treatment on plant aboveground biomass gradually disappeared, possibly because nitrogen deposition enhanced plant nutrient transport capacity, leading to significant increases in stems. In addition, the inhibition effect produced by nitrogen deposition on plant growth may slowly manifest over time. If atmospheric nitrogen deposition is not effectively controlled in the future, its negative impacts on plant growth may become more apparent.

The level of nitrogen application also significantly affects plant aboveground biomass. Aboveground biomass showed the strongest promotion effect at medium nitrogen levels, while higher nitrogen levels reduced the promotion effect. Many studies have found the same conclusion [28,86]. The possible reason for this phenomenon is that long-term high-concentration nitrogen application causes soil acidification [87-88] or nutrient imbalance [89-90], thereby inhibiting plant growth. MetaWin can only be used to analyze the effect of single factors on effect values, while the response of plant biomass allocation to nitrogen deposition is controlled by multiple factors such as nitrogen deposition amount and deposition time. Therefore, there may be some limitations when conducting subgroup analysis on plant biomass allocation response to nitrogen deposition.

The root:shoot ratio plays an important 指示 role in studying carbon and nitrogen allocation and storage in terrestrial ecosystems, and is significant for predicting how plants allocate aboveground and belowground biomass when facing global climate change scenarios. Many nitrogen deposition simulation experiments have shown that external nitrogen application significantly reduces plant root:shoot ratio [85,91-92], consistent with our results. The reduction in root:shoot ratio may be related to the more sensitive response of aboveground biomass to nitrogen deposition. This study found that ecosystem type significantly affects the response of aboveground and belowground biomass allocation to nitrogen deposition. In forest ecosystems, plant root:shoot ratio decreased significantly under nitrogen deposition, but not significantly in grassland ecosystems, consistent with the results of Wang et al. [94]. Compared with forest ecosystems, grassland plant root:shoot ratio did not decrease significantly under nitrogen input. The possible reason is that when nitrogen is input, plant photosynthesis is significantly enhanced, and the demand for water and nutrients also increases accordingly, leading to more organic matter and energy being allocated to roots to maintain water transport and nutrient acquisition between soil and roots [93]. This phenomenon is more obvious in grasslands than in forests [95-96]. In this study, grassland plant belowground biomass showed an increasing trend under external nitrogen input, consistent with the meta-analysis results of Liu et al. [98], which further verified the above explanation.

Differences in plant species significantly affect the response of plant root:shoot ratio to simulated nitrogen deposition [64,97], which confirms the above conclusion. Except for broadleaf trees, the response of root:shoot ratio of other plants to nitrogen deposition differed from that before classification, possibly due to small sample sizes. Unlike this study, the meta-analysis by Fu et al. [82] found that nitrogen deposition had no significant effect on root:shoot ratio, possibly because they only studied changes in root:shoot ratio of alpine plants under nitrogen deposition.

Plant belowground biomass is an important component of global terrestrial ecosystem carbon storage and plays an important role in the global ecosystem carbon cycle. In this study, plant fine root and coarse root biomass did not change significantly under simulated nitrogen deposition conditions, indicating that current plant growth is still in a nitrogen-limited state. However, total belowground biomass increased significantly. Although fine root biomass does not increase significantly under nitrogen input, fine root turnover rate and respiration increase significantly. Plants mainly rely on fine roots to absorb nutrients, and increased fine root turnover rate promotes nutrient absorption [91]. Root respiration is proportional to nitrogen content in roots [99]. Even if fine root biomass does not increase significantly, plants can still enhance absorption of soil available nitrogen under nitrogen deposition. The promotion effect of nitrogen deposition on plant belowground biomass only appears in the short term; when deposition continues, the promotion effect disappears, possibly because long-term continuous nitrogen supply makes the soil nitrogen-saturated, thereby limiting belowground growth.

Currently, a relatively consistent conclusion about the effect of nitrogen input on plant biomass accumulation is that nitrogen input can effectively promote plant biomass accumulation in nitrogen-deficient ecosystems, but has opposite conclusions in nitrogen-saturated ecosystems [100-101]. This study found that although plant biomass accumulation response to nitrogen input was relatively consistent, different factors such as ecosystem type, plant type, and nitrogen application level significantly affected the response. Nitrogen deposition simulation studies have been conducted in different terrestrial ecosystems. Grasslands cover about 40% of the land surface and are usually in nitrogen-limited states [102-103]. In this study, the promotion effect of nitrogen deposition on grassland biomass was significantly higher than on forests. The meta-analysis results of Xia and Wan [104] also showed that nitrogen input had a significantly greater promotion effect on herbaceous biomass than on woody biomass. The possible reason is that nitrogen deposition alleviates nitrogen limitation in grasslands, allowing herbaceous plants to grow vigorously, while for forests, although temperate forests are nitrogen-limited, tropical forests are generally nitrogen-saturated [105]. This well explains why the promotion effect of nitrogen deposition on plant biomass in grasslands is significantly higher than in forests. Most forest experimental sites in this study were in tropical and subtropical regions.

The accumulation of plant biomass at medium nitrogen levels (60–120 kg hm ^{2}) was mainly caused by increased aboveground biomass. This change is important for future community succession and vegetation dynamics. This is consistent with changes in aboveground biomass and further demonstrates that plant biomass in nitrogen deposition simulation studies is primarily affected by aboveground biomass.

Conclusion

Nitrogen deposition significantly affects plant aboveground biomass. Specifically, aboveground biomass increases significantly under external nitrogen input, with both leaf biomass and stem biomass showing significant increasing trends. This may be related to enhanced photosynthesis and nutrient transport under nitrogen input conditions. The promotion effect on aboveground parts indicates that plant canopy structure may expand under nitrogen deposition. Plant belowground biomass receives less promotion than aboveground parts under external nitrogen input. Nitrogen input shows promotion effects on both fine root and coarse root biomass, but these are not significant. The differential response of aboveground and belowground biomass to nitrogen input leads to a significant reduction in root:shoot ratio under nitrogen input, indicating that aboveground parts are more sensitive to nitrogen input than roots and are more likely to benefit from short-term nitrogen deposition.

Ecosystem type and plant species significantly affect the response of plant root:shoot ratio and total biomass to nitrogen input. The promotion effect of nitrogen deposition on grasslands is better than on forests, suggesting that nitrogen deposition may affect future vegetation dynamics and community succession. The response of root:shoot ratio to nitrogen deposition is significantly affected by nitrogen form; ammonium nitrate has a more obvious effect on root:shoot ratio than urea. In simulation experiments of nitrogen deposition effects on plant biomass, nitrogen form may be an important cause of differences among independent studies.

Short-term nitrogen deposition will benefit plant biomass accumulation, but the promotion effect gradually disappears with time extension, implying that plant growth may be limited under future nitrogen deposition scenarios. This serves as a good warning for proactively addressing potential negative impacts of nitrogen deposition on plant growth and provides theoretical guidance and scientific basis for future vegetation and ecosystem management.

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