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Review

Ecosystem responses to reduced and oxidised nitrogen inputs in European terrestrial habitats

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Changing ratios of NH_x and NO_y in deposition has important consequences for ecosystem function.

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ABSTRACT

While it is well established that ecosystems display strong responses to elevated nitrogen deposition, the importance of the ratio between the dominant forms of deposited nitrogen (NH_x and NO_y) in determining ecosystem response is poorly understood. As large changes in the ratio of oxidised and reduced nitrogen inputs are occurring, this oversight requires attention. One reason for this knowledge gap is that plants experience a different NH_x:NO_y ratio in soil to that seen in atmospheric deposits because atmospheric inputs are modified by soil transformations, mediated by soil pH. Consequently species of neutral and alkaline habitats are less likely to encounter high NH_4^+ concentrations than species from acid soils. We suggest that the response of vascular plant species to changing ratios of NH_x:NO_y deposits will be driven primarily by a combination of soil pH and nitrification rates. Testing this hypothesis requires a combination of experimental and survey work in a range of systems.

1. Introduction

Nitrogen (N) is essential for life as a component of amino acids, proteins, and DNA. Much N is present in the Earth's atmosphere, but almost all is in the unreactive form (N_2, gaseous N). The reactive forms of N utilised by organisms (Nr) naturally enter ecosystems via biological N fixation (by legumes, cyanolichens or free-living bacteria), biomass burning, volcanic activity and lightning but human activities over the last century have more than doubled the inputs of Nr into the World's ecosystems. The result has been widespread changes to the global N cycle (e.g. Galloway et al., 2008). Most of this rise in atmospherically deposited N has been in the form of wet deposition, N which enters ecosystems via precipitation, and dry deposition, which is the direct input of atmospheric N gasses and aerosols by wind and gravity. These inputs take two main forms, reduced (NH_x – ammonia and ammonium) and oxidised (NO_y – nitrogen oxides, nitric acid and particulate nitrate) both of which can be deposited as wet or dry deposition depending on climate. For example, wet areas such as Scandinavia will be dominated by wet deposition whereas dry

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areas such as the Mediterranean will be dominated by dry deposition. In Europe and parts of North America, the deposition of NH_x and NO_y strongly increased in the second half of the 20th century, primarily due to increasing agricultural and industrial activities (Fowler et al., 2004; Fenn et al., 2003). Since the 1990s N deposition has also started increasing in eastern Asia and India and it is expected that this dramatic rise will continue in the coming decades (Galloway et al., 2008; Dentener, 2006).

Increased deposition of N can increase net primary productivity in some terrestrial ecosystems (LeBauer and Treseder, 2008) but it has also been demonstrated in both experimental (e.g. Mountford et al., 1993; Wilson et al., 1995; Bobbink et al., 1998) and observational studies (e.g. Stevens et al., 2004; Maskell et al., 2010; Dupré et al., 2010) that increasing N deposition reduces plant species richness, with lichens, bryophytes, low growing forbs and legumes being particularly sensitive (Bobbink and Lamers, 2002; Suding et al., 2005). The mechanisms underlying these changes are yet to be fully understood and, while light exclusion has been demonstrated to be the cause of N induced species losses in mesotrophic grasslands (Hautier et al., 2009), N inputs may also decrease diversity through factors such as nutrient imbalance, soil acidification, ammonium toxicity, and increased susceptibility to pests and frost (see Bobbink et al., 1998, 2010 and references herein).

There have been previous calls that both the amount (load and dose) and form of N inputs need to be considered when considering N deposition effects on ecosystems (e.g. Bobbink and Roelofs, 1995; Bobbink et al., 2003) but in almost all ecological studies of N deposition reduced and oxidised N are considered equivalent, with the total amount of N deposition assumed to determine ecosystem response (e.g. Stevens et al., 2004; Manning et al., 2006). Very few studies have investigated the impact of changing ratios of NH_x and NO_y inputs although a number of studies have investigated the differential effects of reduced and oxidised N on vegetation (e.g. Sanchez-Hoyos and Manrique, 1995; Pearce et al., 2003; Paulissen et al., 2004; Van den Berg et al., 2008; Hogan et al., 2010) with some studies showing different impacts for different N forms. In this paper we argue that the form of N deposition inputs has important consequences for ecosystem response to N enrichment, and that viewing N deposition loads as total inorganic N input may be insufficient to understand ecosystem responses to N deposition.

