Different impacts of external ammonium and nitrate addition on plant growth in terrestrial ecosystems: A meta-analysis

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HIGHLIGHTS

- Growth of terrestrial plants was enhanced more by NH_4-N than NO_3^--N addition.
- Plant allocated more biomass to above- than below-ground parts with NO_3^--N addition.
- NH_4-N addition significantly enhanced below- but not above-ground growth.

GRAPHICAL ABSTRACT
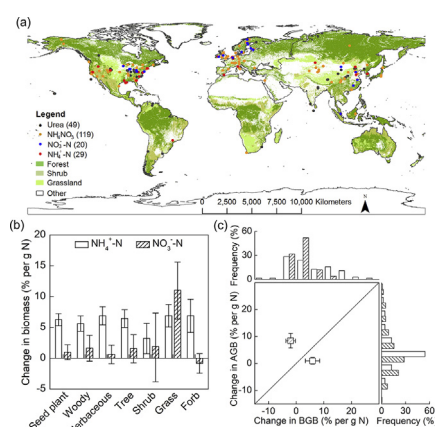
ABSTRACT

Terrestrial plant growth is strongly limited by the availability of nitrogen (N). Atmospheric deposition of N has been rapidly increasing since the industrial revolution, associated with fast compositional shifts between ammonium- (NH_4) and nitrate-N (NO_3^-) globally. However, whether and how such composition changes of deposition will affect the response of terrestrial plant growth to N deposition remains unclear. To fill the gaps, this study quantified the different responses of terrestrial plants to external NH_4-N and NO_3^--N additions. A meta-analysis was applied to compare the growth responses of 367 plant species to different forms of N addition from 210 N-fertilization experiments. In general, a greater response of plant growth to NH_4- N (6 .3% per g N) than NO_3^--N (1.0% per g N) addition was detected across all species. The larger response of plant growth to NH_4-N than NO_3^--N addition was found in trees and forbs but not in shrubs and grasses. The NH_4-N and NO_3^--N additions had contrasting effects on biomass allocation. For example, the NO_3^--N addition increased biomass allocation to above-ground tissues, whereas the NH_4-N addition enhanced below- but not above-ground growth. These results generally reveal a higher response of plant growth to NH_4- N than NO_3^--N addition in terrestrial ecosystems. The findings suggest that future predictions on the vegetation response to atmospheric N enrichment could benefit from a better understanding of plant strategies for acquiring different forms of N.

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1. Introduction

Nitrogen (N) is the most abundant element in the atmosphere and an essential component for organisms on land and in the sea (Vitousek and Howarth, 1991). The deposition rate of atmospheric N to land has dramatically increased by about three-fold since the industrial revolution and is expected to accelerate in the future (Galloway et al., 2008). The loading of N in deposition has two main forms, including ammonium (NH_x) and nitrate (NO_y). NH_x can originate from agriculture (including human and animal excrement, and fertilizer volatilization) and motor vehicles (Fenn et al., 2018), while NO_y mainly stems from fossil-fuel combustion by power plants and automobiles (Hosker and Lindberg, 1982). Although the highly deposited N has been acknowledged to enhance plant growth and primary productivity in many terrestrial ecosystems (LeBauer and Treseder, 2008; Xia and Wan, 2008; Fernandezmartinez et al., 2014), the impacts of chronic depositions of NH_x and NO_y could be different. Some recent observations have even shown large spatial differences in the shifting trend of the composition in N deposition (i.e., NH_x/NO_y). For example, N deposition is shifting from nitrate- to ammonium-dominated in the United States (Du et al., 2014; Li et al., 2016), while a contrasting change is observed in China (Liu et al., 2013, 2016; Yu et al., 2019). Thus, the productivity of terrestrial ecosystem may be largely affected by the different effects between ammonium and nitrate addition on plant growth.

Under natural conditions, plants mainly take up ammonium (NH_4-N) and nitrate (NO_3^--N), although other forms of N such as nitrite and amino acids are utilized as well (Haynes and Goh, 1978; Nasholm et al., 2009). Although NH_4-N and NO_3^--N are considered equivalent in most N fertilization experiments (Stevens et al., 2004; Manning et al., 2006), a number of recent studies have reported differential N preference among plant species (Marschner, 2012; ven den Berg et al., 2016; Tho et al., 2017). For example, plant species that grow in calcareous or slightly acidic soils favor nitrate or a combination of nitrate and ammonium, whereas plants in acidic habitats prefer to uptake ammonium (De Graaf et al., 1998; Falkengren-Grerup and Schottelndreier, 2004; Sheppard et al., 2014). Plant species of different functional types vary in N-use strategy and thus respond differently to N addition (Xia and Wan, 2008). However, it is unclear whether the preference of plant growth for N forms also varies among plant functional types. For some plant species, the addition of NH_4-N appears to be toxic for plant growth (ven den Berg et al., 2005; De Schrijver et al., 2008), while other studies emphasize that the toxic effect might be limited to certain plant functional groups (e.g. bryophyte; Paulissen et al., 2005; Verhoeven et al., 2011) or depended on soil properties (ven den berg et al., 2005; Li et al., 2014). During the past few decades, a tremendous amount of manipulative studies has been conducted to study the response of plant species to N addition (Maaroufi et al., 2015; Stevens and Gowing, 2013; ven Den Berg et al., 2016; Willey and Tang, 2006). Most of these studies have reported the form of added N and the functional type of plant species. These studies enable a quantitative synthesis on the different impacts between ammonium and nitrate additions on plant growth.

Anthropogenic activities are altering both total N loads and the dominant form in N deposition. Global fertilizer use has generally shifted from oxidized- to reduced-N form, surpassing nitrate as the most common N fertilizer worldwide (Glibert et al., 2006). These human activities will, to a certain extent, alter the composition of available N in the soil, eventually indirectly affecting plant growth. For example, urea alone or mixed with ammonium is reported to stimulate soil NH_4-N content (Homann et al., 2001; Ding et al., 2004), but show an inhibitory effect when mixed with nitrate (Silver et al., 2005). By meta-analysis, Lu et al. (2011) has suggested that N fertilizers, mainly as NH_4NO_3 and urea, usually increase the concentration of soil NH_4-N less than NO_3^--N. Thus, the quantification of plant growth responses to different forms of N addition is important to predict the potential trends of vegetation change under the projected compositional shifts in atmospheric N deposition.

In this study, a meta-analysis was applied based on observed plant responses to N addition from 210 manipulative experiments. The effects of different N forms (i.e., nitrate, ammonium, NH_4NO_3, and urea) on plant growth were calculated across the globe and compared among plant functional types. The major question of this study is whether and how the effect of nitrate on plant growth is different from that of ammonium. Because many ecological studies are using NH_4NO_3 or urea as a fertilizer, we also compare their effects on plant growth with the nitrate and ammonium additions. We hypothesize that the growth of plants among different functional types would respond differently to N forms, as plants differ in their preferences for inorganic N source (s). Furthermore, this study also aims to explore the role of N form in affecting the response of biomass allocation to N addition.

2. Materials and methods

2.1. Data collection

2.1.1. Responses of plant growth to N addition

We searched ISI Web of Science with the terms of "nitrogen fertilization (or N addition or N deposition)" and "plant biomass (or plant growth)". Papers meeting the following criteria were selected for further analysis:

(i) The study included both control and N treatments. If N was added together with additional treatments (e.g. CO_2 enrichment), we took the effect of additional treatment (e.g. CO_2 enrichment) as the control, and their combined effect (e.g. CO_2 enrichment plus N addition) as the N treatment;

(ii) Biomass responses to N addition were reported at the species level. Any study conducted in the field (e.g., natural ecosystem) or controlled experimental conditions (e.g., greenhouse, glasshouse, and pot) that reported any part (e.g., leaf, stem, branch, shoot, litter, seed, reproductive organs, and root) or the whole biomass was included;

(iii) Means, sample sizes, and standard deviations or standard errors of plant biomass under both control and N addition treatments were reported;

(iv) N forms, including nitrate (NO_3^--N), ammonium (NH_4-N), ammonium nitrate (NH_4NO_3) and urea, were clarified in the study, and also the N dose was measured as N per unit area per year ($g\ N\ m^{-2}\ yr^{-1}$);

(v) Crop species were excluded from our analysis.

