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Global response patterns of plant photosynthesis to nitrogen addition: A meta-analysis

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Abstract

A mechanistic understanding of plant photosynthetic response is needed to reliably predict changes in terrestrial carbon (C) gain under conditions of chronically elevated atmospheric nitrogen (N) deposition. Here, using 2,683 observations from 240 journal articles, we conducted a global meta-analysis to reveal effects of N addition on 14 photosynthesis-related traits and affecting moderators. We found that across 320 terrestrial plant species, leaf N was enhanced comparably on mass basis (N_{mass}, +18.4%) and area basis (N_{area}, +14.3%), with no changes in specific leaf area or leaf mass per area. Total leaf area (TLA) was increased significantly, as indicated by the increases in total leaf biomass (+46.5%), leaf area per plant (+29.7%), and leaf area index (LAI, +24.4%). To a lesser extent than for TLA, N addition significantly enhanced leaf photosynthetic rate per area (A_{area}, +12.6%), stomatal conductance (g_s, +7.5%), and transpiration rate (E, +10.5%). The responses of A_{area} were positively related with that of g_s, with no changes in instantaneous water-use efficiency and only slight increases in long-term water-use efficiency (+2.5%) inferred from ^{13}C composition. The responses of traits depended on biological, experimental, and environmental moderators. As experimental duration and N load increased, the responses of LAI and A_{area} diminished while that of E increased significantly. The observed patterns of increases in both TLA and E indicate that N deposition will increase the amount of water used by plants. Taken together, N deposition will enhance gross photosynthetic C gain of the terrestrial plants while increasing their water loss to the atmosphere, but the

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effects on C gain might diminish over time and that on plant water use would be amplified if N deposition persists.

KEYWORDS

leaf area, N addition, N deposition, photosynthesis, plant carbon gain, plant functional traits, plant water use

1 | INTRODUCTION

Cycling of C and N is interactively coupled across scales from leaf to the whole plant and ecosystem, thus changes in availability of one are likely to affect the cycling of the other (Zaehle, 2013). Anthropogenic activities have profoundly enhanced N availability for terrestrial ecosystems through increasing atmospheric N deposition (Fowler et al., 2013; Galloway et al., 2008). Even though rates of the atmospheric N deposition in the last two decades have plateaued or declined in some parts of the world (Gilliam et al., 2019; Schmitz et al., 2019; Yu et al., 2019), chronic atmospheric N deposition continues to be a major component of global change, particularly in and around developing nations (BassiriRad, 2015; Stevens, 2019). Therefore, there is a growing need to reliably predict the potential effects of N deposition on terrestrial C gain to understand and attribute C sequestration (Bala, Devaraju, Chaturvedi, Caldeira, &Nemani, 2013; Huntzinger et al., 2017).

At the whole plant level, gross photosynthetic C gain is collectively governed by a suite of traits related to plant photosynthesis (Figure 1; Lambers, Chapin III, & Pons, 2008). Although it has long been acknowledged that N deposition may affect gross plant photosynthetic C gain via affecting total leaf area (TLA) and/or leaf photosynthetic capacity (Janssens & Luyssaert, 2009), we still lack a comprehensive understanding of these photosynthesis-related traits in response to N deposition. On the one hand, to what extent N addition would change TLA remains unknown, although significant enhancements have been reported for plant biomass (Schulte-Uebbing & de Vries, 2018; Sillen & Dieleman, 2012; Song et al., 2019) as well as total leaf biomass (Xia & Wan, 2008), the responses of leaf morphology (e.g., specific leaf area, SLA), and TLA have been largely unknown. On the other hand, the effects of N addition on leaf photosynthetic capacity also remain unclear. Nitrogen addition has been demonstrated to increase mass-based leaf N concentration (N_{mass} in Figure 1; Ostertag & DiManno, 2016; Yuan & Chen, 2015), however, how N addition changes area-based leaf N content (N_{area} in Figure 1) has not been revealed, although N_{area} is the appropriate predictor for area-based leaf photosynthetic capacity (A_{area} in Figure 1; Osnas, Lichstein, Reich, & Pacala, 2013). Furthermore, under some conditions, A_{area} might still be restricted even though leaf N is enhanced, because N addition could reduce base cations (e.g., K^+, Ca^{2+}, and Mg^{2+}) via lowering soil pH (Lucas et al., 2011; Tian & Niu, 2015). For instance, in a tropical forest, N addition increased N_{area} while decreased K^+, Ca^{2+}, and Mg^{2+} in leaves, leading to significant decreases in A_{area} of two tree species (Mao, Lu, Mo, Gundersen, & Mo, 2018). Given the above uncertainties, a meta-analysis integrating multiple photosynthesis-related traits (as shown in Figure 1) is needed to facilitate mechanistic understanding of the effects of N addition on gross plant photosynthetic C gain.

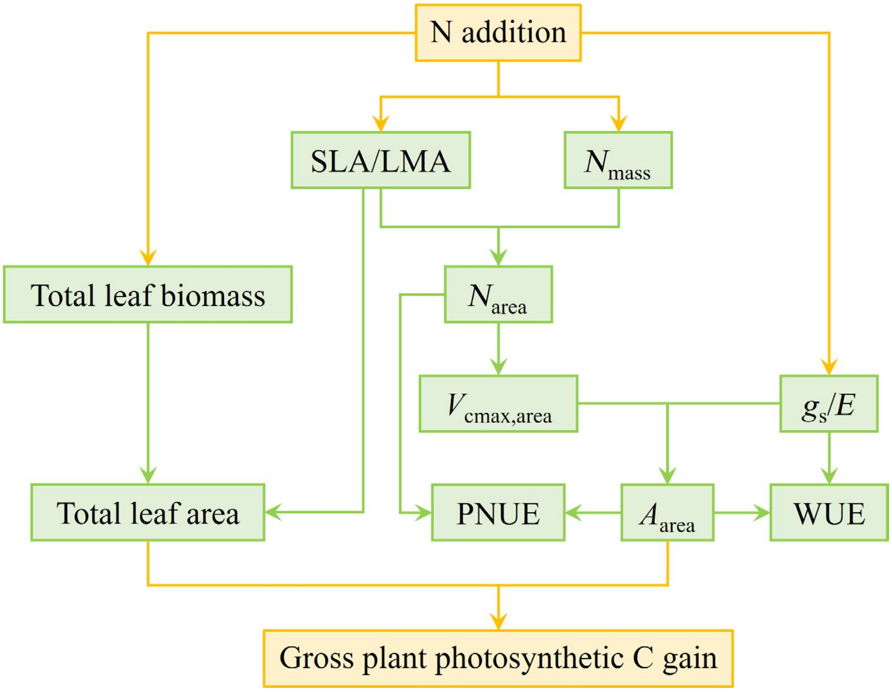

FIGURE 1 Conceptual model depicting the mechanisms that explain effects of N addition on gross plant photosynthetic C gain. Photosynthesis-related traits are shown in green boxes: SLA, specific leaf area; LMA, leaf mass per area; N_{mass}, leaf N per mass; N_{area}, leaf N per area; $V_{cmax,area}$, leaf carboxylation rate per area; g_s, stomatal conductance; E, leaf transpiration rate; A_{area}, leaf photosynthetic rate per area; PNUE, photosynthetic nitrogen use efficiency; WUE, water-use efficiency [Colour figure can be viewed at wileyonlinelibrary.com]

Several moderators are expected to affect the responses of plant photosynthesis-related traits to N addition. First, the responses may depend on biological moderators such as plant functional types. For instance, in a temperate grassland, N supply significantly reduced A_{area} and consequently biomass of forbs but not those of grasses (Tian, Liu, et al., 2016). Across study sites, a meta-analysis reported that N addition significantly enhanced plant biomass of grasses but not that of forbs (You et al., 2017). Several other meta-analyses also showed that the responses of N_{mass} to N addition differed significantly between woody and herb species, conifers and angiosperms, or shrubs and trees (Ostertag & DiManno, 2016; Xia & Wan, 2008; Yuan & Chen, 2015).

