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Nitrogen addition promotes terrestrial plants to allocate more biomass to aboveground organs: A global meta-analysis

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Abstract

A significant increase in reactive nitrogen (N) added to terrestrial ecosystems through agricultural fertilization or atmospheric deposition is considered to be one of the most widespread drivers of global change. Modifying biomass allocation is one primary strategy for maximizing plant growth rate, survival, and adaptability to various biotic and abiotic stresses. However, there is much uncertainty as to whether and how plant biomass allocation strategies change in response to increased N inputs in terrestrial ecosystems. Here, we synthesized 3516 paired observations of plant biomass and their components related to N additions across terrestrial ecosystems worldwide. Our meta-analysis reveals that N addition (ranging from 1.08 to 113.81 $g\,m^{-2}\,year^{-1}$) increased terrestrial plant biomass by 55.6% on average. N addition has increased plant stem mass fraction, shoot mass fraction, and leaf mass fraction by 13.8%, 12.9%, and 13.4%, respectively, but with an associated decrease in plant reproductive mass (including flower and fruit biomass) fraction by 3.4%. We further documented a reduction in plant root-shoot ratio and root mass fraction by 27% (21.8%–32.1%) and 14.7% (11.6%–17.8%), respectively, in response to N addition. Meta-regression results showed that N addition effects on plant biomass were positively correlated with mean annual temperature, soil available phosphorus, soil total potassium, specific leaf area, and leaf area per plant. Nevertheless, they were negatively correlated with soil total N, leaf carbon/N ratio, leaf carbon and N content per leaf area, as well as the amount and duration of N addition. In summary, our meta-analysis suggests that N addition may alter terrestrial plant biomass allocation strategies, leading to more biomass being allocated to aboveground organs than belowground organs and growth versus reproductive trade-offs. At the global scale, leaf functional traits may dictate how plant species change their biomass allocation pattern in response to N addition.

KEYWORDS
biomass partitioning, leaf traits, plant biomass, reproductive trade-offs, terrestrial ecosystem

1 | INTRODUCTION

Plant growth and development depend on environmental variables, such as temperature, light intensity, and the availability of carbon, water, and mineral nutrients (Hermans et al., 2006). As a plant captures carbon and nutrients, the newly formed biomass is allocated to leaves, stems (including bole, branch, and bark), roots, or reproductive parts (Reich et al., 2014). To sustain the required physiological functions and grow normally, a plant must balance the distribution of biomass among its leaves, branches, stems, and roots (Shipley & Meziane, 2002; Yin et al., 2019). Modifying biomass allocation is one of the most fundamental ways to maximize plant growth rate, survival, and adaptability under various biotic and abiotic stresses (Poorter et al., 2015; Puglielli et al., 2021). Consequently, altered biomass allocation has profound implications for plant growth.

Nitrogen (N) is a necessary nutrient for plant growth and ecosystem production in both terrestrial and marine habitats (Elser et al., 2007). N deficit inhibits plant growth and development, lowers photosynthesis and leaf area, accelerates plant senescence, and eventually diminishes plant production (Mu & Chen, 2021). Therefore, N fertilization has been widely used to promote plant growth and production (Frink et al., 1999; Xia & Wan, 2008). Increased reactive N emissions through agricultural fertilization and fossil fuel combustion have resulted in a large amount of atmospheric inorganic N deposition at a global average rate of 105 Tg N $year^{-1}$ (Galloway et al., 2008; Lu et al., 2011). Global N deposition rates are expected to increase 2.5-fold by the end of the century (Janssens et al., 2010; Lamarque et al., 2005). As a result, N addition to terrestrial ecosystems is now considered one of the most widespread drivers of global change (Galloway et al., 2008; Humbert et al., 2016).

In most terrestrial ecosystems, plant growth is typically restricted by soil N availability (LeBauer & Treseder, 2008; Lu et al., 2011). Some previous studies have shown a strong covariation between soil N availability and plant biomass allocation in natural ecosystems (Cambui et al., 2011; Hermans et al., 2006). Therefore, plants, as a fundamental component of the terrestrial ecosystem, may be sensitive to enhanced N deposition in their growth (Bobbink et al., 2010; Phoenix et al., 2012). However, there is still much uncertainty about whether or how plant biomass allocation will change in response to increased N inputs in terrestrial ecosystems. A previous study has shown that plants adapt to environmental changes by changing biomass distribution across different plant organs (Hermans et al., 2006). Besides, leaf functional traits such as leaf carbon and N content (LCC and LNC), specific leaf area (SLA), and leaf area per plant (PLA) have a significant impact on the efficiency of assimilation of photosynthetic active radiation, and hence, plant photosynthetic capacity (Marron et al., 2005; Scott Green et al., 2003). Some research has suggested that leaf functional traits can also be used as potential covariates for understanding biomass allocation (Li et al., 2021; Yin et al., 2019). However, it is unclear whether leaf functional traits and environmental factors jointly drive the response of plant biomass allocation to N addition. Therefore, a quantitative synthesis across multiple studies is urgently needed to quantify the effects of reactive N addition on terrestrial plant biomass and its composition and identify the key drivers accurately.

Previous manipulation experiments have improved our understanding of N addition effects on the allocation of plant biomass (Högberg et al., 2006; Holub & Tůma, 2010; Palmqvist & Dahlman, 2006). However, studies that rely on individual cases or are constrained to specific habitats make it difficult to get a complete picture of the effects of N addition on terrestrial plants. Moreover, the role of global change in promoting the feedback of terrestrial ecosystems and atmospheric N deposition has not been fully elucidated. Previous research has reported the effects of N deposition on plant photosynthesis (Liang et al., 2020), plant diversity (Bobbink et al., 2010), and plant species richness and abundance (Midolo et al., 2019); however, due to a lack of data, a synthesis was not produced. To date, although several studies have attempted to quantify N addition effect on plant biomass (Li et al., 2020; Yue et al., 2020), none of these studies considered the effects of environmental variables (e.g., climate, soil, and N deposition background values) and plant leaf functional traits (such as SLA, PLA, and leaf carbon/nitrogen ratio [LCN]) on the response of terrestrial plants to N addition. Since N availability affects carbon sequestration across terrestrial ecosystems (Gruber & Galloway, 2008), a better understanding of how and to what extent N addition affects biomass allocation in terrestrial plants is essential for accurate quantification of carbon sequestration.

In this study, we compiled a global dataset of 3516 paired sets of experimental field observations from 255 studies covering the majority of the dominant plant species in terrestrial ecosystems. The objectives of this study were to (1) clarify the effects of N addition on plant biomass in terrestrial ecosystems and (2) identify the key drivers and global patterns of biomass accumulation and allocation in response to reactive N addition. We hypothesized that (i) N addition promotes plants to allocate more biomass to vegetative (i.e., roots, stems, and leaves) rather than reproductive (i.e., flowers and fruits) organs and (ii) environmental factors and leaf functional traits jointly drive the response of plant biomass to N addition.

2 | MATERIALS AND METHODS

2.1 | Data collection

We systematically searched the peer-reviewed published literature from the ISI Web of Science and Google Scholar databases for specific search terms (Table S1; Figure S1). Each paper was then screened to determine whether it met the following criteria: (1) the climatic, soil, and vegetation variables (or conditions) were the same between the control and the N addition treatment sites (i.e., studies along gradients of N deposition were not considered); (2) the research only included species that naturally exist in terrestrial habitats; (3) means, standard deviations (SDs), or errors (SEs), and the sampling sizes for both the control and treatment groups could be directly obtained or could be calculated; (4) the statistical assumption of independence across observations for the long-term N addition study were met and, only the most recent results were included; (5) only data from control and N addition plots were collected when global change treatments (e.g., added CO_2 or increased temperature) other than N addition were tested; and (6) data from transgenic plants or plants that had been handled with herbicides, hormones, and/or heavy metals were eliminated since they might have presented a different pattern of biomass distribution. Subsequently, if a publication included several experiments in different locations, these observations were considered independent cases. As supplements, articles used in previous relevant meta-analyses (Liang et al., 2020; Xia & Wan, 2008; Yue et al., 2020) were also included and rescreened according to the above criteria.

For the literature that meets our criteria, we acquired the mean values, SD, and sample size directly from the table, text, and supplementary files or extracted these data indirectly from figures by using GetData software (version 2.26). We also collected geographic variables (i.e., latitude, longitude, and elevation), environmental variables (i.e., MAT, mean annual temperature; MAP, mean annual precipitation), and other reported variables including experimental duration (years, the number of years with N applied repeatedly), the magnitude of N applied (quantity of N addition per year, ranging from 0.3 to 112 $g\,m^{-2}\,year^{-1}$), and the form of N applied (the type or types of N fertilizer). If N addition varied during the N addition experiment, we estimated the total applied dosage based on the amount of N fertilizer used and the duration of the treatment (total N application/duration; Xu et al., 2021). Data on atmospheric inorganic N (ranging from 0.02 to 2.52 $g\,m^{-2}\,year^{-1}$) were acquired from global N deposition maps (Ackerman et al., 2018). Other climatic data such as precipitation in the warmest quarter (WQP) were obtained from WorldClim2 at 1 km spatial resolution (Fick & Hijmans, 2017).

For each species, plants were classified to the family and genus level, and grouped according to their photosynthesis pathway (e.g., C3, C4, or CAM), functional types (i.e., tree, shrub, grass, forb, fern, lichen, and moss), plant N fixation capacity (N-fixing plant or non-N-fixing plant), and life cycles (i.e., annual, biennial, or perennial). As categorical predictors, seven commonly measured plant leaf functional traits were obtained from the TRY plant trait database for each species (Kattge et al., 2020): SLA ($mm^2\,mg^{-1}$), PLA (m^2), LCN, leaf nitrogen/phosphorus (N/P) ratio (LNP), leaf photosynthesis rate (LPR, $\mu mol\,m^{-2}\,s^{-1}$), LCC ($g\,m^{-2}$), and LNC ($g\,m^{-2}$). We averaged every functional trait observed for each species after excluding duplicate functional trait measurements and outliers (values larger than triple standard deviations from the trait mean for each species; Adler et al., 2014). As continuous predictors, four soil variables including soil total nitrogen (TN, %), soil total potassium (TK, %), soil available phosphorus (AP, $mg\,kg^{-1}$), soil pH, and aridity index (AI) were extracted from Global Soil Datasets in Earth System Models (GSDE; Shangguan et al., 2014) and the CGIAR Consortium for Spatial Information (CGIAR-CSI) dataset (Antonio & Robert, 2019) at a 30 arc-second (approximately 1 km^2) spatial resolution. Finally, we compiled a database from 255 published articles, containing a total of 3516 paired observations of 401 terrestrial plant species (see Figure 1; Dataset S1).

2.2 | Data analysis

We used the log response ratio (RR) to conduct a meta-analysis to assess how plant biomass and biomass allocation responded to N addition in terrestrial ecosystems (Hedges et al., 1999). The following is how the RR was calculated:

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

where $\overline{X}_t$ and $\overline{X}_c$ were the means of each observation for the treatment (i.e., elevated N) and the control (i.e., ambient N) groups, respectively. The sampling variation (v) for each RR was calculated as:

$$v = \frac{S_t^2}{N_t \overline{X}_t^2} + \frac{S_c^2}{N_c \overline{X}_c^2}, \quad (2)$$

where N_t and N_c represent the sample size of the treatment and control groups, S_t and S_c were the standard deviation of the treatment and control groups.

For each study, the weighting factor (w) was calculated as:

$$w = \frac{1}{v + \tau^2}, \quad (3)$$

where τ^2 was the estimated between-study variance of estimates. Following that, the overall effects ($\overline{RR}$) for all observations was estimated as:

$$\overline{RR} = \frac{\sum_{i=1}^{m} \sum_{j=1}^{n} w_{ij} \ln RR_{ij}}{\sum_{i=1}^{m} \sum_{j=1}^{n} w_{ij}}, \quad (4)$$

where m ($i = 1, 2, \ldots m$) and n ($j = 1, 2, \ldots n$) indicate the number of groups (e.g., functional type) and the number of observations in the ith group, respectively. For a better interpretation, the mean effect size was transformed back to the percentage change induced by the experimental N addition treatment (Bai et al., 2013):

$$\text{Percentage}\,(\%) = \left[1 - \exp\left(\overline{RR}\right)\right] \times 100. \quad (5)$$

Then, the multilevel mixed-effect meta-analysis was conducted with the rma.mv function in the "metafor" R package (Viechtbauer, 2010) to determine whether N addition had a substantial impact on the biomass accumulation and biomass allocation of terrestrial plants. The effects of the treatment were considered significantly different from the control if their 95% confidence intervals did not include zero (Hedges & Olkin, 1985). The heterogeneity of effect sizes was tested with the Q statistic to determine whether the variability of the observed effect sizes was greater than that anticipated by chance (Cauvy-Fraunié & Dangles, 2019). As projected, a significant residual heterogeneity was found in the mixed effect meta-analysis for the N treatment on plant biomass ($Q_t = 160{,}533.5$, $p < .0001$) and biomass allocation ($Q_t = 18{,}879.8$,

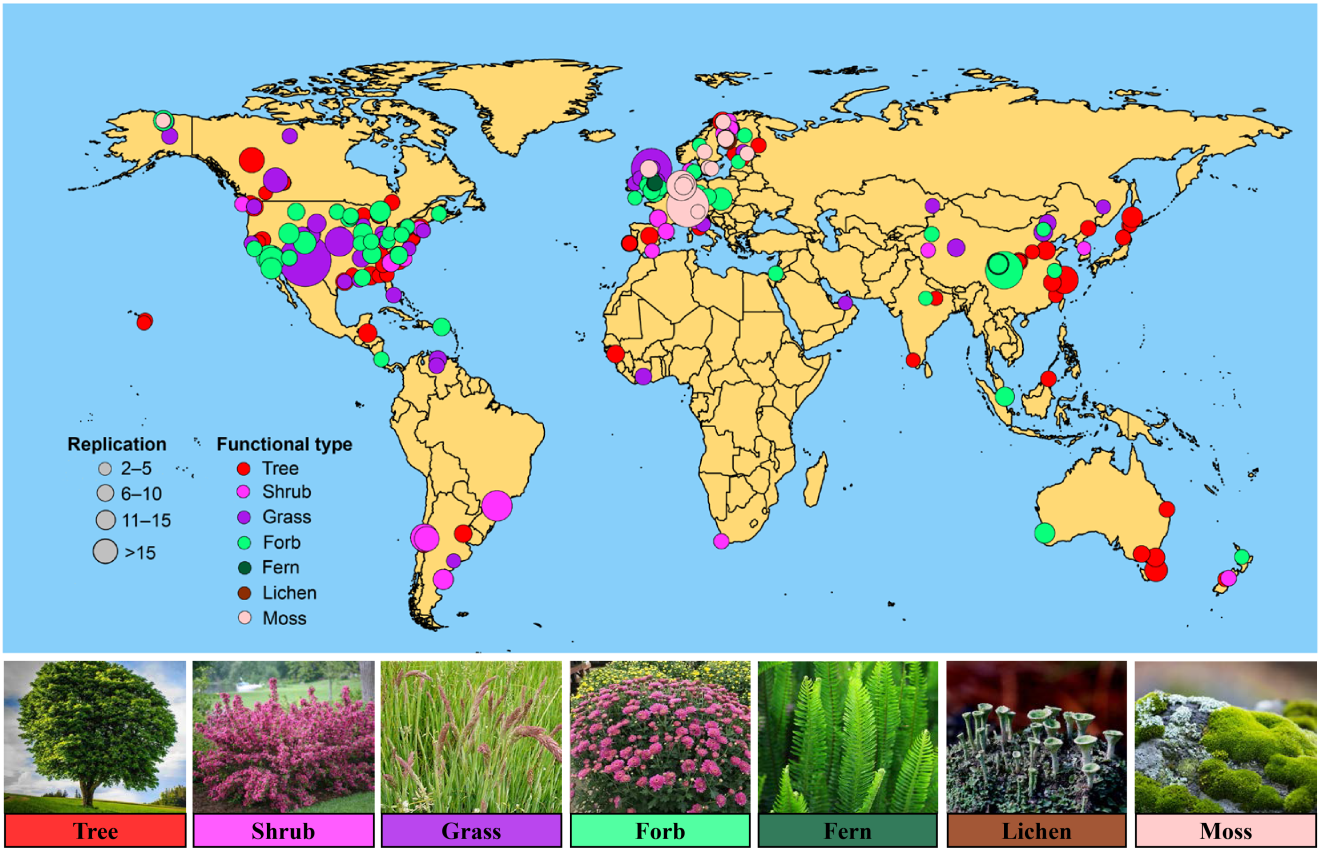

FIGURE 1 Geographical location of study sites in the meta-analysis. The point sizes represent the number of replications. Red, magenta, purple, lime, green, saddle brown, and pink points indicate functional types of tree, shrub, grass, forb, fern, lichen, and moss. Map lines delineate study areas and do not necessarily depict accepted national boundaries. [Colour figure can be viewed at wileyonlinelibrary.com]

$p<.0001$), which we tried to interpret with various moderators (Table S2).

