



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 NH₄⁺ 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.

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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 (N₂, gaseous N). The reactive forms of N utilised by organisms (Nr) naturally enter ecosystems via biological N fixation (by legumes, cyanobacteria 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 $\text{NH}_x:\text{NO}_y$ ratios on soil processes and biogeochemical cycling, and discuss how these changes influence the $\text{NH}_x:\text{NO}_y$ 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 $\text{NH}_x:\text{NO}_y$ 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 $\text{NH}_x:\text{NO}_y$ 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 $\text{NH}_x:\text{NO}_y$ 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 $\text{NH}_x:\text{NO}_y$ 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 $\text{NH}_4^+:\text{NO}_3^-$ ratio. At the same time, the $\text{NH}_4^+:\text{NO}_3^-$ 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 $\text{NH}_x:\text{NO}_y$ 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 $\text{NH}_x:\text{NO}_y$ 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

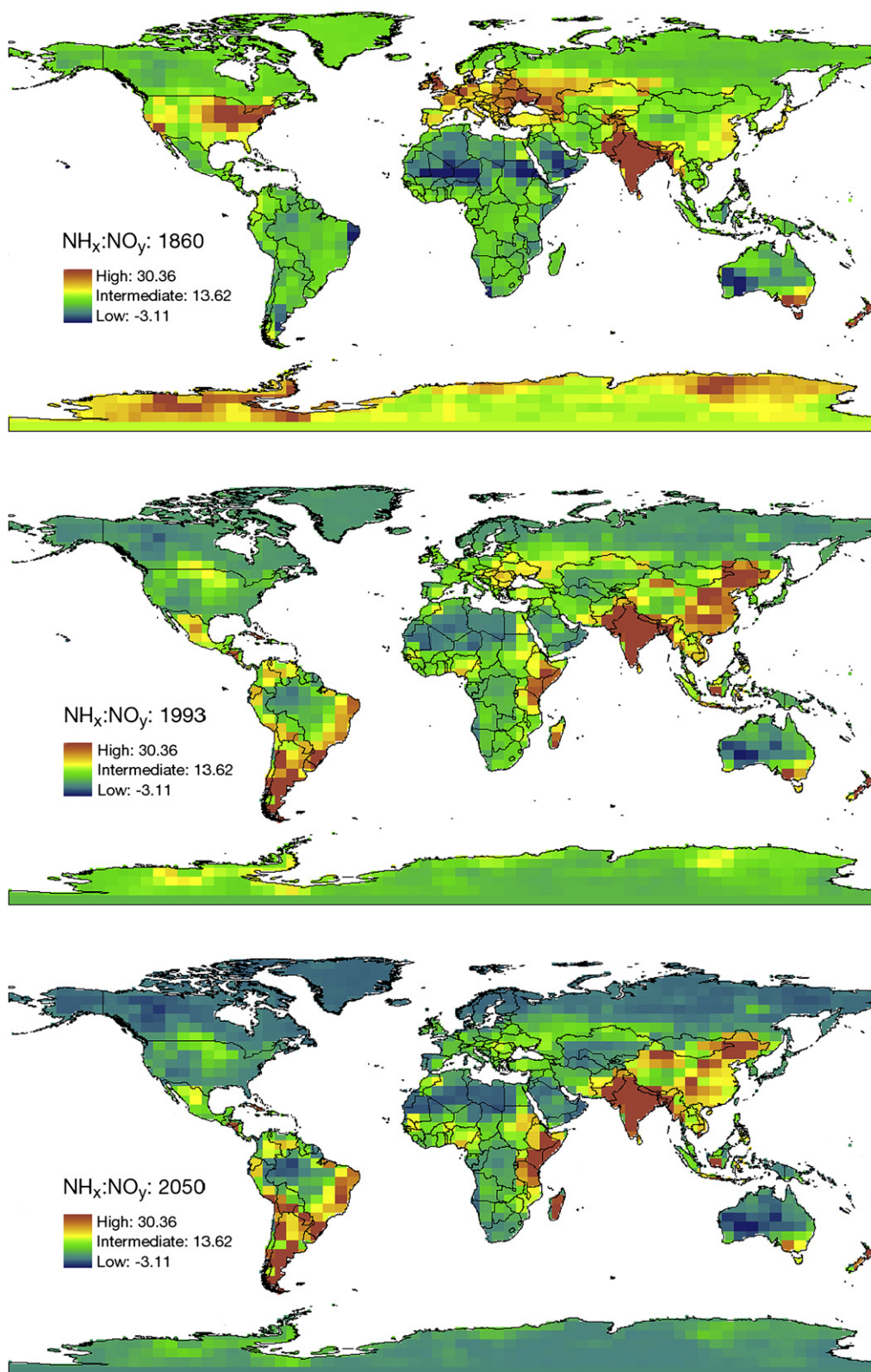


Fig. 1. Ratio between modelled NH_x and NO_y deposits (by mass $\text{NH}_4\text{-N} : \text{NO}_3\text{-N}$) for 1860, 1993 and 2050. Data were taken from the modelled output of Dentener, 2006.

scales by vegetation structure (e.g. Fangmeier et al., 1994) and soil conditions. For example, dry deposition of N onto vegetation with a rough canopy structure, e.g. coniferous forest, is considerably higher (>50%) than that onto smooth surfaces, e.g. a calcareous

grassland. Moreover, the roughness of the vegetation may also influence the $\text{NH}_x:\text{NO}_y$ ratio of deposited N. In coniferous and deciduous forests $\text{NH}_x:\text{NO}_y$ ratios in open field precipitation and throughfall are approximately of the same order of magnitude

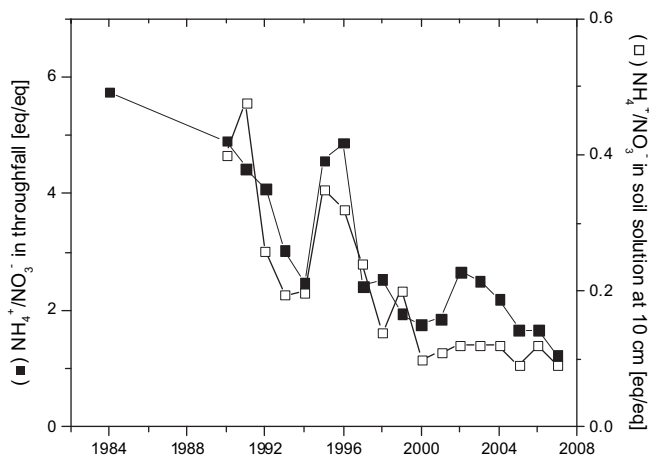


Fig. 2. Ground measurements of $\text{NH}_x:\text{NO}_y$ ratio in throughfall, and in the mineral soil at 10 cm depth [eq/eq] in a Dutch Pine forest. Original data source: Boxman et al., 2008.

