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Current Opinion in Environmental Sustainability

Short and long-term impacts of nitrogen deposition on carbon sequestration by forest ecosystems

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The carbon to nitrogen response of forest ecosystems depends on the possible occurrence of nitrogen limitation versus possible co-limitations by other drivers, such as low temperature or availability of phosphorus. A combination of nitrogen retention estimates and stoichiometric scaling is used to illustrate the most likely carbon–nitrogen responses for needle-leaved and broadleaved forests to atmospheric nitrogen deposition. Results are evaluated against field observations and nitrogen addition experiments. The likely change in carbon to nitrogen response with nitrogen deposition level is hypothesized, distinguishing three threshold values that mark the forest carbon responses. We estimated that at global scale nitrogen deposition currently increases the forest carbon sink by 276–448 Tg C yr^{-1}, with approximately 60% retained in tree wood and 40% in soil. Furthermore, the long-term carbon response to nitrogen, accounting for nitrogen saturation over time is hypothesized. In this context, the role of global scale coupled carbon–nitrogen models is also evaluated in view of current knowledge affecting carbon–nitrogen responses, including interactions with other drivers.

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Current Opinion in Environmental Sustainability 2014, **9–10**:90–104

This review comes from a themed issue on **System dynamics and sustainability — NCGG7**

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Received 20 June 2014; Revised 6 August 2014; Accepted 9 September 2014

http://dx.doi.org/10.1016/j.cosust.2014.09.001

Introduction

Assessments of global carbon (C) budgets over the past 25 years show that more that more than 50% of the anthropogenic CO_2 emissions is stored in oceans and land [1,2]. 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 [2]. The sequestration of anthropogenic CO_2 emissions in terrestrial ecosystems predominantly occurs in forest ecosystems [3••]. In order to predict the long term future global forest C sink, it is crucial to have insight in the (interactions between) environmental drivers affecting the processes that determine the forest C balance, that is, primary production and autotrophic and heterotrophic respiration.

Apart from site disturbance and forest management [4–6], many field studies and model approaches suggest that increasing atmospheric CO_2 concentrations (e.g. [7,8]) and climate warming [9–11] were the major drivers of continental and global carbon sinks. However, the severe perturbation of the nitrogen (N) cycle since the beginning of nineteenth century has caused an enhanced atmospheric N deposition on forests [12] and there is increasing evidence that this has substantially increased forest C sequestration too [13,14,15•,16]. While most forest ecosystems are N limited, increased N deposition increases net primary production (NPP), thus stimulating carbon (C) sequestration in trees [15•,17,18•], but usually also decreases biodiversity [19]. Increased productivity may also increase C sequestration in the soil due to increased soil C inputs by litterfall [20] and reduced decomposition of organic matter [21,22]. There is ample evidence that N availability, or more broadly nutrient availability in general, plays a key role in the response of forest ecosystems to increased CO_2 concentrations, elevated temperature and changed water availability [23–25,26••,27••].

The importance of enhanced historic and future N deposition on global C sequestration has been a topic for research and debate since decades [28–32,33•,34]. Quantification will depend on the magnitude of N deposition and the C sequestration per kg N input, the latter depending on the type of forest. The forest type is important since C–N (deposition) responses or ecosystem N use efficiencies (NUEe) depend on the allocation of N in different vegetation and soil pools with different C:N ratios. The C–N responses are further influenced by the N retention, which depends on the occurrence and severity of N limitation versus limitation by other factors, such as low temperature, limited water availability and/or limited availability of other nutrients such as phosphorus (P) and base cations, which varies across climates. Although N limitation is widespread in terrestrial ecosystems [35], co-limitation of N and P [36,37] or P limitation occurs frequently [38], specifically for tropical forests. Responses thus differ between boreal, temperate and tropical forests. Furthermore, C–N responses will likely change with elevated N inputs and with time, as it will affect both the N retention fractions and the C:N stoichiometry in different vegetation and soil pools.