In addition, we used single mixed-effect meta-regression modeling to investigate the link across effect sizes with moderators. The explained heterogeneity Q statistic (Q_m) was developed to assess for significance in single covariance meta-regressions (Guo et al., 2023). A significant Q_m denotes a statistic in which moderators contribute to the heterogeneity in effect sizes (Cauvy-Fraunié & Dangles, 2019). All parameter estimates reported in this meta-analysis were from the best models fitted by a restricted maximum likelihood approach.

To avoid overfitting, we used the chart.Correlation function in the "PerformanceAnalytics" R package (Peterson & Carl, 2020) to perform Pearson correlation analysis of the predictors to test for multi-collinearity, and then exclude variables with correlation coefficients larger than .7 (Dormann et al., 2013). As a sensitivity test, we ran a model-selection procedure with the maximum likelihood method (Terrer et al., 2021). We used the glmulti function in the "glmulti" package (Calcagno & de Mazancour, 2010) to list all alternative models based on the corrected Akaike information criterion (AICc) values. All models with a ΔAICc value less than 2 were considered equivalent to the best-fitting model (Guo et al., 2023; Table S3).

The robustness of our findings to publication bias was evaluated using the funnel plots, Egger's test (Egger et al., 1997), and Rosenberg's fail-safe numbers (Rosenberg, 2005). The funnel plots found no evidence for funnel asymmetry (Figure S2). Egger's test suggested that the overall effect sizes for N treatment on plant biomass (including biomass accumulation and biomass allocation) were robust (Egger's test: $z=.176$, $p=.860$). Rosenberg's fail-safe numbers were large enough (fail-safe N: 3.86×10^7, $p<.0001$) to be convincing with respect to the estimate's robustness. As a consequence, we did not consider publication bias to be a problem in interpreting the findings. All analyses were carried out using the R 4.1.3 software (R Core Team, 2022).

3 | RESULTS

3.1 | Effects of nitrogen addition on plant biomass accumulation

For all of the terrestrial plants evaluated in this study, N addition increased biomass by 55.6% (back-transformed 95% CI: 51.4–59.8; Figure 2). The biomass of N-fixing plants increased by 53.6% (41.9%–65.4%), which was more variable but on average only slightly less than that of non-N-fixing plants 55.9% (51.4%–60.4%; Figure 3; Table S4). The greatest increase in biomass was for deciduous trees and broadleaved trees which increased by 74.2% (63.3%–85.2%) and 81.3% (70.8%–91.9%), respectively. This was considerably higher than evergreen trees and coniferous trees, which both increased by 57.1% (48%–66.2%) and 40.2%

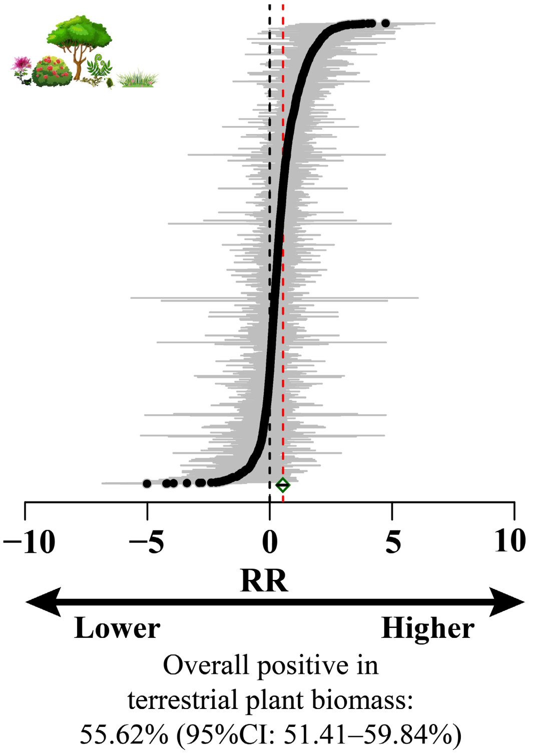

FIGURE 2 Overall effect size estimates of N addition on terrestrial plant biomass at a global scale. RR, log response ratios (effect sizes). RR = 0, black dashed line; overall effect size, red dashed line, and green diamond (with 95% CI in black line). [Colour figure can be viewed at wileyonlinelibrary.com]

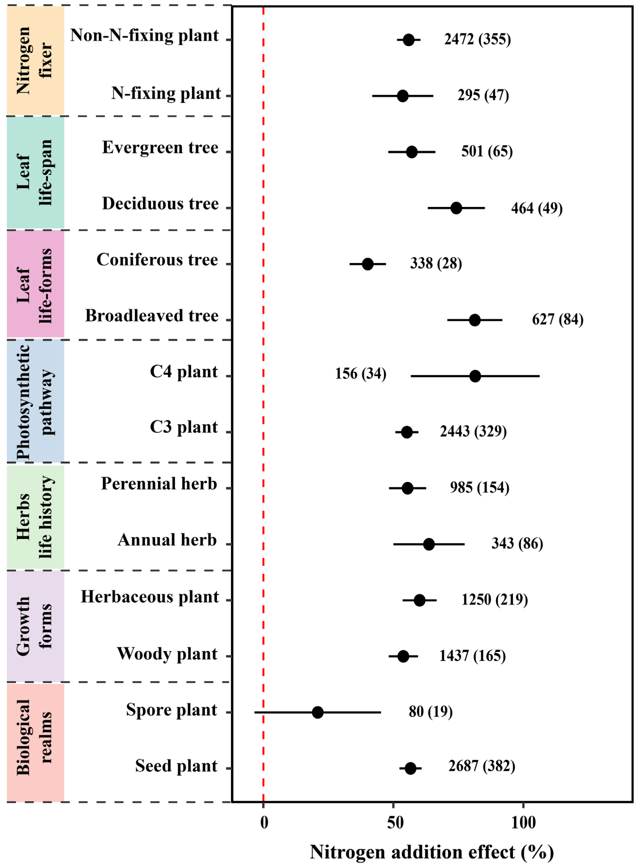

FIGURE 3 Effect size of N addition on terrestrial plant biomass, expressed on the global scale (RR [±95% confidence interval]). The vertical dashed red line denotes a null effect size (RR = 0). The number of observations is beside each attribute without parentheses, and the number of plant species is in parentheses. RR, log response ratio. [Colour figure can be viewed at wileyonlinelibrary.com]

(33.2%–47.2%). For different photosynthesis pathways, N addition increased biomass by 55.2% (50.8%–59.6%) in C3 plants and by 81.5% (56.7%–106.3%) in C4 plants. Our evaluation by life history traits showed that N addition increased the biomass of annual herbs and perennial herbs by 63.7% (50.0%–77.4%) and 55.5% (48.3%–62.6%), respectively.

By the growth forms of plants, we observed that N addition increased the biomass of herbaceous plants and woody plants by 60.1% (53.6%–66.6%) and 53.8% (48.2%–59.5%), respectively (Figure 4; Table S5). Our evaluation of biological realms of plants showed that N addition increased the biomass of seed plants by 56.6% (52.3%–60.9%) but had no effects on spore plants (Figure 3; Table S4). Furthermore, the effects of N addition differed among taxonomic groups, with biomass increasing by 65% for trees (57.9%–72%), 33% for shrubs (24%–42%), 71.4% for grasses (62.4%–80.4%), and 42.7% for forbs (33.6%–51.8%), but had no effects on lichens and mosses.

3.2 | Effects of nitrogen addition on plant biomass allocation

Overall, the meta-analysis demonstrated that N addition had different effects on different functional organs (or tissues) of plants (Figure 5). For the whole plant, N addition increased the biomass by 76.6% (Figure 5a; Table S6). Furthermore, more biomass appeared to be allocated to aboveground (61.7%) than belowground (i.e., root; 42.7%) biomass in response to N addition. Within the components of the aboveground plant structure, plant shoots showed the strongest positive response to N addition, with biomass increasing by 67.3%. Plant leaf and stem biomass, on the other hand, were increased by the addition of N, by 33.2% and 37.2%, respectively The addition of N increased the mass fractions of stem, shoot, and leaf by 13.8%, 12.9%, and 13.4%, respectively (Figure 5b; Table S7). In contrast, plant root-shoot ratio and root mass fraction showed a negative response to N addition, which decreased by 27% and 14.7%, respectively. Although there were no clear directional effects on the reproductive (i.e., flowers and fruits) biomass of plants, more biomass from plants was allocated to vegetative organs than to reproductive organs. And we did note that plant reproductive mass fraction decreased by 3.4% in response to N addition.

3.3 | Moderators of nitrogen addition effects on plant biomass

The meta-regression results revealed that N addition effects on terrestrial plant biomass were positively correlated with MAT

($p < .0001$), AP ($p < .01$), and TK ($p < .01$; Table 1). On the contrary, N addition effects on plant biomass showed a significantly negative correlation with soil TN ($p < .0001$), the duration of the N addition ($p < .0001$), and the amount of N addition ($p < .01$). Furthermore, there was a negative relationship between N addition effects on plant biomass and latitude ($p < .05$). For plant functional traits, the effect size of N addition on plant biomass was positively correlated with SLA ($p < .0001$) and PLA ($p < .01$) and negatively correlated with LCN ($p < .01$), LCC ($p < .0001$), and LNC ($p < .0001$).

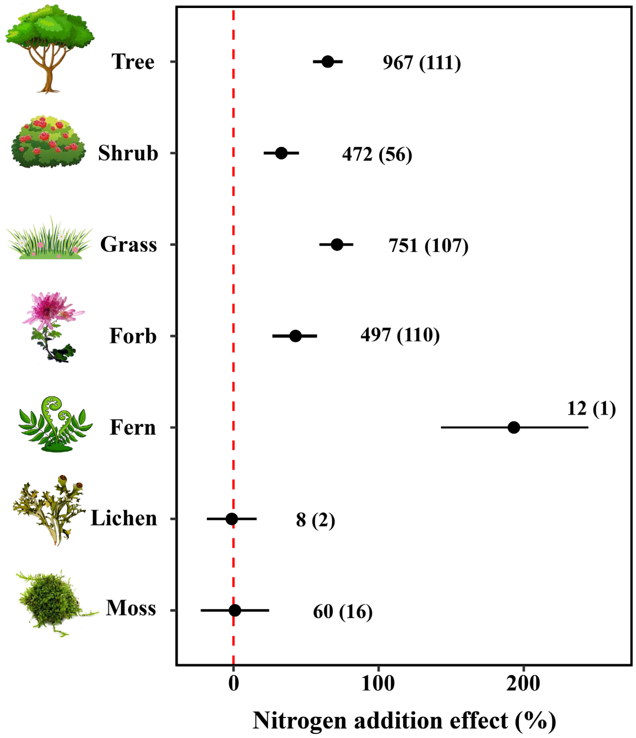

FIGURE 4 Effect size of N addition on terrestrial plant biomass of different growth forms, expressed on the global scale (RR [±95% confidence interval]). The vertical dashed red line denotes a null effect size (RR=0). The number of observations is beside each attribute without parentheses, and the number of plant species is in parentheses. RR, log response ratio. [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

4.1 | Mechanisms of plant biomass allocation in response to nitrogen addition

For most parts of the plants, N resources are limited. Reduced photosynthesis occurs in N-deficient plants due to sugar accumulation, as sugar exerts metabolite feedback and influences many genes responsible for photosynthesis (Bläsing et al., 2005). N addition can therefore reduce sugar accumulation in leaves (Hermans et al., 2006), increase N allocation to photosynthetic apparatus (Li et al., 2019), and promote biomass allocation to vegetative organs (Yan et al., 2019). Consistent with the regulatory mechanisms described above and confirming our hypothesis, our meta-analysis shows that N addition results in a lower biomass fraction of roots and reproductive organs and a decrease in the root-shoot ratio. This indicates that for terrestrial plants, N deficiency may constrain photosynthesis more strongly than reproduction.

Previous research has demonstrated that C4 plants have a higher photosynthetic potential compared to C3 plants. (Zhu et al., 2008). Our research shows that C4 plants also respond more strongly than C3 plants in terms of biomass gain with N addition. Compared with herbaceous plants, the carbon and nutrient storage capacity of woody plants is expected to be much larger (Eyles et al., 2009).

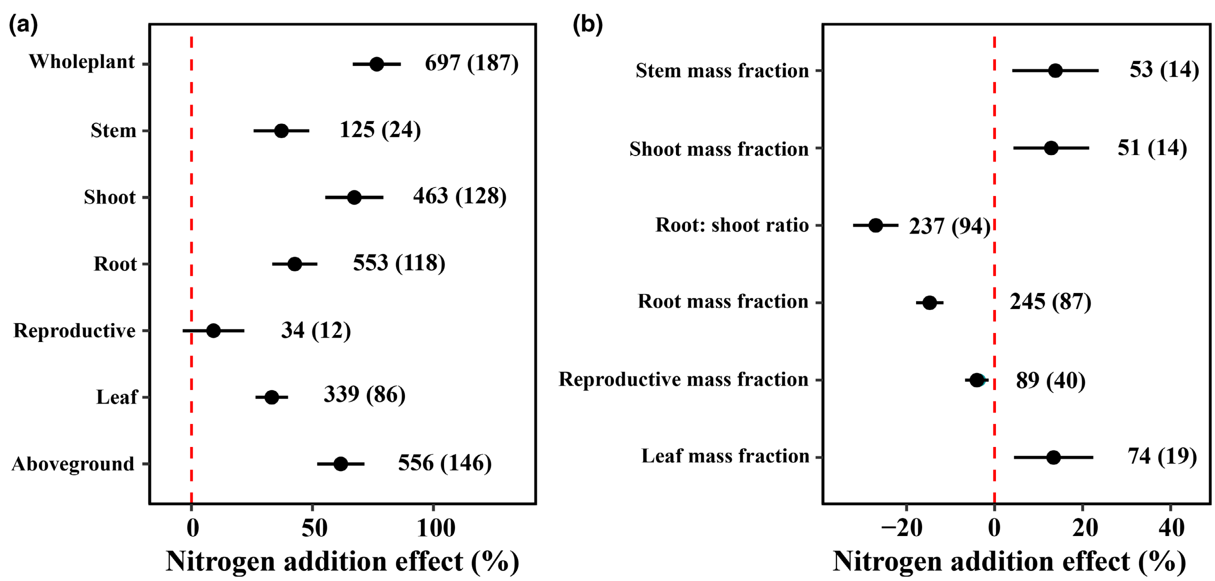

FIGURE 5 Effect size of N addition on terrestrial plant biomass for different tissue types (a) and mass fractions and root-shoot ratio (b), expressed on the global scale (RR [±95% confidence interval]). The vertical dashed red line denotes a null effect size (RR=0). The number of observations is beside each attribute without parentheses, and the number of plant species is in the parentheses. RR, log response ratio. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Effect sizes and regression coefficient of the factors affecting terrestrial plant biomass response to N addition on the global scale.

Fixed effects/ moderators	Mean effect size/regression coefficient	LCI	UCI	*N*	Model support based on omnibus tests (Q_m, df)
MAT				1888	**$Q_{m,1}=29.446$, $p<.0001$**
Intercept	0.2914	0.2476	0.3351		
Slope	0.0101	0.0065	0.0138		
Latitude				1909	**$Q_{m,1}=4.667$, $p=.0307$**
Intercept	0.4199	0.3690	0.4709		
Slope	−0.0012	−0.0023	−0.0001		
AP				821	**$Q_{m,1}=7.469$, $p=.0063$**
Intercept	0.2209	0.0908	0.3510		
Slope	0.0270	0.0076	0.0464		
TK				1658	**$Q_{m,1}=6.999$, $p=.0082$**
Intercept	0.2257	0.1256	0.3257		
Slope	0.0934	0.0242	0.1626		
TN				1772	**$Q_{m,1}=20.416$, $p<.0001$**
Intercept	0.4330	0.3933	0.4727		
Slope	−0.1803	−0.2585	−0.1021		
SLA				1987	**$Q_{m,1}=25.405$, $p<.0001$**
Intercept	0.3138	0.2491	0.3784		
Slope	0.0089	0.0055	0.0124		
PLA				897	**$Q_{m,1}=6.744$, $p=.0094$**
Intercept	0.4373	0.3878	0.4867		
Slope	0.0006	0.0002	0.0011		
LCN				1641	**$Q_{m,1}=10.608$, $p=.0011$**
Intercept	0.5698	0.4939	0.6439		
Slope	−0.0036	−0.0058	−0.0015		
LCC				1510	**$Q_{m,1}=37.941$, $p<.0001$**
Intercept	0.5769	0.5192	0.6346		
Slope	−0.0032	−0.0042	−0.0022		
LNC				1863	**$Q_{m,1}=34.477$, $p<.0001$**
Intercept	0.6211	0.5556	0.6866		
Slope	−0.0997	−0.1330	−0.0664		
N.addition				1607	**$Q_{m,1}=10.087$, $p=.0015$**
Intercept	0.3777	0.3344	0.4210		
Slope	−0.0027	−0.0044	−0.0010		
Duration				2662	**$Q_{m,1}=28.239$, $p<.0001$**
Intercept	0.4835	0.4496	0.5174		
Slope	−0.0259	−0.0354	−0.0163		

Note: LCI and UCI represent the lower and upper bounds of the 95% confidence intervals. Significant influence of moderators is indicated in bold.
Abbreviations: AP, soil available phosphorus; LCC, leaf carbon content per leaf area; LCN, leaf carbon/nitrogen ratio; LNC, leaf nitrogen content per leaf area; MAP, mean annual precipitation; MAT, mean annual temperature; *N*, number of effect sizes; N.addition, nitrogen addition amount (include the experimental N addition and atmospheric inorganic N deposition); Photopathway, photosynthesis pathway; PLA, leaf area per plant; SLA, specific leaf area; TK, soil total potassium; TN, soil total nitrogen.

