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Atmospheric Nitrogen Deposition to Global Forests

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Chapter 4

Impacts of nitrogen deposition on forest productivity and carbon sequestration

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1. Introduction

Nitrogen (N) availability limits primary productivity of many forest ecosystems especially those in boreal and temperate regions (LeBauer and Treseder, 2008; Du et al., 2020a). Available N comes from both internal cycling via soil N mineralization and leaf N resorption, and external inputs via biological N fixation, atmospheric N deposition and bedrock weathering (Cleveland et al., 2013; Du and de Vries, 2018; Morford et al., 2011). As an external N input, N deposition stimulates plant growth and thus increases C sequestration in many terrestrial ecosystems, especially in a world with continuingly rising atmospheric CO_2 concentrations (De Vries et al., 2014; O'Sullivan et al., 2019; Terrer et al., 2019; Thomas et al., 2010).

Global N cycles have been dramatically altered by human activities since the Industrial Revolution accompanying with which anthropogenic N emissions and deposition have been greatly increased (Galloway et al., 2008, 2021). Large amounts of N emissions have been found to cause severe air pollution (e.g., haze, acid rain, and ozone) and result in negative ecological effects (e.g., biodiversity loss, acidification) when deposited to various ecosystems, both in the current hotspot regions, mainly occurring in East and South Asia and the past hotspot regions, mainly in Europe and North America (Fenger, 2009; Bobbink et al., 2010; Liu and Du, 2020; Perring et al., 2023). These negative effects have aroused policies to curb N emissions in European countries from 1980s, the United States from 1990s and China from 2010s (Amann et al., 2013; Li et al., 2017; Zheng et al., 2018). Consequently, N deposition has been greatly decreased in Europe and North America (Du, 2016; Engardt et al., 2017), while it still stays at a high level in many developing countries (e.g., China, India, Russia, and Brazil), driven by agricultural and industrial development (Beachley et al., 2023; Schwede et al., 2018, 2023). Overall, the ecological effects of N deposition will likely shift with its changing rate over time.

Considering that forest biomes account for a major proportion of the total C sinks in global terrestrial ecosystems (Pan et al., 2011), the contribution of N deposition to forest C sequestration has been an important topic for research since decades (Nadelhoffer et al., 1999; Magnani et al., 2007; De Vries et al., 2009; Schulte-Uebbing and de Vries, 2018). The overall effect on C sequestration depends on both the N load and the C−N response (kg C per kg N) that is determined by the N allocation in different vegetation and soil compartments with varying C:N ratios (Du and De Vries, 2018). The C−N response likely varies nonlinearly with increasing levels of N deposition and/or over long time at the same level of N deposition, shifting from an increase when N inputs diminish N limitation to a decline when the negative effects of excess N inputs (e.g., acidification, nutrient imbalances, aluminum mobility) aggravate (De Vries et al., 2014; Etzold et al., 2020; Flechard et al., 2020; Xing et al., 2022). The C−N response is also influenced by a variety of ecological factors, such as mycorrhizal association, temperature, precipitation, and availability of other nutrients such as phosphorus (P) (Du and de Vries, 2018; Thomas et al., 2010). Overall, the C−N response differs largely across boreal, temperate and tropical forest biomes (Du and de Vries, 2018; Schulte-Uebbing and de Vries, 2018).

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Large-scale effects of N deposition on forest productivity and C sequestration are conventionally assessed by four approaches, including field surveys across N deposition gradients, manipulative N addition/removal experiments, stoichiometric scaling, and model simulation (De Vries et al., 2017). Field surveys across spatial gradients or temporal changes of N deposition can be used to evaluate the N deposition-induced effects but the results sometimes are biased due to simultaneous changes in other factors, such as climate, soil nutrient status and plant species composition (Bedison and McNeil, 2009; Solberg et al., 2009). Major knowledge of the N deposition-induced ecological effects is derived from manipulated experiments using low-dose N additions in the range of N deposition levels (e.g., <60 kg N ha^{-1} $year^{-1}$; Schwede et al., 2018, 2023). Such N deposition simulation experiments should be differentiated from N fertilization in agroforestry practices that uses extremely high-level N doses (e.g., >100 kg N ha^{-1} $year^{-1}$) (Bebber, 2021). Meta-analyses or statistical extrapolation of cross-site experimental results can further evaluate the overall effect of N deposition on a large spatial scale (Schulte-Uebbing and de Vries, 2018; Schulte-Uebbing et al., 2022). The stoichiometric scaling approach combines the fate of N estimated from ^{15}N experimental studies and the C:N ratios of forest ecosystem compartments to estimate the response of forest productivity and C sequestration from local to global scales (Du and de Vries, 2018; Gurmesa et al., 2022). Finally, modeling approaches assess the effects of N deposition based on the difference between simulations using different scenarios (Thornton et al., 2007; Thomas et al., 2013; Davies-Barnard et al., 2020). These approaches have greatly improved our understanding of the impacts of N deposition on forest productivity and C sequestration from regional to global scales.

The contribution of the N deposition to forest C sequestration has been a matter of debate for last two decades (Nadelhoffer et al., 1999; Magnani et al., 2007; Sutton et al., 2008; Högberg, 2012; de Vries et al., 2008, 2009; Du and de Vries, 2018; Schulte-Uebbing and de Vries, 2018; Schulte-Uebbing et al., 2022). Some studies support the hypothesis that N deposition strongly favors forest growth and C sequestration (e.g., Magnani et al., 2007), while others have questioned it (e.g., De Vries et al., 2008; Schulte-Uebbing et al., 2022). Based on a literature review, we first summarize the four approaches frequently used to evaluate the ecological effects of N deposition and then synthesize the estimated effects of N deposition on net primary productivity (NPP) and C sequestration in global forest biomes (i.e., boreal forest, temperate forest, and tropical forests). Finally, we discuss the current uncertainties and future research needs to further improve our understanding of N deposition-induced impacts on forest growth and C sequestration.

2. Approaches to assess the effects of nitrogen deposition

Based on a review of literature, we summarize below the basis of field survey across N deposition gradients, manipulative N addition/removal experiment, stoichiometric scaling, and model simulation, and also discuss their potential uncertainties.

2.1 Field survey across nitrogen deposition gradients

Forest growth observations or eddy correlation measurements of CO_2 exchange, either across spatial gradients of N deposition or along re-surveys with long-term changes in N deposition, have been used to assess the impacts of N deposition on forest productivity and C sequestration (e.g., Magnani et al., 2007; Thomas et al., 2010; Fleischer et al., 2013; Etzold et al., 2020). This approach is based on a statistical analysis between measured ecosystem variables (e.g., NPP or NEP) and N deposition, while statistically excluding the potential effects of other covarying environmental factors. However, the application of this approach is limited to regions showing strong spatial gradients of N deposition or experiencing significant changes in N deposition over time. Therefore, this approach has rarely been used to assess the effect of N deposition on a global scale.

Statistical approaches sometimes may fail to disentangle the effect of N deposition when there is a strong collinearity with other drivers (e.g., air CO_2 concentrations, temperature, soil nutrient and forest conditions). Improper attribution may lead to erroneous estimates of the effects caused by N deposition. Using observed data from eddy covariance flux towers in temperate and boreal forests in Europe, Magnani et al. (2007) suggest that after a removal of the age effects forest C sequestration (NEP) was overwhelmingly driven by N deposition and the C−N response was estimated as high as 725 kg C per kg N in wet deposition. This extremely high estimate of the C−N response was likely biased due to the covariation of N deposition with other factors (e.g., positive correlation between air temperature and N deposition), which were not properly accounted for (De Vries et al., 2008; Sutton et al., 2008). By conducting a re-analysis using total N deposition and further accounting for the cross-site climatic differences, Sutton et al. (2008) estimated a much weaker response of NEP to N deposition (50−75 kg C per kg N) for European forests. Using a meta-modeling standardization procedure in combination with eddy covariance CO_2 exchange fluxes from a Europe-wide network of 22 forest flux towers, Flechard et al. (2020) recently estimated that N deposition on average increased NEP by 40−50 kg C per kg N in European forests.