Second, experimental moderators (e.g., N addition rate, duration, cumulative N load, N form, and site management) may exert palpable effects on the responses of photosynthesis-related traits. According to the N saturation hypothesis, plants would perform in different magnitudes or even different directions before and after reaching a threshold of N load (Aber et al., 1998; Aber, Nadelhoffer, Steudler, & Melillo, 1989; Niu et al., 2016). Previous meta-analyses have reported linear or nonlinear relationships between N addition rate and the responses of N_{mass} (Yuan & Chen, 2015) and plant biomass (Schulte-Uebbing & de Vries, 2018; Tian, Wang, Sun, & Niu, 2016; Xu, Liu, Wang, & Song, 2018). Experimental duration also affects the responses of N_{mass} (Zhang et al., 2018) and root biomass (Peng, Guo, & Yang, 2017). Nitrogen form has been demonstrated to influence ecological processes such as soil respiration (Deng, Peng, et al., 2018; Liu & Greaver, 2010), though its effects on plant responses have not been illustrated. Site management might lead plants to respond differently to N addition by affecting resource availability such as light availability.

Third, environmental moderators (e.g., latitude, temperature, precipitation, soil pH) may also be expected to influence the responses of photosynthesis-related traits to N addition. There is a "conventional wisdom" that higher latitude regions with lower temperatures are more N-limited, because soils in higher latitude are younger and N mineralization is suppressed at low temperature (Deng, Liu, et al., 2018; McGroddy, Daufresne, & Hedin, 2004; Reich & Oleksyn, 2004). A recent meta-analysis showed that N addition significantly enhanced aboveground woody biomass for boreal and temperate forests but not that for tropical forests (Schulte-Uebbing & de Vries, 2018). In other meta-analyses, changes in whole plant or root biomass were found to be related linearly to mean annual precipitation (Xia & Wan, 2008) or with mean annual precipitation (Peng et al., 2017). Soil pH has been reported to be related with changes in aboveground net primary productivity (Tian, Wang, et al., 2016) as well as species richness (Simkin et al., 2016; Stevens, Dise, Mountford, & Gowing, 2004).

To date, several studies have examined overall responses of photosynthetically important traits to N addition, including meta-analyses of leaf photosynthetic rate per area (Chen et al., 2015; Zhang et al., 2018), leaf N per mass (N_{mass}; Ostertag & DiManno, 2016; Yuan & Chen, 2015), SLA and leaf area index (LAI; Li et al., 2016), total leaf biomass (Xia & Wan, 2008), and long-term water-use efficiency (Guerrieri et al., 2011). However, these studies are limited either in plant functional types or in the number of traits, with relatively few observations. Moreover, possible biological, experimental, and environmental moderators affecting the responses of photosynthesis-related traits have not been simultaneously considered in previous meta-analyses.

The present study was undertaken to examine the literature to provide a mechanistic understanding of photosynthetic responses to N addition. We were particularly interested to examine a suite of plant traits that have been recognized to affect whole-plant photosynthetic C gain (Cornelissen et al., 2003; Lambers et al., 2008). We also analyzed the effects of biological, experimental, and environmental moderators on the trait responses. To our knowledge, this is the first global analysis that simultaneously examines responses of such a collection of photosynthetically important traits to N addition, and hence can be used to inform large-scale models that incorporate ecosystem function (Bouskill, Riley, & Tang, 2014; Zaehle, 2013).

2 | MATERIALSANDMETHODS

2.1 | Plant functional traits

According to the conceptual model (Figure 1), 14 photosynthesis-related traits were included in the present meta-analysis. Among them were four biochemical/morphological traits: N_{mass}, leaf N per area (N_{area}), SLA, and leaf mass per area (LMA); three structural traits: total leaf biomass, leaf area per plant, and LAI; and seven physiological traits: leaf photosynthetic rate per area (A_{area}), leaf carboxylation rate per area ($V_{\text{cmax,area}}$), stomatal conductance (g_s), leaf transpiration rate (E), photosynthetic nitrogen-use efficiency (PNUE), instantaneous water-use efficiency (inst-WUE, inferred from gas exchange measurement of A_{area} and g_s) and long-term water-use efficiency (long-WUE, calculated from plant ^{13}C composition). We recognized that LMA and SLA are not independent, but studies included in our synthesis reported only the responses of either LMA or SLA. Thus, we quantified the responses of both LMA and SLA to obtain a more comprehensive and robust response pattern of leaf morphology. It is worth noting that leaf area per plant is referring to the summed leaf area of a given plant with a unit of m^2/plant, it is more specific at the individual plant level; whereas LAI is more specific at the community and/or ecosystem level, as it is referring to leaf area per unit ground surface area with a unit of m^2/m^2.

2.2 | Data sources

Article searching and inclusion were performed following the guidelines suggested by PRISMA (Moher, Liberati, Tetzlaff, Altman, & PRISMA Group, 2009; Figure S1). Journal articles published online before April 2019 were searched in Web of Science, using the following search terms: (nitrogen OR fertiliz* OR N OR urea OR manure OR nitri* OR ammon*) AND (effect* OR respon* OR affect* OR impact* OR increas* OR decreas* OR alter* OR deposition OR enrich*) AND (carboxylation OR photosynthe* OR stomatal conductance OR transpiration OR water use efficiency OR 13C OR leaf biomass OR foliage biomass OR needle biomass OR leaf area OR stoichiometr*) NOT (animal* OR medic* OR chemist*). As supplements, journal articles used in related previous meta-analyses (Chen et al., 2015; Fu, Niu, & Dukes, 2015; Li et al., 2016; Xia & Wan, 2008; Yuan & Chen, 2015; Zhang et al., 2018) were also included.

The search results included over 36,000 papers, which were further selected to meet the following criteria: (a) experiments must be carried out in natural soils, excluding experiments using artificially potting soil (i.e., the mixture of sand, clay, and vermiculite, etc.) to grow plants; (b) experiments must be conducted outdoors, all indoor experiments such as greenhouse or close top chamber were excluded; (c) experiments must be conducted with N addition only, that is, any N addition experiments conducted along with P addition (including Hogland nutrient solution), warming, elevated CO_2, or drought were excluded; (d) experiments must be conducted using native species, as we aimed to explore the responses of native vegetation to N addition.

Finally, 240 published articles (Appendix S1), with 2,683 observations (Data S1) of 320 plant species from different functional types (Table S1), were compiled from 184 sites worldwide (Figure S2). Most sites were located in Northern America, Western Europe, and Eastern Asia (Figure S2), covering zones of high anthropogenic N deposition (Galloway et al., 2008).

2.3 | Data extraction

Data with means and standard deviations of both control and N addition groups provided by the original articles were used directly. Data provided by figures in the original articles were extracted using Plot Digitizer (http://plotdigitizer.sourceforge.net). We extracted plant functional type information of each species (i.e., herbaceous vs. woody, legume vs. nonlegume, C3 herb vs. C4 herb, forb vs. grass, shrub vs. tree, broadleaved vs. coniferous tree, broadleaf evergreen vs. broadleaf deciduous tree), experimental factors (i.e., N form [NO_3^--N, NH_4^+-N, NH_4NO_3-N, urea, and others], N addition rate, duration, cumulative N load [total added N during a specific duration calculated as N addition rate multiplied by duration], and site management), and environmental factors (i.e., latitude, longitude, mean annual temperature [MAT] and mean annual precipitation [MAP], soil pH). Note that the duration of an experiment was referring to the interval between the time when the first N addition treatment occurred and the time when plant response was measured. For site management, we distinguished managed and natural plants, with managed plants referred to plants that were grown in plantations, orchards, open top chambers, and pots (filled with natural soil) in the field, while natural plants were referring to plants naturally regenerated in the field. Both managed and natural plants generally have not experienced irrigation, pesticides, or weed. Regarding the environmental factors, if not provided directly, MAT and MAP were extracted from Worldclim (http://www.worldclim.org), and soil pH was extracted from SoilGrids (https://www.isric.org/explore/soilgrids), using the latitude and longitude of the study sites.