Therefore, herbaceous plants are theoretically more responsive to changes in biomass than woody plants to N addition, which we confirmed in this study. Furthermore, the results of our study revealed a significant positive impact of N addition on the biomass of seed plants, but not spore plants. There are several factors that may explain this outcome. Firstly, seed plants typically require higher levels of N than spore plants due to their more intricate vascular system, which allows for more efficient nutrient uptake and transport. In contrast, spore plants lack this specialized system and, thus, may be less responsive to N addition (Xia & Wan, 2008). Secondly, seed plants possess a higher photosynthetic rate than spore plants, enabling them to use the additional N availability to produce more biomass (Sage, 2004). In contrast, spore plants have lower rates of photosynthesis and may not fully benefit from the increased N availability (Flexas & Carriquí, 2020). Overall, the disparate responses of seed and spore plants to N addition can be attributed to their differing nutrient demands, vascular systems, and photosynthetic capacities.

The results of the study indicate that deciduous trees exhibit a more pronounced growth response to N addition compared to evergreen trees. One possible reason for this is that deciduous trees are capable of promptly adjusting their photosynthetic capacity in response to fluctuations in N availability, whereas evergreen trees maintain a relatively stable photosynthetic capacity owing to their long-lived foliage (Li et al., 2020). Additionally, deciduous trees may have a greater requirement for N during the production and replacement of leaves, while evergreen trees demand less N due to their prolonged leaf life (Weng et al., 2017). Another factor that could account for the superior biomass response of deciduous trees to N addition is their greater nutrient-use efficiency (Hiremath, 2000). Research has demonstrated that deciduous trees possess higher N-use efficiency relative to evergreen trees (Liu et al., 2018), enabling them to maintain higher growth rates with reduced N inputs.

The findings from the study indicate that broadleaved trees experience a more substantial increase in biomass following N addition compared to coniferous trees. This phenomenon can be attributed to various factors, including N utilization efficiency and leaf traits. Broadleaved trees typically exhibit higher N utilization efficiency than coniferous trees, which refers to their ability to efficiently acquire and use N for growth and development (Wyka et al., 2012). Furthermore, broadleaved trees possess a more extensive and shallow root system that enables them to take up N from a larger volume of soil (Schenk & Jackson, 2002). In addition, broadleaved trees have a higher leaf N concentration that enhances their photosynthetic capacity and growth rate (Sardans et al., 2011). Leaf traits such as SLA and leaf lifespan can also affect plant response to N addition. Broadleaved trees generally have higher SLA and shorter leaf lifespan compared to coniferous trees (Adler et al., 2014). The higher SLA allows for rapid leaf growth, which results in greater carbon fixation and biomass accumulation following N addition (Augusto & Boča, 2022). The shorter leaf lifespan reduces the carbon costs associated with maintaining old leaves, enabling faster replacement with new, more efficient leaves. Overall, our findings highlight the potential of broadleaved trees as a target for N management strategies aiming at increasing carbon sequestration in terrestrial ecosystems.

4.2 | Leaf functional traits affect plant biomass allocation to nitrogen addition

Plants with high SLA and PLA are capable of high photosynthetic capacity and are considered nitrogennuse efficient as they have a higher capacity to capture nutrients in response to higher N availability in soils (Laliberté et al., 2012). A higher LNC is indicative of more effective N absorption, retention, or both (Gornish & Prather, 2014). We found that the positive effect of N addition on biomass decreased as plant N capture or storage capacity (i.e., LNC) improved, suggesting that when plants have high N-use efficiency or reabsorption efficiency, N resources are not the main source of stress-limiting plant growth. By contrast, the higher the SLA and PLA of terrestrial plants, the higher the positive effect of N addition on biomass (Figure 6a; Table 1), leading to a significantly increased leaf

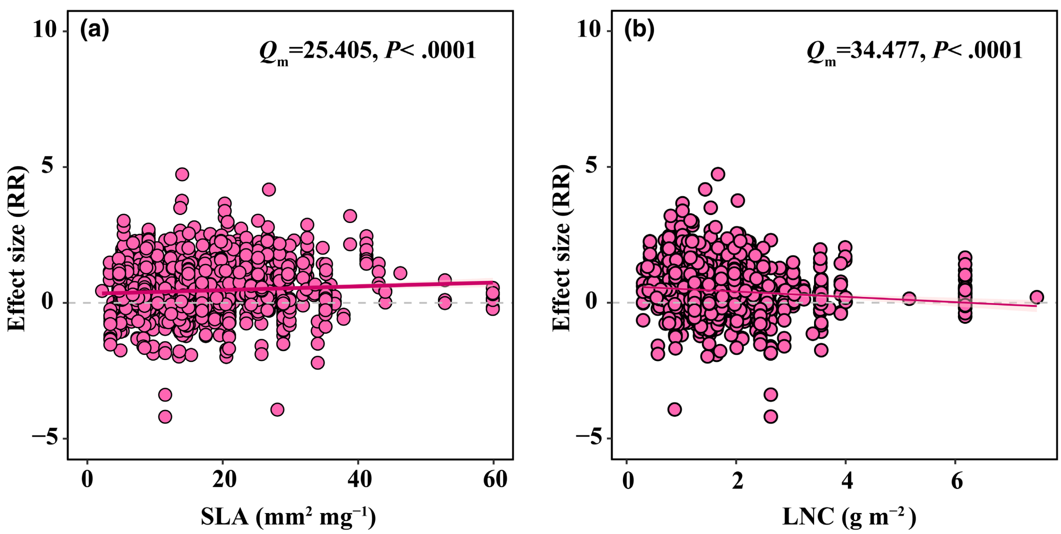

FIGURE 6 Specific leaf area (SLA; a) and leaf N content per leaf area (LNC; b) affecting plant biomass response to N addition. Circles represent the individual experiments under experimental N addition in the meta-analysis. RR, log response ratio. RR = 0, dashed grey line; predicted mean effect size (with 95% CI in grey dashed lines), medium violet red lines. [Colour figure can be viewed at wileyonlinelibrary.com]

mass fraction and a decreased root-shoot ratio. Therefore, terrestrial plants are projected to increase SLA and PLA to be more competitive for light in environments where the N supply is sufficient.

Biomass allocation has been well reported to be a plastic trait of plants adapted to various habitats (Yan et al., 2016). The leaf economics spectrum (Wright et al., 2004) refers to the continuous transition in leaf traits from thin, N-rich, short-lived leaves with high photosynthetic rates, known as the exploitative strategy (Grime, 1977), to thicker, more fibrous, N-poor, long-lived leaves with lower photosynthetic rates, and is known as the conservative growth strategy (Lavorel & Grigulis, 2012). Previous studies have shown that SLA and LNC are effective predictors of where a plant is situated along the leaf economic spectrum. High SLA and LNC imply an exploitative strategy for plants, while low SLA and LNC imply a conservative strategy (Wright et al., 2004). We found that when plants adopt conservative strategies (low SLA and LNC), N addition has a consistently positive effect on plant biomass. However, when plants adopt an exploitative strategy, the positive effect of N addition on plant biomass decreases as LNC increases. It then becomes negative when LNC is greater than 6.23 $g\,m^{-2}$ (Figure 6b). As a result, whereas flexibility in biomass allocation might improve plant adaptation to N addition, the underlying leaf functional traits may dictate how much plant species modify their allocation patterns in response to N addition.

4.3 | Uncertainties and implications for future studies

This global meta-analysis enhances our understanding of the effects of N addition-driven environmental change on biomass accumulation and allocation of terrestrial plants and provides a useful reference for future policymaking and implementation of ecological and environmental protection. However, there are some caveats to be aware of when interpreting the results. First, this meta-analysis focused on the impact of N addition on plant biomass and its components in the terrestrial ecosystem and does not include interactions between other global change factors (e.g., increasing temperature and changing precipitation). Second, a meta-analysis of the effects of N addition on terrestrial plant biomass and its composition was carried out based on the most comprehensive dataset; however, the uneven distribution of field-observed datasets (i.e., the lack of observed data in eastern Africa, Russia, and northern Asia) may cause a bias in the worldwide distribution impacts of increasing N availability. Therefore, more field observations in relevant regions are urgently required to enhance our understanding of the consequences of global N deposition on terrestrial ecosystems.

5 | CONCLUSIONS

Our global synthesis quantified the effects of reactive N addition on terrestrial plant biomass and its allocation in plants, as well as identifying the key drivers of terrestrial plant biomass response to reactive N addition on a global scale. Our findings revealed that N addition had a positive effect on plant biomass, but the positive effect gradually decreased as N load and fertilization duration increased. On the global scale, more plants tend to increase vegetative growth and reduce reproductive allocation under increasing N decomposition. Furthermore, the effects of N addition on plant biomass increased significantly with increasing MAT, AP, TK, SLA, and PLA. However, they decreased significantly with increasing TN, amount of N addition, LCN, LCC, LNC, and duration of the addition. By accelerating growth and reducing reproductive allocations, terrestrial plants may alter their reproductive trade-offs to enhance their competitiveness in response to enhanced competition in N-added plots. Therefore, when simulating global changes related to N deposition and terrestrial carbon sequestration, Earth System Models should be improved to predict the response of plant biomass and its allocations to future N deposition in combination with plant leaf functional traits and environmental variables.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.22584481.

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REFERENCES

Ackerman, D. E., Chen, X., & Millet, D. B. (2018). *Global nitrogen deposition (2°×2.5° grid resolution) simulated with GEOS-Chem for 1984–1986, 1994–1996, 2004–2006, and 2014–2016*. University of Minnesota. https://doi.org/10.13020/D6KX2R

Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C., & Franco, M. (2014). Functional traits explain variation in plant life history strategies. *Proceedings* of the National Academy of Sciences of the United States of America, 111(2), 740–745. https://doi.org/10.1073/pnas.1315179111

Antonio, T., & Robert, Z. (2019). *Global aridity index and potential evapotranspiration (ET0) climate database v2*. https://doi.org/10.6084/m9.figshare.7504448.v3

Augusto, L., & Boča, A. (2022). Tree functional traits, forest biomass, and tree species diversity interact with site properties to drive forest soil carbon. *Nature Communications*, *13*(1), 1097. https://doi.org/10.1038/s41467-022-28748-0

Bai, E., Li, S., Xu, W., Li, W., Dai, W., & Jiang, P. (2013). A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics. *New Phytologist*, *199*(2), 441–451. https://doi.org/10.1111/nph.12252

Bläsing, O. E., Gibon, Y., Günther, M., Höhne, M., Morcuende, R., Osuna, D., Thimm, O., Usadel, B., Scheible, W. R., & Stitt, M. (2005). Sugars and circadian regulation make major contributions to the global regulation of diurnal gene expression in *Arabidopsis*. *Plant Cell*, *17*(12), 3257–3281. https://doi.org/10.1105/tpc.105.035261

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J. W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., & de Vries, W. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications*, *20*(1), 30–59. https://doi.org/10.1890/08-1140.1

Calcagno, V., & de Mazancourt, C. (2010). glmulti: An R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, *34*(12), 1–29. https://doi.org/10.18637/jss.v034.i12

Cambui, C. A., Svennerstam, H., Gruffman, L., Nordin, A., Ganeteg, U., & Nasholm, T. (2011). Patterns of plant biomass partitioning depend on nitrogen source. *PLoS One*, *6*(4), e19211. https://doi.org/10.1371/journal.pone.0019211

Cauvy-Fraunié, S., & Dangles, O. (2019). A global synthesis of biodiversity responses to glacier retreat. *Nature Ecology & Evolution*, *3*(12), 1675–1685. https://doi.org/10.1038/s41559-019-1042-8

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquéz, J. R., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Egger, M., Smith, G. D., Schneider, M., & Minder, C. (1997). Bias in meta-analysis detected by a simple, graphical test. *British Medical Journal*, *315*(7109), 629–634. https://doi.org/10.1136/bmj.315.7109.629

Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B., & Smith, J. E. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, *10*(12), 1135–1142. https://doi.org/10.1111/j.1461-0248.2007.01113.x

Eyles, A., Pinkard, E. A., & Mohammed, C. (2009). Shifts in biomass and resource allocation patterns following defoliation in *Eucalyptus globulus* growing with varying water and nutrient supplies. *Tree Physiology*, *29*(6), 753–764. https://doi.org/10.1093/treephys/tpp014

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Flexas, J., & Carriquí, M. (2020). Photosynthesis and photosynthetic efficiencies along the terrestrial plant's phylogeny: Lessons for improving crop photosynthesis. *The Plant Journal*, *101*(4), 964–978. https://doi.org/10.1111/tpj.14651

Frink, C. R., Waggoner, P. E., & Ausubel, J. H. (1999). Nitrogen fertilizer: Retrospect and prospect. *Proceedings of the National Academy of Sciences of the United States of America*, *96*(4), 1175–1180. https://doi.org/10.1073/pnas.96.4.1175

Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda, M., Cai, Z., Freney, J. R., Martinelli, L. A., Seitzinger, S. P., & Sutton, M. A. (2008). Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. *Science*, *320*(5878), 889–892. https://doi.org/10.1126/science.1136674

Gornish, E. S., & Prather, C. M. (2014). Foliar functional traits that predict plant biomass response to warming. *Journal of Vegetation Science*, *25*(4), 919–927. https://doi.org/10.1111/jvs.12150

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, *111*(982), 1169–1194. https://doi.org/10.1086/283244

Gruber, N., & Galloway, J. N. (2008). An Earth-system perspective of the global nitrogen cycle. *Nature*, *451*(7176), 293–296. https://doi.org/10.1038/nature06592

Guo, J., Feng, H., McNie, P., Liu, Q., Xu, X., Pan, C., Yan, K., Feng, L., Goitom, E. A., & Yu, Y. (2023). Species mixing improves soil properties and enzymatic activities in Chinese fir plantations: A meta-analysis. *Catena*, *220*, 106723. https://doi.org/10.1016/j.catena.2022.106723

Hedges, L. V., Gurevitch, J., & Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, *80*(4), 1150–1156. https://doi.org/10.2307/177062

Hedges, L. V., & Olkin, I. (1985). *Statistical methods for meta-analysis*. Academic Press.