Inventory data from a large number of forest plots have also been used to assess the effects of N deposition on forest productivity and C sinks across a large geographic scale. Using forest inventory data of 24 most common tree species across the north-eastern and north−central US, Thomas et al. (2010) examined the effects of N deposition on tree growth and biomass C storage during the 1980s and 1990s. Their results suggest that N deposition increased aboveground biomass C storage by 61 (51−82) kg C per kg N. In Europe, the influence of N deposition on forest C sequestration by forest growth was investigated at stand level by Solberg et al. (2009) and at tree level by Laubhann et al. (2009) using data on measured bulk and throughfall N deposition and forest biomass for nearly 400 intensively monitored forest plots in Europe, including Norway spruce, Scots pine, common beech, European oak and sessile oak in the period 1993−2000. In their statistical analyses they accounted for the effects of changes in temperature, precipitation and drought and for site factors influencing measured tree growth, including site productivity, stand age and stand density. Overall, they estimated the average response in terms of C sequestration in kg C per kg N near between 21 and 26, based on a growth increase varying between 1.2% and 1.5% per kg N, depending on tree species composition (see also De Vries et al., 2008). More recently, Etzold et al. (2020) conducted a multivariate analysis of forest growth data from 442 even-aged permanent observation plots, mainly overlapping with those by Solberg et al. (2009) and Laubhann et al. (2009), during 1995−2010. They found that stand density and stand age were key predictors of annual stand volume increment while N deposition was the most important environmental driver. Specifically, forest growth showed a positive, but in some cases quadratic response to N deposition, with a threshold at about 30 kg N ha^{-1} $year^{-1}$ (Etzold et al., 2020). Such studies across N deposition gradients have provided spatially extensive evidence for the real effects of N deposition on forest growth and C sequestration.

2.2 Manipulative nitrogen addition/removal experiments

Manipulative N addition/removal experiments provide estimates of the effects of N deposition based on the doses of N addition/removal and the measured differences between treated plots and control plots. Earlier N addition/removal experiments have been mainly conducted in temperate and boreal forests, while the number of experimental studies has lately increased in tropical forests. Cross-site networks and individual studies of N addition/removal experiment have been established in different forest ecosystems globally. Examples of network studies include nitrogen saturation experiments (NITREX) and experimental manipulation of forest ecosystems (EXMAN) in Europe (Wright and Rasmussen, 1998), and nutrient enrichment experiments in China's forests (NEECF) (Du et al., 2013). In view of the difficulty to set up roofing experiments to remove N deposition and consequent biases due to unintended effects (e.g., reduced light and precipitation), N removal experiments have been rarely conducted and relevant insights in N deposition induced effects are thus mainly from N addition experiments.

Meta-analyses of existing N addition experiments can provide assessments of the overall effects of N deposition on C accumulation in forest biomass and soils. Effect size in earlier meta-analyses is mostly defined as the ln-transformed response ratio of treatment plot versus control plot estimating a relative effect of N addition irrespective of the N addition rate, which inhibits the possibility for upscaling as it does not give a C−N response (e.g., Liu and Greaver, 2010; Lu et al., 2011; Janssens et al., 2010; Yan et al., 2019; Deng et al., 2020; Xu et al., 2021). Effect size is also latterly defined as the mean difference between treatment plots and control plots divided by N additions (e.g., Schulte-Uebbing and de Vries, 2018), which provides a useful estimate for assessing the large-scale effects of N deposition (Schulte-Uebbing et al., 2022).

Forest NPP and C sequestration usually respond nonlinearly to increasing N deposition and the effect of N deposition also varies with the background N availability (De Vries et al., 2014). However, many N addition experiments are conducted using high-level N doses (e.g., >100 kg N ha^{-1} $year^{-1}$) and these experimental results may not accurately simulate the actual effects of N deposition that is generally within a range <60 kg N ha^{-1} $year^{-1}$ (Schwede et al., 2018, 2023). Moreover, considering that the C−N responses are also influenced by many biotic and abiotic factors (e.g., forest age, mycorrhizal associations, temperature, water availability and/or availability of other nutrients), uncertainties may increase when extrapolating experimental results to a large scale.

2.3 Stoichiometric scaling combined with ^{15}N tracer experiments

The stoichiometric scaling approach (Fig. 4.1) estimates the effect of N deposition on forest NPP (NPP_{Ndep}) by multiplying the rates of N deposition (N_{dep}), N use efficiency (NUE), the fractions of the N allocation (f_N) to different forest compartments (i.e., stem and branch, coarse root, leaf, fine root and soil) and the corresponding C:N mass ratios ($R_{C:N}$) (Du and de Vries, 2018), as Eq. (4.1),

$$NPP_{Ndep} = N_{dep} \times NUE \times \sum (f_N \times R_{CN}) \tag{4.1}$$

The N use efficiency of N deposition can be derived from ^{15}N tracer experiments (Du and de Vries, 2018). The fractions of the N allocation and C:N ratios in different

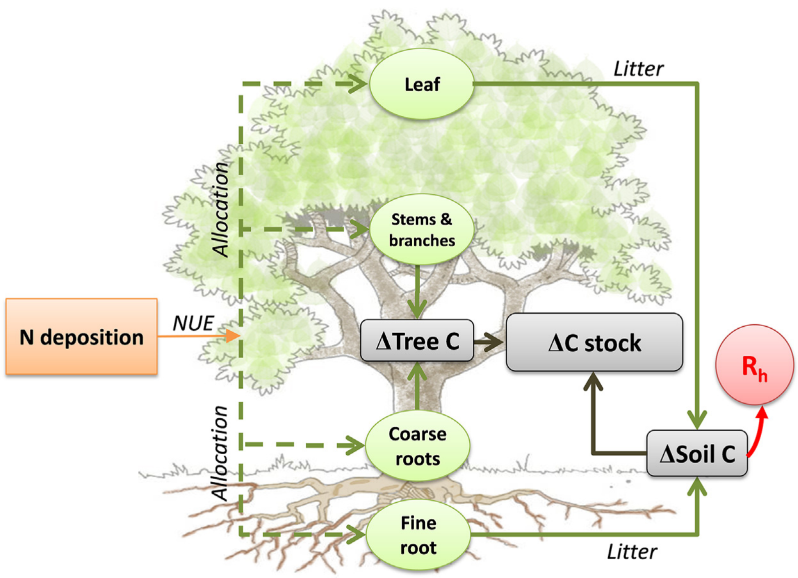

FIG. 4.1 The scheme of stoichiometric scaling approach to estimate the effect of N deposition on forest NPP and C sequestration. *NUE*, nitrogen use efficiency; *Rh*, heterotrophic respiration. *Adapted from Schulte-Uebbing, L., de Vries, W., 2018. Global-scale impacts of nitrogen deposition on tree carbon sequestration in tropical, temperate, and boreal forests: a meta-analysis. Global Change Biol. 24 (2), 416–431, with permission.*

forest compartments can be estimated from allometric and stoichiometric data. The contribution of N deposition to C sequestration can be estimated as the N deposition-induced change in ecosystem C stock ($\Delta C\ stock_{Ndep}$), including an increase of tree woody biomass C stock ($\Delta C\ stock_{tree}$) and an increase of soil C stock ($\Delta C\ stock_{soil}$), as Eq. (4.2),

$$\Delta C\ stock_{Ndep} = \Delta C\ stock_{tree} + \Delta C\ stock_{soil} \tag{4.2}$$