One "mean value ± standard deviation" per trait per species under per N addition rate from a given study was considered as one "observation." Observations for different species from the same study were considered independent, while observations for the same species in the same study were considered non-independent. For example, if a study had several treatments (e.g., N addition rates) or the responses were measured several times over the study period (e.g., annually), the observations were non-independent. However, all these observations were extracted and included into the dataset, to utilize all available data to address relevant questions (Cheung, 2015a, 2019), such as how N addition rate and experimental duration affect the responses. It should be noted that, since multiple observations for the same species in the same study are non-independent, and to take the non-independence into account, they were treated using a "shifting the unit of analysis" approach in the present study (see Section 2.4.2 below).

After the extraction of plant ^{13}C composition ($\delta^{13}C_p$), long-WUE was estimated (Farquhar, Ehleringer, & Hubick, 1989; Guerrieri et al., 2011):

$$\text{long}-\text{WUE}=(c_a/1.6)(b-\delta^{13}C_a+\delta^{13}C_p)/(b-a),$$

where c_a is ambient CO_2 concentration, $\delta^{13}C_a$ is the ^{13}C composition of atmospheric CO_2, a is the fractionation for $^{13}CO_2$ as a result of diffusion through air (4.4‰), and b is the fractionation during carboxylation (27‰) by the CO_2-fixing enzyme Rubisco. c_a and $\delta^{13}C_a$ can be estimated according to the calendar year (t; Feng, 1999):

$$c_a=277.78+1.35\ \exp[0.01572(t-1740)]$$
$$\delta^{13}C_a=-6.429-0.006\ \exp[0.0217(t-1740)].$$

In the present study, t is the calendar year when $\delta^{13}C_p$ was measured, which was provided by the original paper. This approach does not consider local variation in c_a, though c_a is not frequently measured locally in the studies we analyzed anyhow.

2.4 | Statistical analysis

2.4.1 | Response ratios

The natural logarithm-transformed response ratios, ln(RR), of individual observation were calculated using meta-analysis (Hedges, Gurevitch, & Curtis, 1999):

$$\ln(RR)=ln(\bar{X}_t/\bar{X}_c)=ln(\bar{X}_t)-ln(\bar{X}_c),$$

where $\bar{X}_t$ and $\bar{X}_c$ stand for means of the treated and the control groups, respectively.

The variation of ln(RR), that is,v, was calculated as:

$$v=\frac{(SD_t)^2}{n_t\bar{X}_t^2}+\frac{(SD_c)^2}{n_c\bar{X}_c^2},$$

where SD_t and SD_c are the standard deviations of the N addition and the control groups, respectively, and n_t and n_c are the sample sizes of the N addition and the control groups, respectively.

2.4.2 | Independence and weights

The initial weight (w) of each observation was calculated as (Hedges et al., 1999):

$$w = 1/v,$$

where v is the variation of ln(*RR*).

However, if multiple observations for the same species in the same study were included, we must take the non-independence into account. To do this, we used a "shifting the unit of analysis" approach (Cheung, 2015a; Cooper, 2010):

When calculating overall response ratio, the unit of analysis was a species in a study, that is, multiple observations for the same species in the same study were considered to be non-independent. Then, the non-independent response ratios were first averaged within species within studies, by adjusting the weight of each response ratio (Bai et al., 2013):

$$w' = w/n,$$

where w' is the adjusted weight of each observation, n was the total number of observations for a given trait of the same species from the same study.

When evaluating the effects of moderators, such as N addition rate, the unit of analysis was each response ratio, that is, each observation under multiple N addition rates for the same species in the same study was considered to be independent of each other, and thus, the initial weight would be used.

We also conducted a three-level meta-analysis using the *metaSEM* package in R, which was proposed to deal with non-independent effect sizes (Cheung, 2015b, 2019). The results of the conventional meta-analysis and those of the three-level meta-analysis were similar (Table S2). In the main content here, we only reported the conventional results.

2.4.3 | Normality and outliers

Any ln(*RR*) with a standardized residual value exceeding the absolute value of 3 was removed as an extreme value (Anton et al., 2019). After the removal, the distribution of standardized residuals was tested by skew and kurtosis tests (van Valkengoed & Steg, 2019). The test showed that the standardized residuals of 11 traits followed, and the standardized residuals of three traits (i.e., N_{mass}, total leaf biomass, and inst-WUE) asymptotically followed a standard normal distribution (Figure S3 and Table S3), which met the assumptions of meta-analysis (Viechtbauer, 2010). To evaluate the influence of potential outliers, we conducted influential case diagnostics using the *influence* function of *metafor* package in R (Viechtbauer, 2010). If the exclusion of the potential outliers from the analysis leads to considerable changes in the weighted mean of ln(*RR*), then the outliers may be considered to be influential (Viechtbauer, 2010; Viechtbauer & Cheung, 2010). In the present study, 1–74 potential outliers were detected by the diagnostics. However, the exclusion of these potential outliers exerted little influence on the results for all the studied traits (Table S4). We also performed a sensitivity analysis using the *leave1out* function of the *metafor* package (Viechtbauer, 2010). It turned out that leaving out any one of the data points, we did not observe a bias from the overall mean response ratio (Figure S4).

2.4.4 | Publication bias

Publication bias was tested by the "trim and fill" method (Duval & Tweedie, 2000), using the *trimfill* function in the *metafor* package. It is assumed that some studies might be missing from a given meta-analysis. The trim and fill method can be used to estimate the number of missing studies, and then fill the missing data in, to make the funnel plot more symmetric (Duval & Tweedie, 2000). Filled-in values were not used in the final analyses of effect sizes, but were used to evaluate the bias in the results. After the missing data were filled in, a filled response ratio with 95% confidence interval (CI) was calculated for each trait. If there was a significant difference between the initial response ratio and the filled response ratio, that is, the initial response ratio's 95% CI did not overlap with the 95% CI of the filled response ratio, then publication bias was considered to significantly affect the results (Duval & Tweedie, 2000; Viechtbauer, 2010). For our dataset, both the response ratios and the 95% CI values were comparable before and after the missing data were filled in (Table S5 and Figure S5). Therefore, there was little influence of publication bias on the present analyses.

2.4.5 | Weighted mean responses

Weighted means of ln(*RR*), $\overline{\ln(RR)}$ hereafter, with 95% CI were calculated using the mixed-effects model with the R package *metafor* (Viechtbauer, 2010). Finally, values of $\overline{\ln(RR)}$ were transformed back to percentage changes through exponentiation:

$$(e^{\overline{\ln(RR)}} - 1) \times 100\%,$$

with 95% CIs that did not overlap with zero considered statistically significant.

2.4.6 | Meta-regressions

The effects of moderators on the response ratios were evaluated by the meta-regression analysis, using the *rma(mods)* function of the *metafor* package. The moderators included categorical (plant functional type, N form, managed vs. natural plant) and continuous (N addition rate, duration, cumulative N load, absolute latitude, MAT, MAP, and soil pH) moderators. An omnibus test of between-moderator heterogeneity was used, which is based on a χ^2 distribution, with the effects of moderators considered to be significant for $p < .05$.

3 | RESULTS

Leaf N per mass and leaf N per area were increased significantly by 18.4% [95% CI: 15.1%, 21.9%] and 14.3% [8.5%, 20.4%], respectively, with no changes in LMA or SLA (Figure 2).

Nitrogen addition significantly increased total leaf area-related (TLA-related) variables, including total leaf biomass (46.5% [95% CI: 33.1%, 61.4%]), leaf area per plant (29.7% [18.1%, 42.6%]), and LAI (24.1% [16.3%, 33.1%]; Figure 3). Nitrogen addition also significantly increased photosynthetic rate per leaf area (A_{area}; 12.6% [8.5%, 17.0%]), stomatal conductance (g_s; 7.5% [0.4%, 14.9%]), and transpiration rate (E; 10.5% [3.5%, 18.1%]), while it did not significantly increase carboxylation rate per leaf area ($V_{\text{cmax,area}}$; Figure 3). Overall, the responses of all TLA-related traits were greater than that of A_{area} (Figure 3). For 16 studies that have investigated both TLA-related variables and A_{area} (Appendix S1), when plotting the responses of A_{area} against those of TLA-related variables, most of the points and their mean values were found to fall near or below the 1:1 line (Figure 4).

