Impact of Nitrogen Deposition on Tropical Forest Biomass and Carbon Sequestration

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Abstract

Undoubtedly, nitrogen (N) is an essential component of proteins and nucleic acid of cells but in the last few decades it has undergone dramatic changes. Now move nitrogen has come into circulation and thus it has now become an environmental problem. Ndeposition is not always undesirable, in areas with N-limitation, N-deposition enhances the plant growth. Besides, it sequesters more CO₂ into the plant biomass there by lowering greenhouse gas emission into the atmosphere. Forest ecosystems all around the globe have experienced N- deposition and are becoming an important C-sink which has been shown in the table 1of this review article. The C-sink capacity of forest ecosystems have been determined using many approaches which are stochiometric scaling, dynamic global vegetation models and biomass weighting method. All these method used C:N response ratio as a predictor for future rate of C-sequestration in response to N- addition. Nutrient availability increases the production of biomass per unit of photosynthesis and decreases heterotrophic respiration in forests. Nutrient availability also determines net ecosystem productivity (NEP) and ecosystem carbon use efficiency (CUE). Biomass production was found higher in the nutrient rich forests, Increase in biomass production was more in woody biomass while foliage and root biomass production remain unchanged. Indeed, the potential of forest C-sink depends upon the partitioning of the carbon uptaken during photosynthesis. In terrestrial ecosystems, C -sequestration predominantly occur in forests ecosystems. Both C:N ratio and nitrogen use efficiency (NUE) are crucial for determining C-sequestration in different forest types. C-sequestration in response to N-addition shows variation with kind of mycorrhizal association. N-deposition benefitted trees with arbuscular mycorrhizal fungi rather than ectomycorrhizal fungi. Thus, after going thoroughly across number of research articles, we arrived at the conclusion that it is the C:N ratio, NUE, forest type, nutrient availability which determine the C sequestration by forest biomass

1. Introduction

Nitrogen (N) being an essential component of protein and nucleic acid of cells have undergone dramatic changes in recent decades. Evident from human history, available forms of N (nitrogen) for plants have been always in short supply. N then becomes a limiting factor for the growth of forest trees. After the end of second world war the use of artificial fertilizer increased greatly along with the emission of nitric oxide (NO) from motor vehicle and industries. Consequently more nitrogen than before was now brought into circulation. In this way N become an environmental problem. Since 1980 nitrogen started putting adverse effect such as incipient nitrogen separation and reduced productivity of forest land (Cowling et al., 1998). Gradually atmospheric N deposition took the place of sulphur (S) deposition and became an important issue of environmental concern. High level of N causes leaching of nitrate (NO₃) and hence reduces the forest growth. N deposition bears both desirable and undesirable consequences. In areas

of N limitation, N deposition stimulates the forest growth. Also it increases the binding of more CO_2 in plant biomass and thereby lowering the emission of the green house gases to the atmosphere. Meanwhile, N deposition reduces the species richness. Enhanced historic and future N deposition has potential impact on global carbon sequestration.

Forest ecosystems all around the globe have experienced increased N- deposition in the past few decades due to increased rate of anthropogenic emission of N from fossil fuel combustion and modern agriculture (Galloway *et al.*, 2008; Fowler *et al.*, 2013). Increases in atmospheric N-deposition, significantly alters the global N cycle. Alteration in the global N-cycle affects the global (C) cycle by accelerating forest C sequestration. Forests are an important C-sink. Monsoon subtropical forests in East Asia uptake 0.72 Pg C yr¹ and thus they become an important C-sink (Yu *et al.*, 2014). In a terrestrial ecosystem, both C and N cycle are closely linked. Most of the terrestrial ecosystems are N- limited thus the increased N-deposition increases

the biomass production and terrestrial C sequestration (Zaehle, 2013). Nutrients rich forests allocate larger proportion of their photosynthates to wood production in comparison to nutrient poor forest at the cost of producing less root (Vicca *et al.*, 2012). These changes in allocation pattern increase C (carbon) fixation in nutrient rich forest. Nutrient availability is very much crucial in determining forest carbon balances and more particularly the capacity of forest to sequester carbon.