The N deposition-induced increase of woody biomass C stock can be calculated as Eq. (4.3),

$$\Delta C\ stock_{tree} = N_{dep} \times NUE \times \sum (f_{N\ wood} \times R_{CN\ wood}) \tag{4.3}$$

where $f_{N\ wood}$ and $R_{C:N\ wood}$ indicate the fractions of the N allocation to woody compartments (i.e., stem and branch, coarse root) and the corresponding C:N mass ratios. The N deposition-induced increase of soil C stock can be estimated as Eq. (4.4),

$$\Delta C\ stock_{soil} = N_{dep} \times NUE \times \sum (f_{N\ non-wood} \times R_{CN\ non-wood} \times f_{res}) \tag{4.4}$$

where $f_{N\ non-wood}$ and $R_{C:N\ non-wood}$ indicate the fractions of the N allocation to nonwoody compartments (i.e., leaf and fine root) and the corresponding C:N mass ratios, f_{res} is the residual fraction of nonwoody litters after long-term decomposition. The stoichiometric scaling approach can be used to assess the effects of N deposition on forest NPP and C sequestration from ecosystem to global scales.

Several uncertainties remain in the stoichiometric scaling approach and may cause potential biases in the estimated effects of N deposition. For example, the stoichiometric scaling approach usually assumes constant C:N ratios and N allocation fractions for a given forest biomass compartment. However, empirical evidence indicates that a stoichiometric shift (e.g., decreasing C:N ratio) in forest biomass compartments can occur under elevated N deposition (Eastman et al., 2021; De Jong et al., 2022). Moreover, biomass allometric partitioning can be changed by increasing N deposition over time (e.g., increasing ratios of aboveground versus belowground biomass) (Ibáñez et al., 2016). Using standard allometric equations may thus result in biased estimate of biomass and woody C sequestration.

Another key parameter for the stoichiometric scaling approach is the N use efficiency which may vary with the N supply pathway, the forms of deposited N, the rate of N input and the background N availability of the forest ecosystems. By combining several ^{15}N tracer experiments, Nadelhoffer et al. (1999) showed that only a very small proportion of the added N (~5%) was stored in trees whereas most of the deposited N (~70%) was actually stored in soils. A later synthesis of ^{15}N tracer experiments with a duration >1 year estimated average N use efficiencies of 34% in boreal forests, 29% in temperate forests and 21% in tropical forests (Du and de Vries, 2018). Paired ^{15}N tracer experiments further indicate that plants generally take up more labeled nitrate (20%) than ammonium (12%), whereas soils retain more ammonium (57%) than nitrate (46%) (Gurmesa et al., 2022). Nitrogen use efficiency generally decreases nonlinearly with increasing N deposition (Fig. 4.2), thus resulting in lower C−N response ratios (Du and De Vries, 2018). Current estimates of N use efficiency were meanly derived from studies applying ^{15}N tracers to forest floor. Several experiments applying ^{15}N

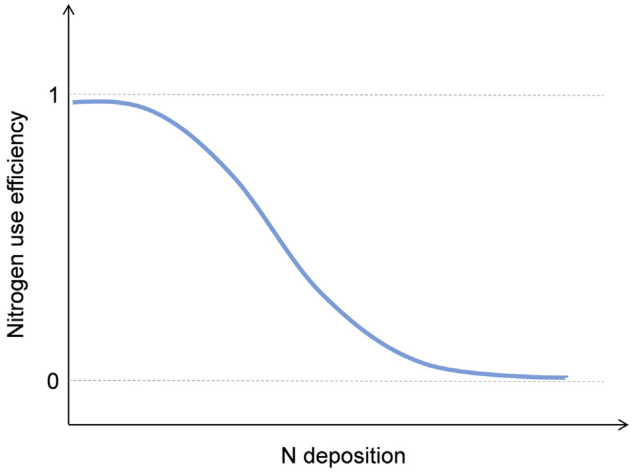

FIG. 4.2 Changes in forest N use efficiency in response to increasing N deposition.

tracers to tree crowns and forest canopies suggest that canopy N uptake can be substantial (Gaige et al., 2007; Nair et al., 2016; Ferraretto et al., 2022). However, canopy N uptake is largely neglected in current estimates of N use efficiency.

2.4 Model simulations

Comprehensive and spatially explicit assessments of the impacts of N deposition on forest NPP and C sequestration can be conducted using earth system models that include global C and N cycles and their interactions (Thornton et al., 2007; Piao et al., 2013; Fleischer et al., 2015; Tharammal et al., 2019; Davies-Barnard et al., 2020). In the Fifth Phase of the Coupled Model Intercomparison Project (CMIP5), only two earth system models incorporated terrestrial N cycling (Taylor et al., 2012; Piao et al., 2013) but the number increased to 10 in the Sixth Phase of the Coupled Model Intercomparison Project (CMIP6) (Arora et al., 2020). The representation of N limitation to C uptake in the land surface module of earth system models is a great progress to address the biggest systematic bias in future projections of land C sinks in response to rising CO_2 concentrations. Simulation experiments have been designed to evaluate the historical or future effects of N deposition in comparison to a control scenario, often simultaneously accounting for elevated CO_2 concentrations and climate change. However, the results of such projections usually vary greatly among different models due to divergent choices in the representation of key N cycle processes (Davies-Barnard et al., 2020).

Further improvement of C−N interactions in earth system models depends on better understanding and more detailed incorporation of key N cycling processes and C−N interactions. For example, some key processes of the N cycle mediated by the microbial organisms are not well represented in current earth system models. Biological N fixation is simply estimated as a function of NPP and evapotranspiration in current earth system models (Davies-Barnard et al., 2022). This results in unreasonable feedbacks that N limitation decreases NPP and evapotranspiration, which further decreases biological N fixation that is theoretically expected to increase in response to N limitation (Kou-Giesbrecht and Arora, 2022; Davies-Barnard et al., 2022). This implies systematic problems of model structures and severe limitations to project the biological N fixation in response to rising CO_2 concentrations. Another potential important limitation of most existing models is the lack of an explicit treatment of microbes as decomposers and related plant-microbe interactions (Zaehle and Dalmonech, 2011). As shown by various authors, neglecting the role of microbial adaptation to changes in CO_2, N deposition and climate, may have important impacts on long-term soil organic matter decay and thus on soil N availability (Allison et al., 2010; Wieder et al., 2013). Furthermore, the mycorrhizal symbiosis has been rarely included in earth system models, although empirical evidences indicate that trees with arbuscular mycorrhizal associations showed stronger growth response to N deposition than those with ectomycorrhizal associations (Thomas et al., 2010).