As recommended by Gurevitch et al. (2018), the flow diagram of the study selection is shown in the Supplementary Fig. S1. According to the above criteria, both seed and spore plant were included. As the number of spore-plant data was small under NO_3^--N and NH_4-N addition, this study only focused on the response of seed plant to N addition. Since plant responses under single N addition showed similar patterns with those under all N treatments, i.e. higher responses with NH_4-N and urea addition relative to that with NO_3^--N and NH_4NO_3 addition, respectively (Fig. S2), this study used data of both single N addition and N with additional treatment. Additionally, within a meta-analysis, some researchers have advocated the inclusion of only one result from each study because of the assumption of independence (Vanderwerf, 1992). However, the omission of multiple results in each study would cause the loss of information, which may be a more serious problem than the violation of the assumption of independence (Gurevitch and Hedges, 1993). Thus, we included more than one sample from a single study in this meta-analysis, whose reliability (or feasibility) had been tested by previous meta-analysis (Maestre et al., 2005). To check our decision, we also compared the results using all data with those using one data from each study, and found these patterns were unchanged. Overall, there were totally 210 papers, 367 species and 2728 data included in

the data set 1 (Appendix Notes S1). The global distribution of study sites is shown in Fig. 1.

The data of means and variations in both control and N addition treatments were collected directly from original tables or extracted from figures using GetData Graph Digitizer 2.24 (http://getdata-graph-digitizer.com/). Species information was completed and species were classified by growth forms: woody plants (tree and shrub) vs herbaceous plants (grass and forb). Plant biomass was categorized by the whole biomass, aboveground biomass (AGB, including the reported aboveground, leaf, litter, shoot, stem, or branch biomass), belowground biomass (BGB, including the reported belowground, rhizome or root biomass), and other-part biomass (e.g., reproductive organs). The duration of N experiments ranged from days to years, while N dose ranged from 0.18 to 120 g m^{-2} yr^{-1} under NO$_3^-$-N and to 48 g m^{-2} yr^{-1} under NH$_4$-N addition, respectively. N dose was divided into <5 and > 5 g m^{-2} yr^{-1} based on the distribution of N dose in this study. Other information, including latitude, longitude, mean annual temperature and precipitation (MAT and MAP) of the field study site was also extracted. MAT and MAP were obtained from the global climate database using the site coordinates (http://www.worldclim.org/) when they were not reported in the study. As a result, the MAT and MAP for NO$_3^-$-N and NH$_4$-N experiments changed from −0.7 to 27.5 °C and from about 200 to 2200 mm, respectively. Detailed information related to species, site, experimental condition, N treatment method and its effect on plant growth, could be found in the Supplementary Table S1.

2.1.2. Responses of soil nitrogen availability to N addition

To evaluate the response of soil NH$_4$-N/NO$_3^-$-N ratio under future enhanced N addition, we updated the dataset of Lu et al. (2011). We only used the results from 29 papers which reported the effect of N addition on soil NH$_4$-N or NO$_3^-$-N pools (Appendix Notes S2, Table S2). Only those studies with NH$_4$NO$_3$ or urea addition were included because these two fertilizers are the most widely used. Meta-analysis was used to estimate the effects of N fertilization on soil NH$_4$-N, NO$_3^-$-N and the ratio of NH$_4$-N/NO$_3^-$-N. Other factors, e.g. the N treatment method, interactive climate variables, or the species information were not considered in this analysis.

2.2. Statistical analyses

2.2.1. Soil ammonium to nitrate ratio (NH$_4^+$-N/NO$_3^-$-N)

When both soil ammonium (NH$_4$-N) and nitrate (NO$_3^-$-N) concentration with the same unit were provided in one study, the soil NH$_4$-N/NO$_3^-$-N ratio was calculated as below:

$$X = \frac{X_{NH_4^+}}{X_{NO_3^-}} \tag{1}$$

where X_{NH_4} and X_{NO_3} are means of the soil ammonium and nitrate concentration, respectively. Its standard deviation (SD) was estimated by:

$$SD = X \sqrt{\left(\frac{S_{NH_4^+}}{X_{NH_4^+}}\right)^2 + \left(\frac{S_{NO_3^-}}{X_{NO_3^-}}\right)^2} \tag{2}$$

where S_{NH_4} and S_{NO_3} are the SD of soil ammonium and nitrate concentration, respectively.

2.2.2. The relative response of plant growth to N addition

In this study, few experiments reported the exact amount of additive N during the whole period. Most of the experiments in this study (~90%) added the N annually (e.g., $N_{add} = 10$ g N m^{-2} yr^{-1}), so the response of plant growth in a certain experimental duration (e.g., $t = 2$ yr) actually is determined by the total N amount (e.g., $N_{amount} = N_{add} * t = 20$ g N m^{-2}). Thus, we first normalized the plant growth and its variation of the N treatment as:

$$X'_e = X_c + \frac{X_e - X_c}{N_{amount}} \tag{3}$$

Its SD is:

$$S'_e = S_c + \frac{S_e - S_c}{N_{amount}} \tag{4}$$

where X_c (or S_c) and X_e (or S_e) are the means (or SD) of the biomass in the control and N addition treatments, respectively. X'_e and S'_e represent
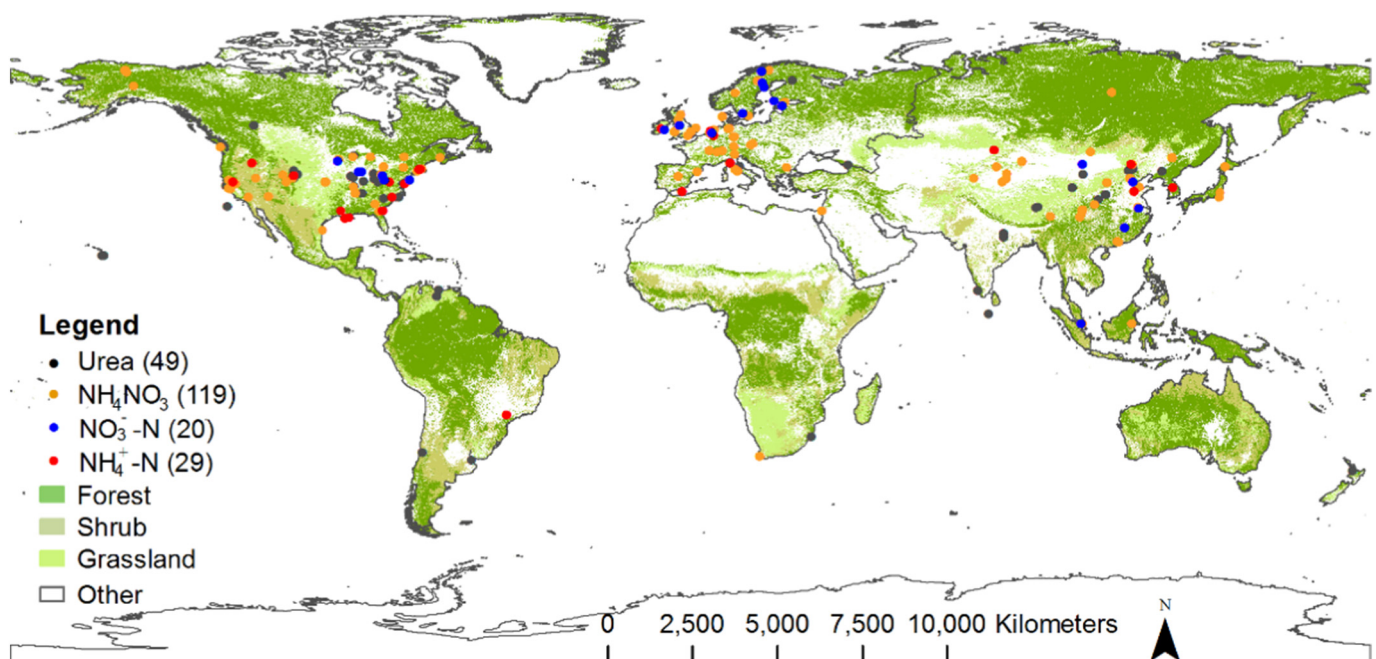

Fig. 1. The global distribution of 210 studies in this meta-analysis.