From the year 2000-2009, forests accounted for 82% of the terrestrial-sink (Le Quere *et al.*, 2015). On the global scale, both forest soil and forest biomass contain roughly equal amount of carbon but living biomass and dead biomass account for 75% of the C-sequestered in forest (Pan *et al.*, 2011). Although most of the carbon is contained in soil, still biomass often accounts for most of the additionally sequestered C. For instance, in a study in Europe, it has been estimated that tree biomass account for 35% of the forest carbon pool 70% of the C-sink lies in the C sequestered in tree biomass and 30% in the C sequestered in soil (Janssens

et al., 2003). Increased N-deposition has potential impacts on forest C-sequestration because the studies done till date have reported limitation in soil (LeBauer et al., 2008; Chen et al., 2015). In order to evaluate the effects of atmospheric N-deposition on forest carbon sequestration, many approaches have been used such as stoichiometric scaling (De Vries et al., 2014), fertilization experiments, model stimulations and biomass weighting method. Despite of all these approaches, still high precision evaluation of how forest C-sequestration responds to atmospheric N-deposition cannot be achieved because of complications in the process of external N-uptake and allocation in natural ecosystem (Templer et al., 2012).

2. Insight into the Datasets Obtained from Various Sites using Different Evaluation Approaches

Among the methods proposed to determine the effect of N deposition on forest carbon sink, stochiometric scaling method is a straight forward empirical approach which is based on the assumption that the effect of the atmospheric N-deposition on C-

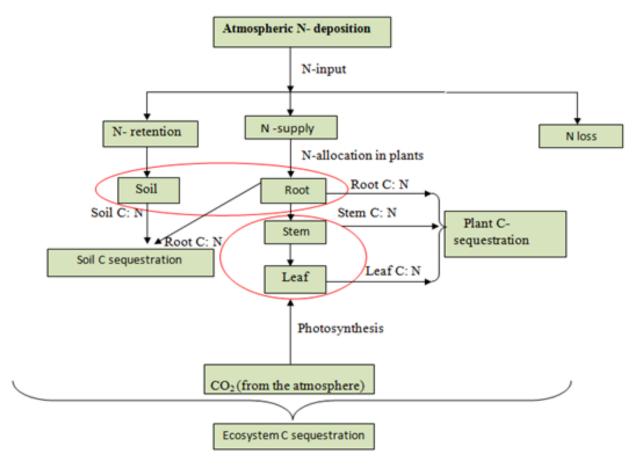


Fig. 1: Forest C sequestration in response to atmospheric nitrogen (N) deposition (Source: Zhu et al., 2017).

sequestration strongly depend on the C:N ratio of soil and plant organ in a forest ecosystem, fraction of external N input retained, relative allocation of the N-uptaken by the plants to different plant organ and N retention fraction in the soil (Zhu *et al.*, 2017) (Fig. 1).

The C:N response ratio is the additional mass unit of C sequestered per additional mass unit of N deposition. In other words, it is the measure of efficiency with which forests use the additional N. When using stoichiometric scaling approach, some studies have kept C:N ratio constant (De Vries et al., 2014; Wang et al., 2017) which will overlook the differences existing in the C:N ratio for different plant organ or communities hence this would restrict the accuracy of estimates to a great extent. Secondly, quantification of relative allocation of N-uptake to different plant organ is very difficult. However, the isotopic labelling technique has helped in determining in the fraction of N allocation to differ plant organ, but major variation among different plant species have been observed (Templer et al., 2012).

Dynamic global vegetation models also estimates C-N responses to N deposition. The advantage of these models is that they include tree species, climate, CO₂ concentration or soil texture which affect forest productivity. However effect of N deposition varies with other environmental factors such as climate and ozone exposure (Fleischer et al., 2013). Fertilization experiments have been conducted in many forests of the world which although provide a powerful insight into the impact of N deposition on forest C sequestration (Vadeboncoeur, 2010) but these results are only valid for the area where experiment has been performed because few experiments show a strong stimulation of forest C sequestration on N addition (Liu et al., 2010) in the other experiments, while in other experiments N addition did not significantly affect tree C-sequestration (Lovett et al., 2013). The latest approach used to assess the impact of N-deposition on C -sequestration at ecosystem level is biomass weighting method (Zhu *et al.*, 2017). Here, by considering the biomass of each plant species in a forest community as weighted values, they scaled up the C:N ratio from plant organ to species, plant functional types, plant communities and whole ecosystem. In this method we did not need to quantify the N allocation fractions of external input among different plant organs. But this method requires the complete community composition information along with the systematic measurement of C:N ratio of different plant species and different organs, which is very troublesome and expensive in practice. (Table 1 representing the forest C-sequestration in response to N-addition.)