The stoichiometric C:N ratios of ecosystem compartments are important parameters for C−N interactions in models. Compared with models using fixed C:N ratios, models using flexible C:N ratios have been shown to make more convincing predictions in agreement with results from N addition experiments (Meyerholt and Zaehle, 2015). The C−N interactions can also be affected by other nutrients (e.g., P, K, Ca, and Mg) that are essential for plant growth and this is particularly crucial for P limitation that occurs widely in terrestrial ecosystems (Du et al., 2020b). However, there are very few models simultaneously including C, N and P cycles (e.g., Goll et al., 2012; Wang et al., 2017) and there was only one CMIP6 earth system model including both N and P cycles (Ziehn et al., 2021). Compared to earth system models without nutrient limitation, model projections generally result in a reduction of land C uptake by 25%−50% when both accounting for N and P limitation (Wieder et al., 2015; Ziehn et al., 2021). Models that did not account for N and P limitations were also found to overestimate the effect of CO_2 fertilization on plant biomass accumulation in comparison to statistically upscaled estimates from observations (Terrer et al., 2019). These studies strongly emphasize that both N and P limitation should be included in earth system models to enable more realistic projections of future land C sinks in view of rising atmospheric CO_2 concentrations.

3. Effects of nitrogen deposition on global forest productivity and carbon sequestration

In this section, the global-scale impacts of N deposition on NPP and C sequestration in forest biomes are synthesized based on a review of literature. We only include global-scale estimates using three approaches, i.e., meta-analysis of manipulative N addition experiments, stoichiometric scaling, and model simulation (Tables 4.1 and 4.2). Results from field survey across spatial gradients of N deposition are not included in this section because this approach is limited to regional scale and have large uncertainties when scaling up to global scale.

3.1 Estimates from meta-analyses approach

Meta-analyses of results from N addition experiments can provide estimates of the overall effects of N deposition in global forest biomes. However, most meta-analysis studies only report the relative effect of N deposition as ln-transformed ratio of treatment plot versus control plot or percentage change per kg N compared to control plots (Liu and Greaver, 2010; Lu et al., 2011; Janssens et al., 2010;

TABLE 4.1 A summary of the estimated responses of C sequestration to N deposition (kg C per kg N) in global forest biomes. The estimates are derived from meta-analysis of N addition experiments (Schulte-Uebbing and de Vries, 2018; Deng et al., 2020; Schulte-Uebbing et al., 2022), stoichiometric scaling (De Vries et al., 2014; Du and de Vries, 2018; Gurmesa et al., 2022), and model simulations (Fleischer et al., 2015).

Compartments	Boreal	Temperate	Tropical
Aboveground woody biomass (AWB)			
Schulte-Uebbing and de Vries (2018)	14 (11–18)	13 (11–15)	1 (−1 to 4)
Schulte-Uebbing et al. (2022)	11 (4–21)	4 (0–8)	0 (−4 to 5)
De Vries et at. (2014)	21 (17–25)	14 (12–17)	5 (3–7)
Du and de Vries (2018)	14 (9–19)	5 (2–9)	4 (1–8)
Belowground woody biomass (BWB)			
De Vries et al. (2014)	5 (4–6)	3 (2–4)	1 (1–2)
Du and de Vries (2018)	3 (2–5)	2 (1–3)	1 (0–2)
Total biomass (AWB + BWB)			
De Vries et al. (2014)	26 (21–31)	17 (14–21)	6 (4–8)
Du and de Vries (2018)	17 (11–24)	7 (3–12)	5 (1–10)
Gurmesa et al. (2022) (NH_x-N)	14 (3–37)	11 (4–20)	12 (6–22)
Gurmesa et al. (2022) (NO_y-N)	45 (17–84)	21 (10–37)	17 (8–32)
Soil			
Deng et al. (2020)	28 (21–35)	18 (16–20)	7 (6–8)
De Vries et al. (2014)	14 (11–18)	14 (11–18)	5 (4–7)
Du and de Vries (2018)	7 (4–11)	3 (1–4)	1 (0–1)
Gurmesa et al. (2022) (NH_x-N)	20 (10–34)	14 (9–19)	8 (4–15)
Gurmesa et al. (2022) (NO_y-N)	14 (8–21)	13 (10–17)	10 (7–16)
Total (soil + biomass)			
De Vries et al. (2014)	40 (32–50)	31 (25–39)	12 (8–15)
Du and de Vries (2018)	24 (15–35)	10 (4–16)	6 (1–11)
Gurmesa et al. (2022) (NH_x-N)	35 (22–54)	16 (18–38)	21 (14–29)
Gurmesa et al. (2022) (NO_y-N)	59 (35–86)	34 (22–50)	28 (19–39)
Fleischer et al. (2015)	17 (12–22)	24 (22–26)	26 (15–37)

TABLE 4.2 A summary of N deposition induced C sink in global forests. The results were based on stoichiometric scaling (De Vries et al., 2014; Du and de Vries, 2018; Wang et al., 2017; Gurmesa et al., 2022), meta-analysis of N addition experiments (Schulte-Uebbing and de Vries, 2018), and model simulations (Fleischer et al., 2015). Units: Area, 10^6 km^2; Ndep, Tg N $year^{-1}$; C sink, Pg C $year^{-1}$.

Study	Period/year	Boreal forest			Temperate forest			Tropical forest			Global		
		Area	Ndep	C sink	Area	Ndep	C sink	Area	Ndep	C sink	Area	Ndep	C sink
Woody biomass C sink													
Du and de Vries (2018)	2001	12.2	1.9	0.04	9.7	9.0	0.08	18.7	10.2	0.07	40.6	21.1	0.19
Schulte-Uebbing and de Vries (2018)	2000	12.1	2.2	0.04	10.2	8.0	0.12	17.9	11.4	0.02	40.2	21.6	0.18
Soil C sink													
Du and de Vries (2018)		12.2	1.9	0.02	9.7	9.0	0.03	18.7	10.2	0.01	40.6	21.1	0.06
Total C sink													
De Vries et al. (2014)	1993	7.8	1.3	0.03	8.6	7.1	0.13	16.2	6.9	0.11	32.6	15.3	0.27
Du and de Vries (2018)	2001	12.2	1.9	0.06	9.7	9.0	0.11	18.7	10.2	0.08	40.6	21.1	0.25
Wang et al. (2017)	2010	7.2	1.7	0.08	7.2	6.6	0.20	11.5	7.9	0.10	25.9	16.2	0.38
Gurmesa et al. (2022)	2010	12	3.7	0.17	7	8	0.24	23	13.1	0.31	42	24.8	0.72
Fleischer et al. (2015)	2000	11.4	4.1	0.07	7.7	4.8	0.11	19.5	10.3	0.27	38.6	19.2	0.46

Yan et al., 2019; Deng et al., 2020). It is not reasonable to extrapolate the relative effect to a large scale because multiplying the same percentage change with spatially varied background NPP or C stocks can lead to largely varied and ecologically implausible C−N responses in kg C per kg N. Therefore, we only rely on two studies by Schulte-Uebbing and de Vries (2018) and Schulte-Uebbing et al. (2022), that report absolute effects as kg C per kg N to avoid possible misleading interpretation.

A meta-analysis of N addition experiments by Schulte-Uebbing and de Vries (2018) suggests that N deposition significantly stimulated aboveground NPP in boreal and temperate forests and resulted in additional C sequestration of 14 and 13 kg C per kg N in aboveground woody biomass, respectively, while the effect on aboveground NPP was not significant in tropical forests (Table 4.1). The latitudinal decrease of C−N response from boreal to tropical forests is likely due to a shift in the strength of N limitation that generally decreases toward lower latitudes (Du et al., 2020a). Combining the C−N responses with forest areas and spatially explicit N deposition (base year 2000), Schulte-Uebbing and de Vries (2018) estimated that N deposition increased C sequestration by 0.15 Pg C year^{-1} in aboveground woody biomass in global forests. Assuming a constant C allocation (20%) to coarse roots versus aboveground woody biomass, they further estimated that N deposition induced woody biomass C sinks of 0.04, 0.12, and 0.02 Pg C year^{-1} in boreal, temperate and tropical forests, respectively, summing up to a total woody biomass C sink of 0.18 Pg C year^{-1} in global forests (Table 4.2). It is worth noting that the low N deposition-induced C sinks in boreal and tropical biomes were due to low levels of N deposition and low C−N response, respectively.

