

Nitrogen effects on plant productivity change at decadal time-scales

Guopeng Liang¹  | Yiqi Luo² | Zhenghu Zhou³ | Bonnie G. Waring¹

¹Department of Biology, Utah State University, Logan, Utah, USA

²Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, Arizona, USA

³Center for Ecological Research, Northeast Forestry University, Harbin, China

Correspondence

Guopeng Liang, Department of Biology, Utah State University, Logan, UT 84321, USA.

Email: guopeng.liang@usu.edu

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Abstract

Aim: Although some long-term studies have been conducted to quantify the impacts of nitrogen (N) on plant productivity, uncertainties remain regarding whether these impacts change over time and the underlying mechanisms. By overlooking this, we might over- or underestimate the impacts of N on terrestrial ecosystems. Our goal was to determine whether the impacts of N on plant productivity change in the long term and what controls these dynamics.

Location: Global.

Time period: 1999–2018.

Major taxa studied: Effects of N on plant productivity.

Methods: We synthesized 63 N addition studies with duration ≥ 8 years in natural terrestrial ecosystems.

Results: Our results showed temporally dynamic impacts of N on plant productivity in terrestrial ecosystems. The interannual coefficient of variation (CV) of N impacts ranged from 19 to 768% across 63 studies, with higher variability in acidic soils. Moreover, a substantial proportion (44%) of studies showed evidence of a consistent directional change in the strength of the impacts of N over time. The direction of change varied with biome type (forests, decrease; grasslands and shrublands, increase). The temporal pattern of the impacts of N was mostly responsive to mean annual precipitation (MAP), mean annual temperature (MAT) and initial soil pH, which accounted for 24%, 19% and 19% of the variation, respectively.

Main conclusions: Our findings indicate that temporally dynamic impacts of long-term N addition on plant productivity and large fluctuations of the impacts of N between years are generally observed among studies in terrestrial ecosystems. Therefore, not only the magnitude of N impacts on plant productivity, but also their temporal pattern and variability should be considered in future experimental and model research.

KEYWORDS

long-term studies, nitrogen addition, plant productivity, temporal pattern, temporal variability, terrestrial ecosystems

1 | INTRODUCTION

Nitrogen (N) addition can enhance the uptake by plants of atmospheric carbon dioxide, increasing plant productivity in terrestrial

ecosystems (Janssens & Luyssaert, 2009; Reay et al., 2008). Although N is considered to be a significant factor affecting plant productivity in terrestrial ecosystems (Du et al., 2020; Dukes et al., 2005; Lebauer & Treseder, 2008; Lu et al., 2018; Vitousek & Howarth, 1991), most

Earth system models implement C–N interactions unfaithfully because the underlying mechanisms of linking terrestrial C and N cycling remain far from clear (Thomas et al., 2015). This leads to large uncertainties in predicting climate change feedbacks in terrestrial ecosystems (Ciais et al., 2019; Green et al., 2019; Wieder et al., 2015). Therefore, in order to provide valuable information for future climate change mitigation and food security policies, a deep understanding of plant productivity responses to N addition is essential.

Given the large impact of N availability on terrestrial ecosystems, many N fertilization experiments have been conducted in the past decades (Kunzová & Hejman, 2010; Oishi et al., 2014; Reich & Hobbie, 2013). However, most of them have focused on short-term N effects, because long-term experiments require enormous resource investment. Moreover, very few meta-analysis studies have been done to collect measurements from long-term N addition experiments. Suding et al. (2005) conducted a meta-analysis study and found that N addition led to declines in plant diversity over time, but studies of this type are rare. As a result, there is much less information regarding long-term effects of N addition on plant productivity when compared with its short-term impacts. Meta-analyses of shorter-term responses have revealed that the impacts of N on plant productivity vary across ecosystem types and in relationship to mean annual temperature (MAT), mean annual precipitation (MAP) and the type and rate of application of N fertilizer (Chen et al., 2015; Lebauer & Treseder, 2008; Yan et al., 2019; Yue et al., 2016). Few of these studies quantified how soil properties (e.g., soil texture, nutrient availability and pH) mediate the impacts of N on plant productivity (Fay et al., 2015). Owing to the limited information that data synthesis can provide, few Earth system models include the roles of soil properties in regulating the impacts of N on terrestrial ecosystems, which might reduce their predictive ability. These models exhibit large divergences among predictions of the terrestrial C sink pattern at decadal and centennial time-scales. This might occur, in part, because the relative contributions of factors affecting the impacts of N on plant productivity change over longer time-scales. Therefore, it is urgent to assess the factors controlling the effects of N on terrestrial ecosystems in both the short and long term.

Although a temporal pattern in the effects of N on plant productivity has been reported in some individual studies (Brooks & Coulombe, 2009), the underlying mechanisms remain poorly explored. On the one hand, addition of N can stimulate plant productivity by relieving nitrogen limitation. However, the magnitude of this stimulation can change over time, owing to the degree of co-limitation by other resources [e.g., phosphorus (P), potassium (K), microelements, light and water] (Du et al., 2020; Fay et al., 2015) and the time needed for the ecosystem to approach N saturation (Aber, 1992; Aber et al., 1998, 2003). On the other hand, N addition can result in soil acidification (Falkengren-Grerup & Tyler, 1993; Tian & Niu, 2015), decrease plant biodiversity (which is positively related to plant productivity) (Chalcraft et al., 2008; Chen, Wang, et al., 2018; Liang et al., 2015; Midolo et al., 2019; Suding et al., 2005) and reduce relative abundances of mycorrhizal fungi and oligotrophic bacteria, which are crucial for nutrient cycling in N-limited ecosystems (Collins et al., 2008; Leff et al., 2015). These negative impacts on plant

productivity may strengthen or weaken over time, depending on the capacities of ecosystems to resist and adapt. The sign and temporal trend of plant responses to N addition will therefore depend both on the absolute magnitude of positive versus negative effects and on the relative rates at which these effects change over time.