Legend

- Urea (49)
- NH$_4$NO$_3$ (119)
- NO$_3^-$-N (20)
- NH$_4^+$-N (29)
- Forest
- Shrub
- Grassland
- Other

0 2,500 5,000 7,500 10,000 Kilometers

the mean and SD of plant growth under the treatment of per unit amount (g N m^{-2}) of N addition.

2.2.3. Meta-analysis

The meta-analysis followed the techniques described in Hedges et al. (1999). For simplicity, we refer to the effects of N addition on plant biomass. N effects on soil ammonium, nitrate, and NH$_4$-N/NO$_3^-$-N were calculated in exactly the same way. The response ratio (*RR*) of plant biomass to per unit amount of N addition was calculated as the log-transformed ratio:

$$LnRR = \ln\left(\frac{X'_e}{X_c}\right) \tag{5}$$

with the variance as:

$$v_{RR} = \frac{(S_c)^2}{n_c(X_c)^2} + \frac{(S'_e)^2}{n_e(X'_e)^2} \tag{6}$$

where n_c and n_e represent the sample size in control and N treatments, respectively. The reciprocal of its variance ($w = \frac{1}{v_{RR}}$) was considered as the weight of each Ln*RR*. Then the mean response ratio (*RR*) and its standard error were calculated as:

$$RR_{++} = \frac{\sum_{i=1}^{m} \sum_{j=1}^{k} w_{ij} LnRR_{ij}}{\sum_{i=1}^{m} \sum_{j=1}^{k} w_{ij}} \tag{7}$$

$$S(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{m} \sum_{j=1}^{k} w_{ij}}} \tag{8}$$

where *m* is the number of groups, and *k* is the number of comparisons in the *i*th group. The 95% confidence interval (95% CI) was calculated as *RR* ± 1.96 *S*(*RR*) by bootstrapping the data using Metawin 2.0. The percentage changes were presented in the figures as back-transformed from the log response ratio (i.e., [exp(*RR*) − 1] × 100%).

Effects of nitrogen addition on plant growth were evaluated as significant if the 95% CI did not overlap zero. This meta-analysis also followed the theory of heterogeneity described by Gurevitch and Hedges (1993), in which total heterogeneity (Q_T) is divided into within-group (Q_w) and between-group (Q_b). If Q_b is larger than a critical value, there would be a significant difference between categories. Statistical significance was tested at the $P < 0.05$ level.

Regression analyses were used to estimate the relationships of plant growth responses under different N forms with climatic factors (MAT and MAP), latitude and the methods of N application (external N dose).

3. Results

3.1. Changes of N forms in the soil under fertilization

In the field N fertilization experiments with NH$_4$NO$_3$ or urea addition, the ratio of NH$_4$-N/NO$_3^-$-N in the soil was significantly decreased by 61.7% (Fig. 2). This decrease was caused more by increases in soil NO$_3^-$-N (415.2%) than by changes in soil NH$_4$-N (87.2%; Fig. 2b). Comparing these two fertilizers, no significant difference was found on the ratio of NH$_4$-N/NO$_3^-$-N (−58.8% vs −70.9%; $P = 0.369$) and soil NO$_3^-$-N concentration (4 77.9% vs 2 50.4%; $P = 0.116$) (Fig. 2a). However, NH$_4$NO$_3$ showed a greater stimulation on soil NH$_4$-N (13 2.4% vs 5.2; $P < 0.001$), compared with urea.

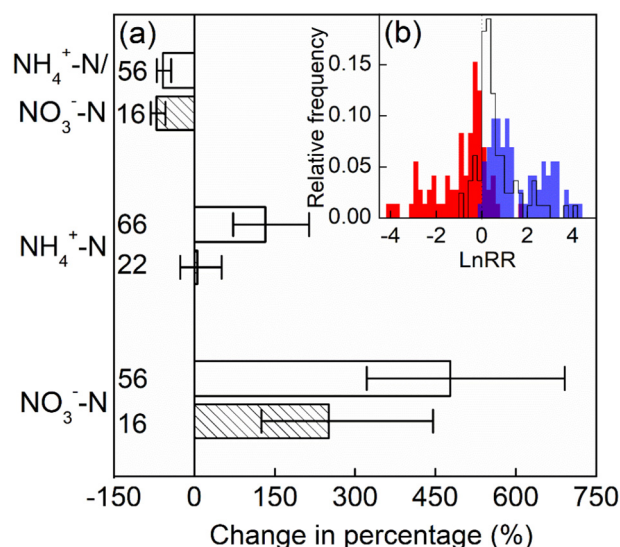**Fig. 2.** Percentage changes (means ±95% CI) of the soil nitrate (NO$_3^-$-N) concentration, ammonium (NH$_4$-N) concentration and the ratio of ammonium to nitrate (NH$_4$-N/NO$_3^-$-N) (a) under NH$_4$NO$_3$ (blank) or urea (shaded) fertilization. Inserted panel b showed the frequency distribution of soil NH$_4$-N (blank), NO$_3^-$-N (blue) and NH$_4$-N/NO$_3^-$-N response (red) under N fertilizations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Responses of plant growth to additive N forms vary with plant functional types

Across all the seed plant species, plant growth increased more with NH$_4$-N (6.3% per g N) than with NO$_3^-$-N addition (1.0% per g N) ($Q_b = 36.8, P < 0.001$; Fig. 3a, Table 1). This higher positive effect of NH$_4$-N than NO$_3^-$-N was found in trees and forbs but not for grasses, which responded marginally less to NH$_4$-N (6.9% per g N) than NO$_3^-$-N (11.1% per g N) addition ($Q_b = 3.5, P = 0.06$; Fig. 3a, Table 1). For shrubs, no difference was found between the two N forms ($Q_b = 0.1, P = 0.72$). The positive effects of NH$_4$-N addition were comparable between woody (5.6% per g N) and herbaceous (6.9% per g N) species ($Q_b = 1.7, P > 0.1$), but a smaller response of herbaceous (0.6% per g N) and woody species (1.6% per g N) ($Q_b = 0.6, P > 0.1$) was detected to NO$_3^-$-N addition (Fig. 3a, Table 2). The positive effects of NH$_4$-N addition among different functional types had no significant difference, with the rank of grasses (6.9% per g N), forbs (6.9% per g N), trees (6.5% per g N) and shrubs (3.2% per g N) ($Q_b = 8.2, P = 0.08$; Fig. 3a, Table 2). However, grasses (11.1% per g N) responded more than shrubs (1.9% per g N), trees (1.6% per g N) and forbs (−0.8% per g N) to NO$_3^-$-N addition ($Q_b = 26.0, P < 0.001$; Fig. 3a, Table 2). These general patterns of Fig. 3a were comparable with the responses when using the whole biomass (Fig. S3). It should also be noted that these response patterns were calculated on all available studies, including experiments which were conducted in both the controlled and field conditions. As shown in the Supplementary Fig. S4, the general patterns of Fig. 3a were similar to that across the field experiments.