Based on a global extrapolation using meta-regression models with important predictors (i.e., potential evapotranspiration, soil N content and stand age), Schulte-Uebbing et al. (2022) lately estimated that the C−N response in aboveground woody biomass were on average 11, 4, and 0 kg C per kg N in boreal, temperate and tropical forests, respectively (Table 4.1). On a global scale, N deposition (base year 2010) thus only resulted in a nearly negligible C sink in aboveground woody biomass (0.04 Pg C year^{-1}) (Schulte-Uebbing et al., 2022), being much lower than their previous estimate (0.15 Pg C year^{-1}) (Schulte-Uebbing and de Vries, 2018). This difference implies the necessity to consider spatially explicit climate, edaphic, and vegetation conditions when upscaling the effects of N deposition globally (Gundale, 2022). However, the extrapolation analysis by Schulte-Uebbing et al. (2022) didn’t include the N deposition-induced changes in soil C stocks, which have been shown to be important in several experimental studies (Janssens et al., 2010; Forsmark et al., 2020; Lu et al., 2021).

The effects of N deposition on soil C sequestration depend on the overall N deposition-induced changes in soil C inputs (e.g., leaf litter, fine root litter) and/or outputs (e.g., soil respiration, leaching of dissolved organic C). However, early meta-analyses have drawn inconsistent conclusions. A meta-analysis of experimental results in forests mainly from North America and Europe suggested no significant effect of N addition on C storage in both organic horizon and mineral soils although N addition significantly increased aboveground and belowground production (Lu et al., 2011). The negligible N stimulation of soil C storage was attributed to a shift toward higher aboveground than belowground biomass allocation and a significant stimulation of soil respiratory C loss (Lu et al., 2011). In contrast, a meta-analysis by Liu and Greaver (2010) suggested that N addition significantly increased the C content of the organic layer but not the mineral soil layer. They also found that N addition reduced heterotrophic respiration and increased litter input from aboveground but not from fine root (Liu and Greaver, 2010). Another meta-analysis indicates that N deposition impeded heterotrophic respiration and substantially increased soil C sequestration (i.e., 19 kg C per kg N) in temperate forests where N was not limiting to microbial growth (Janssens et al., 2010). Although N deposition generally exerts little effects on forest growth in N-rich tropical regions, an experimental study indicates that excess N deposition accelerated soil C storage in subtropical forests (9−11 kg C per kg N) (Lu et al., 2021).

Based on a large empirical data set spanning 60 years across 369 sites, a recent meta-analysis concluded that N addition significantly increased soil organic C content by 4.2% (2.7%−5.8%) across global terrestrial biomes and this effect was amplified over longer N addition durations in both organic and mineral soil layers (Xu et al., 2021). However, another global meta-analysis by Deng et al. (2020) showed that N addition had no significant effect on soil organic C content in boreal, temperate and tropical forests, but it significantly decreased soil respiration in boreal and temperate forests. However, Deng et al. (2020) further estimated that N deposition increased soil C sequestration by 28, 18, and 7 kg C per kg N in boreal, temperate and tropical forests, respectively (Table 4.1). This seems very high, especially for boreal forest, leading to a soil C sink of 0.35 Pg C year^{-1} that is twice as high as the N deposition induced woody biomass C sink (0.18 Pg C year^{-1}) by Schulte-Uebbing and de Vries (2018). Moreover, realistic N deposition at low levels may accelerate heterotrophic respiration under conditions that microbial growth is constrained by N limitation (Janssens et al., 2010; De Vries et al., 2014) but such effect is largely unrepresented in existing studies and this potentially results in an overestimate of the N deposition induced soil C sink.

3.2 Estimates from stoichiometric scaling approach

The stoichiometric scaling approach can give systematic estimates of C−N responses for different forest compartments (e.g., above- and belowground woody biomass and soils) that can further be scaled up to the N deposition-induced productivity and C sink on a large scale. De Vries et al. (2014) estimated that N deposition increased aboveground woody biomass C sequestration by 21, 14, and 5 kg C per kg N in global boreal, temperate and tropical forests, respectively (Table 4.1). Using an updated algorithms and parameters, Du and de Vries (2018) estimated lower aboveground woody biomass C sequestrations by 14, 5, and 4 kg C per kg N in global boreal, temperate and tropical forests, respectively (Table 4.1). Compared with the aboveground compartments, belowground woody biomass production showed much weaker response to N deposition, being 3−5, 2−3 and 1 kg C per kg N in global boreal, temperate and tropical forests, respectively (Table 4.1). Overall, De Vries et al. (2014) estimated that N deposition increased total woody biomass C sequestration by 26, 17, and 6 kg C per kg N in global boreal, temperate and tropical forests, respectively. The estimates by Du and de Vries (2018) were lower (17, 7, and 5 kg C per kg N, respectively) and summed up to 0.19 Pg C $year^{-1}$, divided over 0.04, 0.08, and 0.07 Pg C $year^{-1}$ in global boreal, temperate and tropical forests, respectively (Table 4.2). The estimate of N deposition induced woody biomass C sequestration using stoichiometric scaling approach by Du and de Vries (2018) is comparable to the result based on the meta-analysis approach by Schulte-Uebbing and de Vries (2018), i.e., 0.19 and 0.18 Pg C $year^{-1}$, respectively.

Based on a synthesis of paired ^{15}N tracer experiments in temperate and (sub)tropical forests, Gurmesa et al. (2022) found that plant use efficiency of nitrate was higher than that of ammonium. Therefore, they separately evaluated the effects of these two different N forms. Specifically, they estimated that deposited ammonium potentially increased aboveground woody biomass C sequestration by 14, 11, and 12 kg C per kg N in boreal, temperate and tropical forests, respectively, whereas the effect of nitrate was much higher at 45, 21, and 17 kg C per kg N, respectively (Table 4.1). Their results showed that the woody biomass C−N response in temperate forests was comparable to tropical forests where N is not limiting (Du et al., 2020a). Their estimates are likely subject to large biases because experimental studies commonly show that N addition rarely stimulates NPP in tropical forests (Schulte-Uebbing and de Vries, 2018; Schulte-Uebbing et al., 2022).

Using a stoichiometric scaling approach, Du and de Vries (2018) estimated that N deposition increased soil C sequestration by 7, 3, and 1 kg C per kg N in global boreal, temperate and tropical forests, respectively (Table 4.1), summing up to a global soil C sink of 0.06 Pg C $year^{-1}$ (Table 4.2). In contrast, other two stoichiometric scaling studies estimated much stronger responses of soil C sequestration to N deposition (Table 4.1; De Vries et al., 2014; Gurmesa et al., 2022), corresponding to a high N deposition-induced soil C sink of 0.25−0.28 Pg C $year^{-1}$ given the same forest area and N deposition as Du and de Vries (2018). Considering that both meta-analysis and stoichiometric studies have made inconsistent estimates of N deposition induced soil C sequestration, large uncertainties thus remain in the current understanding of soil C sink due to N deposition.