Temporal patterns in plant responses to fertilization can be mediated by a variety of site-specific factors (e.g., initial soil pH, C:N, P availability, MAT and MAP). For example, in extremely N-limited (high soil C:N) sites, plant productivity might increase over time as added N accumulates in the ecosystem. Consequently, positive impacts of N on plant productivity might predominate and strengthen through time. Conversely, in sites where the soil is extremely acidic, plant productivity responses might diminish over time as soil acidification progresses. Climatic variables, such as MAT and MAP, affect these patterns indirectly, through their influences on soil pH, soil nutrient availability, soil microbial community structure and plant diversity (Crowther et al., 2019; Hou et al., 2018; Jing et al., 2015). Interannual variability in these climatic drivers might also lead to temporal fluctuations in plant community responses to added N; for example, N fertilization might not stimulate plant growth in a drought year, when water becomes limiting. Moreover, the efficiency of use and rate of uptake of N vary across N fertilizer types (Abbasi et al., 2013; Kaštovská & Šantrůčková, 2011), and the magnitude of the decrease in soil pH and the time needed for ecosystems to approach N saturation are dependent on the N application rate (Tian & Niu, 2015; Tian et al., 2016). Consequently, fertilizer type and application rate might also play critical roles in regulating the temporal pattern of effects of N on plant productivity.

The performance of Earth system models has been improved by incorporation of C–N interactions (Tang & Riley, 2018; Thomas et al., 2015; Wieder et al., 2015); however, most models do not consider the potential temporal patterns of the impacts of N. To advance model development, we must determine when and where the impacts of N on plant productivity vary through time. Although the value of long-term studies for advancing knowledge of the effects of global change on ecosystems and C cycling is widely recognized among ecologists (Kuebbing et al., 2018), no study has been done to summarize the results of the temporal pattern and/or interannual variability in plant productivity responses to N addition based on the long-term experiments. Here, we synthesize 63 long-term (≥ 8 years) N-addition studies from around the world to address three research objectives: (1) to determine the short- and long-term and overall effects of N addition on plant productivity in terrestrial ecosystems; (2) to quantify potential temporal patterning and variability in these plant responses; and (3) to identify underlying controls on the magnitude, temporal pattern and variability of plant responses to N.

2 | METHODS

2.1 | Data sources

Publications reporting the response of plant productivity to experimental N addition in terrestrial ecosystems were collected by

searching Web of Science. The keywords used for the literature search consisted of “long-term nitrogen addition” OR “long-term nitrogen fertilizer” OR “long-term nitrogen deposition” AND “biomass” OR “productivity” OR “tree growth”. The dataset provided by a recent meta-analysis about the effect of N addition on forest carbon (Schulte-Uebbing & de Vries, 2018) was also used in the present study.

We screened all resulting publications using the following criteria:

1. The studies were conducted at a field site for ≥ 8 years. After screening the potential papers from which we could extract data, we found that there were nine case studies that reported results from 8-year experiments (14% of the acceptable papers identified); to maximize the size of our dataset, we therefore set the lower bound on study length to 8 years. The distribution of the experimental duration of 63 case studies selected in this study is provided in the Supporting Information (Figures S1 and S2).
2. Plant productivity in both control conditions (0 N kg/ha/year) and N addition treatment was measured continuously every year from the beginning of the experiment.
3. Given that aboveground and belowground plant productivity can show divergent responses to N addition (Chen, Dong, et al., 2018; Cusack et al., 2011; Li et al., 2011), we collected data only from the studies that reported aboveground (56 of 63 studies) or whole-plant productivity (seven of 63 studies) if aboveground plant productivity was not provided.
4. The data from different plant productivity types or N application rates in the same study were regarded as independent observations.
5. Plant productivity was assessed by measuring basal area increment (for forests), biomass (for grasslands) or canopy height (for shrublands). Note that for some experiments, plant productivity was not measured every year. However, if the number of measurements was at least five and the frequency of measurements could capture the short (e.g., < 3 years), medium and long term (e.g., > 8 years) well, they were also included in our study.

The geographical locations (latitude and longitude), climate factors (MAT and MAP), initial soil variables (organic C, total N and P, available N, P and K, pH, clay content and bulk density), N fertilizer variables (N type and application rate) and ecosystem-related variables (ecosystem type and forest age) were also obtained from the papers. If papers did not include MAT and MAP, we extracted them from the database at <http://www.worldclim.org/>, using latitude and longitude with the “raster” package (Hijmans & van Etten, 2012). In the event that soil pH, bulk density and clay content were not provided in the papers, they were extracted from the database at <https://www.isric.org/> using the “GSIF” package, with the help of the latitude and longitude (Hengl, 2020). The data presented in figure form were extracted by using Engauge Digitizer software (Free Software Foundation, Boston, MA, USA). All data were grouped by biome, climate condition, N fertilization rate, initial soil pH, N

fertilizer type and forest age. Given that nearly all long-term studies we collected were conducted in temperate and boreal zones instead of tropical regions, the ranges of MAT and MAP were not wide. Therefore, cut-off values of MAT, MAP, N fertilization rate and forest age were their medians (6.3°C, 875 mm, 50 kg N/ha/year and 30 years), and the cut-off value of pH was 7.