Hermans, C., Hammond, J. P., White, P. J., & Verbruggen, N. (2006). How do plants respond to nutrient shortage by biomass allocation? *Trends in Plant Science*, *11*(12), 610–617. https://doi.org/10.1016/j.tplants.2006.10.007

Hiremath, A. J. (2000). Photosynthetic nutrient-use efficiency in three fast-growing tropical trees with differing leaf longevities. *Tree Physiology*, *20*(14), 937–944. https://doi.org/10.1093/treephys/20.14.937

Högberg, P., Fan, H., Quist, M., Binkley, D., & Tamm, C. O. (2006). Tree growth and soil acidification in response to 30 years of experimental nitrogen loading on boreal forest. *Global Change Biology*, *12*(3), 489–499. https://doi.org/10.1111/j.1365-2486.2006.01102.x

Holub, P., & Tůma, I. (2010). The effect of enhanced nitrogen on aboveground biomass allocation and nutrient resorption in the fern *Athyrium distentifolium*. *Plant Ecology*, *207*(2), 373–380. https://doi.org/10.1007/s11258-009-9681-5

Humbert, J.-Y., Dwyer, J. M., Andrey, A., & Arlettaz, R. (2016). Impacts of nitrogen addition on plant biodiversity in mountain grasslands depend on dose, application duration and climate: A systematic review. *Global Change Biology*, *22*(1), 110–120. https://doi.org/10.1111/gcb.12986

Janssens, I. A., Dieleman, W., Luyssaert, S., Subke, J. A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, A. J., Grace, J., Matteucci, G., Papale, D., Piao, S. L., Schulze, E.-D., Tang, J., & Law, B. E. (2010). Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience*, *3*(5), 315–322. https://doi.org/10.1038/ngeo844

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar, C. C., Aleixo, I., Ali, H., … Wirth, C. (2020). TRY plant trait database—Enhanced coverage and open access. *Global Change Biology*, *26*(1), 119–188. https://doi.org/10.1111/gcb.14904

Laliberté, E., Shipley, B., Norton, D. A., & Scott, D. (2012). Which plant traits determine abundance under long-term shifts in soil resource availability and grazing intensity? *Journal of Ecology*, *100*(3), 662–677. https://doi.org/10.1111/j.1365-2745.2011.01947.x

Lamarque, J.-F., Kiehl, J. T., Brasseur, G. P., Butler, T., Cameron-Smith, P., Collins, W. D., Collins, W. J., Granier, C., Hauglustaine, D., Hess, P. G., Holland, E. A., Horowitz, L., Lawrence, M. G., McKenna, D., Merilees, P., Prather, M. J., Rasch, P. J., Rotman, D., Shindell, D., & Thornton, P. (2005). Assessing future nitrogen deposition and carbon cycle feedback using a multimodel approach: Analysis of nitrogen deposition. *Journal of Geophysical Research: Atmospheres*, *110*, D19303. https://doi.org/10.1029/2005JD005825

Lavorel, S., & Grigulis, K. (2012). How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology*, *100*(1), 128–140. https://doi.org/10.1111/j.1365-2745.2011.01914.x

LeBauer, D. S., & Treseder, K. K. (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, *89*(2), 371–379. https://doi.org/10.1890/06-2057.1

Li, C., Zheng, Z., Peng, Y., Nie, X., Yang, L., Xiao, Y., & Zhou, G. (2019). Precipitation and nitrogen addition enhance biomass allocation to aboveground in an alpine steppe. *Ecology and Evolution*, *9*(21), 12193–12201. https://doi.org/10.1002/ece3.5706

Li, Q., Zhao, C.-Z., Kang, M.-P., & Li, X.-Y. (2021). The relationship of the main root-shoot morphological characteristics and biomass allocation of *Saussurea salsa* under different habitat conditions in Sugan lake wetland on the northern margin of the Qinghai-Tibet Plateau. *Ecological Indicators*, *128*, 107836. https://doi.org/10.1016/j.ecolind.2021.107836

Li, W. B., Zhang, H. X., Huang, G. Z., Liu, R. X., Wu, H. J., Zhao, C. Y., & McDowell, N. G. (2020). Effects of nitrogen enrichment on tree carbon allocation: A global synthesis. *Global Ecology and Biogeography*, *29*(3), 573–589. https://doi.org/10.1111/geb.13042

Liang, X., Zhang, T., Lu, X., Ellsworth, D. S., BassiriRad, H., You, C., Wang, D., He, P., Deng, Q., Liu, H., Mo, J., & Ye, Q. (2020). Global response patterns of plant photosynthesis to nitrogen addition: A meta-analysis. *Global Change Biology*, *26*(6), 3585–3600. https://doi.org/10.1111/gcb.15071

Liu, N., Wu, S., Guo, Q., Wang, J., Cao, C., & Wang, J. (2018). Leaf nitrogen assimilation and partitioning differ among subtropical forest plants in response to canopy addition of nitrogen treatments. *Science of the Total Environment*, *637–638*, 1026–1034. https://doi.org/10.1016/j.scitotenv.2018.05.060

Lu, M., Yang, Y., Luo, Y., Fang, C., Zhou, X., Chen, J., Yang, X., & Li, B. (2011). Responses of ecosystem nitrogen cycle to nitrogen addition: A meta-analysis. *New Phytologist*, *189*(4), 1040–1050. https://doi.org/10.1111/j.1469-8137.2010.03563.x

Marron, N., Villar, M., Dreyer, E., Delay, D., Boudouresque, E., Petit, J.-M., Delmotte, F. M., Guehl, J. M., & Brignolas, F. (2005). Diversity of leaf traits related to productivity in 31 *Populus deltoides* × *Populus nigra* clones. *Tree Physiology*, *25*(4), 425–435. https://doi.org/10.1093/treephys/25.4.425

Midolo, G., Alkemade, R., Schipper, A. M., Benítez-López, A., Perring, M. P., & De Vries, W. (2019). Impacts of nitrogen addition on plant species richness and abundance: A global meta-analysis. *Global Ecology and Biogeography*, *28*(3), 398–413. https://doi.org/10.1111/geb.12856

Mu, X., & Chen, Y. (2021). The physiological response of photosynthesis to nitrogen deficiency. *Plant Physiology and Biochemistry*, *158*, 76–82. https://doi.org/10.1016/j.plaphy.2020.11.019

Palmqvist, K., & Dahlman, L. (2006). Responses of the green algal foliose lichen *Platismatia glauca* to increased nitrogen supply. *New Phytologist*, *171*(2), 343–356. https://doi.org/10.1111/j.1469-8137.2006.01754.x

Peterson, B. G., & Carl, P. (2020). *Performance analytics: Econometric tools for performance and risk analysis* (Version R package version 2.0.4). https://CRAN.R-project.org/package=PerformanceAnalytics

Phoenix, G. K., Emmett, B. A., Britton, A. J., Caporn, S. J. M., Dise, N. B., Helliwell, R., Jones, L., Leake, J. R., Leith, I. D., Sheppard, L. J., Sowerby, A., Pilkington, M. G., Rowe, E. C., Ashmore, M. R., & Power, S. A. (2012). Impacts of atmospheric nitrogen deposition: Responses of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. *Global Change Biology*, *18*(4), 1197–1215. https://doi.org/10.1111/j.1365-2486.2011.02590.x

Poorter, H., Jagodzinski, A. M., Ruiz-Peinado, R., Kuyah, S., Luo, Y., Oleksyn, J., Usoltsev, V. A., Buckley, T. N., Reich, P. B., & Sack, L. (2015). How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytologist*, *208*(3), 736–749. https://doi.org/10.1111/nph.13571

Puglielli, G., Laanisto, L., Poorter, H., & Niinemets, Ü. (2021). Global patterns of biomass allocation in woody species with different tolerances of shade and drought: Evidence for multiple strategies. *New Phytologist*, *229*(1), 308–322. https://doi.org/10.1111/nph.16879

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Reich, P. B., Luo, Y., Bradford, J. B., Poorter, H., Perry, C. H., & Oleksyn, J. (2014). Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(38), 13721–13726. https://doi.org/10.1073/pnas.1216053111

Rosenberg, M. S. (2005). The file-drawer problem revisited: A general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution*, *59*(2), 464–468. https://doi.org/10.1111/j.0014-3820.2005.tb01004.x

Sage, R. F. (2004). The evolution of C_4 photosynthesis. *New Phytologist*, *161*(2), 341–370. https://doi.org/10.1111/j.1469-8137.2004.00974.x

Sardans, J., Rivas-Ubach, A., & Peñuelas, J. (2011). Factors affecting nutrient concentration and stoichiometry of forest trees in Catalonia (NE Spain). *Forest Ecology and Management*, *262*(11), 2024–2034. https://doi.org/10.1016/j.foreco.2011.08.019

Schenk, H. J., & Jackson, R. B. (2002). The global biogeography of roots. *Ecological Monographs*, *72*(3), 311–328. https://doi.org/10.1890/0012-9615(2002)072[0311:TGBOR]2.0.CO;2

Scott Green, D., Erickson, J. E., & Kruger, E. L. (2003). Foliar morphology and canopy nitrogen as predictors of light-use efficiency in terrestrial vegetation. *Agricultural and Forest Meteorology*, *115*(3), 163–171. https://doi.org/10.1016/S0168-1923(02)00210-1

Shangguan, W., Dai, Y. J., Duan, Q. Y., Liu, B. Y., & Yuan, H. (2014). A global soil data set for earth system modeling. *Journal of Advances in Modeling Earth Systems*, *6*(1), 249–263. https://doi.org/10.1002/2013ms000293

Shipley, B., & Meziane, D. (2002). The balanced-growth hypothesis and the allometry of leaf and root biomass allocation. *Functional Ecology*, *16*(3), 326–331. https://doi.org/10.1046/j.1365-2435.2002.00626.x

Terrer, C., Phillips, R. P., Hungate, B. A., Rosende, J., Pett-Ridge, J., Craig, M. E., van Groenigen, K., Keenan, T. F., Sulman, B. N., Stocker, B. D., Reich, P. B., Pellegrini, A. F. A., Pendall, E., Zhang, H., Evans, R. D., Carrillo, Y., Fisher, J. B., van Sundert, K., Vicca, S., & Jackson, R. B. (2021). A trade-off between plant and soil carbon storage under elevated CO_2. *Nature*, *591*(7851), 599–603. https://doi.org/10.1038/s41586-021-03306-8

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*(3), 1–48. https://doi.org/10.18637/jss.v036.i03

Weng, E., Farrior, C. E., Dybzinski, R., & Pacala, S. W. (2017). Predicting vegetation type through physiological and environmental interactions with leaf traits: Evergreen and deciduous forests in an earth system modeling framework. *Global Change Biology*, *23*(6), 2482–2498. https://doi.org/10.1111/gcb.13542

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827. https://doi.org/10.1038/nature02403

Wyka, T. P., Oleksyn, J., Żytkowiak, R., Karolewski, P., Jagodziński, A. M., & Reich, P. B. (2012). Responses of leaf structure and photosynthetic properties to intra-canopy light gradients: A common garden test with four broadleaf deciduous angiosperm and seven evergreen conifer tree species. *Oecologia*, *170*(1), 11–24. https://doi.org/10.1007/s00442-012-2279-y

Xia, J., & Wan, S. (2008). Global response patterns of terrestrial plant species to nitrogen addition. *New Phytologist*, *179*(2), 428–439. https://doi.org/10.1111/j.1469-8137.2008.02488.x

Xu, C., Xu, X., Ju, C., Chen, H. Y. H., Wilsey, B. J., Luo, Y., & Fan, W. (2021). Long-term, amplified responses of soil organic carbon to nitrogen addition worldwide. *Global Change Biology*, *27*(6), 1170–1180. https://doi.org/10.1111/gcb.15489

Yan, B., Ji, Z., Fan, B., Wang, X., He, G., Shi, L., & Liu, G. (2016). Plants adapted to nutrient limitation allocate less biomass into stems in an arid-hot grassland. *New Phytologist*, *211*(4), 1232–1240. https://doi.org/10.1111/nph.13970

Yan, Z., Eziz, A., Tian, D., Li, X., Hou, X., Peng, H., Han, W., Guo, Y., & Fang, J. (2019). Biomass allocation in response to nitrogen and phosphorus availability: Insight from experimental manipulations of *Arabidopsis thaliana*. *Frontiers in Plant Science*, *10*, 598. https://doi.org/10.3389/fpls.2019.00598

Yin, Q., Tian, T., Han, X., Xu, J., Chai, Y., Mo, J., Lei, M., Wang, L., & Yue, M. (2019). The relationships between biomass allocation and plant functional trait. *Ecological Indicators*, *102*, 302–308. https://doi.org/10.1016/j.ecolind.2019.02.047

Yue, K., Fornara, D. A., Li, W., Ni, X., Peng, Y., Liao, S., Tan, S., Wang, D., Wu, F., & Yang, Y. (2020). Nitrogen addition affects plant biomass allocation but not allometric relationships among different organs across the globe. *Journal of Plant Ecology*, *14*(3), 361–371. https://doi.org/10.1093/jpe/rtaa100

Zhu, X.-G., Long, S. P., & Ort, D. R. (2008). What is the maximum efficiency with which photosynthesis can convert solar energy into biomass? *Current Opinion in Biotechnology*, *19*(2), 153–159. https://doi.org/10.1016/j.copbio.2008.02.004

DATA SOURCES

Aerts, R., & de Caluwe, H. (1994). Effects of nitrogen supply on canopy structure and leaf nitrogen distribution in *Carex* species. *Ecology*, *75*(5), 1482–1490. https://doi.org/10.2307/1937471

Aerts, R., de Caluwe, H., & Konings, H. (1992a). Seasonal allocation of biomass and nitrogen in four *Carex* species from mesotorphic and eutrophic fens as affected by nitrogen supply. *Journal of Ecology*, *80*(4), 653–664. https://doi.org/10.2307/2260857

Aerts, R., Wallen, B., & Malmer, N. (1992b). Growth-limiting nutrients in Sphagnum-dominated bogs subject to low and high atmospheric nitrogen supply. *Journal of Ecology*, *80*(1), 131–140. https://doi.org/10.2307/2261070

Aerts, R., Wallen, B., Malmer, N., & de Caluwe, H. (2001). Nutritional constraints on *Sphagnum*-growth and potential decay in northern peatlands. *Journal of Ecology*, *89*(2), 292–299. https://doi.org/10.1046/j.1365-2745.2001.00539.x

Anderson, W. B., & Eickmeier, W. G. (1998). Physiological and morphological responses to shade and nutrient additions of *Claytonia virginica* (Portulacaceae): Implications for the "vernal dam" hypothesis. *Canadian Journal of Botany*, *76*(8), 1340–1349. https://doi.org/10.1046/10.1139/b98-134

Arp, W. J., Van Mierlo, J. E. M., Berendse, F., & Snijders, W. (1998). Interactions between elevated CO_2 concentration, nitrogen and water: Effects on growth and water use of six perennial plant species. *Plant, Cell and Environment*, *21*(1), 1–11. https://doi.org/10.1046/j.1365-3040.1998.00257.x

Báez, S., Fargione, J., Moore, D. I., Collins, S. L., & Gosz, J. R. (2007). Atmospheric nitrogen deposition in the northern Chihuahuan desert: Temporal trends and potential consequences. *Journal of Arid Environments*, *68*(4), 640–651. https://doi.org/10.1016/j.jaridenv.2006.06.011

Bai, X., Cheng, J., Zheng, S., Zhan, S., & Bai, Y. (2014). Ecophysiological responses of *Leymus chinensis* to nitrogen and phosphorus additions in a typical steppe. *Chinese Journal of Plant Ecology*, *38*(2), 103–115.

Bardgett, R. D., Mawdsley, J. L., Edwards, S., Hobbs, P. J., Rodwell, J. S., & Davies, W. J. (1999). Plant species and nitrogen effects on soil biological properties of temperate upland grasslands. *Functional Ecology*, *13*(5), 650–660. https://doi.org/10.1046/j.1365-2435.1999.00362.x

Barger, N. N., D'Antonio, C. M., Ghneim, T., Brink, K., & Cuevas, E. (2002). Nutrient limitation to primary productivity in a secondary savanna in Venezuela. *Biotropica*, *34*(4), 493–501. https://doi.org/10.1111/j.1744-7429.2002.tb00569.x

Barger, N. N., D'Antonio, C. M., Ghneim, T., & Cuevas, E. (2003). Constraints to colonization and growth of the African grass, *Melinis minutiflora*, in a Venezuelan savanna. *Plant Ecology*, *167*(1), 31–43. https://doi.org/10.1023/A:1023903901286

Bazzaz, F. A., & Miao, S. L. (1993). Successional status, seed size, and responses of tree seedlings to CO_2, light, and nutrients. *Ecology*, *74*(1), 104–112. https://doi.org/10.2307/1939505

Bélanger, G., & Richards, J. E. (2000). Dynamics of biomass and N accumulation of alfalfa under three N fertilization rates. *Plant and Soil*, *219*(1), 177–185. https://doi.org/10.1023/A:1004749828745

Bellingham, P. J., Walker, L. R., & Wardle, D. A. (2001). Differential facilitation by a nitrogen-fixing shrub during primary succession influences relative performance of canopy tree species. *Journal of Ecology*, *89*(5), 861–875. https://doi.org/10.1046/j.0022-0477.2001.00604.x

Bennett, J. N., Blevins, L. L., Barker, J. E., Blevins, D. P., & Prescott, C. E. (2003). Increases in tree growth and nutrient supply still apparent 10 to 13 years following fertilization and vegetation control of salal-dominated cedarhemlock stands on Vancouver Island. *Canadian Journal of Forest Research*, *33*(8), 1516–1524. https://doi.org/10.1139/x03-069

Bergamini, A., & Peintinger, M. (2002). Effects of light and nitrogen on morphological plasticity of the moss *Calliergonella cuspidata*. *Oikos*, *96*(2), 355–363. https://doi.org/10.1034/j.1600-0706.2002.960217.x

Birk, E. M., & Vitousek, P. M. (1986). Nitrogen availability and nitrogen use efficiency in loblolly pine stands. *Ecology*, *67*(1), 69–79. https://doi.org/10.2307/1938504

Blanke, V., Renker, C., Wagner, M., Fullner, K., Held, M., Kuhn, A. J., & Buscot, F. (2005). Nitrogen supply affects arbuscular mycorrhizal colonization of *Artemisia vulgaris* in a phosphate-polluted field site. *New Phytologist*, *166*(3), 981–992. https://doi.org/10.1111/j.1469-8137.2005.01374.x

Blicker, P. S., Olson, B. E., & Engel, R. (2002). Traits of the invasive *Centaurea maculosa* and two native grasses: Effect of N supply. *Plant and Soil*, *247*(2), 261–269. https://doi.org/10.1023/a:1021596627967

Bonanomi, G., Caporaso, S., & Allegrezza, M. (2006). Short-term effects of nitrogen enrichment, litter removal and cutting on a Mediterranean grassland. *Acta Oecologica*, *30*(3), 419–425. https://doi.org/10.1016/j.actao.2006.06.007

Boryslawski, Z., & Bentley, B. L. (1985). The effect of nitrogen and clipping on interference between C_3 and C_4 grasses. *Journal of Ecology*, *73*(1), 113–121. https://doi.org/10.2307/2259772

Bowman, W. D., & Bilbrough, C. J. (2001). Influence of a pulsed nitrogen supply on growth and nitrogen uptake in alpine graminoids. *Plant and Soil*, *233*(2), 283–290. https://doi.org/10.1023/a:1010571920890

Bowman, W. D., Gartner, J. R., Holland, K., & Wiedermann, M. (2006). Nitrogen critical loads for alpine vegetation and terrestrial ecosystem response: Are we there yet? *Ecological Applications*, *16*(3), 1183–1193. https://doi.org/10.1890/1051-0761(2006)016[1183:NCLFAV]2.0.CO;2

Bowman, W. D., Theodose, T. A., Schardt, J. C., & Conant, R. T. (1993). Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology*, *74*(7), 2085–2097. https://doi.org/10.2307/1940854

Boyer, K. E., & Zedler, J. B. (1999). Nitrogen addition could shift plant community composition in a restored California salt marsh. *Restoration Ecology*, *7*(1), 74–85. https://doi.org/10.1046/j.1526-100X.1999.07109.x

Brooks, M. L. (2003). Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert.