Across all species, the response of plant growth to NH$_4$NO$_3$ addition (5.5% per g N) was lower than that to NH$_4$-N addition (Fig. 3; Table 1). No significant difference was detected between NH$_4$NO$_3$ and NH$_4$-N effect for each plant functional type, except woody plants and trees ($P < 0.05$). Urea addition showed greater positive effects across all species (11.0% per g N) than both NH$_4$-N and NO$_3^-$-N addition. Its positive impacts were the largest in all plant functional types (e.g., 9.0% per g N and 15.4% per g N in woody and herbaceous species, respectively) (Table 1).
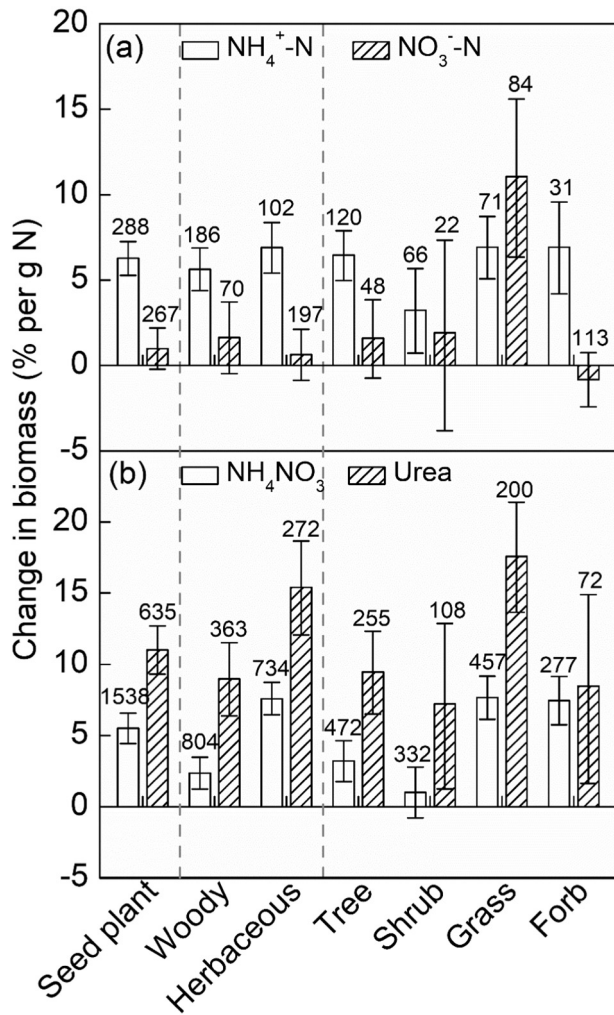
Fig. 3. Percentage changes of plant biomass (% per g N) under NH_4-N and NO_3^--N fertilization (a) and under NH_4NO_3 and Urea addition (b) for all the seed plant and for different plant functional types. Woody = tree s hrub, herbaceous = grass f orb. Values are means ±95% CI.

3.3. Responses of plant growth to NH_4^+- and NO_3^--N addition vary with plant tissues

NO_3^--N addition significantly stimulated the above-ground growth (8.4% per g N), whereas NH_4-N addition showed a greater effect on

Table 1
Between-group heterogeneity (Q_b) and probability (P) of nitrogen effect on plant growth across various nitrogen form (NO_3^--N and NH_4-N; NH_4NO_3 and urea), NO_3^- or NH_4-N effect on above- and below-ground growth within all the seed plant and different plant functional types. The blank cells mean that calculations were not conducted due to limited data.

	NO_3^--N vs NH_4-N		NH_4NO_3 vs urea		NH_4N_3 vs NH_4-N		AGB vs BGB under NO_3^--N		AGB vs BGB under NH_4-N	
	Q_b	P	Q_b	P	Q_b	P	Q_b	P	Q_b	P
Seed plant	36.8	<0.001	29.5	<0.001	7.5	<0.05	44.7	<0.001	12.2	<0.001
Woody	7.1	<0.01	49.0	<0.001	18.8	<0.01	0.2	0.64	4.5	<0.05
Herb	35.5	<0.001	12.4	<0.001	0.0	0.87	51.3	<0.001	0.3	0.60
Trees	7.2	<0.01	34.2	<0.001	11.3	0.06	0.6	0.43	1.6	0.20
Shrubs	0.1	0.72	1.5	0.22	2.4	0.06			35.7	<0.001
Grasses	3.5	0.06	11.3	<0.001	0.0	0.97	0.1	0.74	0.0	1.00
Forbs	29.2	<0.001	0.1	0.70	0.12	0.78	26.3	<0.001	0.3	0.60

Table 2
Between-group heterogeneity (Q_b) and probability (P) of nitrogen effect on plant growth across different functional types within each nitrogen form. The plant functional types include trees, shrubs, grasses and forbs.

	Woody vs herb		Plant functional types	
	Q_b	P	Q_b	P
NO_3^--N	0.6	0.44	26	<0.001
NH_4-N	1.7	0.19	6.6	0.08
NH_4NO_3	41.2	<0.001	45.1	<0.001
Urea	9.3	<0.01	15.1	<0.01

the below-ground growth (5.9% per g N; Fig. 4a, Table 1). NH_4-N addition increased below-ground (7.3% per g N and 9.4% per g N) but not above-ground growth of both woody and herbaceous species. In contrast, NO_3^--N addition significantly increased the above-ground (4.0% per g N and 12.1% per g N) but not below-ground growth of both woody and herbaceous species (Fig. 4b, c).

3.4. Responses of plant growth to NH_4^+- and NO_3^--N addition vary with abiotic factors

By excluding controlled experiments, we found that MAT ($r^2 = 0.17$, $P < 0.001$) and latitude ($r^2 = 0.20$, $P < 0.001$) only affected plant growth response to NO_3^--N addition, while MAP negatively influenced plant growth responses to NH_4-N ($r^2 = 0.29$, $P < 0.001$) and NO_3^--N addition ($r^2 = 0.15$, $P < 0.001$) (Fig. 5). No relationship was shown between the responses of plant growth with the dose, as a minor change in plant responses when N deposition was above 20 g m^{-2} yr^{-1} (Fig. 6a). When separated the field N experiments into two groups in terms of the dose of N addition (i.e., <5 and >5 g m^{-2} yr^{-1}), we found that higher response of plant growth to NH_4-N addition was under the dose of 0–5 g m^{-2} yr^{-1} ($P < 0.001$), while no difference between NH_4-N and NO_3^--N addition with the dose above 5 g m^{-2} yr^{-1} (Fig. 6b).

4. Discussion

4.1. Soil NH_4^+-N/NO_3^--N ratio under artificial fertilization and future atmospheric N deposition

Substantial increases in deposition rates of atmospheric N and its major components (i.e., NH_x and NO_y) are predicted in the coming decades (Galloway et al., 2004; Dentener et al., 2006; Kanakidou et al., 2016). However, the global average cannot reflect the large spatial variation of the trends in the regional NH_4-N/NO_3^--N ratio in N deposition (Tan et al., 2018). For example, N deposition across the US has converted from NO_3^--N in the 1980s to the NH_4-N domination in recent years because the implemented emission control on NO_x but not NH_3 (Li et al., 2016; Sun et al., 2018). On the contrary, the NH_x/NO_y ratio across China has been significantly reduced since the 1980s (Liu et al., 2013, 2016; Yu et al., 2019).