3. Nitrogen as a Key Regulator of Global Forest Carbon Balance

Forests strongly treat climate through the interchange of huge amounts of atmospheric CO₂ (Dixon et al., 1994). The main reasons of local variability in net ecosystem production (NEP) on a global scale are yet poorly known. When nutrient availability increases it increases the production of biomass per unit of photosynthesis and decreases heterotrophic respiration in forests, therefore we must expect nutrients to determine carbon sequestration in forests. Nutrient availability indeed plays an important role in estimating (NEP) and ecosystem carbon-use efficiency /CUE; that is, the ratio of NEP to gross primary production (GPP)]. In nutrients rich forests, forests exhibit high (GPP) and high (NEP). While in nutrientpoor forests, an extremely larger proportion of GPP was released through ecosystem respiration and decreased carbon use efficiency. Our findings that nutrient availability have a powerful control on NEP than on carbon input (GPP) contradicts with assumptions of nearly all global coupled carbon cycle-climate models, which assert that carbon inputs through photosynthesis drive biomass production and carbon sequestration.

Table 1: Forest C-sequestration in response to N deposition in different forests across the world (CSR_N : Carbon sequestration in response to N-addition; NSTEC: north–south transect of eastern China; NA: not available).

| Site | CSR _N (Tg C yr ⁻¹) | C/N (kg C/kg N) | References |
|--|---|-----------------|-------------------------------|
| Eight typical forests along NSTEC | 36.7 | 26.6-48.2 | Zhu <i>et al</i> . (2017) |
| Forest of northern Europe | NA | 25 | Hyvonen <i>et al</i> . (2008) |
| China's forest | 37 | NA | Lu <i>et al</i> . (2012) |
| Monsoon subtropical forests in East Asia | a 720 | NA | Yu et al. (2014) |
| Tropical forests | 15 | 1.3 | Schulte-Uebbing et al. (2017) |
| Temperate forests | 101 | 12.7 | Schulte-Uebbing et al. (2017) |
| Boreal forests | 32 | 14.1 | Schulte-Uebbing et al. (2017) |
| | | | |

4. Impact of N Deposition on Forest Biomass

Increased N input from the atmosphere influences above and below ground production in forest. NPP is converted into plant biomass, root exudation, volatile organic compounds. Biomass production being the largest fraction of NPP, is also used as a proxy for NPP (Goulden et al., 2011). Biomass production was, 78% higher in temperate forest with high nutrient availability than in temperate forest with low nutrient availability (Vicca et al., 2012). In relation to GPP, the disproportionate increase in biomass production was more in woody biomass. Thus, they exhibited higher aboveground wood production in comparison to that at the low nutrient availability status. While foliage and root biomass production remain unchanged. In an analysis of 49 forest sites it was found that nutrient availability is the unifying machinery in regulating the ratio of biomass production (BP) to GPP. The potential of forest to act as carbon sink greatly depends upon the partitioning of carbon taken up during photosynthesis. Photosynthates used up in autotrophic respiration (Ra) do not contribute to C sequestration but those converted to biomass contribute to C sequestration. Then the higher partitioning of carbon to plant biomass with increasing nutrient availability enhances our understanding towards long term C sequestration in forest. This reflects that it is the NEP which regulates the aboveground and belowground biomass which in turn contributes to C-sequestration by trees while the litter fall contributes to soil C-sequestration. In a study by Turnbull et al. (2005), the ratio of leaf respiration to photosynthesis was higher in forest with severe nutrient limitation than in less nutrient limited forest. In forests with high nutrient status a greater fraction of photosynthates is allocated towards wood composition compared to the fraction allocated to wood in forest with low nutrients status (Litten et al., 2007). So the higher wood to foliage production ratio increases the autotrophic respiration (Ra) to GPP ratio in forest with high nutrient availability compared to forest with low nutrient availability Besides, several studies show positive relation between root respiration per unit mass and nutrient concentration (Chapin et al., 1980; Burton et al., 2002). But this is offset by decrease in standing root biomass due to negative fertilization effect on root respiration, found in a recent meta-analysis (Janssens et al., 2010). In a study by Vicca et al. (2012), forest with high nutrient availability use 16±4% more photosynthates for biomass production than in forests with low nutrient availability. This study also hypothesizes that allocation of carbon to root symbionts is a key factor for higher biomass production

efficiency in nutrients rich forest relative to nutrient poor forests.