Journal of Applied Ecology, *40*(2), 344–353. https://doi.org/10.1046/j.1365-2664.2003.00789.x

Bungard, R. A., Scholes, J. D., & Press, M. C. (2000). The influence of nitrogen on rain forest dipterocarp seedlings exposed to a large increase in irradiance. *Plant, Cell & Environment*, *23*(11), 1183–1194. https://doi.org/10.1046/j.1365-3040.2000.00642.x

Burslem, D. F. R. P., Grubb, P. J., & Turner, I. M. (1995). Responses to nutrient addition among shade-tolerant tree seedlings of lowland tropical rain forest in Singapore. *Journal of Ecology*, *83*(1), 113–122. https://doi.org/10.2307/2261155

Burslem, D. F. R. P., Turner, I. M., & Grubb, P. J. (1994). Mineral nutrient status of coastal hill dipterocarp forest and adinandra belukar in Singapore: Bioassays of nutrient limitation. *Journal of Tropical Ecology*, *10*(4), 579–599. https://doi.org/10.1017/S0266467400008257

Cahill, J. F. (1999). Fertilization effects on interactions between above- and belowground competition in an old field. *Ecology*, *80*(2), 466–480. https://doi.org/10.1890/0012-9658(1999)080[0466:Feoiba]2.0.Co;2

Caporn, S. J. M., Brooks, A. L., Press, M. C., & Lee, J. A. (1999). Effects of long-term exposure to elevated CO_2 and increased nutrient supply on bracken (*Pteridium aquilinum*). *Functional Ecology*, *13*(s1), 107–115. https://doi.org/10.1046/j.1365-2435.1999.00013.x

Carswell, F. E., Whitehead, D., Rogers, G. N. D., & McSeveny, T. M. (2005). Plasticity in photosynthetic response to nutrient supply of seedlings from a mixed conifer-angiosperm forest. *Austral Ecology*, *30*(4), 426–434. https://doi.org/10.1111/j.1442-9993.2005.01486.x

Causin, H. F., Tremmel, D. C., Rufty, T. W., & Reynolds, J. E. (2004). Growth, nitrogen uptake, and metabolism in two semiarid shrubs grown at ambient and elevated atmospheric CO_2 concentrations: Effects of nitrogen supply and source. *American Journal of Botany*, *91*(4), 565–572. https://doi.org/10.3732/ajb.91.4.565

Cedergreen, N., & Madsen, T. V. (2002). Nitrogen uptake by the floating macrophyte *Lemna minor*. *New Phytologist*, *155*(2), 285–292. https://doi.org/10.1046/j.1469-8137.2002.00463.x

Chapin, F. S., & Shaver, G. R. (1985). Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology*, *66*(2), 564–576. https://doi.org/10.2307/1940405

Christie, E. K., & Delting, J. K. (1982). Analysis of interferences between C_3 and C_4 grasses in relation to temperature and soil nitrogen supply. *Ecology*, *63*(5), 1277–1284. https://doi.org/10.2307/1938855

Clemmensen, K. E., Michelsen, A., Jonasson, S., & Shaver, G. R. (2006). Increased ectomycorrhizal fungal abundance after long-term fertilization and warming of two arctic tundra ecosystems. *New Phytologist*, *171*(2), 391–404. https://doi.org/10.1111/j.1469-8137.2006.01778.x

Close, D. C., Battaglia, M., Davidson, N. J., & Beadle, C. L. (2004). Within-canopy gradients of nitrogen and photosynthetic activity of Eucalyptus nitens and *Eucalyptus globules* in response to nitrogen nutrition. *Australian Journal of Botany*, *52*(1), 133–140. https://doi.org/10.1071/bt03027

Coyle, D. R., & Coleman, M. D. (2005). Forest production responses to irrigation and fertilization are not explained by shifts in allocation. *Forest Ecology and Management*, *208*(1-3), 137–152. https://doi.org/10.1016/j.foreco.2004.11.022

Cronin, G., & Lodge, D. M. (2003). Effects of light and nutrient availability on the growth, allocation, carbon/nitrogen balance, phenolic chemistry, and resistance to herbivory of two freshwater macrophytes. *Oecologia*, *137*(1), 32–41. https://doi.org/10.1007/s00442-003-1315-3

Daepp, M., Suter, D., Almeida, J. P. F., Isopp, H., Hartwig, U. A., Frehner, M., … Lüscher, A. (2000). Yield response of *Lolium perenne* swards to free air CO_2 enrichment increased over six years in a high N input system on fertile soil. *Global Change Biology*, *6*, 805–816. https://doi.org/10.1046/J.1365-2486.2000.00359.X

Dahlman, L., Nasholm, T., & Palmqvist, K. (2002). Growth, nitrogen uptake, and resource allocation in the two tripartite lichens *Nephroma arcticum* and Peltigera aphthosa during nitrogen stress. *New Phytologist*, *153*(2), 307–315. https://doi.org/10.1046/j.0028-646X.2001.00321.x

De Deyn, G. B., Raaijmakers, C. E., & Van Der Putten, W. H. (2004). Plant community development is affected by nutrients and soil biota. *Journal of Ecology*, *92*(5), 824–834. https://doi.org/10.1111/j.0022-0477.2004.00924.x

de Graaf, M. C. C., Bobbink, R., Roelofs, J. G. M., & Verbeek, P. J. M. (1998). Differential effects of ammonium and nitrate on three heathland species. *Plant Ecology*, *135*(2), 185–196. https://doi.org/10.1023/A:1009717613380

de Valpine, P., & Harte, J. (2001). Plant responses to experimental warming in a montane meadow. *Ecology*, *82*(3), 637–648. https://doi.org/10.1890/0012-9658(2001)082[0637:PRTEWI]2.0.CO;2

Defoliart, L. S., Griffith, M., Chapin, F. S., & Jonasson, S. (1988). Seasonal patterns of photosynthesis and nutrient storage in *Eriophorum vaginatum* L., an Arctic sedge. *Functional Ecology*, *2*(2), 185–194. https://doi.org/10.2307/2389694

DeLaune, R. D., Smith, C. J., & Sarafyan, M. N. (1986). Nitrogen cycling in a freshwater marsh of *Panicum Hemitomon* on the Deltaic Plain of the Mississippi River. *Journal of Ecology*, *74*(1), 249–256. https://doi.org/10.2307/2260361

Denslow, J. S., Vitousek, P. M., & Schultz, J. C. (1987). Bioassays of nutrient limitation in a tropical rain forest soil. *Oecologia*, *74*(3), 370–376. https://doi.org/10.1007/BF00378932

Dighton, J., Tuininga, A. R., Gray, D. M., Huskins, R. E., & Belton, T. (2004). Impacts of atmospheric deposition on New Jersey pine barrens forest soils and communities of ectomycorrhizae. *Forest Ecology and Management*, *201*(1), 131–144. https://doi.org/10.1016/j.foreco.2004.07.038

Drake, D. R., & Ungar, I. A. (1989). Effects of salinity, nitrogen, and population density on the survival, growth, and reproduction of *Atriplex triangularis* (chenopodiaceae). *American Journal of Botany*, *76*(8), 1125–1135. https://doi.org/10.1002/j.1537-2197.1989.tb15097.x

Dyckmans, J., & Flessa, H. (2002). Influence of tree internal nitrogen reserves on the response of beech (*Fagus sylvatica*) trees to elevated atmospheric carbon dioxide concentration. *Tree Physiology*, *22*(1), 41–49. https://doi.org/10.1093/treephys/22.1.41

Eckstein, R. L., & Karlsson, P. S. (2001). The effect of reproduction on nitrogen use-efficiency of three species of the carnivorous genus Pinguicula. *Journal of Ecology*, *89*(5), 798–806. https://doi.org/10.1046/j.0022-0477.2001.00595.x

Ewing, K., McKee, K. L., Mendelssohn, I. A., & Hester, M. W. (1995). A comparison of indicators of sub-lethal untrient stress in the salt marsh grass. *Spartina patens*. *Environmental and Experimental Botany*, *35*(3), 331–343. https://doi.org/10.1016/0098-8472(95)00012-8

Feller, I. C. (1995). Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). *Ecological monographs*, *65*, 477–505. https://doi.org/10.2307/2963499

Fetcher, N., Haines, B. L., Cordero, R. A., Lodge, D. J., Walker, L. R., Fernandez, D. S., & Lawrence, W. T. (1996). Responses of tropical plants to nutrients and light on a landslide in Puerto Rico. *Journal of Ecology*, 331–341. https://doi.org/10.2307/2261196

Forrester, D. I., Cowie, A. L., Bauhus, J., Wood, J. T., & Forrester, R. I. (2006). Effects of changing the supply of nitrogen and phosphorus on growth and interactions between *Eucalyptus globulus* and *Acacia mearnsii* in a pot trial. *Plant and Soil*, *280*(1-2), 267–277. https://doi.org/10.1007/s11104-005-3228-x

Fraser, L. H., & Feinstein, L. M. (2005). Effects of mycorrhizal inoculant, N:P supply ratio, and water depth on the growth and biomass allocation of three wetland plant species. *Canadian Journal of Botany*, *83*(9), 1117–1125. https://doi.org/10.1139/b05-084

Fridley, J. D. (2003). Diversity effects on production in different light and fertility environments: An experiment with communities of annual plants. *Journal of Ecology*, *91*(3), 396–406. https://doi.org/10.1046/j.1365-2745.2003.00775.x

Gaiad, S., Rakocevic, M., & Reissmann, C. B. (2006). N sources affect growth, nutrient content, and net photosynthesis in maté (*Ilex paraguariensis* St. Hil.). *Brazilian Archives of Biology and Technology*, *49*(5), 689–697. https://doi.org/10.1590/s1516-89132006000600001

Gargano, A. O., Aduriz, M. A., & Saldungaray, M. C. (2001). Yield and quality of fertilized deferred forage of *Digitaria eriantha* and *Eragrostis curvula*. *Journal of Arid Environments*, *47*(2), 181–189. https://doi.org/10.1006/jare.2000.0709

Gebauer, G., Schubert, B., Schuhmacher, M. I., Rehder, H., & Ziegler, H. (1987). Biomass production and nitrogen content of C_3- and C_4-grasses in pure and mixed culture with different nitrogen supply. *Oecologia*, *71*(4), 613–617. https://doi.org/10.1007/BF00379307

Gerdol, R., Bragazza, L., & Brancaleoni, L. (2006). Microbial nitrogen cycling interacts with exogenous nitrogen supply in affecting growth of *Sphagnum papillosum*. *Environmental and Experimental Botany*, *57*(1-2), 1–8. https://doi.org/10.1016/j.envexpbot.2005.03.005

Gerdol, R., Brancaleoni, L., Marchesini, R., & Bragazza, L. (2002). Nutrient and carbon relations in subalpine dwarf shrubs after neighbour removal or fertilization in northern Italy. *Oecologia*, *130*(3), 476–483. https://doi.org/10.1007/s00442-001-0823-2

Gleeson, S. K., & Good, R. E. (2003). Root allocation and multiple nutrient limitation in the New Jersey Pinelands. *Ecology Letters*, *6*(3), 220–227. https://doi.org/10.1046/j.1461-0248.2003.00416.x

Gloser, V., Je íková, M., Lüscher, A., Frehner, M., Blum, H., Nösberger, J., & Hartwig, U. A. (2000). Soil mineral nitrogen availability was unaffected by elevated atmospheric pCO_2 in a four year old field experiment (Swiss FACE). *Plant and Soil*, *227*(1), 291–299. https://doi.org/10.1023/A:1026538213199

Gough, C. M., & Seiler, J. R. (2004). Belowground carbon dynamics in loblolly pine (*Pinus taeda*) immediately following diammonium phosphate fertilization. *Tree Physiology*, *24*(7), 845–851. https://doi.org/10.1093/treephys/24.7.845

Gough, L., & Grace, J. B. (1998). Herbivore effects on plant species density at varying productivity levels. *Ecology*, *79*(5), 1586–1594. https://doi.org/10.1890/0012-9658(1998)079[1586:Heopsd]2.0.Co;2

Gough, L., & Hobbie, S. E. (2003). Responses of moist non-acidic arctic tundra to altered environment: Productivity, biomass, and species richness. *Oikos*, *103*(1), 204–216. https://doi.org/10.1034/j.1600-0706.2003.12363.x

Graciano, C., Goya, J. F., Frangi, J. L., & Guiamet, J. J. (2006). Fertilization with phosphorus increases soil nitrogen absorption in young plants of *Eucalyptus grandis*. *Forest Ecology and Management*, *236*(2-3), 202–210. https://doi.org/10.1016/j.foreco.2006.09.005

Graciano, C., Guiamét, J. J., & Goya, J. F. (2005). Impact of nitrogen and phosphorus fertilization on drought responses in *Eucalyptus grandis* seedlings. *Forest Ecology and Management*, *212*(1), 40–49. https://doi.org/10.1016/j.foreco.2005.02.057

Grechi, I., Vivin, P., Hilbert, G., Milin, S., Robert, T., & Gaudillere, J. P. (2007). Effect of light and nitrogen supply on internal C: N balance and control of root-to-shoot biomass allocation in grapevine. *Environmental and Experimental Botany*, *59*(2), 139–149. https://doi.org/10.1016/j.envexpbot.2005.11.002

Green, E. K., & Galatowitsch, S. M. (2001). Differences in wetland plant community establishment with additions of nitrate-N and invasive species (*Phalaris arundinacea* and *Typha ×glauca*). *Canadian Journal of Botany*, *79*(2), 170–178. https://doi.org/10.1139/b00-157

Green, E. K., & Galatowitsch, S. M. (2002). Effects of Phalaris arundinacea and nitrate-N addition on the establishment of wetland plant communities. *Journal of Applied Ecology*, *39*(1), 134–144. https://doi.org/10.1046/j.1365-2664.2002.00702.x

Grelet, G. A., Alexander, I. J., Millard, P., & Proe, M. F. (2003). Does morphology or the size of the internal nitrogen store determine how *Vaccinium* spp. respond to spring nitrogen supply? *Functional Ecology*, *17*(5), 690–699. https://doi.org/10.1046/j.1365-2435.2003.00776.x

Griffin, K. L., Thomas, R. B., & Strain, B. R. (1993). Effects of nitrogen supply and elevated carbon dioxide on construction cost in leaves of *Pinus taeda* (L.) seedlings. *Oecologia*, *95*(4), 575–580. https://doi.org/10.1007/BF00317443

Griffin, K. L., Winner, W. E., & Strain, B. R. (1995). Growth and dry matter partitioning in loblolly and ponderosa pine seedlings in response to carbon and nitrogen availability. *New Phytologist*, *129*(4), 547–556. https://doi.org/10.1111/j.1469-8137.1995.tb03022.x

Grünzweig, J. M., & Körner, C. (2003). Differential phosphorus and nitrogen effects drive species and community responses to elevated CO_2 in semi-arid Grassland. *Functional Ecology*, *17*(6), 766–777. https://doi.org/10.1111/j.1365-2435.2003.00797.x

Gunnarsson, U., Granberg, G., & Nilsson, M. (2004). Growth, production and interspecific competition in *Sphagnum*: Effects of temperature, nitrogen and sulphur treatments on a boreal mire. *New Phytologist*, *163*(2), 349–359. https://doi.org/10.1111/j.1469-8137.2004.01108.x

Gunnarsson, U., & Rydin, H. (2000). Nitrogen fertilization reduces *Sphagnum* production in bog communities. *New Phytologist*, *147*(3), 527–537. https://doi.org/10.1046/j.1469-8137.2000.00717.x

Guo, H., Xu, B., Wu, Y., Shi, F., Wu, C., & Wu, N. (2016). Allometric partitioning theory versus optimal partitioning theory: The adjustment of biomass allocation and internal CN balance to shading and nitrogen addition in *Fritillaria unibracteata* (Liliaceae). *Polish Journal of Ecology*, *64*(2), 189–199. https://doi.org/10.3161/15052249PJE2016.64.2.004

Guo, S.-L., Yan, X.-F., Bai, B., & Yu, S. (2005). Carbon and nitrogen acquisition and allocation in larch seedlings in response to different N supply rates. *Chinese Journal of Plant Ecology*, *29*(4), 550. https://doi.org/10.17521/cjpe.2005.0074

Hamilton Iii, E. W., Giovannini, M. S., Moses, S. A., Coleman, J. S., & McNaughton, S. J. (1998). Biomass and mineral element responses of a Serengeti short-grass species to nitrogen supply and defoliation: Compensation requires a critical [N]. *Oecologia*, *116*(3), 407–418. https://doi.org/10.1007/s004420050604