After this preliminary screening, our meta-analysis included 20 publications providing 63 N fertilizer case studies (44 for forests, 25 for grasslands and four for shrublands) from 20 field sites (Supporting Information Figure S2).

2.2 | Data analysis

2.2.1 | Determining the impacts of N on plant productivity

The means of plant productivity in control conditions (\bar{X}_c) and the N addition treatment (\bar{X}_t) in every year in each case study were used to compute a response ratio (RR), as follows:

$$RR = \ln(\bar{X}_t/\bar{X}_c) = \ln(\bar{X}_t) - \ln(\bar{X}_c). \quad (1)$$

Next, we generated three summary response ratios for each study: (1) RR_{first} , the RR in the first year for each study; (2) RR_{mean} , the average RR across all years for each study; and (3) RR_{last} , the RR in the last year for each study. Most studies did not provide the standard deviation of plant productivity (60 of 63 studies); therefore, RR_{mean} and RR_{last} were weighted by sample size and experimental duration by following Terrer et al. (2016):

$$W = \frac{(n_c \times n_t)}{(n_c + n_t)} + \frac{(yr \times yr)}{(yr + yr)}. \quad (2)$$

The RR_{first} was weighted by sample size:

$$W_{\text{first}} = \frac{(n_c \times n_t)}{(n_c + n_t)}, \quad (3)$$

where W is the weighting factor; n_c and n_t are the sample size in control and N addition treatment, respectively; and yr is the length of the study in years. If sample sizes were not provided (three of 63 studies), they were assigned as the median of sample sizes of the other 60 studies. WRR_{first} , WRR_{mean} and WRR_{last} were weighted RR_{first} , RR_{mean} and RR_{last} , respectively. For WRR_{first} , WRR_{mean} and WRR_{last} , the 95% confidence interval (95% CI) was calculated, and the effects of N on plant productivity were considered significant if the 95% CI did not overlap with zero. Given that some field sites included multiple case studies, we calculated the average of RR_{mean} (RR_{average}) for each field site if appropriate.

The quality check of this meta-analysis and statistical choices were carried out according to previous papers (Gurevitch & Hedges, 1999; Hedges et al., 1999; Viechtbauer, 2010). The

meta-analyses were performed using the “metafor” package in RSTUDIO v.1.2.5033 (Viechtbauer, 2010). We created funnel plots to detect publication bias using the “funnel” function, and no significant publication bias was found. The “leave1out” function was used to perform sensitivity testing, and we found that excluding any one of the studies did not affect the overall results.

2.2.2 | Quantifying temporal pattern and variability in long-term impacts of N on plant productivity

We used simple linear regression to determine the relationship between experimental duration (year) and RR for each study (Supporting Information Figure S3). The slope of this linear regression for each study and the corresponding standard error was recorded. To permit comparison across studies, the weighted mean of slopes (S) was calculated as follows (Kim, 2011):

$$S = \frac{\sum S_i/v_i}{\sum 1/v_i}, \quad (4)$$

where S_i is the slope for each study, and v_i is the squared standard error for each study.

The corresponding standard error of the weighted mean (SE) was given by:

$$SE = \sqrt{\frac{1}{\sum 1/v_i}}. \quad (5)$$

We recognize that a simple linear relationship might not be the best-fitting model to describe the temporal dynamics of N impacts in each study; theoretically, it would be possible to observe exponential relationships, saturating relationships or the absence of a relationship between RR and time. In the context of a meta-analysis, however, we had to derive a summary statistic that could be compared directly across studies. Parsimoniously, we selected a linear model to minimize the number of parameters estimated. We also evaluated the suitability of these linear models by performing Spearman rank-order correlation tests. Thirty-five of the 63 studies had an absolute value of the Spearman correlation coefficient $\geq .40$, above which value we considered the monotonic relationship to be moderately strong (Supporting Information Figure S4). Given that some field sites included multiple case studies, we described the directionality of the temporal pattern of N impacts on plant productivity at one field site as “increased” if the slopes of the linear regression between RR and time were higher than zero in all case studies; as “decreased” if the slopes of the linear regression between RR and time were lower than zero in all case studies; and as “mixed” if the field site included case studies showing both “increased” and “decreased” patterns of N impacts on plant productivity.

Given that there was weak evidence of directional relationships between RR and time in about half of the studies examined, we also determined the temporal variability of long-term N impacts on plant

productivity. The coefficient of variation (CV) for each study was calculated as follows:

$$CV = \frac{\sigma}{\mu}, \quad (6)$$

where σ is the standard deviation of RR for each study, and μ is the absolute value of mean RR for each study.

2.2.3 | Predictors of the impacts of N on plant productivity, and the temporal pattern and variability of these impacts

The relative influences of predictor variables were quantified by using boosted regression tree (BRT) analysis, including predictor variables that were reported in > 50% of studies. Multicollinearity was tested to eliminate the variables that were redundant before running the BRT analysis. We included MAT, MAP, N application rate, RR_{first} , initial soil pH, initial soil clay content and initial soil bulk density as predictor variables (except when the response variable was RR_{first} ; in this case, it was obviously not included as a predictor). The reason why we included RR_{first} as a predictor variable was to determine whether the overall or long-term response of plant productivity to addition of N is predictable based on the short-term response. The BRT analysis was run in R with the “gbm” package (Greenwell, 2019), using the appropriate weighting factor. The three main parameters needing optimization in the BRT analysis were the learning rate (shrinkage), the depth of each regression tree (interaction.depth) and the number of iteration (ntree). In the present study, the three optimized parameters for shrinkage, interaction.depth and ntree were .01, 2 and 12,000, respectively. Overall, the BRT analysis explained 97% of the variation in RR_{first} , 97% in RR_{mean} , 96% in RR_{last} , 89% in S and 87% in CV. All statistical analyses and graphs were performed using RSTUDIO v.1.2.5033.