(Berger et al., 2008). In (grass-dominated) heathlands there are indications that the $\text{NH}_x:\text{NO}_y$ ratio in throughfall is much lower than that of open field precipitation. The latter is solely due to lower NH_x concentrations, with NO_y concentrations remaining unaltered, indicating preferential foliar uptake of NH_x (De Schrijver et al., 2008). Modification of $\text{NH}_x:\text{NO}_y$ ratios also occurs in some moss-dominated ecosystems, where the preferential uptake and sequestration of NH_4^+ in the moss carpet (Wiedermann et al., 2009) regulates the soil $\text{NH}_x:\text{NO}_y$ ratio that is experienced in the rhizosphere of vascular plants (Lamers et al., 2000; Limpens et al., 2003).

3.2. Soil processes affecting $\text{NH}_x:\text{NO}_y$ ratio

In the soil, gaseous forms of NH_x and NO_y dissolve readily to form NH_4^+ and NO_3^- . Typically most NO_3^- is either taken up by

plants and microbes, with a small portion denitrified. Unlike NO_3^- , NH_4^+ can bind strongly to soil cation exchange sites, resulting in soil NH_4^+ accumulation (Fig. 3). In the soil solution, however, plant roots will experience changes in the $\text{NH}_x:\text{NO}_y$ ratio that will influence plant and soil properties, including transformations of N within the soil. All of these effects will be modified by the existing properties of the soil (derived primarily from the type of bedrock), such as its buffer capacity, pH, redox potential, microbial community composition, and climate. However, due to complex interactions between these soil properties it may prove difficult to predict general effects of changing $\text{NH}_x:\text{NO}_y$ ratios on soil N availability.

While the effect of $\text{NH}_x:\text{NO}_y$ ratio on decomposition and mineralisation is poorly known, both direct effects on the activity and abundance of dominant decomposer groups and indirect effects through litter quality are to be expected. For example, increased N input most often stimulates the initial stages of litter decomposition, in which easily degradable materials are consumed by microbes, but suppresses later decomposition stages, in which recalcitrant C is 'mined' for nitrogen (Berg and Matzner, 1997; Knorr et al., 2005); however, exceptions to occur (e.g. Keeler et al., 2009 found no or negative effects on overall rates of litter and organic matter decomposition). The strength of such effects may differ depending on the form of deposited N. DeForest et al. (2004) found chronic NO_3^- additions did not alter the microbial community composition but broadly suppressed all microbial groups which may also impact soil processes. Indirect effects may also occur through changes in plant litter quality (see Section 4.1). The resulting changes to decomposition and N mineralisation rates may subsequently lead to differences in the amount and form of N available to plants. Initial evidence for such effects is provided by Currey et al. (2010), who found that potential mineralisation of labile carbon was higher under NH_4^+ addition than under NO_3^- addition in peat soils. In the same study it was also shown that consumption of the amino acid glutamic acid was higher under NH_4^+ than NO_3^- addition.

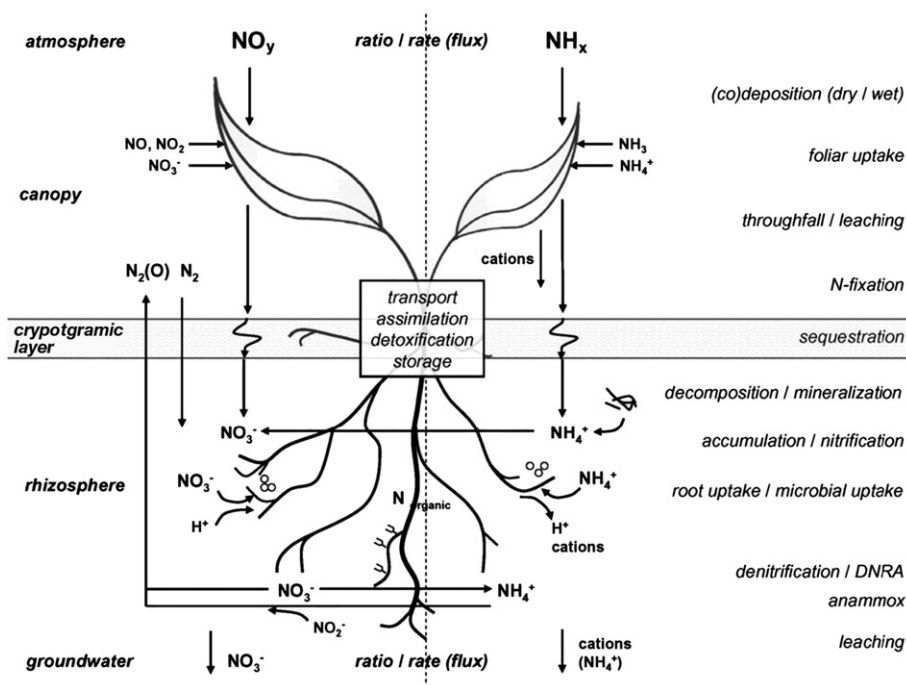


Fig. 3. Processes influencing the availability and ratio of oxidised (NO_y) and reduced (NH_x) nitrogen forms which plants are exposed to DNRA: dissimilatory nitrate reduction to ammonium, anammox: anaerobic ammonium oxidation.

3.2.1. Nitrification and denitrification

The ratio of NH_x and NO_y in soil is strongly influenced by the activity of nitrifying, ammonia oxidizing bacteria (AOB). Nitrification itself is also affected by several soil factors including availability of NH_4^+ (the sole energy source for autotrophic nitrifying bacteria, Booth et al., 2005), pH, O_2 availability (and factors influencing O_2 diffusion through soil such as soil structure), temperature, soil moisture, C:N ratio (e.g. Vestgarden and Kjønaas, 2003) and $\text{DOC}:\text{NO}_3^-$ ratios (Taylor and Townsend, 2010). It is very likely that soil nitrifying activity will increase with increased NH_4^+ availability (in absolute or relative terms), but the magnitude of this increase may depend on soil pH and soil aeration, which are often correlated. In various ecosystems, such as grasslands and heathlands, nitrification is inhibited at low soil pH, resulting in NH_4^+ accumulation (e.g. Roelofs et al., 1985; Dorland et al., 2004). Since nitrification yields protons, it reduces pH and so constitutes a negative feedback, reducing nitrification. As a result high NH_4^+ inputs can acidify the soil and limit future nitrification. In other ecosystems such as forests, nitrification may depend less on soil pH (Booth et al., 2005) or can even be high despite low soil pH, as has been reported for some mature forests (Houdijk et al., 1993). Nitrification also depends on the presence and abundance of the initial bacterial community structure. For example, elevated NH_y concentrations result in increased nitrification rates in the presence of NH_y -tolerant AOB, whereas nitrification will be delayed (or even inhibited) when NH_y -sensitive AOB dominate (Prosser, 1989; Webster et al., 2005). In summary, higher $\text{NH}_x:\text{NO}_y$ ratios in N deposition will only lead to increased ratios of plant-available $\text{NH}_4^+:\text{NO}_3^-$ ratios in soils with low nitrification rates. These soils are characterized by initially low NH_4^+ and low O_2 availability, low pH, and very low or very high soil moisture levels (Booth et al., 2005). In soils with high nitrification rates a high ratio of $\text{NH}_x:\text{NO}_y$ deposits is less likely to be retained in the soils. This conversion of NH_x to NO_y lessens the threat of NH_x toxicity to plants (see below) but poses a greater risk of problems associated with acidification, and NO_y pollution in groundwater and runoff.