It has been demonstrated that the increasing atmospheric N deposition not only stimulates the availability of mineral N but also changes the NH_4-N/NO_3^--N ratio in the soil (Skiba et al., 2004; Boxman et al., 2008). Our results show that although the additions of different N forms affect soil inorganic N stock differently, they all reduced the NH_4-N/NO_3^--N in the soil (Fig. 2). This could be attributed to the fact that soil NH_4-N and NO_3^--N pools depend on not only the N influx but also the transformation processes after they are added into the soil. For example, NH_4-N could be transformed into NO_3^--N via nitrification, and NO_3^--N would be denitrified or leached from the ecosystem (Gundersen and Rasmussen, 1990; Haynes and Goh, 1978). Thus, it remains unclear how the change of NH_x/NO_y in the atmospheric N deposition will affect the availability of soil N. For example, Boxman et al. (2008) have observed a synchronous decline of NH_4-N/NO_3^--N ratio in atmospheric deposition and in the soil solution. They still predict an
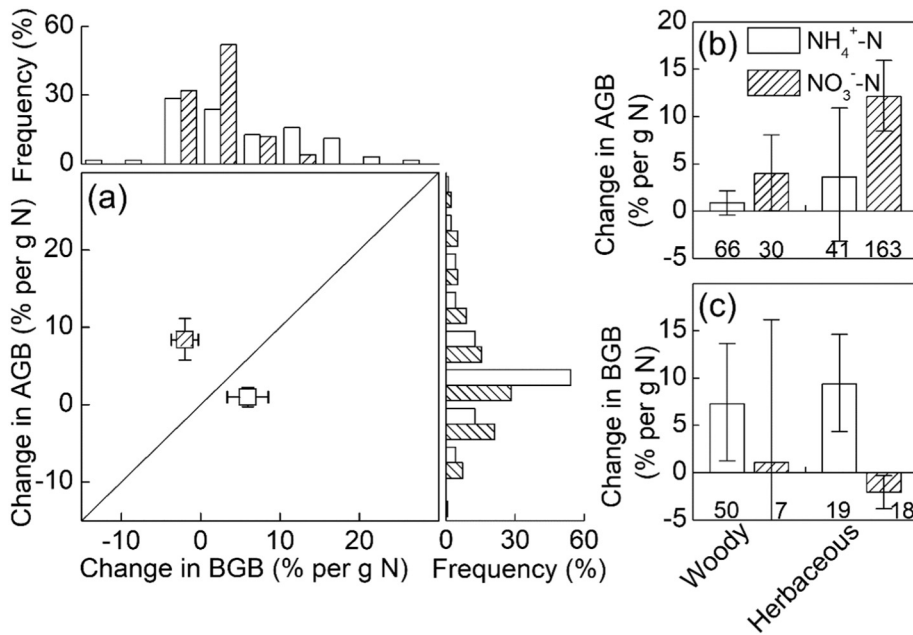
Fig. 4. Comparison the effects of NH$_4$-N and NO$_3^-$-N on plant above-ground (AGB, % per g N) and below-ground biomass (BGB, % per g N) across all the seed plant species (a) and within growth forms (b–c). Open shapes for NH$_4$-N effects and closed ones for NO$_3^-$-N effects. Values are means ±95% CI.

increasing soil NH$_4$-N/NO$_3^-$-N ratio wherein nitrification is inhibited. A global increasing NH$_4$-N concentration in atmospheric deposition may instead increase NO$_3^-$-N content in the soil because of the stimulated nitrification by NH$_4$ supply (Lu et al., 2011). On the other hand, soil acidification under N deposition may play an opposite role (Gundersen and Rasmussen, 1990). These results indicate that an increasing external input of NH$_4$-N or NO$_3^-$-N does not necessarily lead to corresponding changes in the soil. In fact, the observed changes in the soil NH$_4$-N/NO$_3^-$-N ratio (Fig. 2) is the outcome of the responses of multiple N processes. Thus, considering the complicated N cycle in the soil, this study only focused on the impacts of external N forms input on plant growth.

4.2. Different responses of plant growth to NH$_4^+$- and NO$_3^-$-N addition among plant functional types

It is known that ammonium-N addition usually inhibits plant growth compared with the addition of nitrate-N or a mixture of nitrate and ammonium (Paulissen et al., 2005; Willey and Tang, 2006). In this study, however, the response of plant growth to NH$_4$-N addition is about 6-fold as much as that of NO$_3^-$-N addition for terrestrial plants (Fig. 3). The greater positive effect of NH$_4$-N addition is reasonable

because ammonium is less costly in energy than nitrate, which has to be reduced to ammonium before assimilation (Zerihun et al., 1998; Guo et al., 2007). For example, the plants uptake of NH$_4$-N often exceeds that of NO$_3^-$-N when N is the limiting nutrient for growth (Grassein et al., 2015; Konnerup and Brix, 2010; Song et al., 2015). The higher uptake rate of NH$_4$-N means a higher tissue N concentration and then a higher potential N investment in the plant photosynthesis (Gaiad et al., 2006; Huangfu et al., 2016; Konnerup and Brix, 2010). Many studies have found that plant photosynthesis is more stimulated by NH$_4$-N than NO$_3^-$-N addition (Claussen and Lenz, 1999; Hogh-Jensen and Schjoerring, 1997). Thus, ammonium usually acts as a superior N fertilizer than nitrate for plant growth (Gaiad et al., 2006; Huangfu et al., 2016; Konnerup and Brix, 2010).

Among plant functional types, the response of plant growth to NH$_4$-N addition shows lower variability than that to NO$_3^-$-N addition (Fig. 3). This finding is contrary to the observations in an alpine meadow (Song and Yu, 2015), where the synchrony among functional groups was not affected by the addition of different forms of N. NO$_3^-$-N addition only enhances the growth of grasses (Fig. 3), indicating that the nitrate-dominated N deposition would have a greater impact on grassland than other ecosystem types. However, it should be noted that the ratio
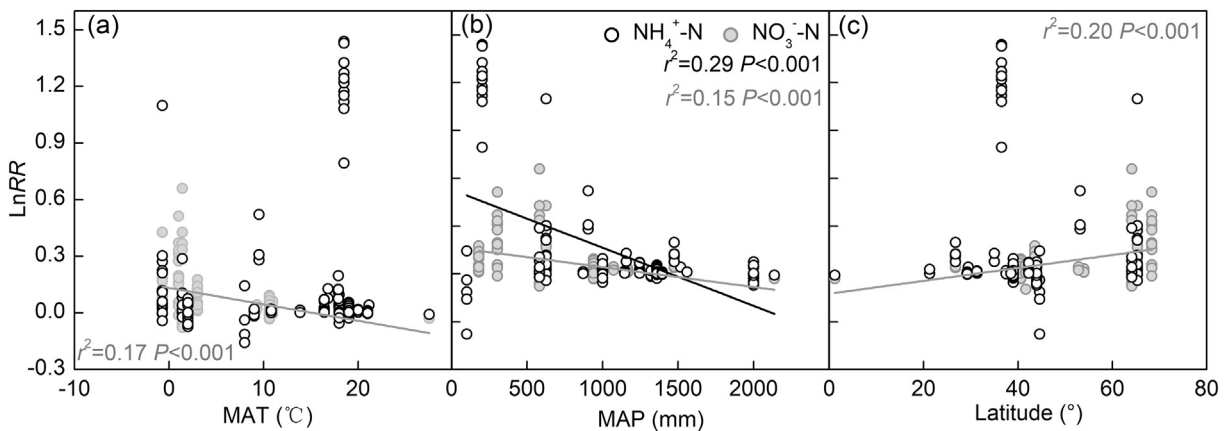