3 | RESULTS

3.1 | Plant productivity responses to N addition

Short-term (WRR_{first}) effects of N addition on plant productivity in terrestrial ecosystems were insignificant, with detectable effects only in conditions of high (> 7) initial soil pH. In contrast, long-term (WRR_{last}) and overall (WRR_{mean}) impacts of N were significantly positive (Figure 1). Positive overall N impacts on plant productivity were found at most field sites (19 of 20), and they were distributed evenly at the global scale, without showing a strong latitudinal pattern (Supporting Information Figure S5). Overall and long-term N impacts showed the same trends regarding their significance and magnitude (Figure 1). The impacts of N on overall productivity were positive in forests and grasslands, but non-significant in shrublands. Nitrogen also boosted productivity in conditions of low MAT (< 6.3°C) and low MAP (< 875 mm), whereas fertilization did not impact productivity in warmer and wetter conditions. Effects were also more positive for

younger forests (< 30 years at the start of the experiment) rather than older stands. Generally speaking, the impacts of N on plant productivity were non-significant in the short term but became significant and positive in the long term in most situations.

MAP was the most influential factor determining the magnitude of overall (WRR_{mean}) plant productivity responses (Figure 2a). In contrast, the influence of N application rate on plant productivity responses to N addition was relatively small, and its influence did not change when measured in the first year, in the last year or as the mean response across all years. Additionally, except for initial soil pH, the overall contribution of soil properties (e.g., initial soil clay content and bulk density) to impacts of N on plant productivity was also relatively minor. The most influential factor determining the magnitude of plant productivity responses varied according to when the productivity response was measured (short term, initial soil pH; long term, MAP).

3.2 | Temporal variability and pattern of long-term N impacts

The impacts of N on plant productivity varied greatly from year to year. The CV of RR ranged from 19 to 768% across studies, and the mean value was $109 \pm 148\%$ (Figure 3b; Supporting Information Figure S6). The CV of RR in alkaline soils (24%) was much lower than

that in acidic soils (121%), but there were no other consistent differences in CV across experimental groups. According to BRT analysis, soil variables (53%) mostly explained cross-study patterns in CV, followed by fertilizer variables (18%), RR_{first} (17%) and climate variables (12%).

Spearman's rank correlation coefficient between RR and experimental duration was $> .5$ in 28 of 63 studies (Supporting Information Figure S4). In other words, 44% of studies showed evidence of a consistent directional change in the strength of the effects of N over time. Although only half of the studies showed a monotonic relationship between RR and time, our overall weighted mean slope estimate was negative but relatively small (.003). In other words, the response ratio of the effect of N on plant productivity in terrestrial ecosystems decreased by .3% annually. This finding suggests that, on average, long-term N effects on plant productivity tend to decrease slightly over time in terrestrial ecosystems (Figure 3a).

The temporal pattern of the impacts of N was randomly distributed at the global scale and did not show specific spatial patterns (Supporting Information Figure S5). Moreover, temporal variations in the sign and magnitude of plant responses were found not only across field sites, but also found from different case studies within one field site. The direction of the temporal pattern of N impacts varied among biomes: N impacts decreased over time in forests but increased in grasslands and shrublands. The effects of N declined