In general, the anaerobic processes denitrification (the conversion of NO_3^- to NO , N_2O and N_2) and DNRA (Dissimilatory Nitrate Reduction to Ammonium, i.e. the conversion of NO_3^- into NO_2^- and subsequently to NH_4^+) play a minor role in well-aerated soils (e.g. De Klein and Van Logtestijn, 1996; Stevens et al., 1998). Consequently, plant-available $\text{NH}_4^+:\text{NO}_3^-$ ratios in soils of temperate European grasslands, heathland and forests will be largely unaffected by these microbial processes. In wetlands however, denitrification and DNRA may play a major role in removing excess NO_3^- from the soil. Once the supply of NO_3^- from either atmosphere or nitrification decreases, denitrification and DNRA rates drop (Paavola and Smolander, 1998; Silver et al., 2001; Sanchez-Martin et al., 2008), resulting in accumulation of NH_4^+ and high $\text{NH}_4^+:\text{NO}_3^-$ ratios. We hypothesize that in wetlands with low nitrification rates (i.e. with low soil redox potential and low availability of carbon and O_2), increasing $\text{NH}_x:\text{NO}_y$ ratios in N deposition leads to lower denitrification and DNRA activity and accumulation of NH_4^+ .

3.3. Interaction with other elements and acidification

Besides differential effects on microbial processes, the dominant form of inorganic soil N also affects several other soil properties affecting plant performance. Increased NH_4^+ deposition may directly and indirectly affect the concentration of essential base cations, such as K^+ , Mg^{2+} and Ca^{2+} , by replacing them on the cation exchange sites in the soil, or by depressing base cation uptake by plants, particularly at low pH (Boxman et al., 1991; Gloser and Gloser, 2000). As a result, base cations are readily leached to deeper soil layers, potentially leading to base cation depletion or trace-element shortages.

Additionally, increased NH_x deposition may lead to soil acidification via a number of pathways including nitrification, with two H^+ produced per mol N, exchange of NH_4^+ with H^+ at the soil complex, or by plant uptake of NH_4^+ (Fig. 3), particularly in weakly buffered soils. This acidification can in turn, reduce plant-available N and N-uptake by plants and their symbionts through changes in the availability of heavy metals and aluminum (e.g. Lazof et al., 1994; Ghnaya et al., 2007).

4. Plant responses

4.1. Root and foliar N uptake

Foliar (including bryophyte shoot system) N uptake (Fig. 3) can be significant in vascular plants, bryophytes and lichens, particularly in N-limited systems (e.g. Pérez-Soba and van der Eerden, 1993; Cape et al., 2009) and during periods of rapid growth when stomatal conductance is high (e.g. Wilson, 1992; Teklemariam and Sparks, 2004). Although many lichens capture both nitrate and ammonium equally under ambient concentrations (Hauck, 2010), in general, in vascular plants foliar uptake of NH_x exceeds that of NO_y (e.g. Garten and Hanson, 1990; Wilson, 1992; Lumme, 1994; Palmqvist and Dahlman, 2006). In an N-limited spruce forest, foliar N uptake was ~90% for NH_4^+ and ~75% for NO_3^- (e.g. Sievering et al., 2007). Foliar NH_4^+ uptake is usually accompanied by an increase in base cation concentration in stem flow and throughflow, implying the loss of base cations from the foliage and potential risk of deficiencies of ions such as K^+ , Mg^{2+} , Ca^{2+} and Mn^{2+} (Roelofs et al., 1987; Garten and Hanson, 1990; Bobbink et al., 1992; De Schrijver et al., 2008). In addition, foliar NH_4^+ uptake affects cell pH regulation as ions (e.g. H^+) are exchanged with the cell apoplasts, potentially resulting in cell acidification and problems relating to cell elongation and growth (Peuke et al., 1998; Paulissen et al., 2004; Van den Berg et al., 2005). In contrast, uptake and assimilation of reduced N by roots is usually accompanied by H^+ exchange with the rhizosphere (Fig. 3) preventing cell acidification, unless pH is low. Under such conditions, root uptake of NH_4^+ may lead to cell acidification in non-adapted plant species, as these plants are not able to exude H^+ to the acid rhizosphere (Lucassen et al., 2003; Van den Berg et al., 2005). In contrast, uptake of NO_3^- by either shoots or roots has no consequences for cell pH.

The rate and form of inorganic N uptake depends heavily upon both plant species and soil properties. Plants adapted to soils with low nitrification rates e.g. many slow growing and perennial groups including Ericaceae and conifers, tend to prefer NH_4^+ as their main N source. They can tolerate high NH_4^+ concentrations and often possess a reduced capacity to utilise NO_3^- (Forde and Clarkson, 1999; Britto and Kronzucker, 2002; Schjoerring et al., 2002). A lack of nitrate reductase synthesis may be one physiological explanation for poor NO_3^- utilisation (Koyama and Tokuchi, 2003).

In contrast, species of less acidic or calcareous, open and disturbed soils (e.g. after fire (Cruz et al., 2008)), which tend to have faster nitrification rates (e.g. fast growing annuals including agricultural crops and pioneer trees), generally prefer NO_3^- or a mixture of both NH_4^+ and NO_3^- (e.g. Pearson and Stewart, 1993; Falkengren-Grerup, 1995; Pearson and Soares, 1995).

As an illustration we use data detailing the presence or absence of 98 plant species in 520 vegetation relevés in which soil $\text{NH}_4^+:\text{NO}_3^-$ ratio was also measured to determine the relationship between species abundance and soil $\text{NH}_4^+:\text{NO}_3^-$ ratio (see Wamelink et al. (2005) for details of survey methods). Species associated with high $\text{NH}_4^+:\text{NO}_3^-$ ratios or independent in their response include some trees (e.g. *Quercus robur*), (dwarf) shrubs and generalist species like *Molinia caerulea* (Fig. 4a and b). Species associated with low $\text{NH}_4^+:\text{NO}_3^-$ ratios include many species of (wet) grasslands, like

Ranunculus repens (Fig. 4c). Other variables such as soil moisture have not been taken into account in these analyses so co-variation cannot be ruled out.

Although plants may have clear preferences in terms of N form, uptake rates do not necessarily reflect this. In the presence of both inorganic N forms, NH_4^+ is more readily taken up by most plants, because its reduced state makes its uptake less energetically costly

than that of NO_3^- (Bloom et al., 1992). Even in plants that can suffer from NH_4^+ toxicity, NH_4^+ uptake often exceeds that of NO_3^- (De Graaf et al., 1998).