Hanley, M. E., Cordier, P. K., May, O., & Kelly, C. K. (2007). Seed size and seedling growth: Differential response of Australian and British Fabaceae to nutrient limitation. *New Phytologist*, *174*(2), 381–388. https://doi.org/10.1111/j.1469-8137.2007.02003.x

Harrington, R. A., Fownes, J. H., & Cassidy, T. M. (2004). Japanese barberry (*Berberis thunbergii*) in forest understory: Leaf and whole plant responses to nitrogen availability. *The American Midland Naturalist*, *151*(2), 206–216, 211. https://doi.org/10.1674/0003-0031(2004)151[0206:-JBBTIF]2.0.CO

Hartley, S. E., & Amos, L. (1999). Competitive interactions between *Nardus stricta* L. and *Calluna vulgaris* (L.) Hull: The effect of fertilizer and defoliation on above- and below-ground performance. *Journal of Ecology*, *87*(2), 330–340. https://doi.org/10.1046/j.1365-2745.1999.00353.x

Hartwig, U. A., Wittmann, P., Braun, R., Hartwig-Räz, B., Jansa, J., Mozafar, A., … Nösberger, J. (2002). Arbuscular mycorrhiza infection enhances the growth response of *Lolium perenne* to elevated atmospheric pCO_2. *Journal of Experimental Botany*, *53*(371), 1207–1213. https://doi.org/10.1093/jexbot/53.371.1207

Hatcher, P. E., Paul, N. D., Ayres, P. G., & Whittaker, J. B. (1997). Added soil nitrogen does not allow *Rumex obtusifolius* to escape the effects of insect-fungus interactions. *Journal of Applied Ecology*, *34*(1), 88–100. https://doi.org/10.2307/2404850

Hättenschwiler, S., & Körner, C. (1997). Biomass allocation and canopy development in spruce model ecosystems under elevated CO_2 and increased N deposition. *Oecologia*, *113*(1), 104–114. https://doi.org/10.1007/s004420050358

Hawkins, B. J., Burgess, D., & Mitchell, A. K. (2005). Growth and nutrient dynamics of western hemlock with conventional or exponential greenhouse fertilization and planting in different fertility conditions. *Canadian Journal of Forest Research*, *35*(4), 1002–1016. https://doi.org/10.1139/x05-026

Hebeisen, T., LÜScher, A., Zanetti, S., Fischer, B., Hartwig, U., Frehner, M., … NÖSberger*, J. (1997). Growth response of *Trifolium repens* L. and *Lolium perenne* L. as monocultures and bi-species mixture to free air CO_2 enrichment and management. *Global Change Biology*, *3*(2), 149–160. https://doi.org/10.1046/j.1365-2486.1997.00073.x

Heijmans, M. M. P. D., Berendse, F., Arp, W. J., Masselink, A. K., Klees, H., De Visser, W., & Van Breemen, N. (2001). Effects of elevated carbon dioxide and increased nitrogen deposition on bog vegetation in the Netherlands. *Journal of Ecology*, *89*(2), 268–279. https://doi.org/10.1046/j.1365-2745.2001.00547.x

Heijmans, M. M. P. D., Klees, H., & Berendse, F. (2002). Competition between *Sphagnum magellanicum* and *Eriophorum angustifolium* as affected by raised CO_2 and increased N deposition. *Oikos*, *97*(3), 415–425. https://doi.org/10.1034/j.1600-0706.2002.970311.x

Heisler, J. L., Briggs, J. M., Knapp, A. K., Blair, J. M., & Seery, A. (2004). Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. *Ecology*, *85*(8), 2245–2257. https://doi.org/10.1890/03-0574

Hill, P. W., Marshall, C., Williams, G. G., Blum, H., Harmens, H., Jones, D. L., & Farrar, J. F. (2007). The fate of photosynthetically-fixed carbon in *Lolium perenne* grassland as modified by elevated CO_2 and sward management. *New Phytologist*, *173*(4), 766–777. https://doi.org/10.1111/j.1469-8137.2007.01966.x

Hobbie, S. E., Gough, L., & Shaver, G. R. (2005). Species compositional differences on different-aged glacial landscapes drive contrasting responses of tundra to nutrient addition. *Journal of Ecology*, *93*(4), 770–782. https://doi.org/10.1111/j.1365-2745.2005.01006.x

Hochwender, C. G., Marquis, R. J., & Stowe, K. A. (2000). The potential for and constraints on the evolution of compensatory ability in *Asclepias syriaca*. *Oecologia*, *122*(3), 361–370. https://doi.org/10.1007/s004420050042

Hodge, A., Stewart, J., Robinson, D., Griffiths, B. S., & Fitter, A. H. (2000). Spatial and physical heterogeneity of N supply from soil does not influence N capture by two grass species. *Functional Ecology*, *14*(5), 645–653. https://doi.org/10.1046/j.1365-2435.2000.t01-1-00470.x

Holub, P., & Tůma, I. (2010). The effect of enhanced nitrogen on aboveground biomass allocation and nutrient resorption in the fern *Athyrium distentifolium*. *Plant Ecology*, *207*(2), 373–380. https://doi.org/10.1007/s11258-009-9681-5

Huang, C., Zeng, F., & Lei, J. (2016). Growth and functional trait responses of *Alhagi sparsifolia* seedlings to water and nitrogen addition. *Acta Prataculturae Sinica*, *25*(12), 150–160.

Imo, M., & Timmer, V. R. (2001). Growth and nitrogen retranslocation of nutrient loaded *Picea mariana* seedlings planted on boreal mixedwood sites. *Canadian Journal of Forest Research*, *31*(8), 1357–1366. https://doi.org/10.1139/x01-063

Islam, M. A., & Macdonald, S. E. (2005). Effects of variable nitrogen fertilization on growth, gas exchange, and biomass partitioning in black spruce and tamarack seedlings. *Canadian Journal of Botany*, *83*(12), 1574–1580. https://doi.org/10.1139/b05-123

Jackson, R. B., & Reynolds, H. L. (1996). Nitrate and ammonium uptake for single-and mixed-species communities grown at elevated CO_2. *Oecologia*, *105*(1), 74–80. https://doi.org/10.1007/BF00328793

Jaramillo, V. J., & Detling, J. K. (1992). Small-scale heterogeneity in a semi-arid North American grassland. I. tillering, N uptake and retranslocation in simulated urine patches. *Journal of Applied Ecology*, *29*(1), 1–8. https://doi.org/10.2307/2404340

Jing, Y., Guan, D., Wu, J., Wang, A., Jin, C., & Yuan, F. (2016). Photosynthate supply drives soil respiration of *Fraxinus mandshurica* seedlings in northeastern China: Evidences from a shading and nitrogen addition experiment. *Journal of Forestry Research*, *27*(6), 1271–1276. https://doi.org/10.1007/s11676-016-0255-9

Joel, G., Chapin, F. S., Chiariello, N. R., Thayer, S. S., & Field, C. B. (2001). Species-specific responses of plant communities to altered carbon and nutrient availability. *Global Change Biology*, *7*(4), 435–450. https://doi.org/10.1046/j.1365-2486.2001.00420.x

Johansson, M. (2000). The influence of ammonium nitrate on the root growth and ericoid mycorrhizal colonization of *Calluna vulgaris* (L.) Hull from a Danish heathland. *Oecologia*, *123*(3), 418–424. https://doi.org/10.1007/s004420051029

Johnson, D., Geisinger, D., Walker, R., Newman, J., Vose, J., Elliot, K., & Ball, T. (1994). Soil pCO_2, soil respiration, and root activity in CO_2-fumigated and nitrogen-fertilized ponderosa pine. *Plant and Soil*, *165*(1), 129–138. https://doi.org/10.1007/BF00009969

Johnson, D. W., Ball, J. T., & Walker, R. F. (1997). Effects of CO_2 and nitrogen fertilization on vegetation and soil nutrient content in juvenile ponderosa pine. *Plant and Soil*, *190*(1), 29–40. https://doi.org/10.1023/A:1004213826833

Johnson, N. C., Wolf, J., & Koch, G. W. (2003). Interactions among mycorrhizae, atmospheric CO_2 and soil N impact plant community composition. *Ecology Letters*, *6*(6), 532–540. https://doi.org/10.1046/j.1461-0248.2003.00460.x

Johnson, R. H., & Lincoln, D. E. (1991). Sagebrush carbon allocation patterns and grasshopper nutrition: The influence of CO_2 enrichment and soil mineral limitation. *Oecologia*, *87*(1), 127–134. https://doi.org/10.1007/BF00323790

Jongen, M., Jones, M. B., Hebeisen, T., Blum, H., & Hendrey, G. (1995). The effects of elevated CO_2 concentrations on the root growth of *Lolium perenne* and *Trifolium repens* grown in a face system. *Global Change Biology*, *1*(5), 361–371. https://doi.org/10.1111/j.1365-2486.1995.tb00034.x

Jouquet, P., Tavernier, V., Abbadie, L., & Lepage, M. (2005). Nests of subterranean fungus-growing termites (*Isoptera, Macrotermitinae*) as nutrient patches for grasses in savannah ecosystems. *African Journal of Ecology*, *43*(3), 191–196. https://doi.org/10.1111/j.1365-2028.2005.00564.x

Jung, J. Y., & Lal, R. (2011). Impacts of nitrogen fertilization on biomass production of switchgrass (*Panicum Virgatum* L.) and changes in soil organic carbon in Ohio. *Geoderma*, *166*(1), 145–152. https://doi.org/10.1016/j.geoderma.2011.07.023

Kercher, S. M., & Zedler, J. B. (2004). Multiple disturbances accelerate invasion of reed canary grass (*Phalaris arundinacea* L.) in a mesocosm study. *Oecologia*, *138*(3), 455–464. https://doi.org/10.1007/s00442-003-1453-7

Kern, C. C., Friend, A. L., Johnson, J. M. F., & Coleman, M. D. (2004). Fine root dynamics in a developing *Populus deltoides* plantation. *Tree Physiology*, *24*(6), 651–660. https://doi.org/10.1093/treephys/24.6.651

Keski-Saari, S., & Julkunen-Tiitto, R. (2003). Early developmental responses of mountain birch (*Betula pubescens* subsp. *czerepanovii*) seedlings to different concentrations of phosphorus. *Tree Physiology*, *23*(17), 1201–1208. https://doi.org/10.1093/treephys/23.17.1201

Khurana, E., & Singh, J. S. (2004). Impact of elevated nitrogen inputs on seedling growth of five dry tropical tree species as affected by life-history traits. *Canadian Journal of Botany*, *82*(2), 158–167. https://doi.org/10.1139/b03-132

Kitao, M., Koike, T., Tobita, H., & Maruyama, Y. (2005). Elevated CO_2 and limited nitrogen nutrition can restrict excitation energy dissipation in photosystem II of Japanese white birch (*Betula platyphylla* var. japonica) leaves. *Physiologia Plantarum*, *125*(1), 64–73. https://doi.org/10.1111/j.1399-3054.2005.00540.x

Kolb, A., Alpert, P., Enters, D., & Holzapfel, C. (2002). Patterns of invasion within a grassland community. *Journal of Ecology*, *90*(5), 871–881. https://doi.org/10.1046/j.1365-2745.2002.00719.x

Kuers, K., & Steinbeck, K. (1998). Foliar nitrogen dynamics in *Liquidambar styraciflua* saplings: Response to nitrogen fertilization. *Canadian Journal of Forest Research*, *28*(11), 1671–1680. https://doi.org/10.1139/x98-156

Kummerow, J., Avila, G., Aljaro, M.-E., Araya, S., & Montenegro, G. (1982). Effect of fertilizer on fine root density and shoot growth in Chilean Matorral. *Botanical Gazette*, *143*(4), 498–504. https://doi.org/10.1086/337327

Lappalainen, Janne, H., Martel, J., Lempa, K., Wilsey, B., & Ossipov, V. (2000). Effects of resource availability on carbon allocation and developmental instability in cloned birch seedlings. *International Journal of Plant Sciences*, *161*(1), 119–125. https://doi.org/10.1086/314228

Launonen, T. M., Ashton, D. H., & Keane, P. J. (2005). Growth, nutrient acquisition and ectomycorrhizae of *Eucalyptus regnans* F. Muell. seedlings in fertilized or diluted air-dried and undried forest soil. *Plant and Soil*, *268*(1), 221–231. https://doi.org/10.1007/s11104-004-0279-3

Lawrence, D. (2001). Nitrogen and phosphorus enhance growth and luxury consumption of four secondary forest tree species in Borneo. *Journal of Tropical Ecology*, *17*(6), 859–869. https://doi.org/10.1017/S0266467401001638

Ledgard, S. F., Sprosen, M. S., Penno, J. W., & Rajendram, G. S. (2001). Nitrogen fixation by white clover in pastures grazed by dairy cows: Temporal variation and effects of nitrogen fertilization. *Plant and Soil*, *229*(2), 177–187. https://doi.org/10.1023/a:1004833804002

Lee, K. H., & Jose, S. (2003). Soil respiration, fine root production, and microbial biomass in cottonwood and loblolly pine plantations along a nitrogen fertilization gradient. *Forest Ecology and Management*, *185*(3), 263–273. https://doi.org/10.1016/s0378-1127(03)00164-6

Leith, I. D., Hicks, W. K., Fowler, D., & Woodin, S. J. (1999). Differential responses of UK upland plants to nitrogen deposition. *New Phytologist*, *141*(2), 277–289. https://doi.org/10.1046/j.1469-8137.1999.00333.x

L'Hirondelle, S. J., Jacobson, J. S., & Lassoie, J. P. (1992). Acidic mist and nitrogen fertilization effects on growth, nitrate reductase activity, gas exchange, and frost hardiness of red spruce seedlings. *New Phytologist*, *121*(4), 611–622. https://doi.org/10.1111/j.1469-8137.1992.tb01132.x

Li, M., Wang, J., Wang, Z., Wu, X., Huang, R., & Zhu, J. (2013). Photosynthetic characteristics, biomass allocation C, N and P distribution of *Schima superba* seedlings in response to simulated nitrogen deposition. *Acta Ecologica Sinica*, *33*, 1569–1572.

Liberloo, M., Dillen, S. Y., Calfapietra, C., Marinari, S., Bin Luo, Z., De Angelis, P., & Ceulemans, R. (2005). Elevated CO_2 concentration, fertilization and their interaction: Growth stimulation in a short-rotation *Poplar coppice* (Euroface). *Tree Physiology*, *25*(2), 179–189. https://doi.org/10.1093/treephys/25.2.179

Lim, W. H. L., & Turner, I. M. (1996). Resource availability and growth responses to defoliation in seedlings of three early-successional, tropical, woody species. *Ecological Research*, *11*(3), 321–324. https://doi.org/10.1007/BF02347789

Limpens, J., & Berendse, F. (2003). Growth reduction of *Sphagnum magellanicum* subjected to high nitrogen deposition: The role of amino acid nitrogen concentration. *Oecologia*, *135*(3), 339–345. https://doi.org/10.1007/s00442-003-1224-5

Limpens, J., Berendse, F., & Klees, H. (2003). N deposition affects N availability in interstitial water, growth of *Sphagnum* and invasion of vascular plants in bog vegetation. *New Phytologist*, *157*(2), 339–347. https://doi.org/10.1046/j.1469-8137.2003.00667.x

Limpens, J., Berendse, F., & Klees, H. (2004). How phosphorus availability affects the impact of nitrogen deposition on *Sphagnum* and vascular plants in bogs. *Ecosystems*, *7*(8), 793–804. https://doi.org/10.1007/s10021-004-0274-9

Liu, L., Zuo, S., Ma, M., Li, J., Guo, L., & Huang, D. (2021). Appropriate nitrogen addition regulates reproductive strategies of *Leymus chinensis*. *Global Ecology and Conservation*, *27*, e01599. https://doi.org/10.1016/j.gecco.2021.e01599

Liu, Y., Li, P., Wang, G., Liu, G., & Li, Z. (2016). Above- and below-ground biomass distribution and morphological characteristics respond to nitrogen addition in *Pinus tabuliformis*. *New Zealand Journal of Forestry Science*, *46*(1), 25. https://doi.org/10.1186/s40490-016-0083-x

Liu, Y., Zhang, J., Chen, Y., Chen, L., & Liu, Q. (2013). Effect of nitrogen and phosphorus fertilization on biomass allocation and C: N: P stoichiometric characteristics of *Eucalyptus grandis* seedlings. *Chinese Journal of Plant Ecology*, *37*(10), 933–941.