Photosynthetic nitrogen-use efficiency was not changed significantly under N addition (Figure 3). Both inst-WUE (calculated as A_{area}/g_s) and long-WUE (inferred from plant δ^{13}C value) showed a slight increase in response to N addition, but only the response in long-WUE (2.5% [1.1%, 4.0%]) was statistically significant (Figure 3). The responses among A_{area}, g_s, and $V_{\text{cmax,area}}$ were significantly correlated with each other (Figure 5).

The effects of N addition on photosynthesis-related traits depended on the plant functional types (Table S6; Figure 6). The most striking differences were found between forb and grass species (Figure 6a), with grasses showed significantly greater enhancement across N_{mass} (grass: 34.0% vs. forb: 20.3%), SLA (6.2% vs. −4.9%), total leaf biomass (57.6% vs. 14.2%), A_{area} (20.0% vs. −3.1%), g_s (17.4% vs. −15.5%), and E (21.3% vs. 0.7%). The enhancements of N_{mass} were significantly greater in herb (29.2%) than in woody species (12.2%; Figure 6b). The responses of leaf area per plant were significantly greater in broadleaf (31.8%) than in conifer trees (6.9%), also the responses of E were greater in broadleaf (22.3%) than in conifer trees (−5.1%; Figure 6c). There were significant differences in the responses of inst-WUE and PNUE between broadleaf deciduous and broadleaf evergreen trees, both inst-WUE and PNUE were significantly decreased for broadleaf evergreen trees but were not changed significantly for broadleaf evergreen trees (Figure 6d). Legumes exhibited significantly greater responses in A_{area} and E to N addition than did nonlegumes (Table S6). Compared to C4 herbs, C3 herbs showed a significantly greater response in long-WUE (Table S6; Figure 6e).

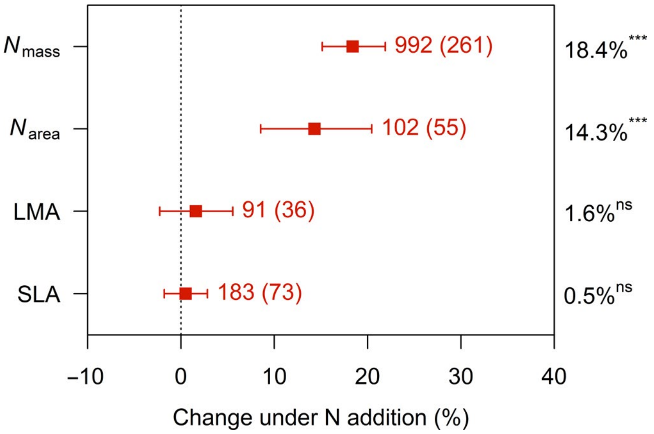

FIGURE 2 Overall responses (±95% CI) of the four biochemical/morphological traits to N addition. N_{mass}, leaf N per mass; N_{area}, leaf N per area; LMA, leaf mass per area; SLA, specific leaf area. The number of observations (species) for each trait is shown near the bar. The numbers on the right of the figure represent the mean percentage changes of the tested traits, with p-values denoted by $^{\text{ns}}p > .05$; $^{***}p < .001$ [Colour figure can be viewed at wileyonlinelibrary.com]

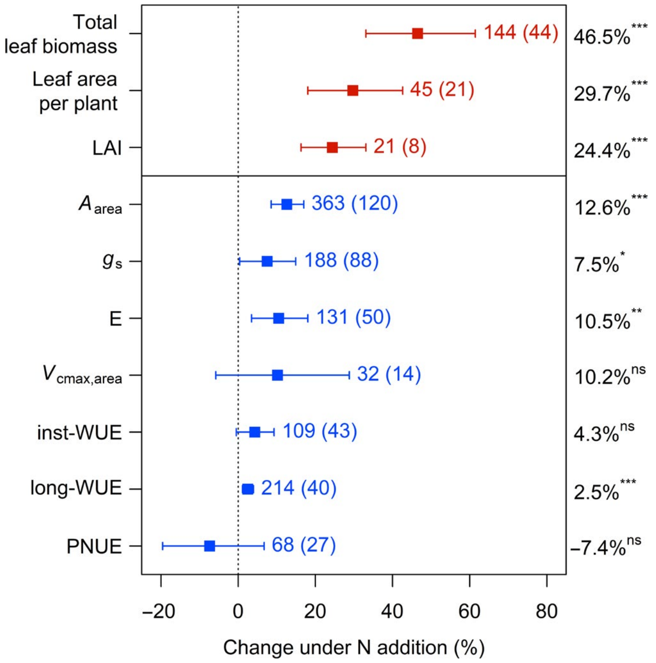

FIGURE 3 Overall responses (±95% CI) of the three structural traits (in red) and the seven physiological traits (in blue) to N addition. LAI, leaf area index; A_{area}, leaf photosynthetic rate per area; g_s, stomatal conductance; E, leaf transpiration rate; $V_{\text{cmax,area}}$, leaf carboxylation rate per area; inst-WUE, instantaneous water-use efficiency; long-WUE, long-term water-use efficiency; PNUE, photosynthetic nitrogen use efficiency. The number of observations (species) for each trait is shown near the bar. The numbers on the right of the figure represent the mean percentage changes of the tested traits, with p-values denoted by $^{\text{ns}}p > .05$; $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$ [Colour figure can be viewed at wileyonlinelibrary.com]

Nitrogen addition rate significantly affected the responses of leaf N, PNUE, and inst-WUE but not that of other traits (Figure 7; Table S7). As N addition rate increased, both N_{mass} and N_{area} increased to greater extents, but PNUE decreased to greater extents and the response of A_{area} did not change significantly (Figure 7a–d). Experimental duration showed significant influences on the responses of LAI, A_{area}, and E, with the enhancements of LAI and

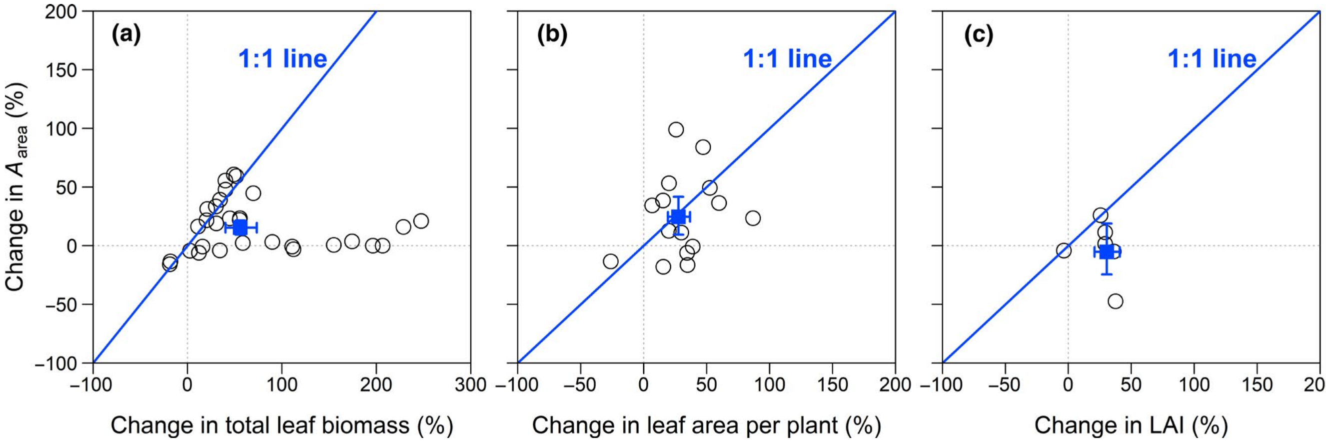

FIGURE 4 Responses of A_{area} against that of (a) total leaf biomass, (b) leaf area per plant and (c) LAI to N addition. The blue points indicate the weighted mean, with error bars indicating ±95% CI of the variables in each panel. LAI, leaf area index [Colour figure can be viewed at wileyonlinelibrary.com]