Combining the effects on woody biomass and soils, Du and de Vries (2018) estimated that N deposition on average increased total C sequestration by 24, 10, and 6 kg C per kg N in boreal, temperate and tropical forests, respectively (Table 4.1), leading to a total C sink of 0.25 Pg C $year^{-1}$on a global scale (Table 4.2). Although De Vries et al. (2014) estimated much higher C−N responses (Table 4.1), they estimated a similar C sink of 0.27 Pg C $year^{-1}$ by using lower forest area and N deposition (Table 4.2). Using lower forest areas and N deposition, Wang et al. (2017) estimated an N deposition induced increase of C sink by 0.38 Pg $year^{-1}$ in global forests. However, Gurmesa et al. (2022) estimated that N deposition increases global forest C sink by 0.72 Pg C $year^{-1}$, being 2−3 times of the previous estimates using the stoichiometric scaling approach (Table 4.2; De Vries et al., 2014; Wang et al., 2017; Du and de Vries, 2018). The estimate of high N deposition-induced C sink by Gurmesa et al. (2022) is mainly attributable to higher C−N response especially in tropical forests and higher levels of N deposition (Tables 4.1 and 4.2).

3.3 Estimates from modeling simulation

An increasing number of earth system models have incorporated terrestrial N cycling and its interactions with C cycling (Arora et al., 2020; Davies-Barnard et al., 2020) because of the essential role of N limitation in constraining future C sinks in response to rising atmospheric CO_2 and climate change (Thornton et al., 2007; Wieder et al., 2015; Ziehn et al., 2021). Such improvement of earth system models enable an evaluation of the effects of N deposition on terrestrial C sink, but the modeling results frequently deviate from those of empirical studies mainly due to the inaccurate representation of key N cycle processes, lack of including P limitation and other model limitations, as discussed in Section 2.4 (see also Davies-Barnard et al., 2020). For example, Fleischer et al. (2015) estimated that the C−N deposition response increased toward lower latitudes, on average being 17, 24, and 26 kg C per kg N in boreal, temperate and tropical forests, respectively (Table 4.1), summing up to a global C sink of 0.46 Pg C $year^{-1}$ (Table 4.2). Their estimates, however, showed an opposite latitudinal trend in comparison with results from empirical studies and stoichiometric scaling (Table 4.1). The failure to capture the spatial pattern of N deposition induced C sequestration is likely due to the fact that P limitation was not well represented in their model simulations (Fleischer et al., 2015).

Model simulations are frequently used to evaluate N deposition induced NPP and C sink in historical periods and make projections for future scenario. Using the Community Land Model 4.0 (CLM4), Bala et al. (2013) estimated that increased N deposition caused an additional NPP of 175 Pg C in global terrestrial ecosystems from preindustrial period to 2000, being comparable to the effect of CO_2 fertilization (242 Pg C). Another simulation using fully coupled NCAR Community Earth System Model (CESM1.0.4) also suggested that N deposition contributed to comparable NPP as CO_2 fertilization (2.0 versus 2.3 Pg C $year^{-1}$) during the period 1850–2005 (Devaraju et al., 2016). Moreover, an overview of model simulations suggests that CO_2 fertilization is the primary driver (up to 85%) of the recent increase in land C sink followed by N deposition (~10%–20%) while the effects of N deposition on future C sink are likely small (~2%–10%) (Tharammal et al., 2019).

3.4 Overall effect of nitrogen deposition on greenhouse gas emissions

Based on a review of literature, we show that the global estimates of N deposition induced C sink in global forests range from 0.25 to 0.72 Pg C $year^{-1}$. Considering that the lower-end estimates of C–N responses by stoichiometric scaling showed better agreement with the result from meta-analyses of N addition experiments (Table 4.2), we can infer that current N deposition more reasonably increases the C sink by ~0.3 Pg C $year^{-1}$ in global forests. In that case, the N deposition induced C sink only accounts for 15% of the total C sink in global forests (~2.0 Pg C $year^{-1}$) (Pan et al., 2011).

Based on a meta-analysis of experimental results, Xia et al. (2023) have estimated that N deposition currently decreases the soil CH_4 sink by 0.18 Tg CH_4 $year^{-1}$ in global forests, being equivalent to an increase of 5.4 Tg CO_2 $year^{-1}$ using a global warming potential of 29.8 kg CO_2 equivalents per kg CH_4 for a 100-year timescale based on the most recent insight of IPCC AR6. Additionally, N deposition has been estimated to cause an overall emission of 0.17 Tg N_2O $year^{-1}$ from global forest soils (Du et al., 2023), being equivalent to an increase of 46 Tg CO_2 $year^{-1}$ assuming a global warming potential of 273 kg CO_2 equivalents per kg CH_4 for a 100-year timescale according to IPCC AR6. Combining the effects of N deposition on soil CH_4 uptake and N_2O emissions, we estimate an overall increase of global warming potential by 51 Tg CO_2 $year^{-1}$. This is negligible compared with the N deposition induced C sink in global forests (1100 Tg CO_2 $year^{-1}$ when using a sink of 0.3 Pg C $year^{-1}$, being 300 Tg CO_2 -C $year^{-1}$ multiplied by 44/12). Therefore, we can conclude that N deposition causes an overall reduction of global warming potential (1050 Tg CO_2 $year^{-1}$) via changing uptake/emissions of the three major greenhouse gases in global forests.

4. Discussion and future research needs

Although great efforts have been made to understand the effects of N deposition on forest growth and C sequestration in global forests, several key knowledge gaps remain in this research topic. Future research efforts are needed to elucidate (i) the difference between the responses of C fluxes and C stocks to N deposition, (ii) the effect of canopy interactions with N deposition, (iii) the response to decreasing rates and shifting chemical composition of N deposition, (iv) interactions with P limitation, (v) the interactions with other global change drivers, and (vi) the effect of N deposition on growth and C sequestration of managed forests. The new insights will better inform earth system models to predict the effects of N deposition under future environmental change.

4.1 Difference between the responses of carbon fluxes and carbon stocks

Empirical studies generally show that N deposition altered various C fluxes in forest ecosystems, such as soil respiration, NPP and NEP. For instance, N deposition generally simulates NPP and NEP in N-limited forests, but it exerts no significant effects on forest growth in N-rich conditions (Schulte-Uebbing et al., 2022). Low-level N deposition provides external N supply for the growth of microbial organisms and thus accelerate soil organic matter decomposition in N-limited ecosystem, while high-level N inputs are found to inhibit soil respiration (Janssens et al., 2010; De Vries et al., 2014; Xing et al., 2022; Kuyper et al., 2023). Previous studies mainly focused on measured C fluxes on an annual basis and assume that higher annual CO_2 uptake can be transformed to larger C stocks over time. However, it is questionable whether the N deposition-induced transient increase in C fluxes can be actually transformed to long-term ecosystem C storage. A long-term N addition experiment (0, 10, 50, and 100 kg N ha^{-1} $year^{-1}$) showed that N addition increased plant biomass production but had no significant effect on soil C storage in a temperate grassland (Wilcots et al., 2022), whereas such studies are still rare in forest ecosystems.

It also remains unexamined whether N deposition only accelerates the accumulation of ecosystem C stocks tracking an intrinsic curve during forest succession or it can finally enlarge the maximum potential of the ecosystem C stock (Fig. 4.3). The answer to this question is crucial to understand the actual effects of N deposition on forest C sinks in the long term. This calls for long-term experimental studies on a perspective of forest succession.