Firstly, we explore the spatial and temporal patterns of NH_x and NO_y inputs (Section 2), the effects of changing NH_x and NO_y inputs and NH_x:NO_y ratios on soil processes and biogeochemical cycling, and discuss how these changes influence the NH_x:NO_y ratio which plants are exposed to in European terrestrial habitats (Section 3). We synthesise findings on plant species differences in their preference and tolerance of these two N forms (Section 4), identify situations where NH_x:NO_y ratio needs to be considered when explaining community-level responses to N deposition, and make predictions regarding these community responses (Section 5). Finally, we discuss the science required to confirm these predictions and the implications of changing NH_x:NO_y ratios for biodiversity conservation and habitat management (Section 6). This review will focus on the impacts of the changing inputs and ratios of N deposition in European terrestrial habitats because they have been most intensively studied. While we do not expect the mechanistic basis to change, translating our hypotheses to areas of the world not covered by our data (e.g. South America, East Asia and East Africa) must be treated with caution.

2. The cause of differences in N input ratios

There are considerable differences in the temporal and spatial patterns of NH_x and NO_y emissions (Holland et al., 2005), and there is evidence that ratios of reduced to oxidised N deposition are changing at regional scales as a result of land use, technology and policy changes.

Nitrogen oxides (NO_y) are emitted mainly from stationary combustion sources (industrial processes and power plants) and transport activities (road and ship traffic), while reduced N (NH_x) emissions are mostly a result of agricultural activities such as animal husbandry (livestock wastes) and fertiliser application (e.g. Asman et al., 1998; Holland et al., 2005). Because of the differences in sources and their distribution, atmospheric transformations and deposition velocities, clear regional N deposition patterns have been observed. In general, total N deposition is spatially highly variable, with the highest deposition rates often dominated by dry deposition of NH_3 close to its source, and declining rapidly with distance (see Stevens and Tilman (2010) for an example). In contrast, wet deposition of both NH_x and NO_y and dry deposition of NO_y display less spatial variability, as a result of the diffuse and point source origins of these two forms of pollutant. The result of this variability is spatial heterogeneity in the pattern of NO_y and NH_x deposition at a local scale (Sutton et al., 1998).

This local variability is nested within large scale patterns of N deposition. In western Europe, the highest values were observed in the 1980s and 1990s, with hot spots of NH_x deposition (>70% of total deposition) in intensively farmed regions such as Netherlands, Belgium, Denmark, north-west Germany and Italy's Po Valley. Contrary to this, NO_y deposition peaked in the 1980s in parts of Eastern Europe (Van Leeuwen et al. 1996). Over Europe as a whole NO_y deposition decreased between 1990 and 2005 as a result of a change from coal burning to gas or nuclear power, while NH_x deposition stabilised after 1995, resulting in an increased NH_x:NO_y ratio (Fagerli and Aas, 2008). Significant differences in the input of NO_y and NH_x are even seen at the continental scale. In the 1990s the NH_x:NO_y ratio for the USA was 0.64, in contrast to 1.02 in Europe and 2.48 in Asia as a result of different energy production, farming and waste management practices (Galloway et al., 2004; Fig. 1).

Galloway et al. (2004) predict that by 2050 terrestrial NO_y deposits will have increased by up to 70% from levels in the 1990s, while NH_x deposits will increase by 133% over the same period primarily due to increased demand for food. This trend towards increased NH_x deposits relative to those of NO_y is already being observed in Europe (Fagerli and Aas, 2008). However, in the Netherlands NH_x deposition has decreased considerably through legislation, which significantly reduced NH_x emissions. Detailed measurements from a Dutch pine forest have shown that NH_4^+ deposition in throughfall decreased by 40% since 1984, while NO_3^- deposition increased, resulting in significant decrease in throughfall NH_4^+:NO_3^- ratio. At the same time, the NH_4^+: NO_3^- ratio in the mineral soil solution at 10 cm depth also decreased (Fig. 2; Boxman et al., 2008), indicating that changes in the ratio of deposits may be experienced by plant roots.

3. Factors controlling plant responses

After deposition, N is affected by a number of factors, influencing the ratio of reduced and oxidised N that plants are exposed to (Fig. 3). Where plants take up N via their leaves, the NH_x:NO_y ratio they experience will often be similar to atmospheric N deposits. In contrast, N deposits to the soil may be strongly modified by chemical and biological transformations in the heterogeneous soil environment, and so soil NH_x:NO_y ratios may be very different to those of N deposits (Fig. 3).

3.1. Stratification by vegetation

Spatial patterns of reduced and oxidised N deposition, and the relative abundances of these two forms, will be modified at local