The form of N taken up or experienced by a plant may affect its health and performance. There is considerable evidence that sole NH_4^+ -N nutrition and high $\text{NH}_4^+:\text{NO}_3^-$ ratios are toxic to plants (e.g. Dijk and Eck, 1995; De Graaf et al., 1998; Van den Berg et al., 2005). NH_4^+ toxicity is manifested by leaf chlorosis, stunted root growth, increased shoot: root ratio, decreased fine: coarse root ratio, growth retardation and, in extreme cases, plant death (Britto and Kronzucker, 2002; Van den Berg et al., 2005; Boxman et al., 1991). Several non-exclusive mechanisms have been postulated as the cause of this toxicity. These are (1) NH_4^+ uptake reduces the uptake of important cations such as Ca^{2+} , Mg^{2+} and K^+ (Marschner, 1995); (2) NH_4^+ is metabolised immediately to N-rich amides and amino acids within plant cells (Raven and Smith, 1976), diverting resources away from plant growth (Schortemeyer et al., 1997); (3) NH_4^+ uptake and assimilation imposes homeostatic energetic costs on the plant to maintain cytosol pH, potentially retarding growth (Bligny et al., 1997; Gerendas and Ratcliffe, 2000).

4.2. Variation in plant tolerance to NH_x

Regardless of the mechanism by which NH_x impairs plant performance, it is clear that plant species differ strongly in their tolerance of high NH_x concentrations. For species of originally weakly acid soils ($4.5 < \text{pH} < 6.5$) NH_4^+ toxicity occurs at external concentrations of $100 \mu\text{mol l}^{-1}$ or less (Dijk and Eck, 1995; De Graaf et al., 1998; Van den Berg et al., 2005), but in species from acid soils it is only manifested at much higher concentrations (Boxman et al., 1991; De Graaf et al., 1998). Underlying these patterns are physiological differences between species. Many plants, including bryophytes, respond to NH_4^+ uptake by synthesising specific amino acids and amides, particularly amino acids with a low C:N ratio (e.g. Lucassen et al., 2003; Limpens and Berendse, 2003), and this may help to prevent NH_4^+ toxicity. Bryophyte and herb species have shown increases in the fraction of N-rich free amino acids when grown at increased N supply, with NH_4^+ as the dominant N form, in both greenhouse and field experiments (Fig. 5).

Differences in the sensitivity of plant species to reductions in their cytoplasmic pH (acidosis) and in the capacity of species to buffer their cytoplasm, may also explain species-specific responses to NH_x deposition (Pearson and Stewart, 1993). For appropriate cell functioning, the pH of the cytosol should be maintained within an appropriate range. Plants which predominantly take up and assimilate NO_3^- generate bases and thereby buffering capacity, either through OH^- release or by base cation uptake. This reduces their sensitivity to cytoplasmic acidosis. In contrast, with NH_x -uptake plants generate acidity instead of OH^- . Though it has been shown that NH_4^+ nutrition does not always lead to decreased cytosol pH (Bligny et al. 1997; Gerendas and Ratcliffe, 2000), maintaining optimal cytosol pH is an energy demanding process. This energy is not available for plant maintenance or growth and may therefore, at least partly explain the retarded growth of many species grown on NH_4^+ nutrition (Britto and Kronzucker, 2002).

Light may also play a role in modifying species responses to NH_x as its toxicity is less pronounced at low-light intensity (Britto and Kronzucker, 2002). This may mean that understory species are less likely to be sensitive to increases in the ratio of $\text{NH}_x:\text{NO}_y$ inputs but more research is needed to test this. Plants susceptible to NH_4^+ toxicity might be afflicted by reduced rates of net photosynthesis, and thus, are in lower need of N. However, understory plants are most likely well adapted to these low-light conditions, with 'normal' photosynthesis rates in shaded conditions.

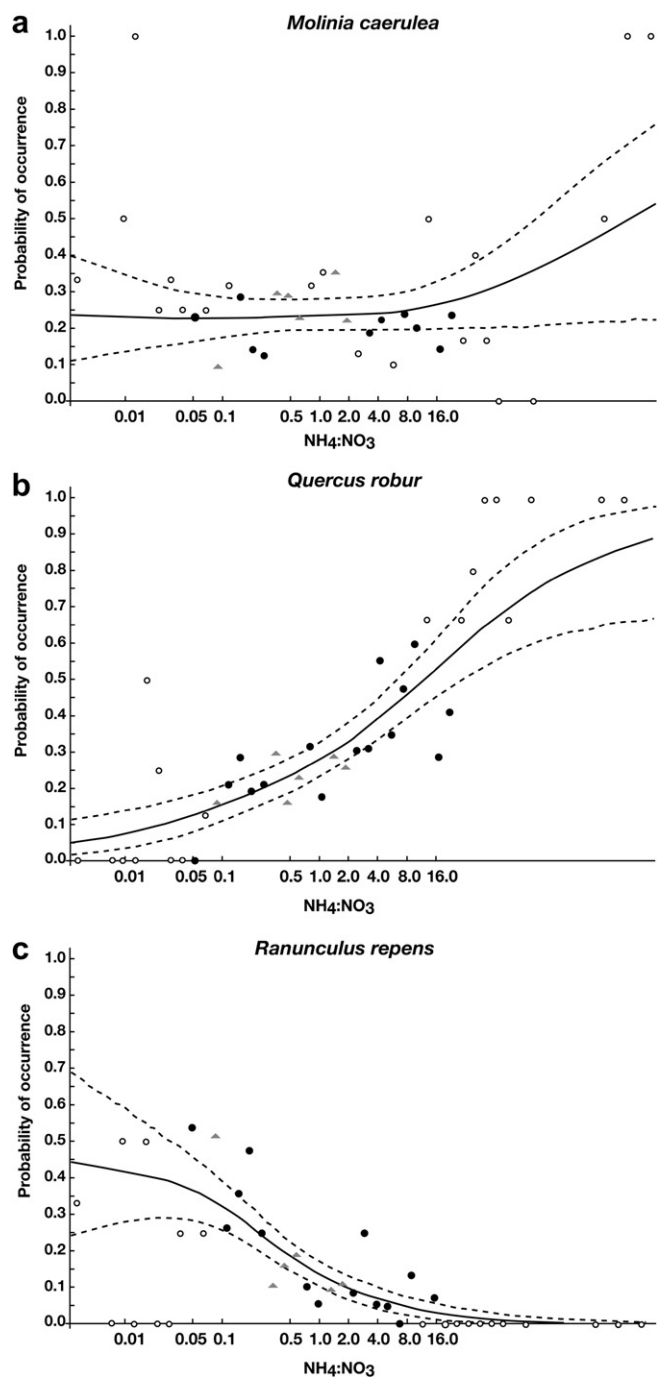


Fig. 4. Response curves and 95% confidence intervals (broken lines) of three plant species across a $\text{NH}_4^+:\text{NO}_3^-$ ratio gradient. The curves represent species with (a) a positive association with high $\text{NH}_4^+:\text{NO}_3^-$ ratios, (b) abundance independent of $\text{NH}_4^+:\text{NO}_3^-$ ratio, and (c) a species associated with low $\text{NH}_4^+:\text{NO}_3^-$ ratios. Open circles are those in which the probability of occurrence is calculated from ≤ 10 relevés, filled circles were drawn from 11 to 25 relevés and triangles 26–50 relevés. See Wamelink et al. (2005) for methods, soils were collected in the field, extracted using 0.01 M CaCl_2 solution and analysed using an autoanalyser.