Loveland, D. G., & Ungar, I. A. (1983). The effect of nitrogen fertilization on the production of halophytes in an inland salt marsh. *American Midland Naturalist*, *346-354*. https://doi.org/10.2307/2425415

Lowe, P. N., Lauenroth, W. K., & Burke, I. C. (2003). Effects of nitrogen availability on competition between *Bromus tectorum* and *Bouteloua gracilis*. *Plant Ecology*, *167*(2), 247–254. https://doi.org/10.1023/A:1023934515420

Lüscher, A., Hartwig, U. A., Suter, D., & Nösberger, J. (2000). Direct evidence that symbiotic N_2 fixation in fertile grassland is an important trait for a strong response of plants to elevated atmospheric CO_2. *Global Change Biology*, *6*(6), 655–662. https://doi.org/10.1046/j.1365-2486.2000.00345.x

Lusk, C. H., Contreras, O., & Figueroa, J. (1996). Growth, biomass allocation and plant nitrogen concentration in Chilean temperate rainforest tree seedlings: Effects of nutrient availability. *Oecologia*, *109*(1), 49–58. https://doi.org/10.1007/s004420050057

Maestre, F. T., & Reynolds, J. F. (2006). Spatial heterogeneity in soil nutrient supply modulates nutrient and biomass responses to multiple global change drivers in model grassland communities. *Global Change Biology*, *12*(12), 2431–2441. https://doi.org/10.1111/j.1365-2486.2006.01262.x

Magill, A. H., Aber, J. D., Currie, W. S., Nadelhoffer, K. J., Martin, M. E., McDowell, W. H., . . . Steudler, P. (2004). Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA. *Forest Ecology and Management*, *196*(1), 7-28. https://doi.org/10.1016/j.foreco.2004.03.033.

Mäkipää, R. (1995). Sensitivity of forest-floor mosses in boreal forests to nitrogen and sulphur deposition. *Water, Air, and Soil Pollution*, *85*(3), 1239–1244. https://doi.org/10.1007/BF00477151

Malmer, N., Albinsson, C., Svensson, B. M., & Wallén, B. (2003). Interferences between *Sphagnum* and vascular plants: Effects on plant community structure and peat formation. *Oikos*, *100*(3), 469–482. https://doi.org/10.1034/j.1600-0706.2003.12170.x

Mao, Q., Watanabe, M., Makoto, K., Kita, K., & Koike, T. (2014a). High nitrogen deposition may enhance growth of a new hybrid larch F1 growing at two phosphorus levels. *Landscape and ecological engineering*, *10*(1), 1–8.

Mao, R., Zhang, X., & Song, C. (2014b). Effects of nitrogen addition on plant functional traits in freshwater wetland of Sanjiang Plain, Northeast China. *Chinese Geographical Science*, *24*(6), 674–681. https://doi.org/10.1007/s11769-014-0691-4

Maroco, J. P., Breia, E., Faria, T., Pereira, J. S., & Chaves, M. M. (2002). Effects of long-term exposure to elevated CO_2 and N fertilization on the development of photosynthetic capacity and biomass accumulation in *Quercus suber* L. *Plant, Cell & Environment*, *25*(1), 105–113. https://doi.org/10.1046/j.0016-8025.2001.00800.x

Marriott, C. A., & Zuazua, M. T. (1996). Tillering and partitioning of dry matter and nutrients in *Lolium perenne* growing with neighbours of different species: Effects of nutrient supply and defoliation. *New Phytologist*, *132*(1), 87–95. https://doi.org/10.1111/j.1469-8137.1996.tb04512.x

Matsushima, M., & Chang, S. X. (2006). Vector analysis of understory competition, N fertilization, and litter layer removal effects on white spruce growth and nutrition in a 13-year-old plantation. *Forest Ecology and Management*, *236*(2), 332–341. https://doi.org/10.1016/j.foreco.2006.09.018

Maurer, D. A., & Zedler, J. B. (2002). Differential invasion of a wetland grass explained by tests of nutrients and light availability on establishment and clonal growth. *Oecologia*, *131*(2), 279–288. https://doi.org/10.1007/s00442-002-0886-8

McKinnon, L. M., & Mitchell, A. K. (2003). Photoprotection, not increased growth, characterizes the response of Engelmann spruce (*Picea engelmannii*) seedlings to high light, even when resources are plentiful. *New Phytologist*, *160*(1), 69–79. https://doi.org/10.1046/j.1469-8137.2003.00854.x

Michelsen, A., Jonasson, S., Sleep, D., Havström, M., & Callaghan, T. V. (1996). Shoot biomass, $\delta^{13}C$, nitrogen and chlorophyll responses of two arctic dwarf shrubs to in situ shading, nutrient application and warming simulating climatic change. *Oecologia*, *105*(1), 1–12. https://doi.org/10.1007/BF00328785

Minchinton, T. E., & Bertness, M. D. (2003). Disturbance-mediated competition and the spread of *Phragmites australis* in a coastal marsh. *Ecological Applications*, *13*(5), 1400–1416. https://doi.org/10.1890/02-5136

Monaco, T. A., Johnson, D. A., & Creech, J. E. (2005). Morphological and physiological responses of the invasive weed *Isatis tinctoria* to contrasting light, soil-nitrogen and water. *Weed Research*, *45*(6), 460–466. https://doi.org/10.1111/j.1365-3180.2005.00480.x

Munoz, A., Celedon-Neghme, C., Cavieres, L. A., & Arroyo, M. T. K. (2005). Bottom-up effects of nutrient availability on flower production, pollinator visitation, and seed output in a high-Andean shrub. *Oecologia*, *143*(1), 126–135. https://doi.org/10.1007/s00442-004-1780-3

Murray, M. B., Smith, R. I., Friend, A., & Jarvis, P. G. (2000). Effect of elevated [CO_2] and varying nutrient application rates on physiology and biomass accumulation of Sitka spruce (*Picea sitchensis*). *Tree Physiology*, *20*(7), 421–434. https://doi.org/10.1093/treephys/20.7.421

Nakaji, T., Fukami, M., Dokiya, Y., & Izuta, T. (2001). Effects of high nitrogen load on growth, photosynthesis and nutrient status of *Cryptomeria japonica* and *Pinus densiflora* seedlings. *Trees*, *15*(8), 453–461. https://doi.org/10.1007/s00468-001-0130-x

Newman, J. A., Abner, M. L., Dado, R. G., Gibson, D. J., Brookings, A., & Parsons, A. J. (2003). Effects of elevated CO_2, nitrogen and fungal endophyte-infection on tall fescue: Growth, photosynthesis, chemical composition and digestibility. *Global Change Biology*, *9*(3), 425–437. https://doi.org/10.1046/j.1365-2486.2003.00601.x

Niu, J., Zhang, W., Feng, Z., Wang, X., & Tian, Y. (2011). Impact of elevated O_3 on visible foliar symptom, growth and biomass of *Cinnamomum camphora* seedlings under different nitrogen loads. *Journal of Environmental Monitoring*, *13*(10), 2873–2879.

Noaman, M. N. (2004). Effect of potassium and nitrogen fertilizers on the growth and biomass of some halophytes grown under high levels of salinity. *Journal of Agronomy*, *3*, 25–30. https://doi.org/10.3923/ja.2004.25.30

Nordin, A., & NÄsholm, T., & Ericson, L. (1998). Effects of simulated N deposition on understorey vegetation of a boreal coniferous forest. *Functional Ecology*, *12*(4), 691–699. https://doi.org/10.1046/j.1365-2435.1998.00240.x

Nordin, A., Strengbom, J., & Ericson, L. (2006). Responses to ammonium and nitrate additions by boreal plants and their natural enemies. *Environmental Pollution*, *141*(1), 167–174. https://doi.org/10.1016/j.envpol.2005.08.017

Øien, D.-I. (2004). Nutrient limitation in boreal rich-fen vegetation: A fertilization experiment. *Applied Vegetation Science*, *7*(1), 119–132. https://doi.org/10.1111/j.1654-109X.2004.tb00602.x

Olff, H., Van Andel, J., & Bakker, J. P. (1990). Biomass and shoot/root allocation of five species from a grassland succession series at different combinations of light and nutrient supply. *Functional Ecology*, *4*(2), 193–200. https://doi.org/10.2307/2389338

Oliet, J. A., Planelles, R., Artero, F., & Jacobs, D. F. (2005). Nursery fertilization and tree shelters affect long-term field response of *Acacia salicina* Lindl. planted in Mediterranean semiarid conditions. *Forest Ecology and Management*, *215*(1-3), 339–351. https://doi.org/10.1016/j.foreco.2005.05.024

Pakeman, R. J., & Lee, J. A. (1991). The ecology of the strandline annuals *Cakile maritime* and *Salsola kali*. II. The role of nitrogen in controlling plant performance. *Journal of Ecology*, *79*(1), 155–165. https://doi.org/10.2307/2260790

Parsons, L. S., & Zedler, J. B. (1997). Factors affecting reestablishment of an endangered annual plant at a California salt marsh. *Ecological Applications*, *7*(1), 253–267. https://doi.org/10.1890/1051-0761(1997)007[0253:FAROAE]2.0.CO;2

Patterson, T. B., Guy, R. D., & Dang, Q. L. (1997). Whole-plant nitrogen- and water-relations traits, and their associated trade-offs, in adjacent muskeg and upland boreal spruce species. *Oecologia*, *110*(2), 160–168. https://doi.org/10.1007/s004420050145

Peace, W. J. H., & Grubb, P. J. (1982). Interaction of light and mineral nutrient supply in the growth of *Impatiens parviflora*. *New Phytologist*, *90*(1), 127–150. https://doi.org/10.1111/j.1469-8137.1982.tb03247.x

Phoenix, G. K., Booth, R. E., Leake, J. R., Read, D. J., Grime, J. P., & Lee, J. A. (2003). Effects of enhanced nitrogen deposition and phosphorus limitation on nitrogen budgets of semi-natural grasslands. *Global Change Biology*, *9*(9), 1309–1321. https://doi.org/10.1046/j.1365-2486.2003.00660.x

Pieters, A., & Baruch, Z. (1997). Soil depth and fertility effects on biomass and nutrient allocation in Jaragua grass. *Journal of Range Management*, *50*(3), 268–273. https://doi.org/10.2307/4003728

Piippo, S., Huhta, A. P., Rautio, P., & Tuomi, J. (2005). Resource availability at the rosette stage and apical dominance in the strictly biennial *Erysimum strictum* (Brassicaceae). *Canadian Journal of Botany*, *83*(4), 405–412. https://doi.org/10.1139/b05-015

Polley, H. W., & Detling, J. K. (1989). Defoliation, nitrofen, and competition: Effects on plant growth and nitrogen nutrition. *Ecology*, *70*(3), 721–727. https://doi.org/10.2307/1940222

Portsmuth, A., & Niinemets, Ü. (2006). Interacting controls by light availability and nutrient supply on biomass allocation and growth of *Betula pendula* and *B. pubescens* seedlings. *Forest Ecology and Management*, *227*(1), 122–134. https://doi.org/10.1016/j.foreco.2006.02.020

Portsmuth, A., & Niinemets, U. (2007). Structural and physiological plasticity in response to light and nutrients in five temperate deciduous woody species of contrasting shade tolerance. *Functional Ecology*, *21*(1), 61–77. https://doi.org/10.1111/j.1365-2435.2006.01208.x

Pratt, C. R. (1984). The response of *Solidago graminifolia* and *S. juncea* to nitrogen fertilizer application: Changes in biomass allocation and implications for community structure. *Bulletin of the Torrey Botanical Club*, *111*(4), 469–478. https://doi.org/10.2307/2995897

Pregitzer, K. S., Zak, D. R., Curtis, P. S., Kubiske, M. E., Teeri, J. A., & Vogel, C. S. (1995). Atmospheric CO_2, soil nitrogen and turnover of fine roots. *New Phytologist*, *129*(4), 579–585. https://doi.org/10.1111/j.1469-8137.1995.tb03025.x

Qi, Y., Huang, Y., Wang, Y., Zhao, J., & Zhang, J. (2011). Biomass and its allocation of four grassland species under different nitrogen levels. *Acta Ecologica Sinica*, *31*(18), 5121–5129.

Rautio, P., Huhta, A.-P., Piippo, S., Tuomi, J., Juenger, T., Saari, M., & Aspi, J. (2005). Overcompensation and adaptive plasticity of apical dominance in *Erysimum strictum* (Brassicaceae) in response to simulated browsing and resource availability. *Oikos*, *111*(1), 179–191. https://doi.org/10.1111/j.0030-1299.2005.14045.x

Reich, P. B., Tilman, D., Craine, J., Ellsworth, D., Tjoelker, M. G., Knops, J., … Lee, T. D. (2001). Do species and functional groups differ in acquisition and use of C, N and water under varying atmospheric CO_2 and N availability regimes? A field test with 16 grassland species. *New Phytologist*, *150*(2), 435–448. https://doi.org/10.1046/j.1469-8137.2001.00114.x

Retzlaff, W. A., Handest, J. A., O'Malley, D. M., McKeand, S. E., & Topa, M. A. (2001). Whole-tree biomass and carbon allocation of juvenile trees of loblolly pine (*Pinus taeda*): Influence of genetics and fertilization. *Canadian Journal of Forest Research*, *31*(6), 960–970. https://doi.org/10.1139/x01-017

Rickey, M. A., & Anderson, R. C. (2004). Effects of nitrogen addition on the invasive grass *Phragmites australis* and a native competitor *Spartina pectinata*. *Journal of Applied Ecology*, *41*(5), 888–896. https://doi.org/10.1111/j.0021-8901.2004.00948.x

Ringwall, K. D., Biondini, M. E., & Grygiel, C. E. (2000). Effects of nitrogen fertilization in leafy spurge root architecture. *Journal of Range Management*, *53*, 228–232. https://doi.org/10.2307/4003288

Robinson, D. E., Wagner, R. G., & Swanton, C. J. (2002). Effects of nitrogen on the growth of jack pine competing with Canada blue-joint grass and large-leaved aster. *Forest Ecology and Management*, *160*(1), 233–242. https://doi.org/10.1016/S0378-1127(01)00448-0

Rogers, W. E., & Siemann, E. (2003). Effects of simulated herbivory and resources on Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasion of native coastal prairie. *American Journal of Botany*, *90*(2), 243–249. https://doi.org/10.3732/ajb.90.2.243

Rubio, G., Zhu, J. M., & Lynch, J. P. (2003). A critical test of the two prevailing theories of plant response to nutrient availability. *American Journal of Botany*, *90*(1), 143–152. https://doi.org/10.3732/ajb.90.1.143

Ryan, M. G., Binkley, D., Fownes, J. H., Giardina, C. P., & Senock, R. S. (2004). An experimental test of the causes of forest growth decline with stand age. *Ecological monographs*, *74*(3), 393–414. https://doi.org/10.1890/03-4037

Saarinen, T. (1998). Internal C:N balance and biomass partitioning of *Carex rostrata* grown at three levels of nitrogen supply. *Canadian Journal of Botany*, *76*(5), 762–768. https://doi.org/10.1139/b98-046

Samuelson, L. J., Johnsen, K., & Stokes, T. (2004). Production, allocation, and stemwood growth efficiency of *Pinus taeda* L. stands in response to 6 years of intensive management. *Forest Ecology and Management*, *192*(1), 59–70. https://doi.org/10.1016/j.foreco.2004.01.005

Sardans, J., Peñuelas, J., & Rodà, F. (2006). The effects of nutrient availability and removal of competing vegetation on resprouter capacity and nutrient accumulation in the shrub *Erica multiflora*. *Acta Oecologica*, *29*(2), 221–232. https://doi.org/10.1016/j.actao.2005.10.006

Shaver, G. R., Bret-Harte, M. S., Jones, M. H., Johnstone, J., Gough, L., Laundre, J., & Chapin Iii, F. S. (2001). Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology*, *82*(11), 3163–3181. https://doi.org/10.1890/0012-9658(2001)082[3163:SCIWFT]2.0.CO;2

Shaver, G. R., Chapin, F., & Gartner, B. L. (1986). Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaskan tussock tundra. *Journal of Ecology*, *74*(1), 257–278. https://doi.org/10.2307/2260362

Shevtsova, A., Nilsson, M.-C., Gallet, C., Zackrisson, O., & Jäderlund, A. (2005). Effects of long-term alleviation of nutrient limitation on shoot growth and foliar phenolics of *Empetrum hermaphroditum*. *Oikos*, *111*(3), 445–458. https://doi.org/10.1111/j.0030-1299.2005.13524.x

Shujauddin, N., & Kumar, B. M. (2003). *Ailanthus triphysa* at different densities and fertiliser regimes in Kerala, India: Growth, yield, nutrient use efficiency and nutrient export through harvest. *Forest Ecology and Management*, *180*(1-3), 135–151. https://doi.org/10.1016/s0378-1127(02)00609-6

Siegenthaler, A., Buttler, A., Grosvernier, P., Gobat, J.-M., Nilsson, M. B., & Mitchell, E. A. (2013). Factors modulating cottongrass seedling growth stimulation to enhanced nitrogen and carbon dioxide: Compensatory tradeoffs in leaf dynamics and allocation to meet potassium-limited growth. *Oecologia*, *171*(2), 557–570. https://doi.org/10.1007/s00442-012-2415-8

Siemann, E., & Rogers, W. E. (2003). Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. *Journal of Ecology*, *91*(6), 923–931. https://doi.org/10.1046/j.1365-2745.2003.00822.x

Silletti, A. M., Knapp, A. K., & Blair, J. M. (2004). Competition and coexistence in grassland codominants: Responses to neighbour removal and resource availability. *Canadian Journal of Botany*, *82*(4), 450–460. https://doi.org/10.1139/b04-016

Simms, E. L. (1985). Growth response to clipping and nutrient addition in *Lyonia lucida* and *Zenobia pulverulenta*. *The American Midland Naturalist*, *114*(1), 44–50. https://doi.org/10.2307/2425239

Singh, H., Menka, P. S., & Singh, V. (2011). Effect of nitrogen addition on the architecture and biomass allocation of two invasive plant species (*Ageratum conyzoides* L. and *Parthenium hysterophorus* L.). *Proceedings of the National Academy of Sciences, India Section B: Biological Sciences*, *81*, 348–358.