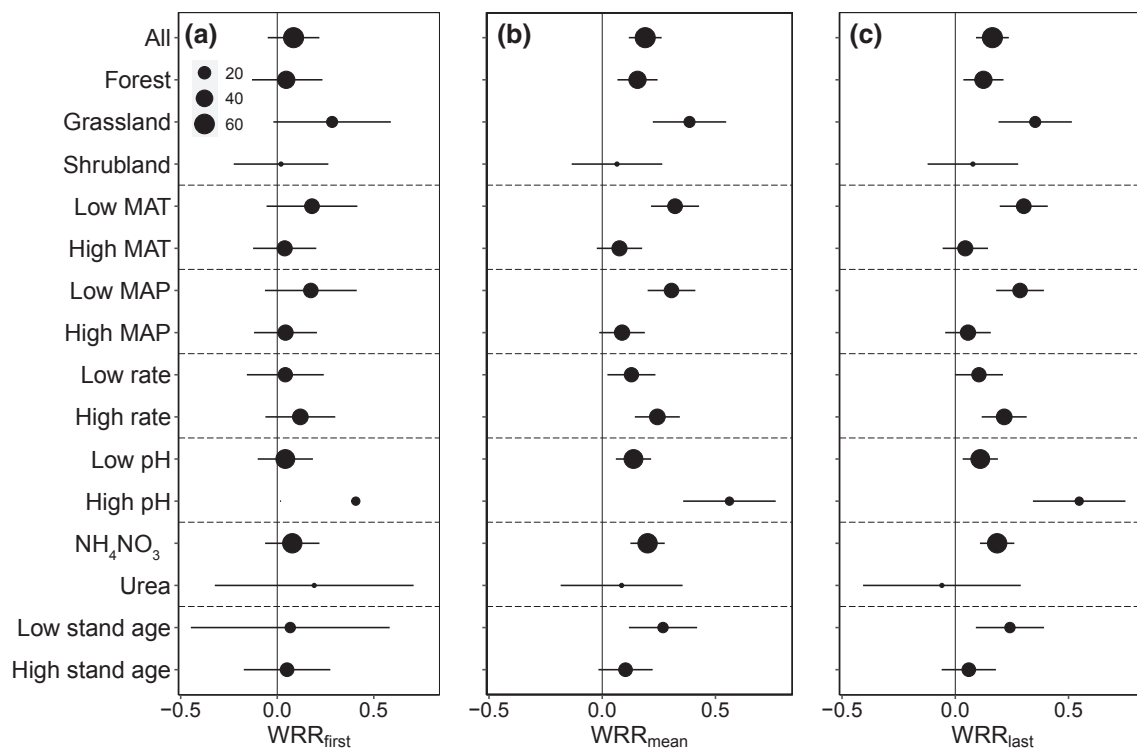


FIGURE 1 Weighted response ratios of plant productivity (WRR) under N addition in studies grouped by biome, climate condition, N fertilization rate, initial soil pH, N fertilizer type and forest age. These weighted response ratios were calculated using: (a) data from only the first year (WRR_{first}); (b) all timepoints (WRR_{mean}); and (c) only the most recent timepoint (WRR_{last}). Values represent effect sizes $\pm 95\%$ confidence intervals. The size of each point is proportional to the sample size. Cut-off values of mean annual temperature (MAT), mean annual precipitation (MAP), N fertilization rate and forest age were their medians (6.3°C, 875 mm, 50 kg N/ha/year and 30 years, respectively). The cut-off value of the initial soil pH (pH) was 7

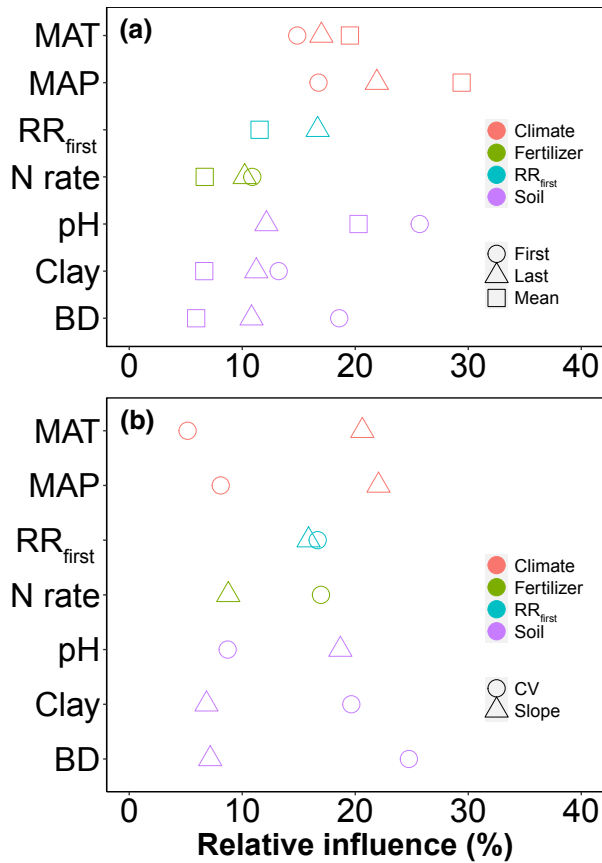


FIGURE 2 Relative influence of predictor variables on (a) RR_{first} (circles), RR_{mean} (squares) and RR_{last} (triangles) or (b) the coefficient of variation (CV) of the response ratio of the effect of N addition on plant productivity (RR) (circles) and the slope of the linear regression between RR and time (triangles). BD = initial soil bulk density; Clay = initial soil clay content; MAP = mean annual precipitation; MAT = mean annual temperature; N rate = nitrogen application rate; pH = initial soil pH; RR_{first} = RR in the first year; RR_{last} = RR in the last year; RR_{mean} = average RR across all years

over time in sites characterized by warm or wet climates or acidic soils. In contrast, N effects strengthened over time in sites characterized by cold, dry climates or alkaline soils (Figure 3a). However, the temporal pattern of N fertilization was not dependent on N application rate, N fertilizer type or forest age. MAP had the greatest influence on the temporal response of plant productivity to N addition, accounting for 24% of the variation among studies. Additional variance was explained by MAT (19%), initial soil pH (19%), RR_{first} (15%), N application rate (9%), initial soil bulk density (8%) and initial soil clay content (6%) (Figure 2b).

3.3 | Relationship between N effect sizes and their temporal patterns

The magnitude of the effects of N on productivity (i.e., the degree to which N increased growth at the first, last or time-integrated measurement intervals) was not related consistently to the temporal

trend of these responses (Supporting Information Figure S7). For studies that showed decreases in the impacts of N through time, the effect of N addition on plant productivity was positive in the first year (WRR_{first}) but became insignificant by the last year (WRR_{last}). For studies that showed increases in the impacts of N through time, the effect of N addition on plant productivity was positive in both the first and last year.