In this paper, we first present a range of likely global average C–N responses for needle-leaved forests, deciduous broadleaved forests and evergreen broadleaved forests, mainly representative for boreal, temperate and tropical regions, respectively, based on N retention measurements combined with stoichiometric scaling. Results thus obtained are compared to (meta-analysis of) experimental N addition studies and field based monitoring studies across N deposition gradients and used to estimate the contribution of N deposition to the current global forest C sink. The impacts of the level of N deposition on N retention, NPP, heterotrophic respiration and NEP are then discussed. We also consider that the C–N response is likely to change with accumulated N deposition over time in view of changes in N retention and stoichiometry in soil and vegetation compartments. In this context, we finally present an overview of the current status of global carbon–nitrogen (C–N) cycle modeling approaches, predicting long-term impacts N on global CO_2–C exchange by forest ecosystems, accounting for interactions with climate change and elevated CO_2 concentrations.

Carbon response to nitrogen inputs in forest ecosystems

Carbon response parameters

In assessing the role of N deposition on forest C sequestration, it is important to make a distinction between the contribution to net primary production (NPP), being equal to the gross primary production by photosynthesis (GPP) minus autotrophic (plant) respiration (Ra), and net ecosystem production (NEP), being equal to the NPP minus heterotrophic respiration (Rh) (see Figure 1). Net primary production is the total forest production in stem and branch wood (also denoted as above-ground woody biomass production; AGWB), coarse roots (also denoted as below-ground woody biomass production; BGWB), leaves (also denoted as above-ground litter production; ALP, being near equal to litter fall) and fine roots (also denoted as root litter production; RLP, being near equal to fine root turnover). Due to the much longer turn over times, it is the total woody biomass production (TWB = AGWB + BGWB) that determines the C sequestration by forest trees. The change in total litter production (TLP = ALP + RLP) is affecting the C input to soil and thereby the soil C sequestration, in combination with soil respiration. The sum of both tree and soil C sequestration is the NEP. On a large scale and/or over longer time periods, the C sequestration is further determined by disturbances, such as forest harvesting, fires, insect outbreaks and wind throws. The so-called net biome production (NBP), being equal to NEP minus disturbances, is thus the ultimate regional scale carbon sequestration (Figure 1). In this paper, we focus on the evaluation of the NEP response, being the tree and soil C sequestration in an undisturbed system, to N inputs for present day environmental conditions.

Stoichiometric scaling approach

A relative simple empirical approach to assess the impact of N deposition on forest C sequestration is to multiply the N deposition with the C response per kg N input for major forest ecosystem types, such as boreal, temperate and tropical forests (e.g. [13,28,39]). A straightforward approach to assess C–N (deposition) responses of forest ecosystems is stoichiometric scaling. Stoichiometric scaling is based on the principle that effects of N deposition on C sequestration strongly depend on the proportions of external N inputs that is retained in forest ecosystems (the ecosystem nitrogen use efficiency; NUEe), the relative allocation of the assimilated N to woody and non-woody tissues and the immobilization in the soil.

The C–N responses of trees is determined by the overall N retention fraction in vegetation ($frN_{ret,veg}$) and the allocation of N (frN_{all}) over different forest vegetation pools (stems, leaves, coarse-roots and fine-roots, denoted as st, lv, cr and fr) and the CN stoichiometry in those pools, according to:

$$\begin{aligned} C{-}N_{tree} = {} & frN_{ret,veg} \times \big(frN_{all,st} \times (C/N)_{st} + frN_{all,lv} \\ & \times (C/N)_{lv} + frN_{all,cr} \times (C/N)_{cr} + frN_{all,fr} \\ & \times (C/N)_{fr}\big) \end{aligned} \quad (1)$$

Similarly, the C–N response of soil is determined by the overall soil N immobilization fraction (frN_{im}) and the allocation of N over the organic layer (ol) and in the mineral soil (ms), according to [13]:

$$\begin{aligned} C{-}N_{soil} = {} & frN_{im,soil} \\ & \times \big(frN_{ol} \times (C/N)_{ol} + frN_{ms} \times (C/N)_{ms}\big) \end{aligned} \quad (2)$$

The fraction part of N that is not retained in vegetation or soil ($frNl_{oss}$) is lost to air (as N_2O, NO_x or N_2) via (de)nitrification or leached to surface and ground-water, mainly as NO_3.

The fate of N inputs to forest ecosystems can be derived from N application experiments, either including recorded changes of biomass and N concentrations in various forest ecosystem compartments and soil organic matter (e.g. [40,41•]) or based on ^{15}N tracer experiments [39,42,43]. Table 1 gives overall average N allocation fractions and C/N ratios for needle-leaved forests, deciduous broadleaved forests and evergreen broadleaved forests as summarized in Cleveland *et al.* [44••],