Fig. 5. Dependence of the plant growth response to N addition (i.e., LnRR) upon mean annual temperature (MAT), mean annual precipitation (MAP) and latitude. Only data from the field experiments were shown.
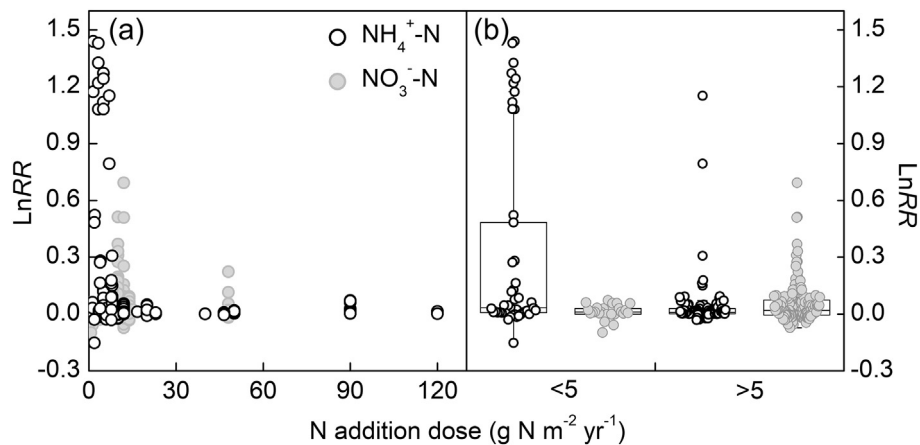
Fig. 6. Dependence (a) of plant growth response to N addition (i.e., Ln*RR*) upon N dose and the distribution of N effects in various groups of N dose (b). The dots in panels represent each data. In panel b, the box indicates the 25th and 75th percentile, and the whiskers show the 10th and 90th percentile, with the line in each box as the median.

of NH_4-N/NO_3^--N in N deposition shows contrasting trends in different grassland regions, for example, increasing in North America (Kanakidou et al., 2016) but decreasing in Asia (Tan et al., 2018). Furthermore, the preference for ammonium or nitrate may vary among species within an ecosystem (Metcalfe et al., 2011; Sheppard et al., 2014). These results call for more research on the different impacts of NH_4-N and NO_3^--N addition on plant community composition in the future.

4.3. Different responses of plant growth to NH_4^+- and NO_3^--N addition among plant tissues

Plants growing in the infertile or low N soils usually allocate more biomass to roots for acquiring nutrients. The increase of soil N availability, on the contrary, enhances the allocation of plant biomass from below- to above-ground (Müller et al., 2000; Song et al., 2010). Our meta-analysis also shows that above-ground growth is stimulated more under NO_3^--N addition but below-ground growth is more responsive to NH_4-N addition across all growth forms.

The N form, including N availability, is another important determinant of plant biomass allocation (Cambui et al., 2011; Willey and Tang, 2006). The energy cost for the reduction of NO_3^- to NH_4 is lower if the conversion takes place in photosynthetic leaves, in where photons are directly used to fuel the NO_3^- reduction (Raven, 1985; Gerendás et al., 1997). Thus, the relative increase of NO_3^- supply in leave tends to enhance biomass allocation to shoot. The NH_4 is primarily assimilated by roots (Marschner, 2012; Schjoerring et al., 2002), so more root growth is required for acquiring NH_4-N (Gerendás et al., 1997) and constructing C-N bonds related to the critical pathways of ammonium detoxification (Bittsánszky et al., 2015). Thus, this study found more biomass allocation to root under NH_4-N supply than NO_3^--N addition at the global scale (Fig. 3). On the other hand, plants have a protective mechanism to keep the balance between the lowered root water-uptake capacity and the high root C demand for NH_4 uptake (Guo et al., 2007). All of these findings indicate that plants have evolved different specialized strategies for adapting to the changing N environments.

4.4. Limitations and implications

It should be noted that there are several limitations in this study. First, the meta-analysis combines results from previous studies to calculate a weighted average of the measures, and identifies patterns based on results from different studies. To test the robustness of the key findings in this study, we further studied the experiments which simultaneously added NH_4- and NO_3^--N (totally 42 paired data and 12 species from 7 independent studies, Appendix Table S3). The results (Appendix

Fig. S5) were consistent with the general patterns found in Fig. 3. Second, this study tried to discuss the plant preference for different N forms under the scenario of future atmospheric N deposition. However, the increasing NH_x/NO_y ratio in the atmospheric N deposition does not necessarily lead to enhanced NH_4-N/NO_3^--N in the soil, because NH_4 could be quickly transformed to NO_3^- by nitrification. Only a few studies have reported the associated changes between ratios of atmospheric NH_x/NO_y and soil NH_4-N/NO_3^--N at the site level (e.g., Skiba et al., 2004). Third, some of the discussions are based on the global trends of atmospheric NH_x/NO_y, but the projection itself has great uncertainty. Fourth, the durations of most experiments in this study was less than five years (Appendix Fig. S6), suggesting that the long-term biological impacts of N addition are not considered in our analyses. Fifth, the woody plants under the controlled experimental condition were generally concentrated in the seedling stage. Lastly, neither NH_4-N nor NO_3^--N could be added in the experiments without an inorganic anion or cation. Although no difference was detected between treatments with anions or cations (Appendix Fig. S7), their effects could have been included in the NH_4-N or NO_3^--N addition in this study.

Overall, the findings in this study have some additional important implications for the widespread N-addition manipulative experiments:

1. NH_4NO_3 and urea are widely used as the major fertilizers in most field ecological experiments. We found the effect of NH_4NO_3 addition was slightly lower than NH_4-N addition but was much lower than urea addition (Fig. 3b). This suggests that the N effect on plant growth in the manipulative experiments could be larger than that in the natural ecosystems, especially in those regions with increasing deposition of NO_3^--N.

2. The ratio of NH_4-N/NO_3^--N in the soil is reduced under the addition of NH_4NO_3 or urea (Fig. 2b). However, the responses of soil NH_4-N/NO_3^--N ratio to atmospheric N deposition with changing NH_4-N/NO_3^--N are complicated (Skiba et al., 2004; Boxman et al., 2008), so attention should be paid to the scaling of experimental results up to the real ecosystems.

3. Plants growing in drier regions are more sensitive to NH_4-N and NO_3^--N addition than those growing in wetter regions (Fig. 5b). Experimental studies are needed to explore whether this pattern is attributed to the water-limited N availability in the dry environments (Giese et al., 2011) or a higher potential nitrification rate leading to a more pronounced nitrate preference in wetter regions (Olsson and Falkengren-Grerup, 2000).

4. The higher response of plant growth to NH_4-N addition was showed under the dose of 0–5 g m^{-2} yr^{-1} ($P < 0.001$), while no response difference was detected with the N dose above 5 g m^{-2} yr^{-1} (Fig. 6b). Thus,

future N-addition experiments need to consider the natural N deposition rate (e.g., 0–5 g m^{-2} yr^{-1} at present, Dentener et al., 2006).

5. Conclusions

Using the meta-analysis, this study reveals a general higher growth response of terrestrial plants to NH$_4$-N than NO$_3^-$-N addition. Addition of NO$_3^-$-N promotes more growth allocation to above-ground, whereas NH$_4$-N addition significantly enhances below- but not above-ground growth. Given that the atmospheric inputs of NH$_4$-N and NO$_3^-$-N are uneven in most areas of the globe, plant strategies for acquiring different forms of N would play an important role in vegetation response to future atmospheric N enrichment. In some regions, e.g., eastern Asia, the rate of N deposition could exceed the critical loads of N and trigger sudden harmful impacts on plant growth (Bobbink et al., 2010; Pardo et al., 2011). It also should be noted that plants in the real ecosystems could respond to future N enrichment differently from that have been reported by the manipulative field experiments in this study. Thus, we recommend future manipulative experiments with N addition to consider the realistic compositional features of local N deposition. Terrestrial biogeochemical models should also need to incorporate different preferences of plant species for acquiring ammonium and nitrate.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.05.448.

References

Bittsánszky, A., Pilinszky, K., Gyulai, G., Komives, T., 2015. Overcoming ammonium toxicity. Plant Sci. 231, 184–190.