4 | DISCUSSION

4.1 | Overall impacts of N on plant productivity and the controls

Our study found significant and positive overall impacts of N on plant productivity in terrestrial ecosystems (Figure 1), which is consistent with previous studies (Lebauer & Treseder, 2008; Vitousek & Howarth, 1991). However, negative effects of N addition on plant productivity were found in six studies (Supporting Information Figure S5). Most Earth system models do not incorporate the mechanisms by which N addition might slow plant productivity (e.g., soil acidification and micronutrient losses associated with N leaching), which might result in large uncertainties in their predictions.

The most influential factor determining the magnitude of the impacts of N on plant productivity changed according to the time frame over which productivity responses were measured (short term, initial soil pH; long term, MAP; Figure 2a). The positive impact of N on plant growth was, in general, relatively minor for the first year of N application, which could be attributable to the initial soil pH and its significant negative effect on plant growth. Soils with lower initial soil pH have greater resistance to the soil acidification caused by N application when compared with soils having higher initial soil pH (Tian & Niu, 2015). Furthermore, Tian and Niu (2015) found that soil pH decreased by .25, .34, .24 and .12 for a study with duration of < 5, 5–10, 10–20 and > 20 years, respectively. This suggests that the impacts of fertilizer-related soil acidification could weaken over time. Meanwhile, the importance of MAP for predicting long-term growth responses might relate to the availability of non-N nutrients, in that P limitation becomes more severe with increasing MAP. Overall, our study indicates that the controls of N impacts on plant productivity change over time. This finding might be used to calibrate Earth system models to improve their long-term predictive ability.

4.2 | Temporal variability of long-term impacts on plant productivity and the controls

Our study found that for most long-term studies, the impacts of N on plant productivity showed enormous variation between years (Figure 3b). This finding could reflect that the response of plant productivity to N addition in a particular year would be highly dependent on the local precipitation and temperature in that year. We

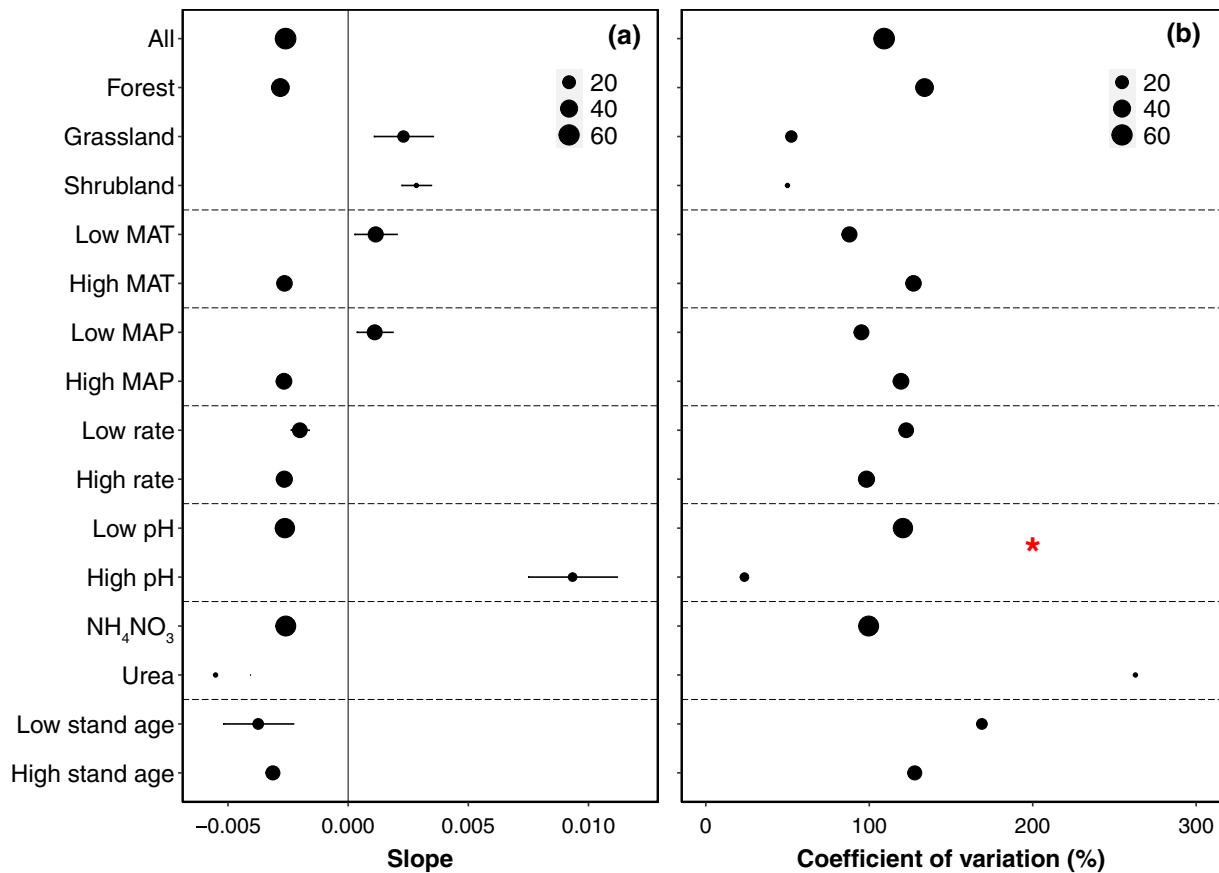


FIGURE 3 (a) The slope of the linear regression between response ratio (RR) and time and (b) the coefficient of variation (CV) of RR in studies grouped by biome, climate condition, N fertilization rate, initial soil pH, N fertilizer type and forest age. Values represent effect sizes $\pm 95\%$ confidence intervals. The size of each point is proportional to the sample size. Cut-off values of mean annual temperature (MAT), mean annual precipitation (MAP), N fertilization rate and forest age were their medians (6.3°C, 875 mm, 50 kg N/ha/year and 30 years, respectively). The cut-off value of pH was 7