5. Impact of N Deposition on Carbon Sequestration by Forest Ecosystem

Evaluation of global carbon (C) budget over the last 25 years show that more than 50% of the anthropogenic CO₂ emissions is stored in oceans and terrestrial ecosystems (Bousquet et al., 1999; Le Quere et al., 2013). The most recent global estimate of C sinks are 2.6±0.5 Pg C yr⁻¹ for oceans and 2.6±0.8 Pg C yr⁻¹ for terrestrial ecosystems (Le Quere et al., 2013). The sequestration of CO₂ released by human activities in terrestrial ecosystems, predominantly occurs in forest ecosystems (Le Quere et al., 2013). Therefore for the prediction of the long term future global forest C sink, it is vital to have insight in the (interactions between) environmental drivers affecting the processes that sort out the forest C balance, that is, primary production and autotrophic and heterotrophic respiration. Inspite of, the drastic dearrangement of the nitrogen (N) cycle since the beginning of nineteenth century, has caused an increased atmospheric N deposition on forests (Piao et al., 2009) and there is increasing evidence that this has virtually increased forest C sequestration too (De Vries et al., 2006, 2009; Churkina et al., 2009; Thomas et al., 2010). As the most forest ecosystems are N limited, therefore increased N deposition increases the net primary production (NPP) and thus stimulating carbon (C) sequestration in trees (LeBauer et al., 2008; Thomas et al., 2010; Zaehle et al., 2011), but also declined the biodiversity (Bobbink et al., 2010). Increased NPP also increases C sequestration in the soil due to increased soil C inputs by litterfall (Lu et al., 2011) and reduced decomposition of organic matter (Berg and Matzner, 1997; Janssens et al., 2010). There is sufficient evidence that N availability, plays a key role in the response of forest ecosystems to increased CO₂ concentrations, elevated temperature and changed water availability (Poorter and Nagel, 2000; Wamelink et al., 2009; De Vries and Posch, 2011; Goll et al., 2012). The importance of future N deposition on global C sequestration has been a broad topic for research and debate since decades (Peterson and Melillo, 1985; Townsend et al., 1996; Holland et al., 1997; Oren et al., 2001; Magnani et al., 2007; De Vries et al., 2008; Sutton et al., 2008). The forest type is crucial because Ndeposition effect on ecosystem N use efficiency (NUE) depends on the allocation of N in vegetation and soil pools with various C:N ratios. The C:N responses are further influenced by the N retention, which depends up on the factors, such as low temperature, limited water availability, limited availability of other nutrients

such as phosphorus (P) and base cations. Although N limitation is prevalent in terrestrial ecosystems (Vitousek and Howarth, 1991). While co-limitation of N and P (Elser *et al.*, 2007) is specifically for tropical forests. Responses thus varied between boreal, temperate and tropical forests.

Impact of Nitrogen (N) deposition on forest ecosystems have recognized global attention. Most important role of plantations in mitigating climate change is through assimilating atmospheric CO₂. However, the mechanisms by which increasing N additions affect net ecosystem production (NEP) of plantations remained poorly understood. In 2009, a field experiment was conducted in a locality that contained the largest area of plantations in China, which incorporated additions of four rates of N. (1) Control (no N addition), (2) Low-N (5 g N m⁻² yr⁻¹), (3) Medium-N (10 g N m^2 yr¹), and (4) High-N (15 g N m^2 yr¹) and measured the following: Net primary production (NPP), soil respiration, and its autotrophic and heterotrophic constituents and soil pH, extracellular enzyme activities ,microbial biomass, microbial community composition and plant tissue carbon (C) and N concentrations (including foliage, litter, and fine roots). When N was added in the experimental plots it significantly increased NPP, which was associated with increased litter N concentrations therefore, autotrophic respiration (AR) means respiration by photosynthetic organisms (e.g., plants and algae) increased but heterotrophic respiration (HR) decreased in the high and the medium N plots. While the HR in high and medium N plots did not significantly differ from that in the control. While the HR was significantly inhibited in the high-N plots though no significant changes were observed in soil microbial biomass, composition, or activity of extracellular enzymes. Also reduced pH with fertilization could not explain the pattern of HR. The decrease in HR may be related to changed microbial C use efficiency. NEP was significantly increased by N addition, from 149 to 426.6 g C m⁻² yr⁻¹. Short-term N addition may significantly increase the role of plantations as an important C sink.