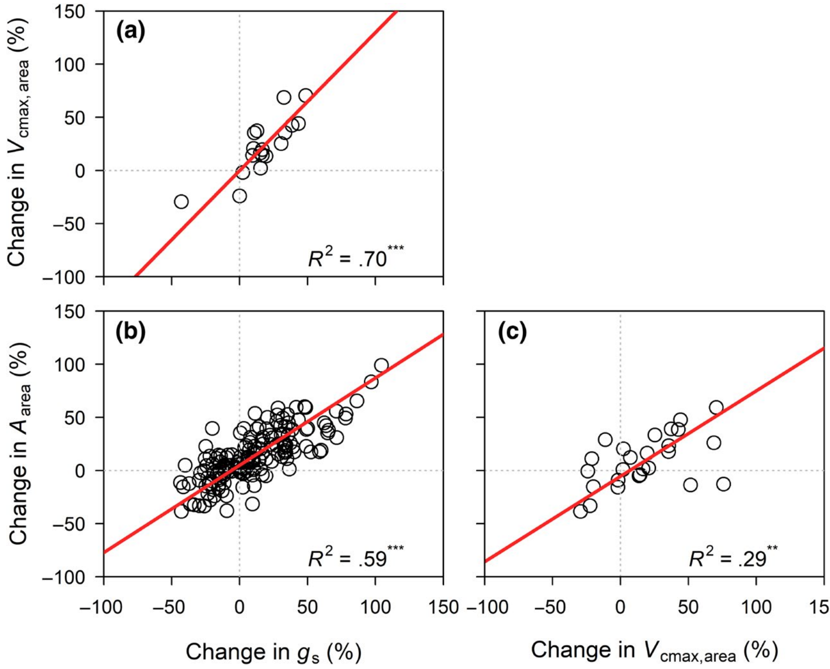

FIGURE 5 Correlations between the responses of (a) $V_{cmax,area}$ and g_s, (b) A_{area} and g_s and (c) A_{area} and $V_{cmax,area}$. See Figure 3 for abbreviations. $^{**}p < .01$; $^{***}p < .001$ [Colour figure can be viewed at wileyonlinelibrary.com]

A_{area} weakening with longer durations (Figure 7e–g). Accumulated N load exhibited significant positive effects on the responses of N_{mass} and E (Figure 7i,k). Nitrogen form was not found to affect the responses of all the 14 traits (Table S6). The responses in all traits did not differ significantly between managed and natural plants (Table S6).

Environmental moderators also exhibited significant effects on the responses of photosynthesis-related traits (Figure 8; Table S7). With increasing latitude and decreasing MAP/MAT, the log response ratios of N_{mass} increased significantly (Figure 8a,e,i), while that of PNUE decreased significantly (Figure 8b,f,j). The responses of leaf area per plant or total leaf biomass showed contradictory trends compared to those of LAI along the latitude and MAP (Figure 8c,d,g,h). Soil pH showed a positive relationship with the responses of N_{mass} but negative relationships with that of PNUE, leaf area per plant, and E (Figure 8m–p).

4 | DISCUSSION

4.1 | N addition increases leaf nitrogen

One of the most universal drivers of plant photosynthesis is leaf concentration of N(Evans, 1989; Field & Mooney, 1986; Nijs, Behaeghe, & Impens, 1995). Although leaf N on area basis is the appropriate predictor of photosynthesis on area basis (Osnas et al., 2013), previous meta-analyses have largely reported how N addition affected leaf N on mass basis rather than area basis

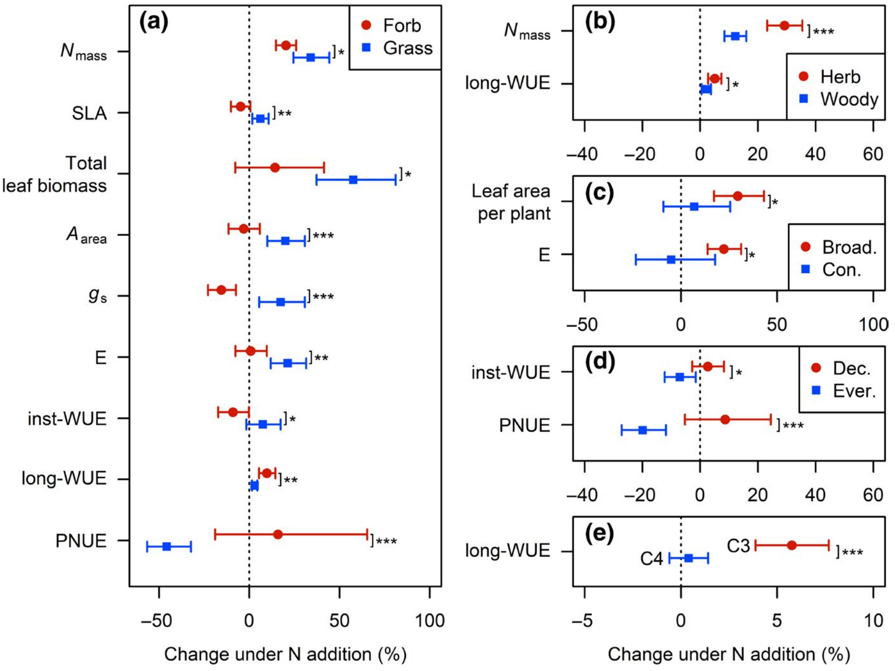

FIGURE 6 Responses (±95% CI) of photosynthesis-related traits to N addition between different plant functional types. (a) Forb versus grass species; (b) Herb versus woody species; (c) Broadleaf (Broad.) versus conifer (Con.) trees; (d) Broadleaf deciduous (Dec.) versus broadleaf evergreen (Ever.) trees; (e) C3 versus C4 herbs. See Figures 2and3 for abbreviations. **p* < .05; ***p* < .01; ****p* < .001. Only significant results are reported, the details of test results and other traits are found in Table S6 [Colour figure can be viewed at wileyonlinelibrary.com]

(Bejarano-Castillo, Campo, & Roa-Fuentes, 2015; Ostertag & DiManno, 2016; Xia & Wan, 2008;Yuan & Chen, 2015; Zhang et al., 2018). To our knowledge, this is the first examination of the global data focusing on the effects of N addition on leaf N expressed in both ways. We found that N_{area} and N_{mass} increased comparably owing largely to the fact that leaf morphological traits particularly SLA or LMA did not change in response to N addition (Figure 2). Overall, N_{mass} was enhanced by 18.4% [95% CI: 15.1%, 21.9%], which was comparable with an earlier study that N_{mass} was enhanced by 19.6% [15.3%, 24.2%] (Ostertag & DiManno, 2016). Given the strong interdependence of plant photosynthesis on leaf N, our data indicate that chronic N addition will enhance gross photosynthesis of the terrestrial systems at least in part by improving leaf N status.

4.2 | N addition enhances total leaf area and leaf photosynthetic capacity

Nitrogen addition can increase plant carbon uptake by stimulating leaf production and/or leaf photosynthetic capacity (Janssens & Luyssaert, 2009). We found that N addition significantly enhanced both. The response in total leaf biomass was analogous to that in TLA, as TLA equals total leaf biomass times SLA, and SLA did not change significantly under N addition (Figure 2). With large sample sizes, the average responses of total leaf biomass (+46.5%), leaf area per plant (+29.7%), and LAI (+24.1%) found here are stronger than those reported in previous meta-analyses. For instance, Xia and Wan (2008), using 71 observations (i.e., *n* = 71), showed that total leaf biomass at the species level was increased by 14.7%, and with a larger sample size (*n* = 103), they updated the value to 33.2%–36.2% (Xu, Yan, & Xia, 2019). Li et al. (2016) found that total leaf biomass of trees was increased by 20.9% but leaf area per plant did no change significantly, and Zhang et al. (2018) reported LAI of woody plants to increase significantly by 10.3%.