did not find any evidence that mean climatic conditions (i.e., MAT or MAP) mediated the degree of interannual variability in plant responses. However, the CV was lower on alkaline soils, although this might be an artefact of the relatively small number of studies conducted in high-pH sites. Most studies determining the impacts of N are conducted only over short time frames. If any one of these years is particularly hot, dry, etc., the study might not capture representative responses of plant production to N inputs. Therefore, more long-term studies should be encouraged, and climatic covariates should be measured and reported in each year to gain a better understanding of ecosystem responses to N deposition.

4.3 | Temporal pattern of long-term impacts on plant productivity and the controls

Ecologists have argued that global change experiments might overestimate impacts on terrestrial ecosystems because the effects of global change drivers (e.g., elevated CO₂, warming and N deposition) can diminish over time at the local scale (Leuzinger et al., 2011). However, given that few studies have synthesized the results from long-term N fertilization studies at the global scale, it remains

unknown whether impacts of N on plant productivity also shift over time. We found that within any given ecosystem, the impacts of N on plant productivity were extremely variable from year to year; in many cases, this interannual variability showed no consistent pattern. Yet on average, we found that impacts of N on plant productivity in the present study decreased very weakly through time (Figure 3a), which indicates that the effect of N on plant productivity can be temporally dynamic in terrestrial ecosystems. It should be noted that large variations in the directionality of response (i.e., increasing vs. decreasing slopes of RR vs. time) were found not only across field sites but also from different case studies within one field site (Supporting Information Figure S5). A field site with multiple case studies usually included different plant species or N application rates. Likewise, Chalcraft et al. (2008) found that impacts of N on plant biodiversity vary from small to large spatial scale. Therefore, in order to improve the accuracy of estimation of N impacts on terrestrial ecosystems, it is necessary to consider the drivers of variation at both small and large scales.

Changing plant responses to N might be explained by concomitant shifts in soil pH, nutrient availability, microbial community and plant biodiversity. However, most long-term experiments do not measure these variables continuously together with plant

productivity, which complicates efforts to unravel the underlying mechanisms. Yet site-specific variables (e.g., MAT, MAP, initial soil pH, N application rate and fertilizer type) can provide clues about the drivers of temporal pattern in the effects of N on plant productivity. The direction of temporal pattern of long-term N impacts on plant productivity was different between sites with low and high MAT, between sites with low and high MAP, between sites with low and high initial soil pH, and between ecosystem types (Figure 3a). This finding was supported by the BRT analysis, which showed that the temporal pattern of N impacts was regulated mostly by MAP, MAT and initial soil pH (Figure 2b). The effects of N tended to decrease in sites characterized by warm and wet climates or acidic soils, but tended to increase in sites characterized by cold and dry climates or alkaline soils (Figure 3a). These patterns are likely to reflect non-target effects of N on soil properties. The N leaching rate is higher with high MAP and MAT, and it becomes more severe with continuous N application. Soil acidification, base cation (Ca²⁺, K⁺, Mg²⁺ and Na⁺) losses and soil erosion can occur with N leaching and become more serious over time. Additionally, soil acidification caused by N addition and Al³⁺ accumulation associated with soil acidification tend to be more severe in acidic soils (Tian & Niu, 2015).

4.4 | Limitations of the study

First, the goal of this study was to determine whether N impacts on plant productivity change over time; we used the slope of the relationship between RR and time to assess this. This simple linear

model might not be the best-fitting model for any particular study, especially in the case of a non-monotonic relationship (e.g., a hump-shaped relationship between RR and time). When inspecting the raw data (Supporting Information Figure S4), we saw that the vast majority of studies displayed: (1) a monotonic relationship between RR and time, which could be described well by a linear model; or (2) no relationship, in which case the slope estimate was small and the SE large. Our meta-analysis calculations captured both of these scenarios accurately, because they incorporated slope estimates and their associated standard errors. It should be noted that the linear slopes ranged from -0.03 to 0.02 (i.e., the magnitude of plant responses to N declined $\leq 3\%$ annually or increased $\leq 2\%$ annually). In other words, directional changes in plant responses to N, when present, are relatively mild.

Second, we were not able to assess the mechanisms that drove the temporal pattern of ecosystem response to N. This mainly reflects a lack of time-series data related to changes in soil pH, nutrient availability, microbial communities and plant biodiversity. Further studies should measure these variables together with plant productivity continuously.

Third, we used the data in the first year and in the last year to represent short- and long-term responses, respectively. It should be noted that the response of plant productivity to N addition in a particular year would be highly dependent on the local climatic conditions in that year; a conclusion that is highlighted by the extremely high interannual variability in N responses observed within and among studies.