Bobbink, R., Hicks, K., Galloway, J.N., Spranger, T., Alkemade, R., Ashmore, M.R., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., et al., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecol. Appl. 20 (1), 30–59.

Boxman, A.W., Peters, R.C., Roelofs, J.G., 2008. Long term changes in atmospheric N and S throughfall deposition and effects on soil solution chemistry in a Scots pine forest in the Netherlands. Environ. Pollut. 156, 1252–1259.

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.

Claussen, W., Lenz, F., 1999. Effect of ammonium or nitrate nutrition on net photosynthesis, growth, and activity of the enzymes nitrate reductase and glutamine synthetase in blueberry, raspberry and strawberry. Plant Soil 208, 95–102.

De Graaf, M.C., Bobbink, R., Roelofs, J.G., Verbeek, P.J., 1998. Differential effects of ammonium and nitrate on three heathland species. Plant Ecol. 135, 185–196.

De Schrijver, A., Staelens, J., Wuyts, K., Van Hoydonck, G., Janssen, N., Mertens, J., Gielis, L., Geudens, G., Augusto, L., Verheyen, K., 2008. Effect of vegetation type on throughfall deposition and seepage flux. Environ. Pollut. 153, 295–303.

Dentener, F., Drevet, J., Lamarque, J.F., Bey, I., Eickhout, B., Fiore, A.M., Hauglustaine, D.A., Horowitz, L.W., Krol, M.C., Kulshrestha, U.C., et al., 2006. Nitrogen and sulfur deposition on regional and global scales: A multimodel evaluation. Global Biogeochem. Cy. 20, 1–21.

Ding, W.X., Cai, Z.C., Tsuruta, H., 2004. Cultivation, nitrogen fertilization, and set-aside effects on methane uptake in a drained marsh soil in Northeast China. Glob. Change Biol. 10, 1801–1809.

Du, E., de Vries, W., Galloway, J.N., Hu, X., Fang, J., 2014. Changes in wet nitrogen deposition in the United States between 1985 and 2012. Environ. Res. Lett. 9, 095004.

Falkengren-Grerup, U., Schottelndreier, M., 2004. Vascular plants as indicators of nitrogen enrichment in soils. Plant Ecol. 172, 51–62.

Fenn, M.E., Bytnerowicz, A., Schilling, S.L., Vallano, D.M., Zavaleta, E.S., Weiss, S.B., Morozumi, C., Geiser, L.H., Hanks, K., 2018. On-road emissions of ammonia: an underappreciated source of atmospheric nitrogen deposition. Sci. Total Environ. 625, 909–919.

Fernandezmartinez, M., Vicca, S., Janssens, I.A., Sardans, J., Luyssaert, S., Campioli, M., Penuelas, J., 2014. Nutrient availability as the key regulator of global forest carbon balance. Nat. Climate Change 4, 471–476.

Gaiad, S., Rakocevic, M., Reissmann, C.B., 2006. N sources affect growth, nutrient content, and net photosynthesis in mate (Ilex paraguariensis St. Hil.). Braz Arch Biol Techn 49, 689–697.

Galloway, J.N., Dentener, F.J., Capone, D.G., et al., 2004. Nitrogen cycles: past, present, and future. Biogeochemistry 70, 153–226.

Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z.C., 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, 889–892.

Gerendás, J., Zhu, Z.J., Bendixen, R., Ratcliffe, R.G., Sattelmacher, B., 1997. Physiological and biochemical processes related to ammonium toxicity in higher plants. J. Plant Nutr. Soil Sci. 160, 239–251.

Giese, M., Gao, Y.Z., Lin, S., Brueck, H., 2011. Nitrogen availability in a grazed semi-arid grassland is dominated by seasonal rainfall. Plant Soil 340, 157–167.

Glibert, P.M., Harrison, J.A., Heil, C.A., Seitzinger, S.P., 2006. Escalating worldwide use of urea - a global change contributing to coastal eutrophication. Biogeochemistry 77, 441–463.

Grassein, F., Lemauviellavenant, S., Lavorel, S., Bahn, M., Bardgett, R.D., Desclosthéveniau, M., Laine, P., 2015. Relationships between functional traits and inorganic nitrogen acquisition among eight contrasting European grass species. Annals Bot 115, 107–115.

Gundersen, P., Rasmussen, L., 1990. Nitrification in forest soils: effects from nitrogen deposition on soil acidification and aluminum release. Rew. Environ. Contam. T. 113, 1–45.

Guo, S., Zhou, Y., Shen, Q., Zhang, F.S., 2007. Effect of ammonium and nitrate nutrition on some physiological processes in higher plants-growth, photosynthesis, photorespiration, and water relations. Plant Biol. 9, 21–29.

Gurevitch, J., Hedges, L.V., 1993. Meta-analysis: combining the results of independent experiments. In: Scheiner, S.M., Gurevitch, J. (Eds.), Design and Analysis of Ecological Experiments. Chapman and Hall, New York, pp. 378–398.

Gurevitch, J., Koricheva, J., Nakagawa, S., Stewart, G., 2018. Meta-analysis and the science of research synthesis. Nature 555, 175–182.

Haynes, R.J., Goh, K.M., 1978. Ammonium and nitrate nutrition of plants. Biol. Rew. 53, 465–511.

Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156.

Hogh-Jensen, H., Schjoerring, J.K., 1997. Effects of drought and inorganic N form on introgen fixation and carbon isotope discrimination in Trifolium repens. Plant Phy. Biochem. 35, 55–62.

Homann, P.S., Caldwell, B.A., Chappell, H.N., Sollins, P., Swanston, C.W., 2001. Douglas-fir soil C and N properties a decade after termination of urea fertilization. Can. J. For. Res. 31, 2225–2236.

Hosker, R.P., Lindberg, S.E., 1982. Review: atmospheric deposition and plant assimilation of gasses and particles. Atmos. Environ. 16, 889–910.

Huangfu, C., Li, H., Chen, X., Liu, H., Wang, H., Yang, D., 2016. Response of an invasive plant, Flaveria bidentis, to nitrogen addition: a test of form-preference uptake. Biol. Invasions 18, 3365–3380.

Kanakidou, M., Myriokefalitakis, S., Daskalakis, N., Fanourgakis, G.S., Nenes, A., Baker, A.R., Tsigaridis, K., Mihalopoulos, N., 2016. Past, present, and future atmospheric nitrogen deposition. J. Atmos. Sci. 73, 2039–2047.

Konnerup, D., Brix, H., 2010. Nitrogen nutrition of Canna indica: effects of ammonium versus nitrate on growth, biomass allocation, photosynthesis, nitrate reductase activity and N uptake rates. Aquat. Bot. 92, 142–148.

LeBauer, D.S., Treseder, K.K., 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89, 371–379.

Li, B.H., Li, G.J., Kronzucker, H.J., Baluska, F., Shi, W.M., 2014. Ammonium stress in Arabidopsis: signaling, genetic loci, and physiological targets. Trends Plant Sci. 19, 107–114.

Li, Y., Schichtel, B.A., Walker, J.T., Schwede, D.B., Chen, X., Lehmann, C.M.B., Puchalski, M.A., Gay, D.A., Collett, J.L., 2016. Increasing importance of deposition of reduced nitrogen in the United States. P. Natl. Acad. Sci. USA. 113, 5874–5879.

Liu, X., Zhang, Y., Han, W., Tang, A., Shen, J., Cui, Z., Zhang, F., 2013. Enhanced nitrogen deposition over China. Nature 494, 459–462.

Liu, X., Xu, W., Du, E., Pan, Y., Goulding, K., 2016. Reduced nitrogen dominated nitrogen deposition in the United States, but its contribution to nitrogen deposition in China decreased. P. Natl. Acad. Sci. USA 113, E3590–E3591.