Here we propose three hypothesized scenarios for the long-term changes of forest C stock under elevated N deposition (Fig. 4.3). For a given condition with low N deposition, total C stock in a forest ecosystem accumulates over time and approaches a maximum (C_{max}) at a certain age (T_0) without severe disturbances. The first hypothesized scenario (Hypothesis 1: faster and larger) predicts that elevated N deposition both increases the accumulation rate of the ecosystem C stock ($T_1 < T_0$) and enlarges the maximum size of the ecosystem C stock, being in line with the view of many previous studies. The second scenario (Hypothesis 2: faster but not larger) predicts that elevated N deposition may only shorten the time ($T_2 < T_0$) to approach the maximum ecosystem C stock but don't enlarge it. The third scenario (Hypothesis 3: larger but not faster) predicts that ecosystem C stock increases with forest age in line with an intrinsic curve during forest succession but elevated N deposition can further enlarge the final ecosystem C stock mainly via increasing soil C storage. The first and second scenarios might occur in N-limited forests (e.g., boreal forest) while the third scenario may occur in forest ecosystems (e.g., tropical and subtropical forests) where N is not limiting. These hypothesized scenarios can be tested by long-term N addition experiments (e.g., >30 years).

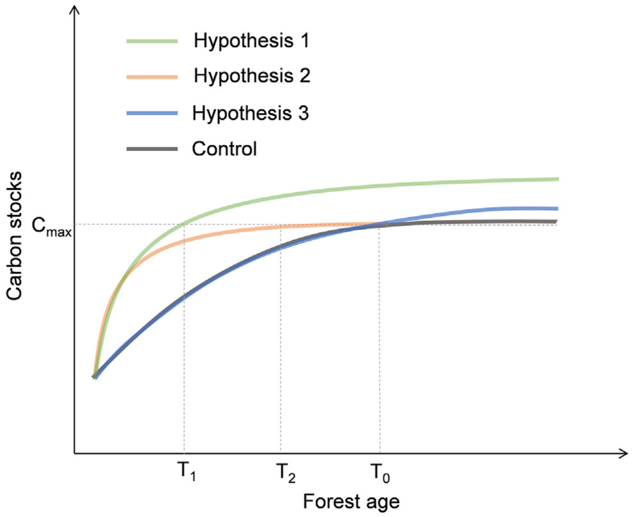

FIG. 4.3 Hypotheses of long-term changes in forest C stocks with forest age under elevated N deposition. C_{max} indicates the maximum C stock of the forest ecosystem for a given low N deposition condition (control). T_1 and T_2, and T_0 indicate the time approaching C_{max} in three hypothesized scenarios under elevated N deposition with T_0 being the time in the control situation. Note that the control scenario overlaps with hypothesis 3 up to T_0.

4.2 Effects of canopy interactions with nitrogen deposition

Major knowledge of the ecological effects of N deposition on forest growth and C sequestration has been derived from manipulative experiments that directly apply N additions to forest floors. These experiments ignore the strong interactions between forest canopy and N deposition (Fig. 4.4; Lovett and Lindberg, 1993; Bortolazzi et al., 2021; Beachley et al., 2023). Tree leaves can both assimilate soluble N during wet deposition and take up airborne N in gaseous forms (e.g., NH_3 and NO_2) during rainless periods, potentially contributing to N supply for photosynthesis and growth (Sievering et al., 2000; Sparks, 2009; Nair et al., 2016). The rates of canopy N uptake can be derived from experimental studies that apply ^{15}N tracer to foliage of saplings or forest canopies. A mesocosm canopy ^{15}N tracer experiment indicates that 60% of ^{15}N tracer was recovered in needles, stem and branches of Sitka spruce saplings (Nair et al., 2016). A field canopy ^{15}N tracer experiment in Sitka spruce plantation further showed that the canopy was a sink of N deposition (Ferraretto et al., 2022). Moreover, a large-scale experiment of helicopter N spraying in central Maine suggested that more than 70% of the applied N was retained in forest canopy (Gaige et al., 2007). These results imply that direct N addition to forest floor most likely underestimates the C−N response since part of the canopy retained N is used for photosynthesis and transformed to NPP and C stock. Canopy interactions with N deposition should be considered in the new generation of canopy N addition experiments (Zhang et al., 2015) and represented in process-based models.

4.3 Response to decreasing rates and shifting composition of nitrogen deposition

Although N deposition has increased in many developing regions, it has decreased for decades in Europe and the US

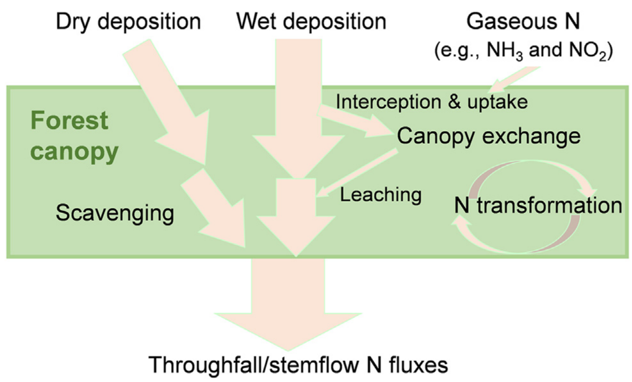

FIG. 4.4 Conceptual diagram of the interactions between forest canopy and N deposition. These interactions include interception of wet and dry deposition, scavenging of dry deposited N, foliar N uptake, canopy N leaching and N transformation.

and recently in China, all being major hotspots of N deposition over the world (Du, 2016; Engardt et al., 2017; Liu and Du, 2020). Previous studies have mostly focused on the effects of elevated N deposition on forest growth and C sequestration, while the effects of decreasing N deposition remain less-well understood (Gilliam et al., 2023; Schmitz et al., 2023). The ecosystem response to decreasing N deposition likely differs from the response to increasing N deposition. A hysteretic model predicts a legacy of ecosystem response to decreasing N deposition (Gilliam et al., 2023), but the proposed legacy effect on plant productivity and C sequestration remains to be tested in various forest ecosystems. The effects of decreasing N deposition can be quantified via progressively cessation of N additions in long-term experiments, monitoring ecosystem changes in areas with decreasing N deposition, and roofing experiments where rain is collected and cleaned. Such experimental studies will update our understanding of future forest C sinks in regions with a further decrease in N deposition.

In accompany with a rapid change in the rate of N deposition, chemical composition also shifts substantially with an increasing dominance of ammonium over nitrate, since NO_x emission reduction is until now faster than NH_3 emission reduction (Du, 2016; Engardt et al., 2017; Schwede et al., 2023). Such a change in chemical composition may affect the forest growth response to N deposition due to different fates and effects of deposited ammonium and nitrate. As mentioned above, an analysis of ecosystem-scale paired ^{15}N tracer experiments in forest ecosystem indicated that plants took up more labeled nitrate than ammonium (Gurmesa et al., 2022). Using a stoichiometric scaling approach, they further estimated a much stronger increase of C sequestration in response to nitrate deposition than ammonium deposition, mainly due to a stronger C accumulation in woody biomass (Gurmesa et al., 2022). However, a meta-analysis of N addition experiments suggest that tree growth showed greater response to ammonium additions than nitrate additions (Yan et al., 2019), implying an opposite effect compared to the stoichiometric scaling approach (Gurmesa et al., 2022). This inconsistency implies that the different roles of ammonium and nitrate should be better elucidated.