Last, most long-term N studies were conducted in the temperate and continental regions, which means that our study cannot shed light on the long-term N pattern in tropical zones. More studies in

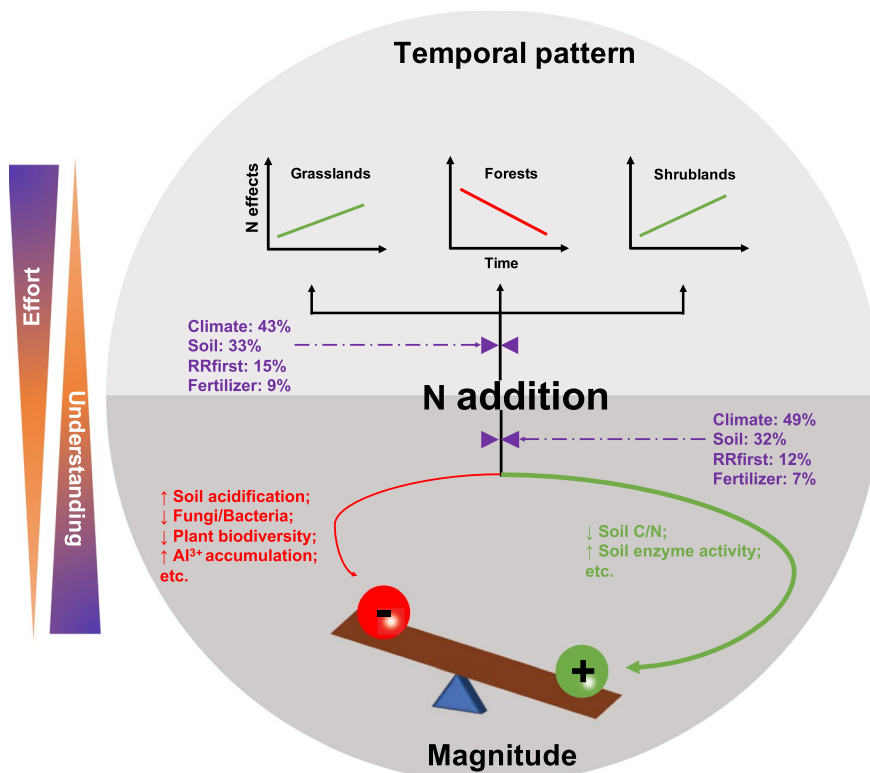


FIGURE 4 Long-term impacts of N addition on plant productivity and their temporal patterns. Red arrows represent negative N impacts/decreasing plant productivity responses, whereas green arrows represent positive N impacts/increasing plant productivity responses. The purple bowties represent the factors influencing the overall N impact or its temporal pattern; the relative contribution is shown next to the corresponding factor

tropical ecosystems should be done in the future because of their great role in climate change mitigation (Bonan, 2008).

4.5 | Implications

Our study found that long-term impacts of N on plant productivity in terrestrial ecosystems are positive, because higher N availability generally stimulates plant growth. However, the degree of stimulation shows large temporal variability from year to year, with a substantial number of ecosystems displaying consistent increases or declines in the magnitude of response (Figures 1 and 3). This finding indicates that we might over- or underestimate the effects of N on terrestrial ecosystems by making inferences based on short-term measurements. Unfortunately, the magnitude of N impact in the short term (RR_{first}) was not a very strong predictor of the magnitude of long-term N impacts, their temporal pattern or their temporal variability (Figure 2). This result demonstrates the value of long-term experiments, which can be used to explore the mechanisms that drive decadal responses to N addition. Most field experiments last < 3 years, which means that patterns extrapolated from short-term measurements might not reflect long-term ecosystem dynamics. Our study highlights the necessity of long-term experiments. It is essential for funding agencies to invest more in experiments at multi-decadal time-scales.

Terrestrial ecosystems play a large role in mitigation of climate warming by absorbing atmospheric carbon dioxide. For Earth system models that include C–N interactions, most consider the positive effect of N on plant growth rate, which has been widely observed from many experimental studies. However, they do not incorporate the mechanisms of potentially decreased N impacts on plant productivity over time via soil acidification, N saturation, etc. As a result, Earth system models might overestimate the potential of terrestrial ecosystems for future climate mitigation. In order to predict C cycling in terrestrial ecosystems under future climate change, it is urgent to pay more attention to the underlying mechanisms that drive the temporal pattern of plant responses to N (Figure 4). Moreover, when quantifying the impacts of N on terrestrial ecosystems in the long term, future meta-analysis studies should generate time-integrated response metrics to avoid inaccurate estimation.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

G.L. designed the study and collected the data. G.L. and B.G.W. analysed the data. G.L., B.G.W., Y.L. and Z.Z. contributed significantly to the writing of the manuscript.

DATA AVAILABILITY STATEMENT

All data are given in the Supporting Information and are also available on Figshare at: <https://doi.org/10.6084/m9.figshare.14698794.v1>.

ORCID

Guopeng Liang  <https://orcid.org/0000-0001-5514-785X>

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BIOSKETCH

Guopeng Liang is a PhD student in the Department of Biology at Utah State University. His research interests include global change ecology, ecosystem carbon cycling and soil microbiology.

Yiqi Luo is a Professor at the Northern Arizona University. His research programmes are designed to advance predictive understanding of ecosystem ecology and biogeochemistry under global environmental change via data–model integration.

Zhenghu Zhou is a Professor of the Center for Ecological Research at Northeast Forestry University. His research interests are soil microbial ecology, ecological stoichiometry and global change.

Bonnie Waring is a Senior Lecturer of Grantham Institute – Climate Change and Environment at Imperial College London. Her research focuses on investigating how the ecology of plant and soil microbial communities influences the carbon cycle and its feedbacks on climate change.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX

DATA SOURCES

Avolio, M. L., Koerner, S. E., La Pierre, K. J., Wilcox, K. R., Wilson, G. W. T., Smith, M. D., & Collins, S. L. (2014). Changes in plant

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