6. Response of Mycorrhizal Association to N Deposition

N deposition stimulates carbon sequestration in forests (Melillo and Gosz., 1983). In a study at a northeastern and north-central USA during the year 1980s and 1990s it was found that N deposition enhances the tree growth which had arbuscular mycorrhizal fungal association. Five tree species (*Acer rubrum, A. saccharum, Fraxinus americana, Liriodendron tulipifera,* and *Prunus serotina*) showed positive response to N deposition because they exhibited arbuscular

mycorrhizal associations. Contrary to ectomycorrhizal, fungi, arbuscular mycorrhizal fungi are not able to produces enzyme which break down soil organic N into inorganic N (Chalot and Brun, 1998) hence N deposition benefitted the tree species where arbuscular mycorrhizal association was present by increasing the availibility of soil inorganic N to them. Eight species which showed decreased survivorship had ectomycorrhizal association. This case study suggested that response of tree species to N deposition also depend upon the type of mycorrhizal association present.

7. Conclusions

Since trees being important primary producers in forest ecosystems, so how they get affected by N-deposition will crucially determine changes in other parts of the system. The latest scaling-up method based on biomass weighting provided a new way for estimating C-sequestration in response to N-addition by forest ecosystems. Reported ranges and trends of $\text{CSR}_{\scriptscriptstyle N}$ and NUE in various forests mentioned in various literatures provided an important reference for future analyses of C-sequestration in response to N-addition.

An increased supply of N, probably leads to decrease in its uptake by forest ecosystem i.e. instantaneous uptake rate. As a consequence, more N will be present in the soil system and will cause increased leaching (Bertills and Näsholm, 2000). Increased nitrogen availability leads to higher levels of N in aboveground tissues (leaves or needles) of the trees and also alters the patterns of forest growth. Increased N- deposition causes increased forest growth and hence increased C-sequestration by increased biomass and humus. Also, the binding of N to humus results in slower decomposition of organic C.

Gradually, it has been realized that in the long term, increased C-sequestration due to N-deposition would have only minor effects on atmospheric concentration of CO₂. Despite of increased N-input, CO₂ level has doubled in the last hundred years (Bertills and Näsholm, 2000). So, nitrogen addition, has detrimental effects which should also be taken into account.

Amongst the changes that occured due to N-deposition, the response of different types of mycorrhizal associations was particularly striking. Studies till date do not give clear-cut evidence that the N- deposition is the main driver of increased forest growth. Swedish (Elfving and Tegnhammar, 1996) and European studies (Spiecker *et al.*, 1996) showed that forest growth is also increasing in areas with low N-deposition thus indicating that there are various factors

other than nitrogen also which significantly contribute to forest growth.

We still need to focus to a large extent on the relationship between levels of nitrogen deposition and response (biomass production and C-sequestration) including differences between different forest ecosystems.

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References

- Berg, B. and Matzner, E. 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. *Environmental Reviews* 5(1):1-25.
- Bertills, U. and Näsholm, T. 2000. Effects of nitrogen deposition on forest ecosystems. Swedish Environmental Protection Agency, Trelleborg.
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F. and Emmett, B. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications* **20**(1):30-59.
- Bousquet, P., Peylin, P., Ciais, P., Ramonet, M. and Monfray, P. 1999. Inverse modeling of annual atmospheric CO₂ sources and sinks: 2. Sensitivity study. *Journal of Geophysical Research: Atmospheres* **104**(D21):26179-26193.
- Burton, A., Pregitzer, K., Ruess, R., Hendrick, R. and Allen, M. 2002. Root respiration in North American forests: effects of nitrogen concentration and temperature across biomes. *Oecologia* **131**(4):559-568.
- Chalot, M. and Brun, A. 1998. Physiology of organic nitrogen acquisition by ectomycorrhizal fungi and ectomycorrhizas. FEMS Microbiology Reviews 22(1):21-44.
- Chapin III, F.S. 1980. The mineral nutrition of wild plants.