Lu, M., Yang, Y., Luo, Y., Fang, C.M., Zhou, X.H., Chen, J.K., Yang, X., Li, B., 2011. Responses of ecosystem nitrogen cycle to nitrogen addition: a meta-analysis. New Phytol. 189, 1040–1050.

Maaroufi, N.I., Nordin, A., Hasselquist, N.J., Bach, L.H., Palmqvist, K., Gundale, M.J., 2015. Anthropogenic nitrogen deposition enhances carbon sequestration in boreal soils. Glob. Change Biol. 21, 3169–3180.

Maestre, F.T., Valladares, F., Reynolds, J.F., 2005. Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. J. Ecol. 93, 748–757.

Manning, P., Newington, J.E., Robson, H.R., Saunders, M., Eggers, T., Bradford, M.A., Rees, M., 2006. Decoupling the direct and indirect effects of nitrogen deposition on ecosystem function. Ecol. Lett. 9, 1015–1024.

Marschner, H., 2012. Marschner's Mineral Nutrition of Higher Plants. 3rd ed. Academic press, London.

Metcalfe, R.J., Nault, J., Hawkins, B.J., 2011. Adaptations to nitrogen form: comparing inorganic nitrogen and amino acid availability and uptake by four temperate forest plants. Can. J. For. Res. 41, 1626–1637.

Müller, I., Schmid, B., Weiner, J., 2000. The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. Perspect. Plant Ecol. 3, 115–127.

Nasholm, T., Kielland, K., Ganeteg, U., 2009. Uptake of organic nitrogen by plants. New Phytol. 182, 31–48.

Olsson, M.O., Falkengren-Grerup, U., 2000. Potential nitrification as an indicator of preferential uptake of ammonium or nitrate by plants in an oak woodland understory. Ann. Bot. 85, 299–305.

Pardo, L.H., Fenn, M.E., Goodale, C.L., Geiser, L.H., Driscoll, C.T., Allen, E.B., Baron, J.S., Bobbink, R., Bowman, W.D., Clark, C.M., et al., 2011. Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecol. Appl. 21, 3049–3082.

Paulissen, M.P., Besalu, L.E., De Bruijn, H., Paulissen, M.P., Besalu, L.E., De Bruijn, H., Van Der Ven, P.J., Bobbink, R., 2005. Contrasting effects of ammonium enrichment on fen bryophytes. J. Bryol. 27, 109–117.

Raven, J.A., 1985. Regulation of pH and generation of osmolarity in vascular plants: a cost-benefit analyses in relation to efficiency of use of energy, nitrogen and water. New Phytol. 101, 25–77.

Schjoerring, J.K., Husted, S., Mäck, G., Mattsson, M., 2002. The regulation of ammonium translocation in plants. J. Exp. Bot. 53, 883–890.

Sheppard, L., Leith, I.D., Mizunuma, T., Leeson, S.R., Kivimaki, S., Neil Cape, J., Smart, S., 2014. Inertia in an ombrotrophic bog ecosystem in response to 9 years' realistic perturbation by wet deposition of nitrogen, separated by form. Glob. Change Biol. 20, 566–580.

Silver, W.L., Thompson, A.W., Reich, A., Ewel, J.J., Firestone, M.K., 2005. Nitrogen cycling in tropical plantation forests: potential controls on nitrogen retention. Ecol. Appl. 15, 1604–1614.

Skiba, U., Pitcairn, C.E., Sheppard, L.J., Kennedy, V., Fowler, D., 2004. The influence of atmospheric N deposition on nitrous oxide and nitric oxide fluxes and soil ammonium and nitrate concentrations. Water Air Soil Poll 4, 37–43.

Song, M.H., Yu, F.H., 2015. Reduced compensatory effects explain the nitrogen-mediated reduction in stability of an alpine meadow on the Tibetan Plateau. New Phytol. 207, 70–77.

Song, C.J., Ma, K.M., Qu, L.Y., Liu, Y., Xu, X.L., Fu, B.J., Zhong, J.F., 2010. Interactive effects of water, nitrogen and phosphorus on the growth, biomass partitioning and water-use efficiency of Bauhinia faberi seedlings. J. Arid Environ. 74, 1003–1012.

Song, M.H., Zheng, L.L., Suding, K.N., Yin, T.F., Yu, F.H., 2015. Plasticity in nitrogen form uptake and preference in response to long-term nitrogen fertilization. Plant Soil 394, 215–224.

Stevens, C.J., Gowing, D.J., 2013. Effect of nitrogen addition, form and clipping on competitive interactions between grassland species. J. Plant Ecol. 7, 222–230.

Stevens, C.J., Dise, N.B., Mountford, J.O., Gowing, D.J.G., 2004. Impact of nitrogen deposition on the species richness of grasslands. Science 303, 1876–1879.

Sun, W., Shao, M., Granier, C., Liu, Y., Ye, C.S., Zheng, J.Y., 2018. Long-term trends of anthropogenic SO₂, NOx, CO, and NMVOCs emissions in China. Earth's Future 6, 1112–1133.

Tan, J., Fu, J.S., Dentener, F., Sun, J., Emmons, L., Tilmes, S., Sudo, K., Flemming, J., Jonson, J.E., Gravel, S., Bian, H., Henze, D., Lund, M.T., Kucsera, T., Takemura, T., Keating, T., 2018. Multi-model study of HTAP II on sulphur and nitrogen deposition. Atmos. Chem. Phys. 18, 6847–6866.

Tho, B.T., Lambertini, C., Eller, F., Brix, H., Sorrell, B.K., 2017. Ammonium and nitrate are both suitable inorganic nitrogen forms for the highly productive wetland grass Arundo donax, a candidate species for wetland paludiculture. Ecol. Eng. 105, 379–386.

Vanderwerf, E., 1992. Lack's clutch size hypothesis: an examination of the evidence using meta-analysis. Ecology 73, 1699–1705.

ven Den Berg, L.J., Dorland, E., Vergeer, P., Hart, M.A.C., Bobbink, R., Roelofs, J.G.M., 2005. Decline of acid-sensitive plant species in heathland can be attributed to ammonium toxicity in combination with low pH. New Phytol. 166, 551–564.

ven Den Berg, L.J., Jones, L., Sheppard, L., Smart, S.M., Bobbink, R., Dise, N.B., Ashmore, M.R., 2016. Evidence for differential effects of reduced and oxidised nitrogen deposition on vegetation independent of nitrogen load. Environ. Pollut. 208, 890–897.

Verhoeven, J.T., Beltman, B., Dorland, E., Robat, S.A., Bobbink, R., 2011. Differential effects of ammonium and nitrate deposition on fen phanerogams and bryophytes. Appl. Veg. Sci. 14, 149–157.

Vitousek, P.M., Howarth, R.W., 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13, 87–115.

Willey, N., Tang, S., 2006. Some effects of nitrogen nutrition on caesium uptake and translocation by species in the Poaceae, Asteraceae and Caryophyllidae. Environ. Exp. Bot. 58 (1–3), 114–122.

Xia, J., Wan, S., 2008. Global patterns of terrestrial plant species to nitrogen addition. New Phytol. 179, 428–439.

Yu, G., Jia, Y., He, N., Zhu, J., Chen, Z., Wang, Q., Piao, S., Liu, X., He, H., Guo, X., Wen, Z., Li, P., Ding, G., Goulding, K., 2019. Stabilization of atmospheric nitrogen deposition in China over the past decade. Nat. Geosci. https://doi.org/10.1038/s41561-019-0352-4.

Zerihun, A., Mckenzie, B.A., Morton, J.D., 1998. Photosynthate costs associated with the utilization of different nitrogen-forms: influence on the carbon balance of plants and shoot–root biomass partitioning. New Phytol. 138, 1–11.