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EDITORIAL: NITROGEN DEPOSITION REASSESSED

Consequences of atmospheric nitrogen deposition in terrestrial ecosystems: old questions, new perspectives

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The anthropogenic production of reactive nitrogen (N) and the atmospheric fluxes of this growth-limiting resource onto native ecosystems have been the focus of thousands of papers over the past four decades. Records from the 1960s, 1970s and 1980s document unprecedented levels of N depositions, often exceeding tens of kilograms per hectare per year in Europe and North America. During the last decade or so, regulatory measures have led to the significant decline of the emission and deposition of reactive N (especially the oxidized forms) in eastern North America and Europe (Eshleman et al. 2013; Strock et al. 2014). While these declines may be interpreted as diminishing the importance of N deposition as a component of global change, there are compelling reasons to suggest just the opposite.

First, in regions of the world where N deposition rates have either stabilized or been reduced, they continue to be far above the background level. Despite the recent reduction in the emission rates of N, eastern North America and Europe still remain as regions with some of the highest N deposition rates in the world (Vet et al. 2014; Zhang et al. 2012). For example, Zhang et al. (2012) estimated that over 35 % of the contiguous US still receives more than 10 kg ha^{-1} year^{-1} of atmospheric N deposition. This is particularly revealing because we now know that deposition rates as low as $1-5$ kg N ha^{-1} year^{-1} can have significant effects on ecosystem processes (Arens et al. 2008). It must also be noted that in regions where N deposition has stabilized or declined, the legacy effects of decades of N deposition are likely to override the declining rates of deposition, but little is known about such effects. Secondly, atmospheric N deposition in many regions of the world, including China and India (Vet et al. 2014; Liu et al. 2013), and most likely Brazil (Allen et al. 2011), is on the rise. These regions are home to some of the most productive and diverse ecosystems of the world whose responses to N deposition are still unknown. Third, even in regions where N deposition has been on the decline, the decrease is predominantly in the oxidized ($\mathrm{NO_3}^-$) and not the reduced N form ($\mathrm{NH_4}^+$). Consequently, in many of these regions the ratio of the inorganic N forms is decisively shifting in favor of $\mathrm{NH_4}^+$ (Vet et al. 2014). It has been argued that the relative abundance of inorganic N forms may be a more important factor than the absolute amount that affects community-level processes (Lane and BassiriRad 2002; Boudsocq et al. 2012; Britto and Kronzucker 2013).

Much of the earlier research designed to better understand the consequences of N deposition on terrestrial ecosystems was shaped by the N saturation model first proposed by Aber et al. (1989). More specifically, this model proposed a broader set of biogeochemical mechanisms that triggered N saturation followed by a decrease in net primary productivity (NPP) and forest decline. This conceptual framework is based on a reasonable set of theoretical assumptions, and early research provided numerous empirical confirmation of it in some systems. However, two and a half decades of cumulating research point out that the N saturation model may not fully capture the end results and/or the underlying mechanisms. In fact, Aber et al. (1998) were among the first to revisit the N saturation model and pose a number of challenges that needed to be met to

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Dedication: to the memory of John Lussenhop (1941–2009) for his passion and contributions to soil ecology and an understanding of mycorrhizal fungi responses to N deposition

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improve its predictive ability. For example, they proposed that the onset of N saturation in some systems could be considerably delayed if the biological uptake capacity of the system is poorly understood or underestimated.

This special section includes six papers which highlight a subset of such challenges. The papers presented here cover a range of topics and ecosystem types from acidic grasslands in Europe, to boreal forests in Canada, to alpine grasslands in China, to temperate forests in the Midwest and Northeastern USA. The main theme and focus of these papers fall into two distinct areas:

1. How do biological uptake capacity, specific pools and fluxes of N respond to chronic N inputs? Now more than ever before, improved techniques make it possible for accurate identification and assessment of important pools and fluxes of N. The relative importance of these particular pools and fluxes is likely to be site specific and this highlights why we are currently unable to propose a mechanism that universally predicts ecological consequences.
2. Do plant species differ significantly in their responses to chronic N addition and what are the potential consequences for biodiversity? In many ecosystems that are experiencing high N input, a shift in species composition, encroachment of invasive species and more broadly, biodiversity, may be more critical response variables than NPP.

The first three papers focus largely on biological uptake and/or transformation of deposited N. The study by Templer et al. focuses on two class I wilderness areas of the Northeastern United States. These high-elevation forest ecosystems may be particularly sensitive to atmospheric pollution, but the scale of N deposition in these ecosystems and their responses are poorly understood. Comparative analysis of stable isotope of NO_3^- in atmospheric deposition and streams led this team to conclude that atmospheric N is being biologically converted as it moves through the watersheds, rather than directly passing through. They also found that the cycling of N, particularly the rate of throughfall for NH_4^+, is significantly different in conifer compared to deciduous forest sites. Finally, they concluded that these class I wilderness areas are not N saturated.

The rate of gaseous losses specifically through denitrification and how this responds to increased N deposition is the subject of the paper by Morse et al. The study was conducted at three hardwood forest sites in the Northeastern US representing a gradient of N deposition. They found that while denitrification in these forest sites is a significant proportion of the total N budget, the gaseous N losses through this pathway did not respond to increased N deposition rates. This conclusion is particularly important for modeling efforts designed to assess the critical N load (see Pardo et al. 2011), and whether atmospheric N input can be markedly offset by denitrification. In the third paper featured here, Houle et al. examined long-term flux patterns for bulk precipitation, throughfall and canopy N uptake between 1997 and 2012 at two boreal forest sites in Quebec, Canada. The paper reports that overall, these boreal forest canopies retain more than 50 % of the deposited N. However, the rate of canopy inorganic N retention was generally higher for NH_4^+ than for NO_3^-. More specifically, canopies retained an average of 65 and 50 % of the deposited NH_4^+ and NO_3^-, respectively.

The remaining three papers focus on community assemblages and whether individual species or functional groups respond differently to chronic N deposition. The study presented by Pannek et al. targeted a number of acidic grasslands in Northwestern Europe, including Germany and the Netherlands. They used both spatial and temporal gradient of N deposition along with other soil variables such as soil pH and P to assess the performance of 44 native species in these sites. N deposition was one of the most influential factors negatively affecting growth of 12 species, but positively affecting four others. The remaining target species did not significantly respond to deposition. The study has implications for conservation restoration of these acidic grasslands, but also provides strong evidence that N deposition can act as a strong selective force in shaping plant community dynamics.

Similarly, BassiriRad et al. found that the two dominant tree species, red oak and sugar maple, from Midwestern US temperate forest sites responded differently to N deposition. More specifically they reported that seedlings of oak, but not maple, responded negatively to 7 years of experimental N addition. They concluded that decades of N deposition is potentially a contributing factor to the observed historical trend of oak replacement by maple in these forest communities. Finally, Li et al. conducted a 4-year field experiment in an alpine grassland system in China and concluded that the effect of N deposition was conditioned by water availability. They found that increased N deposition rates generally improved the growth of grasses, but had a negative effect on forbs. Despite a clear difference between responses of grasses and forbs to increased N availability, there was no significant shift in species richness or other indexes of species composition.

Atmospheric N deposition will continue to be a major component of global change with potentially serious consequences for unmanaged ecosystems and plant communities. We hope the collection of papers assembled here sparks new ideas and approaches that would better inform experimental and modeling efforts yet to come.

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