We found that A_{area} was also significantly enhanced in response to N addition, although the magnitude of this response was markedly lower than those reported above for TLA. The effects of N addition on A_{area}, g_s, and carboxylation rate ($V_{cmax,area}$) were correlated with each other (Figure 5), suggesting that N addition might affect leaf photosynthesis via simultaneously affecting leaf carboxylation capacity and stomatal conductance. Overall, we found that N addition increased A_{area} by 12.6%, which is higher than the response (5.2%) reported by Chen et al. (2015). It should be noted that 80% of the observations (i.e., 32 of 40) for A_{area} in Chen et al. (2015)were from forests in Dinghushan, a subtropical area in southern China, where plant photosynthesis has been demonstrated to respond moderately even negatively to N addition (Lu et al., 2018; Mao et al., 2018). Zhang et al. (2018) reported that A_{area} of woody plants was enhanced by 16.1% [95% CI: 12.4%, 19.1%], which is similar to our result for woody species (13.3% [95% CI: 8.2%, 18.6%]; Table S6).

The greater increases in TLA than A_{area} (Figures and) indicate that higher leaf area may be the main response across plant species to N enrichment. This finding can be confirmed by studies explored responses of both TLA and A_{area}. For example, Krause, Cherubini, Bugmann, and Schleppi (2012) found that experimental N addition significantly enhanced C gain of *Picea abies* trees, mainly via increasing TLA rather than leaf-level photosynthetic capacity. The results indicate that the available space for leaves (and light) would critically limit responses of plant carbon uptake to N addition. For example, former studies showed that tree carbon sequestration of old forests responded less strongly to N addition than young forests (Magnani et al., 2007; Schulte-Uebbing & de Vries, 2018), one

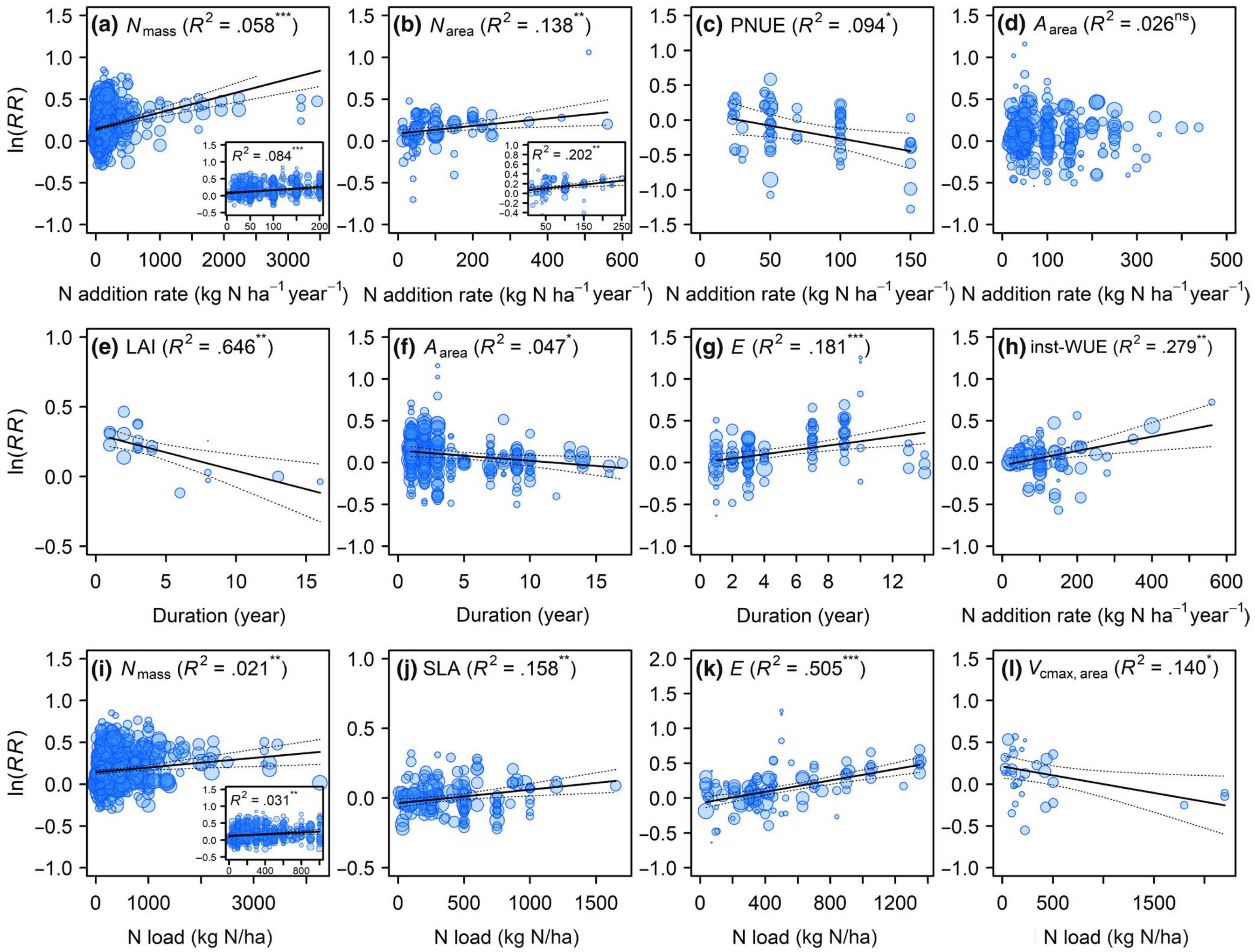

FIGURE 7 Correlations between the natural logarithm-transformed response ratio of (a) leaf N per mass and N addition rate, (b) leaf N per area and N addition rate, (c) photosynthetic nitrogen use efficiency and N addition rate, (d) leaf photosynthetic rate per area and N addition rate, (e) leaf area index and experimental duration, (f) leaf photosynthetic rate per area and experimental duration, (g) leaf transpiration rate and experimental duration, (h) instantaneous water-use efficiency and N addition rate, (i) leaf N per mass and N load, (j) specific leaf area and N load, (k) leaf transpiration rate and N load, and (l) leaf carboxylation rate per area and N load. Symbol size depicts observation's weights [Colour figure can be viewed at wileyonlinelibrary.com]

possible explanation is that the canopy of old forests is closed and consequently limiting the response of TLA.

4.3 | Effects of N addition on plant water-use efficiency

We did not find inst-WUE to change significantly under N addition (Figure 3), which can be explained by a positive linear relationship between the responses of A_{area} and g_s (Figure 5b). By contrast, long-WUE was increased significantly under N addition (Figure 3). The long-WUE captures variability in availability of other resources such as light, nutrients, and water, which is not the case for the instantaneous measure (Farquhar et al., 1989; van der Sleen, Zuidema, & Pons, 2017). Nonetheless, long-WUE was enhanced slightly by 2.5%, indicating a minor if any impact of N addition on plant carbon–water relations. A previous study showed that long-WUE was increased by 16.1% between 1850 and 2000, which was mainly driven by N deposition (Leonardi et al., 2012). These results together suggest that the positive effect of increased N availability on WUE has been declining, due to long-term N deposition around the world.

4.4 | Moderators affecting the responses of photosynthesis-related traits

4.4.1 | Biological moderators

Decades of manipulative experiments and gradient studies provide strong evidence that plant species differ markedly in response to increased N availability (Clark & Tilman, 2008; Lane & BassiriRad,