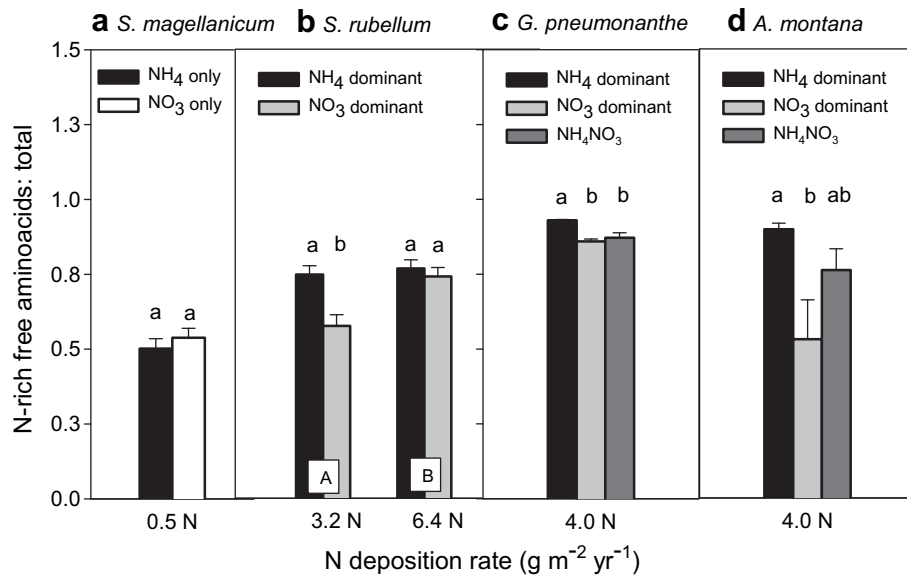


Fig. 5. The ratio between the concentrations of the three main N-rich free amino acids (arginine, glutamine and asparagine) and all free amino acids (g g^{-1}) in bryophytes from N-poor acidic ecosystems ((a) *Sphagnum magellanicum*, (b) *Sphagnum rubellum*) and in two perennial herbs from N-poor, weakly buffered ecosystems ((c) *Gentiana pneumonanthe*, (d) *Arnica montana*) subjected to different $\text{NH}_4^+:\text{NO}_3^-$ ratios and N supply. Reduced or oxidised N treatments were applied to the bryophytes and plants in the greenhouse for three months (a), in the field for three years at $\text{NH}_4^+:\text{NO}_3^-$ ratios of 1:9 and 9:1 (b) or in a climate chamber for three months at $\text{NH}_4^+:\text{NO}_3^-$ ratios of 4:1, 1:1 and 1:4 (c, d). Different capital letters indicate significant effects of N load (ANOVA, $p < 0.05$), different lower case letters indicate effects of N form (paired t -test). Data sources: (a) J. Limpens (unpublished) and (b–d) L.J.L. van den Berg (unpublished).

In addition to these effects on mature plants $\text{NH}_4^+:\text{NO}_3^-$ ratio may also influence germination and early seedling establishment. Both N forms are known to break seed dormancy but germination effects will be species specific as not all species are stimulated, some only respond to NO_3^- or NH_4^+ , and responses may be both positive and negative (e.g. Singh and Amritphale, 1992; Dorland et al., 2003; Luna and Moreno, 2009).

Plant species sensitivity to $\text{NH}_4^+:\text{NO}_3^-$ ratio may also depend upon the preferences and sensitivities of their associated symbionts. A meta-analysis of N addition effects on mycorrhizal fungi found negative effects of N addition but no significant impact of N form (Treseder, 2004). However, some individual studies have found an impact of N form, for example, Yoshida and Allen, 2001 found a large mycorrhizal response to ammonium addition but not nitrate addition in coastal sage scrub species in California. Ectomycorrhizal plants appear to prefer NH_4^+ (e.g. Cumming, 1990), whereas arbuscular mycorrhizal (AM) plants seem to prefer NO_3^- (e.g. Cuenca and Azcon, 1994; Persson et al., 2003) although this is not always the case (e.g. Yoshida and Allen, 2001). These preferences are consistent with the natural patterns of N availability and plant uptake, and mycorrhizal distribution (Nordin et al., 2001). This implies that AM plant species may decline when the $\text{NH}_4^+:\text{NO}_3^-$ ratio in the soil is high or increasing.

5. Community and ecosystem responses to changing $\text{NH}_4^+:\text{NO}_3^-$

Despite strong evidence that $\text{NH}_4^+:\text{NO}_3^-$ ratio affects plant species differentially with respect to germination, growth and survival it is still not known how important the form of N is relative to the amount of N being deposited in determining community responses to N enrichment. Where ratio effects are important the mechanism is likely to differ depending on soil NH_4^+ and NO_3^- concentrations as determined by the factors and processes explained above, and by their differential effects (toxicity, growth etc) on species performance.

Based on the preceding review we hypothesize that there is a gradient of $\text{NH}_4^+:\text{NO}_3^-$ ratios in the soil, driven primarily by soil pH and subsequently nitrification rates, with plant species life history strategies evolving to specialise at different points on this gradient and thus displaying a range of inherent sensitivities to NH_4^+ (Fig. 6). We also predict that the relationship between $\text{NH}_4^+:\text{NO}_3^-$ ratios in the soil and plant species is general, with these patterns being found in a wide range of habitats. Such a natural gradient generates context dependency in the effects of NH_4^+ and NO_3^- deposits and makes the prediction of responses to changing $\text{NH}_4^+:\text{NO}_3^-$ input ratios challenging.

In acid environments ($\text{pH} < 4.5$) where nitrification rates are frequently low, N will accumulate as NH_4^+ , potentially reaching toxic concentrations. In such cases species differences in sensitivity to high NH_4^+ concentration will determine community response (Fig. 6).

Acidification processes related to high NH_4^+ concentrations result in the mobilisation of metals and an increase in metal concentrations such as aluminium (Al^{3+}) and iron (Fe^{3+}) (Stevens et al., 2009). In addition base cation (Ca^{2+} , Mg^{2+}) concentrations decline. Tolerance to free metal concentrations may also be important in determining community response (e.g. De Graaf et al., 1994). While some species found at these sites may tolerate these increases in NH_4^+ and metal ion concentrations, species growth rates and thresholds for tolerance may differ within a community (Kleijn et al., 2008). For any given community it is likely to be those species with the lowest tolerance to NH_4^+ and metals and strongest preference for NO_3^- that will decline when the ratio of $\text{NH}_4^+:\text{NO}_3^-$ inputs increases. Evidence for this has been found in dry heaths ($\text{pH} 3.8\text{--}4.9$), where soil NH_4^+ concentrations were strongly negatively correlated with the number of plant species and a better predictor for plant diversity in this ecosystem than pH or Al^{3+} (De Graaf et al., 2009).