4.4 Interactions with phosphorus limitation

Nitrogen is conventionally believed to limit plant growth globally since the publication of a review paper by Vitousek and Howarth (1991), who concluded that N limits NPP in most terrestrial biomes and many marine ecosystems. This point of view has lately been strengthened by meta-analyses of fertilization experiments (Elser et al., 2007; LeBauer and Treseder, 2008). However, such meta-analyses are strongly affected by publication bias because experimental results with no significant fertilization effects are less likely published. Using a new approach based on leaf N and P resorption ratios of dominant species, a recent assessment indicates that 18% of the natural terrestrial area is limited by N, whereas 43% is P limited (Du et al., 2020a). Human-induced N inputs in terrestrial ecosystems may further strengthen P limitation in terrestrial ecosystems (Luo et al., 2022). For example, anthropogenic emissions generally cause a much stronger increase in N deposition than P deposition and the imbalanced N and P deposition may further shift ecosystems toward P limitation (Du et al., 2016). Experimental studies suggest that N deposition can result in lower foliar P concentrations and thus in turn increase P limitation to forest growth (Braun et al., 2010; Du et al., 2021). These evidences imply that N limitation likely occurs in a lower proportion of land area in comparison to the conventional view. The interactions with P should thus be considered in empirical and modeling studies when extrapolating the effects of N deposition on NPP and C sequestration to a global scale because the expected growth acceleration by N deposition can be constrained by P limitation.

4.5 Interactions with other global change drivers

Forest growth and consequent C sequestration are simultaneously affected by N deposition and many other global change factors, such as climate warming, elevated concentrations of CO_2 and O_3, drought, and P deposition (Fig. 4.5). For example, the fertilization effect of rising atmospheric CO_2 concentrations and longer growing season caused by climate warming will likely increase biotic N demand for plant growth and thus decline terrestrial N availability (Mason et al., 2022). Moreover, a global meta-analysis of CO_2 enrichment experiments indicate that N and P availability significantly limits the strength of CO_2 fertilization on vegetation productivity (Terrer et al., 2019).

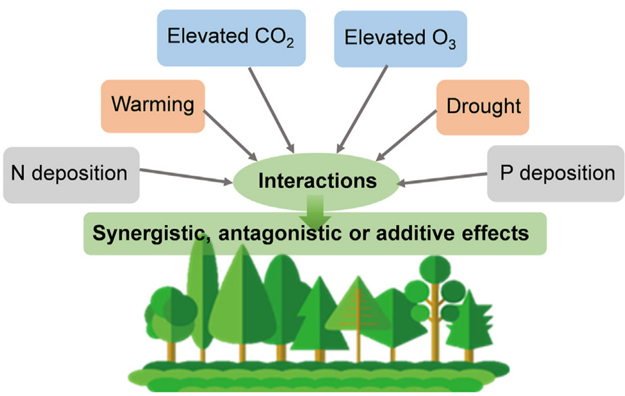

FIG. 4.5 Interactive effects of multiple global change factors on forest ecosystems.

A large number of single-factor experiments and meta-analyses of these experiments have been conducted to improve our understanding of the effects caused by individual global change factors (e.g., Norby et al., 2005; Wittig et al., 2009; Lin et al., 2010; Janssens et al., 2010; Lu et al., 2013; Schulte-Uebbing and de Vries, 2018; Song et al., 2019; Terrer et al., 2019; Zhou et al., 2022). However, there are much less experimental studies on the response of forest growth and C sequestration to N deposition in combination with other global change factors (Song et al., 2019).

Two-factor experiments usually indicate that ecosystem responses are mostly nonlinear due to interacting effects between factors (e.g., N deposition and rising CO_2 concentrations) (Kardol et al., 2012). Theoretically, there can be synergistic, antagonistic, and additive effects for different combinations of global change factors, while several meta-analyses of experimental results suggest that the interactive effects of two global change factors are mostly additive (Zhou et al., 2016; Yue et al., 2017; Song et al., 2019). Experiments considering three or more factors are extremely rare and the interactive effects of the multiple factors remain poorly understood especially in forest ecosystems (Song et al., 2019).

The overall effect of multiple global change factors depends on their interactions. A mesocosm pot experiment with six global change factors suggests that multiple factors can affect plant communities in a different way from those expected from single factor effects (Speißer et al., 2022). Therefore, future efforts are needed to conduct multi-factor experiments with a standardized methodology especially in forest ecosystems (Kardol et al., 2012). The improved understanding will better inform earth system models to predict forest growth and C stocks in response to future changes in N deposition and other simultaneously acting global change factors.

4.6 Effects of nitrogen deposition on managed forests

Managed forests, such as plantations and urban forests, occupy a growing area globally and provide important ecosystem services (Payn et al., 2015; Zhou et al., 2022). In comparison with natural forest, many plantations are generally located in areas with relatively high-level N deposition. Plantations are characterized by relatively simple species composition (e.g., mono-plantations) and strong management, implying that the negative effect of N deposition on plant diversity is not likely an important issue. Additionally, N inputs from atmospheric deposition can provide an important N supply to plantations that require large amounts of N for rapid growth. However, the effects of N deposition on NPP and C sequestration remain less well understood in global plantations.

Urban areas are hotspots of N deposition and thus urban forests are subject to much higher levels of N deposition in comparison with their natural counterparts (Du et al., 2022). Different from natural forests, urban forests grow in soil conditions with substantial artificial materials (Kaushal et al., 2020) and are affected by strong urban heat island effects, high-level atmospheric CO_2 and ozone concentrations and frequent horticultural practices (Du et al., 2022; Wang et al., 2023), implying potentially distinct growth responses of urban forests to high-level N deposition. High-level N deposition to urban forests may result in soil acidification, increase toxicity of heavy metals, cause imbalances between N and other nutrients, and even induce ecosystem N saturation. As a result, high-level N deposition may cause a decline of tree growth in urban forests when it exceeds a certain threshold (Du et al., 2022). Further experimental and observational research efforts are needed to gain more insights into the effects of high-level N deposition on urban forest growth and C sequestration.

5. Conclusions

Nitrogen deposition has exerted profound effects on NPP and C sequestration in global forests. The effects of N deposition generally vary with the status of N limitation across forest biomes. Specifically, N deposition increases NPP in N-limited boreal forest and many temperate forests, while it only makes a minor contribution to NPP in N-rich tropical and subtropical forests. Moreover, N deposition increases soil C sequestration via inhibiting decomposition of soil organic matter and/or increase aboveground litter inputs, while low-level N deposition has been found to increase soil heterotrophic respiration in N-limited forests and this effect has largely been unrepresented in literature.

Based on results of N addition experiments, stoichiometric scaling, and model simulation, N deposition is estimated to increase C sequestration by 0.25−0.72 Pg C $year^{-1}$ in global forests, where the lower-end estimate agrees best with experimental results. Considering a total C sink ~2.0 Pg C $year^{-1}$ in global forests this implies that N deposition contributes 12%−36% to the global, with the lower estimate (near 15%) being most likely. Uncertainties, however, largely remain in the effect of N deposition on soil C sequestration considering the inconsistent results of existing studies using different approaches.

Nitrogen deposition shows large spatial heterogeneity in its trends over the world, including an increase in regions with growing anthropogenic N emissions and a decrease in regions with abatement of N emissions. The spatial patterns of N deposition-induced forest growth and C sequestration will thus likely change over time. Meanwhile, the fertilization effect of rising atmospheric CO_2 concentrations and longer growing season caused by climate warming will likely increase the N demand and thereby the response ratio of NPP and C sequestration to N deposition in a future world. Further experimental and modeling efforts are in need to track the future effect of N deposition on global forest growth and C sequestration.

Acknowledgments

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