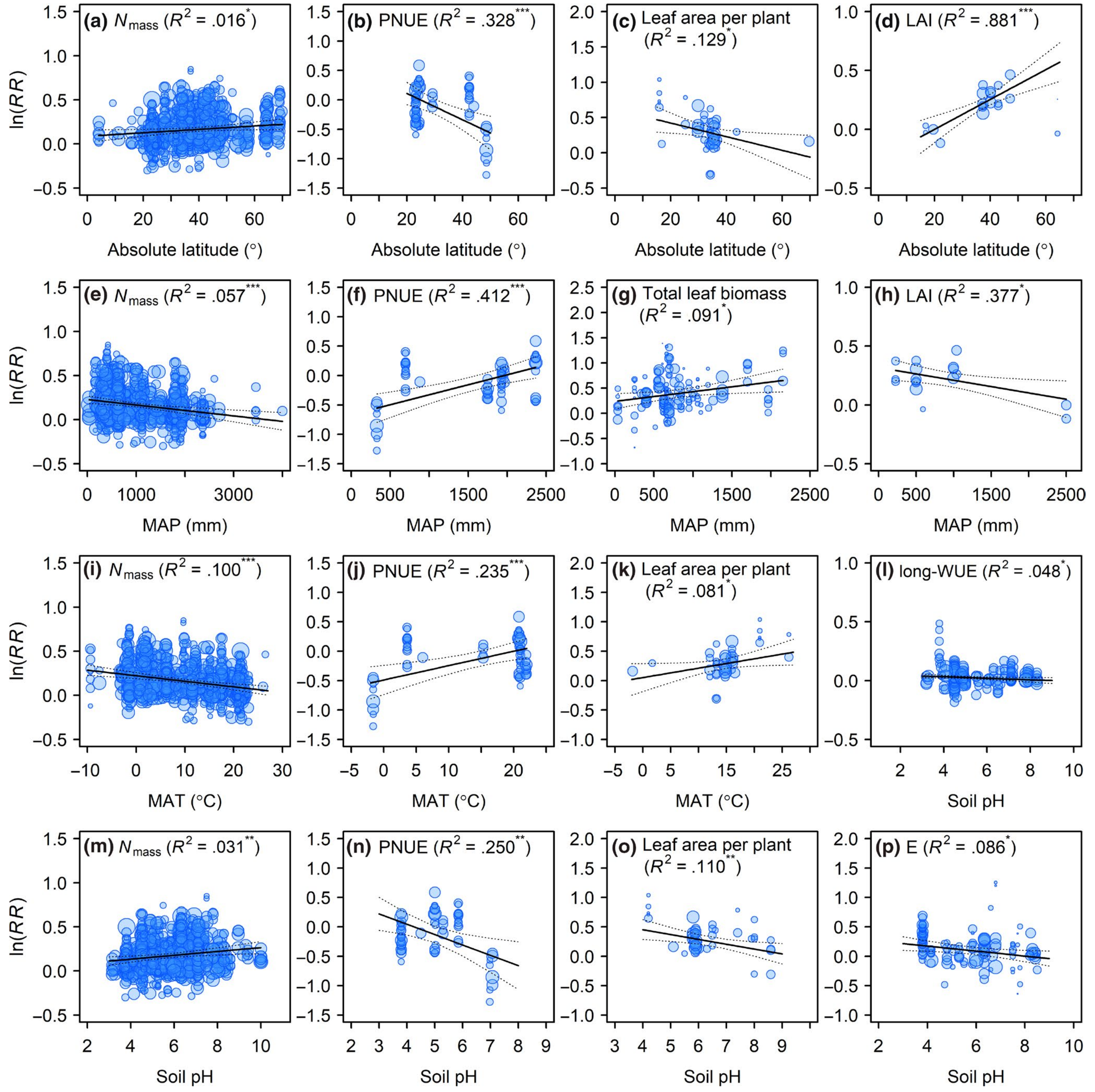

FIGURE 8 Correlations between the natural logarithm-transformed response ratio of (a) leaf N per mass and absolute latitude, (b) photosynthetic nitrogen use efficiency and absolute latitude, (c) leaf area per plant and absolute latitude, (d) leaf area index and absolute latitude, (e) leaf N per mass and mean annual precipitation, (f) photosynthetic nitrogen use efficiency and mean annual precipitation, (g) total leaf biomass and mean annual precipitation, (h) leaf area index and mean annual precipitation, (i) leaf N per mass and mean annual temperature, (j) photosynthetic nitrogen use efficiency and mean annual temperature, (k) leaf area per plant and mean annual temperature, (l) long-term water-use efficiency and soil pH, (m) leaf N per mass and soil pH, (n) photosynthetic nitrogen use efficiency and soil pH, (o) leaf area per plant and soil pH, and (p) leaf transpiration rate and soil pH. Symbol size depicts observation's weight [Colour figure can be viewed at wileyonlinelibrary.com]

2002; Lu, Mo, Gilliam, Zhou, & Fang, 2010; Midolo et al., 2019; Simkin et al., 2016; Stevens et al., 2004; Wedin & Tilman, 1996). Different responses of photosynthesis-related traits among plant functional types revealed here can provide mechanistic understanding of plant responses to N deposition. For example, total leaf biomass (and consequently TLA) and A_{area} were enhanced significantly in grass but not in forb (Figure 6a), suggesting that grass would outcompete forb under increased N availability. Consistent with our results, previous studies repeatedly reported that N addition/deposition significantly stimulated total or aboveground biomass of grass but not that of forb both across biomes (De Schrijver et al., 2011; Xia & Wan, 2008; Xu et al., 2019; You et al., 2017) and within a biome such as grasslands (Fu & Shen, 2016; Humbert, Dwyer, Andrey, & Arlettaz, 2016; Stevens, Dise, Gowing, & Mountford, 2006).

The enhancement of leaf area per plant was significantly greater for broadleaf than for conifer trees (Figure 6c). Given greater enhancement of TLA indicates greater enhancement of competition for light and space, the greater enhancement of TLA for broadleaf than conifer trees found here suggests that chronic N deposition gives broadleaves benefits relative to conifers in terms of light interception and consequently gross photosynthesis and growth. This inference is supported by results of two previous meta-analyses that N addition enhanced plant biomass more for broadleaf than conifer trees (Xia & Wan, 2008; Xu et al., 2019).

The results showed that compared to nonlegumes, legumes exhibited significantly greater responses in two out of the 14 studied traits, namely A_{area} and E (Table S6). However, it should be noted that the sample sizes for legumes were rather small, that is, with $n = 13$ and 350 for A_{area} of legumes and nonlegumes, respectively, and $n = 4$ and 127 for E of legumes and nonlegumes, respectively. Clearly, future work is needed to reveal how legumes and nonlegumes differ in photosynthesis under N addition. With regard to C3 and C4 herbs, the results showed that they only differed significantly in long-WUE, which was enhanced significantly by N addition for C3 but not C4 herbs (Figure 6e), indicating that C4 plants are more efficient in water use under N addition (Yang, Yu, Sheng, Li, & Tian, 2017). We also found that C3 and C4 herbs did not differ in the responses of TLA or leaf photosynthetic rate, which are in line with results of Xia and Wan (2008), who showed nonsignificant differences in plant biomass and N concentration between C3 and C4 herbs.

4.4.2 | Experimental moderators

An important driver of variability in responses to N deposition is the rate at which the system is approaching the critical load (Aber et al., 1989,1998; Niu et al., 2016). Consequently, deposition rates as well as the biological retention capacity of the system are likely to affect the outcome of the results. We found that, with increasing N addition rate, leaf N (both N_{mass} and N_{area}) increased to a greater extent. However, greater enhancement in leaf N did not lead to greater enhancement in A_{area}, because PNUE was decreased to a greater extent (Figure 7). Leaf photosynthesis was increased to the same extent from low (as 10 kg N ha^{-1} year^{-1}) to high (as 400 kg N ha^{-1} year^{-1}) N addition rate (Figure 7), consistent with previous findings that global canopy A_{area} leveled off at N deposition rate greater than 8 kg N ha^{-1} year^{-1} (Fleischer et al., 2013), and that positive effects of N deposition on growth rate of beech trees tended to level off at N deposition over 10 kg N ha^{-1} year^{-1} (Gentilesca et al., 2018). The results might indicate that terrestrial ecosystem gross primary productivity (GPP) would level off at N deposition rates from 10 up to 400 kg N ha^{-1} year^{-1}.

Experimental duration negatively affected the responses of LAI and A_{area} (Figure 7e,f), while accumulative N load did not (Table S7), suggesting that experimental duration may affect the photosynthetic responses indirectly via plant ontogeny. That is, as experimental duration persists, plants also get older and larger. In two prior meta-analyses, stand age was found to negatively affect the response ratio of primary production of forests to N addition (Schulte-Uebbing & de Vries, 2018; Vadeboncoeur, 2010). In three forest sites across China, N addition stimulated the growth of small trees (DBH < 15 cm) but not that of large trees (DBH > 15 cm; Li, Tian, Yang, & Niu, 2018). Interestingly, although accumulative N load did not affect the response of leaf photosynthetic rate, it did positively affect the response of leaf transpiration rate ($R^2 = .505$, $p < .001$; Figure 7k). This might be related with reduction of Ca^{2+} under lowered soil pH. First, N addition would intensify soil acidification, leading to leaching of base cations (e.g., Ca^{2+}, K^+, and Mg^{2+}; Lucas et al., 2011; Tian & Niu, 2015). Then, reduction in Ca^{2+} can affect the regulation of stomatal aperture, preventing stomatal closure and sustaining the transpiration, and thus intensifying plant water use (Lanning et al., 2019). Taken together, our results indicate that the positive effects of N addition on plant photosynthetic C gain might not be lasting in the long term, while the positive effects on plant water consumption seem to become greater if increased levels of N addition persist.