As the initial soil pH increases and nitrification rates increase a greater proportion of NH_4^+ deposition inputs will be converted into the non-toxic NO_3^- form. We predict that in soil of intermediate pH (4.5–6.0) nitrification rates will be sufficient to convert a large

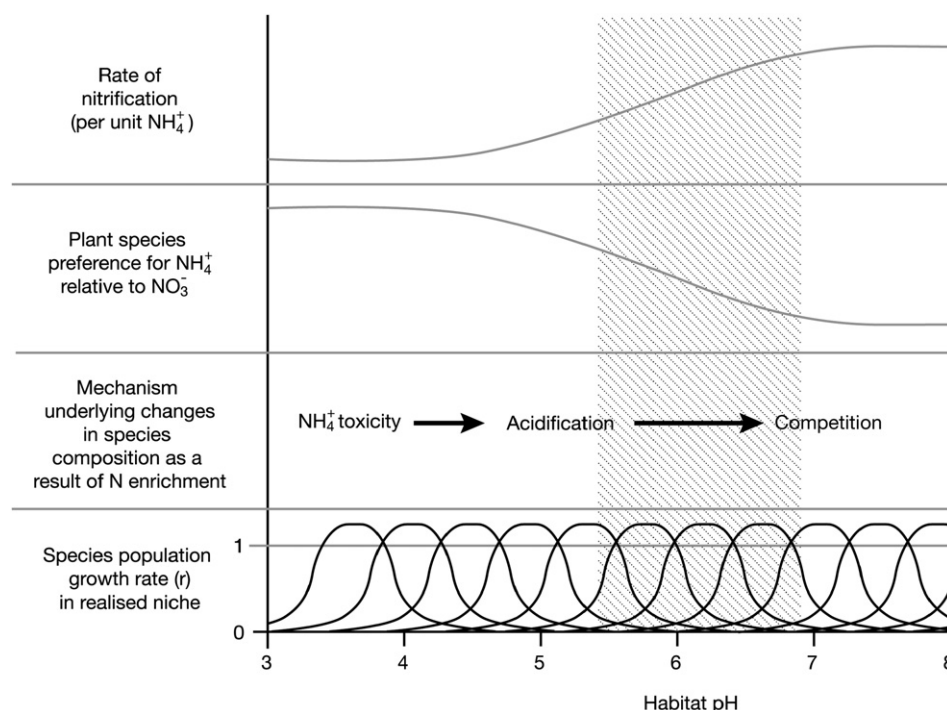


Fig. 6. Hypothetical relationships between the background soil pH and the mechanisms regulating plant community composition responses to N addition. The performance of different species, as represented by r , with each hump equivalent to a species' realised niche, differs across the pH gradient and so any shift in conditions results in compositional change. In low pH systems high $\text{NH}_x:\text{NO}_y$ inputs move the community to the left and low $\text{NH}_x:\text{NO}_y$ inputs shift the community to the right. At higher pH (probably ~ 5.5) most NH_4^+ is nitrified and the form of N addition becomes less important in predicting plant community response. The hatched area represents the region of uncertainty in which high nitrification rates and buffering capacity render the form of N inputs unimportant.

proportion of the deposited NH_x into NO_y . However, if associated pH decline is large, and soil pH approaches 4.5, then deposition of NH_x may cause species loss via Al^{3+} or H^+ toxicity, and shift conditions towards low pH conditions in which NH_4^+ accumulates (Fig. 6). Species that are adapted to very acid conditions will not suffer from NH_4^+ toxicity. For them, the enhanced N-availability will lead to increased productivity and enhanced competitive ability. In wet heathlands this has resulted in vegetation changes from dwarf shrub dominated heaths to domination of grasses such as *M. caerulea* and *Deschampsia flexuosa*. We therefore hypothesize that in soil of intermediate pH species typically found on soils with pH 4.5–6 will decrease in abundance with increasing $\text{NH}_x:\text{NO}_y$ inputs and that species typical of soils of pH < 4.5, or insensitive species e.g. *M. caerulea*, will increase in abundance. In heathlands and grasslands on weakly buffered soils, it has been shown that soil acidification was the main factor in explaining plant species richness declines, thereby supporting the current hypothesis (De Graaf et al. 2009). In summary, we predict that in soils of low and intermediate pH the species with the highest pH and lowest $\text{NH}_4^+:\text{NO}_3^-$ optima are most at risk if the system experiences an increase in $\text{NH}_x:\text{NO}_y$ input ratios.

In more neutral soils (pH 6.0–7.5) an increase in the $\text{NH}_x:\text{NO}_y$ ratio of inputs will be mitigated by rapid nitrification of NH_4^+ to NO_3^- , thereby preventing ammonium toxicity from occurring. The high initial soil pH will also mean that the soils are initially well buffered against the effects of acidification. In these soils with a high NH_4^+ turnover, N deposition is more likely to have a fertilising effect and it may be the degree of N limitation and the total amount of N deposited, rather than its form that is important to plant community dynamics. In such cases community response to N is most likely driven by increases in plant productivity (Clark et al., 2007), with tall, rapidly growing and canopy forming species casting a shade which excludes smaller plants (Bobbink, 1991;

Manning et al., 2009; Hautier et al., 2009) and legumes, which lose their N fixing advantage and are outcompeted at high N availability (Suding et al., 2005).

Further research is required to confirm the relationship we suggest between soil $\text{NH}_4^+:\text{NO}_3^-$ ratios and plant species composition. A number of modifying factors need to be assessed including the habitat specific threshold of soil conditions above which high nitrification rate renders the form of N inputs unimportant, and the degree of generality in the relationship between pH and nitrification rates should be evaluated. The potential for acidification is also likely to vary between sites depending on their soil buffering system. We therefore need to identify the positions on natural environmental gradients above which plant community responses to N addition are no longer predominantly determined by NH_4^+ sensitivity mechanisms, but by acidification and light or other nutrient competition. Although this hypothesis is community dependent in its details, and there are likely to be exceptions to the hypothesized trends, its principles are general and so it could be tested with a combination of experimental and survey work across a range of systems, adopting an approach similar to that of Kleijn et al. (2008).

6. Assessment and management of the ecosystem impacts of changing $\text{NH}_x:\text{NO}_y$ ratios

While the synthesis presented here suggests an important role of N form in determining ecosystem responses to N deposition there is great difficulty in assessing these effects. One such hurdle is that the largest values of N deposition are always dominated by gaseous NH_x deposition. As a result it is difficult to distinguish the effects of high $\text{NH}_x:\text{NO}_y$ ratio and high total N load. The observational data of Stevens et al. (2004) and Kleijn et al. (2008) for instance, show correlations (Pearson's r) of 0.42 and 0.35 ($p < 0.001, 0.07$) between

total N load and $\text{NH}_x:\text{NO}_y$ ratio respectively (data taken from species level means from Table 1 of Kleijn et al. 2008). The correlation between NH_4^+ deposition and total N deposition is high ($r = 0.98$ and 1.00 ; $p < 0.001$ in both cases), making it difficult to distinguish whether fertilization, acidification or NH_4^+ toxicity, or a combination of these mechanisms, may be responsible for compositional change of ecosystems. Their relative importance can only be found by acquiring data from ecosystems in which the NH_4^+ N deposition load and $\text{NH}_x:\text{NO}_y$ ratio correlations are absent, in combination with experimental work which removes this correlation (e.g. Van den Berg et al., 2008). Experimental work in mesocosms or in low N input regions may overcome this problem but measurements must distinguish between the acidifying and toxic effects of NH_4^+ . Here, plant community data may be combined with physiological measures of plant health, e.g. amino acid concentrations, pigment content and chlorophyll fluorescence, that may indicate which stresses are the causes of species loss.