 Annual Review of Ecology and Systematics 11(1):233-260
- Chen, H., Li, D., Gurmesa, G.A., Yu, G., Li, L., Zhang, W., Fang, H. and Mo, J. 2015. Effects of nitrogen deposition on carbon cycle in terrestrial ecosystems of China: A meta-analysis. *Environmental Pollution* **206**:352-360.
- Churkina, G., Brovkin, V., Von Bloh, W., Trusilova, K., Jung, M. and Dentener, F. 2009. Synergy of rising nitrogen depositions and atmospheric CO₂ on land carbon uptake moderately offsets global warming. *Global Biogeochemical Cycles* 23(4).
- Cowling, E.B., Erisman, J.W., Smeulders, S.M., Holman, S.C. and Nicholson, B.M. 1998. Optimizing air quality management in Europe and North America: Justification for integrated management of both oxidized and reduced forms of nitrogen. *In Nitrogen, the*

- Confer-Ns pp. 599-608.
- De Vries, W. and Posch, M. 2011. Modelling the impact of nitrogen deposition, climate change and nutrient limitations on tree carbon sequestration in Europe for the period 1900–2050. *Environmental Pollution* **159**(10):2289-2299.
- De Vries, W., Du, E. and Butterbach-Bahl, K. 2014. Short and long-term impacts of nitrogen deposition on carbon sequestration by forest ecosystems. *Current Opinion in Environmental Sustainability* **9**:90-104.
- De Vries, W., Solberg, S., Dobbertin, M., Sterba, H., Laubhahn, D., Reinds, G.J., Nabuurs, G.J., Gundersen, P. and Sutton, M.A. 2008. Ecologically implausible carbon response? Nature **451**:E1–E3.
- De Vries, W., Solberg, S., Dobbertin, M., Sterba, H., Laubhann, D., Van Oijen, M., Evans, C., Gundersen, P., Kros, J., Wamelink, G.W.W. and Reinds, G.J. 2009. The impact of nitrogen deposition on carbon sequestration by European forests and heathlands. *Forest Ecology and Management* **258**(8):1814-1823.
- De Vries, W.I.M., Reinds, G.J., Gundersen, P.E.R. and Sterba, H. 2006. The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. *Global Change Biology* **12**(7):1151-1173.
- Dixon, R.K., Solomon, A.M., Brown, S., Houghton, R.A., Trexier, M.C. and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. *Science* **263** (5144):185-190.
- Elfving, B. and Tegnhammar, L. 1996. Trends of tree growth in Swedish forests 1953–1992: an analysis based on sample trees from the National Forest Inventory. Scandinavian Journal of Forest Research 11(1-4):26-37.
- Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B. and Smith, J.E. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology letters* **10**(12):1135-1142.
- Fleischer, K., Rebel, K. T., van der Molen, M. K., Erisman, J. W., Wassen, M. J., van Loon, E. E., Dolman, A. J. 2013. The contribution of nitrogen deposition to the photosynthetic capacity of forests. *Global Biogeochemical Cycles* 27:187-199.
- Fowler, D., Coyle, M., Skiba, U., Sutton, M.A., Cape, J.N., Reis, S., Sheppard, L.J., Jenkins, A., Grizzetti, B., Galloway, J.N. and Vitousek, P. 2013. The global nitrogen cycle in the twenty-first century. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 368:20130164.
- Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L.A., Seitzinger, S.P. and Sutton, M.A. 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science* **320**:889-892.
- Goll, D.S., Brovkin, V., Parida, B.R., Reick, C.H., Kattge, J., Reich, P.B., Van Bodegom, P.M. and Niinemets, Ü. 2012. Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen

- and phosphorus cycling. Biogeosciences 9:3547-3569.
- Goulden, M.L., McMillan, A.M.S., Winston, G.C., Rocha, A.V., Manies, K.L., Harden, J.W. and Bond-Lamberty, B.P. 2011. Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Global Change Biology* 17(2):855-871.
- Holland, E.A., Braswell, B.H., Lamarque, J.F., Townsend, A., Sulzman, J., Müller, J.F., Dentener, F., Brasseur, G., Levy, H., Penner, J.E. and Roelofs, G.J. 1997. Variations in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems. *Journal of Geophysical Research: Atmospheres* **102**(D13):15849-15866.
- Hyvonen, R., Persson, T., Andersson, S., Olsson, B., Ågren, G.I. and Linder, S. 2008. Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. *Biogeochemistry* **89**(1):121-137.
- Janssens, I.A., Dieleman, W., Luyssaert, S., Subke, J.A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, A.J., Grace, J., Matteucci, G. and Papale, D. 2010. Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geosciences* 3(5):315.
- Janssens, I.A., Freibauer, A., Ciais, P., Smith, P., Nabuurs, G.J., Folberth, G., Schlamadinger, B., Hutjes, R.W., Ceulemans, R., Schulze, E.D. and Valentini, R. 2003. Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic CO₂ emissions. *Science* 300(5625):1538-1542.
- Le Quere, C., Moriarty, R., Andrew, R. M., Canadell, J. G., Sitch, S., Kors-bakken, J. I., Zeng, N. 2015. Global carbon budget 2015. Earth System Science Data 7:349-396
- Le Quere, C., Peters, G.P., Andres, R.J., Andrew, R.M., Boden, T., Ciais, P. and Friedlingstein, P. 2013. Global carbon budget. Earth System Science Data Discussion 6:689-760.
- LeBauer, D.S. and Treseder, K.K. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* **89**(2):371-379.
- Litton, C.M., Raich, J.W. and Ryan, M.G. 2007. Carbon allocation in forest ecosystems. *Global Change Biology* **13**(10):2089-2109.
- Liu, J.X., Zhou, G.Y., Zhang, D.Q., Xu, Z.H., Duan, H.L., Deng, Q. and Zhao, L. 2010. Carbon dynamics in subtropical forest soil: effects of atmospheric carbon dioxide enrichment and nitrogen addition. *Journal of Soils and sediments* 10(4):730-738.
- Lovett, G.M., Arthur, M.A., Weathers, K.C., Fitzhugh, R.D. and Templer, P.H. 2013. Nitrogen addition increases carbon storage in soils, but not in trees, in an eastern US deciduous forest. *Ecosystems* **16**(6):980-1001.
- Lu, C., Tian, H., Liu, M., Ren, W., Xu, X., Chen, G. and Zhang, C. 2012. Effect of nitrogen deposition on China's terrestrial carbon uptake in the context of multifactor environmental changes. *Ecological Applications* **22**(1):53-75.
- Lu, M., Zhou, X., Luo, Y., Yang, Y., Fang, C., Chen, J. and Li, B. 2011. Minor stimulation of soil carbon storage by nitrogen