Son, Y., & Hwang, J. H. (2003). Fine root biomass, production and turnover in a fertilized *Larix leptolepis* plantation in central Korea. *Ecological Research*, *18*(3), 339–346. https://doi.org/10.1046/j.1440-1703.2003.00559.x

Steinbachová-Vojtíšková, L., Tylová, E., Soukup, A., Novická, H., Votrubová, O., Lipavská, H., & Čížková, H. (2005). Influence of nutrient supply on growth, carbohydrate, and nitrogen metabolic relations in *Typha angustifolia*. *Environmental and Experimental Botany*, *57*(3), 246–257. https://doi.org/10.1016/j.envexpbot.2005.06.003

Strengbom, J., Nasholm, T., & Ericson, L. (2004). Light, not nitrogen, limits growth of the grass *Deschampsia flexuosa* in boreal forests. *Canadian Journal of Botany*, *82*(4), 430–435. https://doi.org/10.1139/b04-017

Strengbom, J., & Reich, P. B. (2006). Elevated [CO_2] and increased N supply reduce leaf disease and related photosynthetic impacts on *Solidago rigida*. *Oecologia*, *149*(3), 519–525. https://doi.org/10.1007/s00442-006-0458-4

Sundberg, B., Näsholm, T., & Palmqvist, K. (2001). The effect of nitrogen on growth and key thallus components in the two tripartite lichens, *Nephroma arcticum* and *Peltigera aphthosa*. *Plant, Cell and Environment and Environment*, *24*(5), 517–527. https://doi.org/10.1046/j.1365-3040.2001.00701.x

Tang, Z. M., Sayer, M. A., Chambers, J. L., & Barnett, J. P. (2004). Interactive effects of fertilization and throughfall exclusion on the physiological responses and whole-tree carbon uptake of mature loblolly pine. *Canadian Journal of Botany*, *82*(6), 850–861. https://doi.org/10.1139/b04-064

Thomas, R. B., Bashkin, M. A., & Richter, D. D. (2000). Nitrogen inhibition of nodulation and N_2 fixation of a tropical N_2-fixing tree (*Gliricidia sepium*) grown in elevated atmospheric CO_2. *New Phytologist*, *145*(2), 233–243. https://doi.org/10.1046/j.1469-8137.2000.00577.x

Tilman, G. D. (1984). Plant dominance along an experimental nutrient gradient. *Ecology*, *65*(5), 1445–1453. https://doi.org/10.2307/1939125

Tjoelker, M. G., & Luxmoore, R. J. (1991). Soil nitrogen and chronic ozone stress influence physiology, growth and nutrient status of *Pinus taeda* L. and *Liriodendron tulipifera* L. seedlings. *New Phytologist*, *119*(1), 69–81. https://doi.org/10.1111/j.1469-8137.1991.tb01009.x

Tomassen, H. B. M., Smolders, A. J. P., Lamers, L. P. M., & Roelofs, J. G. M. (2003). Stimulated growth of *Betula pubescens* and *Molinia caerulea* on ombrotrophic bogs: Role of high levels of atmospheric nitrogen deposition. *Journal of Ecology*, *91*(3), 357–370. https://doi.org/10.1046/j.1365-2745.2003.00771.x

Tomassen, H. B. M., Smolders, A. J. P., Limpens, J., Lamers, L. P. M., & Roelofs, J. G. M. (2004). Expansion of invasive species on ombrotrophic bogs: Desiccation or high N deposition? *Journal of Applied Ecology*, *41*(1), 139–150. https://doi.org/10.1111/j.1365-2664.2004.00870.x

Treseder, K. K., & Vitousek, P. M. (2001). Effects of soil nutrient availability on investment in acquisition of N and P in Havaiian rain forests. *Ecology*, *82*(4), 946–954. https://doi.org/10.1890/0012-9658(2001)082[0946:Eosnao]2.0.Co;2

Tungate, K. D., Susko, D. J., & Rufty, T. W. (2002). Reproduction and offspring competitiveness of *Senna obtusifolia* are influenced by nutrient availability. *New Phytologist*, *154*(3), 661–669. https://doi.org/10.1046/j.1469-8137.2002.00407.x

Tyler, A. C., Mastronicola, T. A., & McGlathery, K. J. (2003). Nitrogen fixation and nitrogen limitation of primary production along a natural marsh chronosequence. *Oecologia*, *136*(3), 431–438. https://doi.org/10.1007/s00442-003-1277-5

Urbas, P., & Zobel, K. (2000). Adaptive and inevitable morphological plasticity of three herbaceous species in a multi-species community: Field experiment with manipulated nutrients and light. *Acta Oecologica*, *21*(2), 139–147. https://doi.org/10.1016/S1146-609X(00)00115-6

Uselman, S. M., Qualls, R. G., & Thomas, R. B. (1999). A test of a potential short cut in the nitrogen cycle: The role of exudation of symbiotically fixed nitrogen from the roots of a N-fixing tree and the effects of increased atmospheric CO_2 and temperature. *Plant and Soil*, *210*(1), 21–32. https://doi.org/10.1023/A:1004619509878

van der Hoek, D., van Mierlo Anita, J. E. M., & van Groenendael, J. M. (2004). Nutrient limitation and nutrient-driven shifts in plant species composition in a species-rich fen meadow. *Journal of Vegetation Science*, *15*(3), 389–396. https://doi.org/10.1111/j.1654-1103.2004.tb02276.x

van der Wal, R., Pearce, I., Brooker, R., Scott, D., Welch, D., & Woodin, S. (2003). Interplay between nitrogen deposition and grazing causes habitat degradation. *Ecology Letters*, *6*(2), 141–146. https://doi.org/10.1046/j.1461-0248.2003.00407.x

Vilela, A. E., Rennella, M. J., & Ravetta, D. A. (2003). Responses of tree-type and shrub-type *Prosopis* (Mimosaceae) taxa to water and nitrogen availabilities. *Forest Ecology and Management*, *186*(1-3), 327–337. https://doi.org/10.1016/s0378-1127(03)00299-8

Villar-Salvador, P., Planelles, R., Enríquez, E., & Rubira, J. P. (2004). Nursery cultivation regimes, plant functional attributes, and field performance relationships in the Mediterranean oak *Quercus ilex* L. *Forest Ecology and Management*, *196*(2), 257–266. https://doi.org/10.1016/j.foreco.2004.02.061

Vinton, M. A., & Burke, I. C. (1995). Interactions between individual plant species and soil nutrient status in shortgrass steppe. *Ecology*, *76*(4), 1116–1133. https://doi.org/10.2307/1940920

Vitousek, P. (1983). Nitrogen turnover in a ragweed-dominated 1st-year old field in southern Indiana. *The American Midland Naturalist*, *110*(1), 46–53. https://doi.org/10.2307/2425212

Voisin, A.-S., Salon, C., Munier-Jolain, N. G., & Ney, B. (2002). Effect of mineral nitrogen on nitrogen nutrition and biomass partitioning between the shoot and roots of pea (*Pisum sativum* L.). *Plant and Soil*, *242*(2), 251–262. https://doi.org/10.1023/A:1016214223900

Volin, J. C., & Reich, P. B. (1996). Interaction of elevated CO_2 and O_3 on growth, photosynthesis and respiration of three perennial species grown in low and high nitrogen. *Physiologia Plantarum*, *97*(4), 674–684. https://doi.org/10.1111/j.1399-3054.1996.tb00531.x

Vose, J. M., Elliott, K. J., Johnson, D. W., Walker, R. F., Johnson, M. G., & Tingey, D. T. (1995). Effects of elevated CO_2 and N fertilization on soil respiration from ponderosa pine (*Pinus ponderosa*) in open-top chambers. *Canadian Journal of Forest Research*, *25*(8), 1243–1251. https://doi.org/10.1139/x95-137

Walters, J. R., House, A. P. N., & Doley, D. (2005). Water and nutrient availabilities do not affect lignotuber growth and sprouting ability of three eucalypt species of south-eastern Queensland. *Australian Journal of Botany*, *53*(3), 251–257. https://doi.org/10.1071/bt04021

Wang, A.-Y., Wang, M., Yang, D., Song, J., Zhang, W.-W., Han, S.-J., & Hao, G.-Y. (2016). Responses of hydraulics at the whole-plant level to simulated nitrogen deposition of different levels in *Fraxinus mandshurica*. *Tree Physiology*, *36*(8), 1045–1055. https://doi.org/10.1093/treephys/tpw048

Wang, D., He, H. L., Gao, Q., Zhao, C. Z., Zhao, W. Q., Yin, C. Y., … Liu, Q. (2017). Effects of short-term N addition on plant biomass allocation and C and N pools of the *Sibiraea angustata* scrub ecosystem. *European Journal of Soil Science*, *68*(2), 212–220. https://doi.org/10.1111/ejss.12414

Wang, G., & liu, F. (2014). Carbon allocation of Chinese pine seedlings along a nitrogen addition gradient. *Forest Ecology and Management*, *334*, 114–121. https://doi.org/10.1016/j.foreco.2014.09.004

Wang, M., Shi, S., Lin, F., Hao, Z., Jiang, P., & Dai, G. (2012). Effects of soil water and nitrogen on growth and photosynthetic response of Manchurian ash (*Fraxinus mandshurica*) seedlings in northeastern China. *PLoS ONE*, *7*(2), e30754. https://doi.org/10.1371/journal.pone.0030754

Wang, M., Zhang, W.-W., Li, N., Liu, Y.-Y., Zheng, X.-B., & Hao, G.-Y. (2018). Photosynthesis and growth responses of *Fraxinus mandshurica* Rupr. seedlings to a gradient of simulated nitrogen deposition. *Annals of Forest Science*, *75*(1), 1. https://doi.org/10.1007/s13595-017-0678-2

Wang, W., Franklin, S. B., & Cirtain, M. C. (2007). Seed germination and seedling growth in the arrow bamboo *Fargesia qinlingensis*. *Ecological Research*, *22*(3), 467–474. https://doi.org/10.1007/s11284-006-0027-7

Wang, X. Z., & Curtis, P. S. (2001). Gender-specific responses of *Populus tremuloides* to atmospheric CO_2 enrichment. *New Phytologist*, *150*(3), 675–684. https://doi.org/10.1046/j.1469-8137.2001.00138.x

Wang, Y., Xi, B., Bloomberg, M., Moltchanova, E., Li, G., & Jia, L. (2015). Response of diameter growth, biomass allocation and N uptake to N fertigation in a triploid *Populus tomentosa* plantation in the North China Plain: Ontogenetic shift does not exclude plasticity. *European Journal of Forest Research*, *134*(5), 889–898. https://doi.org/10.1007/s10342-015-0897-8

Watanabe, M., Ryu, K., Kita, K., Takagi, K., & Koike, T. (2012). Effect of nitrogen load on growth and photosynthesis of seedlings of the hybrid larch F1 (*Larix gmelinii* var. *japonica*×*L. kaempferi*) grown on serpentine soil. *Environmental and Experimental Botany*, *83*, 73–81. https://doi.org/10.1016/j.envexpbot.2012.04.011

Weih, M. (2000). Delayed growth response of Mountain Birch seedlings to a decrease in fertilization and temperature. *Functional Ecology*, *14*(5), 566–572. https://doi.org/10.1046/j.1365-2435.2000.t01-1-00452.x

Weih, M., & Karlsson, P. S. (2001). Growth response of Mountain birch to air and soil temperature: Is increasing leaf-nitrogen content an acclimation to lower air temperature? *New Phytologist*, *150*(1), 147–155. https://doi.org/10.1046/j.1469-8137.2001.00078.x

Whitehead, S. J., Caporn, S. J. M., & Press, M. C. (1997). Effects of elevated CO_2, nitrogen and phosphorus on the growth and photosynthesis of two upland perennials: *Calluna vulgaris* and *Pteridium aquilinum*. *New Phytologist*, *135*(2), 201–211. https://doi.org/10.1046/j.1469-8137.1997.00651.x

Will, R. E., Munger, G. T., Zhang, Y. J., & Borders, B. E. (2002). Effects of annual fertilization and complete competition control on current annual increment, foliar development, and growth efficiency of different aged *Pinus taeda* stands. *Canadian Journal of Forest Research*, *32*(10), 1728–1740. https://doi.org/10.1139/x02-095

Willey, N., & Tang, S. (2006). Some effects of nitrogen nutrition on caesium uptake and translocation by species in the Poaceae, Asteraceae and Caryophyllidae. *Environmental and Experimental Botany*, *58*(1-3), 114–122. https://doi.org/10.1016/j.envexpbot.2005.07.001

Wilson, F. E. A., Harvey, B. M. R., McAdam, J. H., & Walton, D. W. H. (2001). The response of Whitegrass [*Cortaderia pilosa* (D' Urv.) Hack.] to nitrogen nutrition. *Grass and Forage Science*, *56*(1), 84–91. https://doi.org/10.1046/j.1365-2494.2001.00252.x

Witkowski, E. T. F. (1989). Effects of nutrients on the distribution of dry mass, nitrogen and phosphorus in seedlings of *Protea repens* (L.) L. (Proteaceae). *New Phytologist*, *112*(4), 481–487. https://doi.org/10.1111/j.1469-8137.1989.tb00341.x

Wu, F., Bao, W., & Wu, N. (2008). Growth, accumulation and partitioning of biomass, C, N and P of *Sophora davidii* seedlings in response to N supply in dry valley of upper Minjiang River. *Acta Ecologica Sinica*, *28*(8), 3817–3824.

Wu, L. H., Li, H., Luo, Y. M., & Christie, P. (2004). Nutrients can enhance phytoremediation of copper-polluted soil by Indian mustard. *Environmental Geochemistry and Health*, *26*(2-3), 331–335. https://doi.org/10.1023/B:EGAH.0000039598.24033.4e

Wu, Q., Ding, J., Yan, H., ZHANG, S.-R., Fang, T., & MA, K.-P. (2011). Effects of simulated precipitation and nitrogen addition on seedling growth and biomass in five tree species in Gutian Mountain, Zhejiang Province. *China. Chinese Journal of Plant Ecology*, *35*(3), 256.

Xiao, D., Wang, X., Zhang, K., Kang, F., He, N., & Hou, J. (2015). Effects of simulated nitrogen deposition on growth of *Acer mono* seedlings. *Journal of Beijing Forestry University*, *37*(10), 50–57.

Yao, X., & Liu, Q. (2006). Changes in morphological, photosynthetic and physiological responses of Mono Maple seedlings to enhanced UV-B and to nitrogen addition. *Plant Growth Regulation*, *50*(2), 165. https://doi.org/10.1007/s10725-006-9116-4

Yao, X., & Liu, Q. (2009a). The effects of enhanced ultraviolet-B and nitrogen supply on growth, photosynthesis and nutrient status of *Abies faxoniana* seedlings. *Acta physiologiae plantarum*, *31*(3), 523–529.

Yao, X., & Liu, Q. (2009b). Photosynthetic and physiological responses of *Swida hemsleyi* (C.K. Schneid. et Wangerin) subjected to enhanced UV-B enhanced and to nitrogen suppy. *Polish Journal of Ecology*, *57*(3), 483–494.

Zak, D. R., Pregitzer, K. S., Curtis, P. S., Vogel, C. S., Holmes, W. E., & Lussenhop, J. (2000). Atmospheric CO_2, soil N availability, and the allocation of biomass and nitrogen in *Populus tremuloides*. *Ecological Applications*, *10*(1), 34–46. https://doi.org/10.1890/1051-0761(2000)010[0034:ACSNAA]2.0.CO;2

Zamin, T. J., Bret-Harte, M. S., & Grogan, P. (2014). Evergreen shrubs dominate responses to experimental summer warming and fertilization in Canadian mesic low arctic tundra. *Journal of Ecology*, *102*(3), 749–766. https://doi.org/10.1111/1365-2745.12237

Zanetti, S., Hartwig, U. A., Luscher, A., Hebeisen, T., Frehner, M., Fischer, B. U., . . . Nosberger, J. (1996). Stimulation of symbiotic N_2 fixation in *trifolium repens* L. under elevated atmospheric pCO_2 in a grassland ecosystem. *Plant Physiology*, *112*(2), 575-583. https://doi.org/10.1104/pp.112.2.575.

Zhang, Z., Niu, K., Liu, X., Jia, P., & Du, G. (2013). Linking flowering and reproductive allocation in response to nitrogen addition in an alpine meadow. *Journal of Plant Ecology*, *7*(3), 231–239. https://doi.org/10.1093/jpe/rtt030

Zhao, C., & Liu, Q. (2009). Growth and photosynthetic responses of two coniferous species to experimental warming and nitrogen fertilization. *Canadian Journal of Forest Research*, *39*(1), 1–11. https://doi.org/10.1139/x08-152

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