Using conservation management to mitigate N deposition impacts is challenging. Many of the available techniques for removing N also involve the removal of carbon and other nutrients, thus potentially altering a range of ecosystem functions. As a result the only truly effective way of managing for N deposition is the reduction of N inputs to the ecosystem by the reduction of N emissions. Critical loads for N deposition are currently based on total reactive N deposition but devising habitat specific critical loads for the components of deposition and $\text{NH}_x:\text{NO}_y$ ratio could be beneficial in some ecosystems. This still leaves the problem of potentially high amounts of NH_4^+ accumulated in the soil and slow recovery. Suggestions for deposition management on a local scale have been made, such as the use of tree shelter belts to capture NH_3 (Theobald et al., 2001), but generally, the reduction of N deposition requires action at a national or international level. Unfortunately, the formulation and delivery of policy at these levels is a slow process and more immediate action is often required if sites of conservation importance are to be protected and restored. An understanding of the mechanisms underlying ecosystem responses to different ratios N input should allow for the development of management and mitigation options.

The most appropriate form of management to apply in a habitat will depend on the vegetation community and its position along the pH gradient described above and in Fig. 6. In low pH soils (to the left of Fig. 6), where NH_4^+ and heavy metal toxicity are likely to be the key processes associated with changes in species composition caused by N enrichment, management must change soil properties to restore low NH_x concentration and reduce the $\text{NH}_x:\text{NO}_y$ ratio (Kleijn et al., 2008). One of the most effective ways to do this is by turf cutting and liming. Turf (or sod) cutting removes excess nutrients and restores damaged ecosystems. It has been used successfully in a range of habitats (e.g. heathland: Dorland et al., 2005a; De Graaf et al. 1998; grassland: Jansen and Roelofs, 1996; fens: Beltman et al., 2001; pine forest: Boxman and Roelofs, 2006), especially in the Netherlands. It may, however, decrease the nitrification potential of acidified soils and lead to a rapid increase in soil NH_4^+ concentrations (Dorland et al., 2003). The addition of lime after cutting has been found to successfully prevent NH_4^+ accumulation by increasing nitrification (Dorland et al., 2004; De Graaf et al., 1998; Van den Berg et al., 2003). While a powerful tool, turf cutting is a dramatic and expensive form of management with a number of potential problems (see Klap and Schmidt, 1995; Van den Berg et al., 2003; Dorland et al., 2004; Vergeer et al., 2006).

An alternative and emerging option for removing reactive N from soils is the addition of carbon (C). The addition of organic C to the soil increases the C:N ratio and could be expected to induce microbial communities to immobilize N. Several studies have reported successful reduction of soil N availability and a reduction

in nitrophilous species as a result of addition of C supplements (e.g. Török et al., 2000; Eschen et al., 2007). While there are a limited number of C addition studies on soils that are likely to have naturally low nitrification rates, results to date suggest that carbon addition may be more effective in reducing soil NO_3^- concentrations than those of NH_4^+ (Török et al., 2000; Blumenthal et al., 2003; Prober et al., 2005; Eschen et al., 2007). It may therefore be more suitable for systems with naturally high nitrification rates (the right of Fig. 6).

At slightly higher pH, moving towards the centre of Fig. 6, where acidification rather than the toxicity is the main driver of compositional changes resulting from N enrichment, liming is an effective management option. Liming has been widely used in many terrestrial habitats to counteract acidification from atmospheric pollutants (e.g. forests: Löfgren et al., 2009; heathland: Dorland et al. 2005b; grassland: Blake et al., 1999; bogs: Sanger et al., 1993). Increasing the pH also has the potential to increase nitrification, thus reducing the $\text{NH}_x:\text{NO}_y$ ratio. In areas fed by base-rich groundwater restoration of hydrology by blocking drainage ditches has been used as an alternative method to reduce acidification in combination with sod cutting (Roelofs et al., 1987). Increasing the pH has the potential to increase nitrification reducing the $\text{NH}_x:\text{NO}_y$ ratio.

In high pH and nitrification rate systems, where most species have a preference for NO_3^- (i.e. those found at the far right of Fig. 6) canopy closure and light limitation are likely to be the most important mechanisms driving species changes as a result of N deposition. Here measures can be taken to reduce competition for light. This could include an increase in cutting frequency or grazing intensity, especially in ecosystems dominated by herbaceous vegetation (e.g. Bobbink and Willems, 1988). Nutrient levels can also be reduced when these methods are combined with the removal of cut vegetation or the folding of livestock (Ausden, 2007). This method is commonly used in the restoration of grasslands on former agricultural land (e.g. Walker et al., 2003) and can change species composition, reducing the cover of productive grasses promoted by N enrichment.

7. Conclusion

Future changes in the ratio of NH_y and NO_x inputs have the potential to alter numerous soil processes, plant N uptake, community composition and ecosystem functioning. This has important implications for plant community composition as, depending on soil type and habitat, some species may be favoured by the changing ratio to the expense of others. Further research is needed to test the hypothesis that there is a natural spectrum of $\text{NH}_x:\text{NO}_y$ ratios in the soil, driven primarily by soil pH and buffer capacity and subsequently nitrification rates. The response of plants to $\text{NH}_x:\text{NO}_y$ ratios at different points on this gradient also needs to be investigated, as does its generality to a wide range of ecosystems as it is in many poorly studied regions of the world, e.g. South America, East Africa and East Asia where $\text{NH}_x:\text{NO}_y$ ratios are expected to show the greatest increases. If this hypothesis is supported, and found to be general across a range of ecosystems it may enable us to predict ecosystem responses to changing $\text{NH}_x:\text{NO}_y$ ratios, increasing the effectiveness of the management and mitigation of N deposition impacts.