- addition: a meta-analysis. *Agriculture, Ecosystems and Environment* **140**(1-2):234-244.
- Magnani, F., Mencuccini, M., Borghetti, M., Berbigier, P., Berninger, F., Delzon, S., Grelle, A., Hari, P., Jarvis, P.G., Kolari, P. and Kowalski, A.S. 2007. The human footprint in the carbon cycle of temperate and boreal forests. *Nature* **447**(7146):849.
- Melillo, J.M. and Gosz, J.R. 1983. Interactions of biogeochemical cycles in forest ecosystems, The Major Biogeochemical Cycles and their Interactions B. Bolin, RB Cook 177–222.
- Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C., Schäfer, K.V., McCarthy, H., Hendrey, G., McNulty, S.G. and Katul, G.G. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature* **411**(6836):469.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G. and Ciais, P. 2011. A large and persistent carbon sink in the world's forests. *Science* **333**:988–993.
- Peterson, B.J. and Melillo, J.M. 1985. The potential storage of carbon caused by eutrophication of the biosphere. *Tellus B* **37**(3):117-127.
- Piao, S., Friedlingstein, P., Ciais, P., Peylin, P., Zhu, B. and Reichstein, M., 2009. Footprint of temperature changes in the temperate and boreal forest carbon balance. *Geophysical Research Letters* **36**(7).
- Poorter, H. and Nagel, O. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review. *Functional Plant Biology* **27**(12):1191-1191.
- Schulte-Uebbing, L. and 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 Biology* **24**(2):416-431.
- Spiecker, H., Mielikainen, K., Kohl, M. and Skovsgaard, J.P. (Eds.) 1996. Growth trends of European forests. Studies from 12 countries. *Springer Verlag*, New York.
- Sutton, M.A., Simpson, D., Levy, P.E., Smith, R.I., Reis, S., Van Oijen, M. and De Vries, W.I.M. 2008. Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration. *Global Change Biology* 14(9):2057-2063.
- Templer, P.H., Mack, M.C., FS III, C., Christenson, L.M., Compton, J.E., Crook, H.D., Currie, W.S., Curtis, C.J., Dail, D.B., D'Antonio, C.M. and Emmett, B.A. 2012. Sinks for nitrogen inputs in terrestrial ecosystems: a meta-analysis of 15N tracer field studies. *Ecology* 93(8):1816-1829.
- Thomas, R.Q., Canham, C.D., Weathers, K.C. and Goodale, C.L. 2010. Increased tree carbon storage in response to nitrogen deposition in the US. *Nature Geoscience* **3**(1):13.
- Townsend, A.R., Braswell, B.H., Holland, E.A. and Penner, J.E. 1996. Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen. *Ecological Applications* **6**(3):806-814.

- Turnbull, M.H., Tissue, D.T., Griffin, K.L., Richardson, S.J., Peltzer, D.A. and Whitehead, D. 2005. Respiration characteristics in temperate rainforest tree species differ along a long-term soil-development chronosequence. *Oecologia* **143**(2):271-279.
- Vadeboncoeur, M.A. 2010. Meta-analysis of fertilization experiments indicates multiple limiting nutrients in northeastern deciduous forests. *Canadian Journal of Forest Research* **40**(9):1766-1780.
- Vicca, S., Luyssaert, S., Penuelas, J., Campioli, M., Chapin, F.S., Ciais, P., Heinemeyer, A., Högberg, P., Kutsch, W.L., Law, B.E. and Malhi, Y. 2012. Fertile forests produce biomass more efficiently. *Ecology Letters* **15**(6):520-526.
- Vitousek, P.M. and Howarth, R.W. 1991. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* 13(2):87-115.
- Wamelink, G.W.W., Wieggers, H.J.J., Reinds, G.J., Kros, J., Mol-Dijkstra, J.P., Van Oijen, M. and De Vries, W. 2009. Modelling impacts of changes in carbon dioxide concentration, climate and nitrogen deposition on carbon sequestration by European forests and forest soils. Forest Ecology and Management 258(8):1794-1805.

- Wang, R., Goll, D., Balkanski, Y., Hauglustaine, D., Boucher, O., Ciais, P., Janssens, I., Penuelas, J., Guenet, B., Sardans, J. and Bopp, L. 2017. Global forest carbon uptake due to nitrogen and phosphorus deposition from 1850 to 2100. Global Change Biology 23:4854–72
- Yu, G., Chen, Z., Piao, S., Peng, C., Ciais, P., Wang, Q., Li, X. and Zhu, X. 2014. High carbon dioxide uptake by subtropical forest ecosystems in the East Asian monsoon region. *Proceedings of the National Academy of Sciences* 111(13):4910-4915.
- Zaehle, S. 2013. Terrestrial nitrogen-carbon cycle interactions at the global scale. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**(1621):20130125.
- Zaehle, S., Ciais, P., Friend, A.D. and Prieur, V. 2011. Carbon benefits of anthropogenic reactive nitrogen offset by nitrous oxide emissions. *Nature Geoscience* **4**(9):601.
- Zhu, J., He, N., Zhang, J., Wang, Q., Zhao, N., Jia, Y., Ge, J. and Yu, G. 2017. Estimation of carbon sequestration in China's forests induced by atmospheric wet nitrogen deposition using the principles of ecological stoichiometry. *Environmental Research Letters* 12(11):114038.