Another important aspect of plant N nutrition is the complexity associated with forms of N. Plants can effectively utilize N in inorganic (NO_3^- and NH_4^+) and organic forms, but the relative abundance of different inorganic N forms in atmospheric deposition varies significantly depending on identity of the sources of the pollution (BassiriRad, 2015). Typically, N deposition generated from industrial sources is dominated by NO_3^- whereas farming practices often result in preponderance of NH_4^+ in the deposition. Previous studies found that N form could significantly affect the responses of belowground C processes such as soil respiration (Liu & Greaver, 2010). In the present study, N form was not found to have a significant effect on the responses of all the photosynthesis-related traits (Table S6). Our finding is consistent with the results of former meta-analyses that neither net primary productivity (LeBauer & Treseder, 2008) nor aboveground plant biomass (Schulte-Uebbing & de Vries, 2018) responded differently with N forms added. These results suggest that N form might not be an important factor for aboveground C processes in response to N deposition (Schulte-Uebbing & de Vries, 2018). Although the forms of atmospheric N deposition change over time and space (BassiriRad, 2015; Liu, Xu, Du, Pan, & Goulding, 2016; Yu et al., 2019), the effects of N deposition on plant photosynthesis should remain unchanged.

4.4.3 | Environmental moderators

It is commonly hypothesized that N-limitation on plant productivity is greater in higher latitudes with lower MAT because N mineralization is suppressed at low temperature (Deng, Liu, et al., 2018; Reich & Oleksyn, 2004). In the present study, we found that the responses of N_{mass} were greater in higher latitudes (Figure 8a) and under lower MAP (Figure 8e) or MAT (Figure 8i), suggesting that plants in higher latitudes and under lower MAT are more sensitive to N addition.

However, a similar pattern of A_{area} in response to N addition along latitude or MAT could not be confirmed by the present dataset (Table S7). The results indicate that greater enhancement in leaf N of plants in higher-latitudes did not lead to greater enhancement in leaf photosynthetic rate, likely owing to that low precipitation and temperature limited the physiological responses of plants (Liang, Xia, Liu, & Wan, 2013; Reich & Oleksyn, 2004). Oddly, two agencies of TLA varied inconsistently along latitude, that is, as latitude increased, the response of leaf area per plant decreased (Figure 8c) while that of LAI increased (Figure 8d). This may be because the sample size used to compare the low and high altitude was small (Figure 8c,d). Some studies have reported a latitudinal pattern of ecosystem C uptake under N addition. For example, using a stoichiometric scaling method, Du and de Vries (2018) revealed that N deposition lead to a larger C sink in midlatitude temperate forests than low-latitude tropical and high-latitude boreal forests, and in a meta-analysis, Schulte-Uebbing and de Vries (2018) showed that aboveground woody biomass of tropical forests did not respond significantly to N addition. However, LeBauer and Treseder (2008) found that net primary productivity was enhanced by N addition similarly among tropical, temperate, and boreal forests. More recently, a meta-analysis by Wright (2019) reported that N addition significantly enhanced plant growth rates in tropical forests. However, more photosynthesis-related data in future investigations are needed, especially at low and high latitudes, to draw a solid conclusion about latitudinal effects on leaf-level photosynthesis under N addition.

Soil pH plays a critical role in N availability and thus may affect plant responses to N addition. At low soil pH, nitrification is inhibited because pH 7–8 is the optimum condition for the *Nitrosomas* bacteria (Stevens, Thompson, Grime, Long, & Gowing, 2010). In addition, the release of free Al^{3+} at low pH can reduce nitrate uptake by plants (Lazof, Rincón, Rufty, Mackown, & Carter, 1994). Therefore, plants grown under lower soil pH may be unable to uptake N (especially nitrate) efficiently, and thus could be more N limited. Consistent with this expectation, N_{mass} enhancements were smaller under lower soil pH (Figure 8m), while leaf area per plant was enhanced to greater extents with decreasing soil pH (Figure 8o). Our results are in line with a prior meta-analysis, which reported a negative relationship between the response of ecosystem aboveground net primary productivity and soil pH (Tian, Wang, et al., 2016). In this study, we also found a negative relationship between the response of leaf transpiration rate and soil pH (Figure 8p), possibly owing to greater reduction in Ca^{2+} under lower pH, which can intensify plant water use (Lanning et al., 2019; McLaughlin & Wimmer, 1999).

4.5 | Implications for plant carbon and water processes

The pattern of enhanced TLA and A_{area} responses to N addition indicates a mechanistic basis for postulating that global primary productivity and C sequestration are likely to increase if N deposition remains high. Obviously, much work is needed to fine-tune the offsetting effects of changes in canopy architecture, vertical N distribution within the canopy, leaf display, and self-shading. Nevertheless, our results could help to explain the increases of plant biomass and ecosystem productivity under N enrichment found in previous studies (de Vries, Reinds, Gundersen, & Sterba, 2006; Elser et al., 2007; LeBauer & Treseder, 2008; Schulte-Uebbing & de Vries, 2018; Wright, 2019; Xia & Wan, 2008). However, as the responses of both LAI and A_{area} weaken with increasing experimental duration, the positive effects of N addition on plant gross photosynthetic C gain might diminish with time.

Our global analyses of TLA, g_s, E, and WUE data provide, fortuitously, an insight into how elevated N availability may impact hydrologic dynamics. Increased leaf area and transpiration rate together suggest a greater water requirement by plants under N addition, which could have important implications for both plant hydraulics and regional hydrology. First, plants may become more sensitive to drought under higher N deposition (Gessler, Schaub, & McDowell, 2017), as they need to modify their hydraulic architecture to meet the higher requirement of water. Indeed, there are reports that the sizes of vessel and tracheid were increased significantly by N addition (Jiang et al., 2018; Lovelock et al., 2006; Wang et al., 2016). Furthermore, a meta-analysis reported that plant hydraulic conductivity was enhanced significantly, and water potential corresponding to 50% loss of hydraulic conductivity (P_{50}) became less negative under N addition (Zhang et al., 2018). Second, regional hydrological cycling might change under N addition. Supporting this inference, a recent study found that the plant transpiration increased while the soil water leaching below the rooting zone decreased in a tropical forest after a decade of N addition (Lu et al., 2018). Nevertheless, it is notable that these results were merely based on transpiration of plants, not including soil evaporation. Evapotranspiration (sum of soil evaporation and plant transpiration) at the ecosystem level may be not changed (Jassal et al., 2010; Tian, Niu, et al., 2016; Yan, Zhang, Liu, & Zhou, 2014), or even decreased(Lu et al., 2019) under N addition, because N addition can accelerate canopy closure, and consequently reduce soil evaporation through the shading effect.

In summary, this meta-analysis has three key findings: (a) TLA and, to a lesser extent, leaf photosynthetic capacity were increased by N addition, helping to explain previous findings of stimulations in plant biomass and ecosystem productivity; however, our results also indicate that the positive effects might diminish in the long term; (b) higher leaf area and transpiration rate together suggest that N deposition will intensify plant water use, and this effects would become stronger as accumulative N load increases; and (c) N addition would stimulate both plant C uptake and water consumption, with little changes in water-use efficiency. These findings facilitate mechanistic understanding and model projections of the effects of future N deposition on plants and ecosystems, including carbon and water cycles.

AUTHOR'S CONTRIBUTION

X.L., T.Z., and Q.Y. designed the study; X.L. and T.Z. collected and analyzed the data; X.L. and T.Z. drafted the manuscript; X.L., D.E., H.B., C.Y., D.W., P.H., Q.D., H.L., J.M., and Q.Y. revised the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

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

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