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References

- Asman, W.A.H., Sutton, M.A., Schjoerring, J.K., 1998. Ammonia: emission, atmospheric transport and deposition. *New Phytologist* 139, 27–48.
- Ausden, M., 2007. Habitat Management for Conservation: A Handbook of Techniques. Oxford University Press, Oxford.
- Beltman, B., Van den Broek, T., Barendregt, A., Bootsma, M.C., Grootjans, A.P., 2001. Rehabilitation of acidified and eutrophied fens in the Netherlands: effects of hydrologic manipulation and liming. *Ecological Engineering* 17, 21–31.
- Berg, B., Matzner, E., 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest ecosystems. *Environmental Reviews* 5, 1–25.
- Berger, T.W., Untersteiner, H., Schume, H., Jost, G., 2008. Throughfall fluxes in a secondary spruce (*Picea abies*), a beech (*Fagus sylvatica*) and a mixed spruce-beech stand. *Forest Ecology and Management* 255, 605–618.
- Blake, L., Goulding, K.W.T., Mott, C.J.B., Johnstone, A.E., 1999. Changes in soil chemistry accompanying acidification over more than 100 years under woodland and grass at Rothamsted Experimental Station, UK. *European Journal of Soil Science* 50, 401–412.
- Bligny, R., Gout, E., Kaiser, W., Heber, U., Walker, D., Douce, R., 1997. pH regulation in acid-stressed leaves of pea plants grown in the presence of nitrate or ammonium salts: studies involving P-31-NMR spectroscopy and chlorophyll fluorescence. *Biochimica et Biophysica Acta – Bioenergetics* 1320, 142–152.
- Bloom, A.J., Sukrapanna, S.S., Warner, R.L., 1992. Root respiration associated with ammonium and nitrate absorption and assimilation by barley. *Plant Physiology* 99, 1294–1301.
- Blumenthal, D.M., Jordan, N.R., Russelle, M.P., 2003. Soil carbon addition controls weeds and facilitates prairie restoration. *Ecological Applications* 13, 605–615.
- Bobbink, R., 1991. Effects of nutrient enrichment in Dutch chalk grassland. *Journal of Applied Ecology* 28, 28–41.
- Bobbink, R., Hornung, M., Roelofs, J.G.M., 1998. The effects of air borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology* 86, 717–738.
- Bobbink, R., Ashmore, M., Braum, S., Flückinger, W., Van den Wyngaert, I.J., 2003. Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update. In: Achermann, B., Bobbink, R. (Eds.), *Empirical Critical Loads for Nitrogen*. Environmental Documentation No. 164 Air. Swiss Agency for Environment, Forest and Landscape SAEFL, Berne.
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinnerby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., De Vries, W., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* 20, 30–59.
- Bobbink, R., Lamers, L.P.M., 2002. Effects of increased nitrogen deposition. In: Bell, J.N.B., Treshow, M. (Eds.), *Air Pollution and Plant Life*, second ed. John Wiley & Sons, Ltd, Oxford, pp. 201–235.
- Bobbink, R., Roelofs, J.G.M., 1995. Nitrogen critical loads for natural and semi-natural ecosystems: the empirical approach. *Water, Air and Soil Pollution* 85, 2413–2418.
- Bobbink, R., Willems, J.H., 1988. Effects of management and nutrient availability on vegetation structure of chalk grasslands. In: During, H.J., Wager, M.J.A., Willems, J.H. (Eds.), *Diversity and Pattern in Plant Communities*. Academic Publishing House, The Hague, pp. 183–193.
- Booth, M.S., Stark, J.M., Rastetter, E., 2005. Controls on nitrogen cycling in terrestrial ecosystems: a synthetic analysis of literature data. *Ecological Monographs* 75, 139–157.
- Boxman, A.W., Krabbendam, H., Bellemakers, M.J.S., Roelofs, J.G.M., 1991. Effects of ammonium and aluminium on the development and nutrition of *Pinus nigra* in hydroculture. *Environmental pollution* 73, 119–136.
- Boxman, A.W., Peters, C.H.J., Roelofs, J.G.M., 2008. Long term changes in atmospheric N and S throughfall deposition and effects on soil solution chemistry in a Scots pine forest in the Netherlands. *Environmental Pollution* 156, 1252–1259.
- Boxman, A.W., Roelofs, J.G.M., 2006. Effects of liming, sod-cutting and fertilization at ambient and decreased nitrogen deposition on the soil solution chemistry in a Scots pine forest in the Netherlands. *Forest Ecology and Management* 237, 237–245.
- Britto, D.T., Kronzucker, H.J., 2002. NH_4^+ toxicity in higher plants: a critical review. *Journal of Plant Physiology* 159, 567–584.
- Cape, J.N., van der Eerden, L.J., Sheppard, L.J., Leith, I.D., Sutton, M.A., 2009. Evidence for changing the critical level for ammonia. *Environmental Pollution* 157, 1033–1037.
- Clark, C., Cleland, E.E., Collins, S.C., Fargione, J., Gough, L., Gross, K.L., Pennings, S., Suding, K.N., Grace, J., 2007. Environmental and plant community determinants of species loss following nitrogen enrichment. *Ecology Letters* 10, 596–607.
- Cruz, C., Bio, A.M.F., Jullioti, A., Tavares, A., Dias, T., Martins-Loucao, M.A., 2008. Heterogeneity of soil surface ammonium concentration and other characteristics, related to plant specific variability in a Mediterranean-type ecosystem. *Environmental Pollution* 154, 414–423.
- Cuenca, G., Azcon, R., 1994. Effects of ammonium and nitrate on the growth of vesicular-arbuscular mycorrhizal *Eruthrina poeppigiana* O.I. Cook seedlings. *Biology and Fertility of Soils* 18, 249–254.
- Currey, P.M., Johnson, D., Sheppard, L.J., Leith, I.D., Toberman, H., van der Wal, R., Dawson, L.A., Artz, R.R.E., 2010. Turnover of labile and recalcitrant soil carbon differ in response to nitrate and ammonium deposition in an ombrotrophic peatland. *Global Change Biology* 16, 2307–2321.
- Cumming, J.R., 1990. Nitrogen-source effects on Al-toxicity in nonmycorrhizal and mycorrhizal pitch pine (*Pinus rigida*) seedlings 2. Nitrate reduction and NO_3^- uptake. *Canadian Journal of Botany* 68, 2653–2659.
- De Graaf, M.C.C., Verbeek, P.J.M., Cals, P.J.M., Roelofs, J.G.M., 1994. Restoration of Acidified and Eutrophied Species Rich Heathlands and Acidic Grasslands 1990–1994. Report to the Department of Ecology, University of Nijmegen, 248pp.
- De Graaf, M.C.C., Verbeek, P.J.M., Bobbink, R., Roelofs, J.G.M., 1998. Restoration of species-rich dry heaths. The importance of appropriate soil conditions. *Acta Botanica Neerlandica* 47, 89–111.
- De Graaf, M.C.C., Bobbink, R., Smits, N.A.C., Van Diggelen, R., Roelofs, J.G.M., 2009. Biodiversity, vegetation gradients and key biogeochemical processes in the heathland landscape. *Biological Conservation* 142, 2191–2201.
- Dentener, F.J., 2006. Global maps of atmospheric nitrogen deposition, 1860, 1993, and 2050. Data set. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A. doi:10.3334/ORNLDAAC/830. Available from: <http://daac.ornl.gov>.
- DeForest, J.L., Zak, D.R., Pregitzer, K.S., Burton, A.J., 2004. Atmospheric nitrate deposition, microbial community composition, and enzyme activity in northern hardwood forests. *Soil Science Society of America Journal* 68, 132–138.
- De Schrijver, A., Staelens, J., Wuyts, K., Van Hoydonck, G., Janssen, N., Mertens, J., Gielis, L., Geudens, G., Augusto, L., Verheyen, K., 2008. Effect of vegetation type on throughfall deposition and seepage flux. *Environmental Pollution* 153, 295–303.
- De Klein, C.A.M., Van Logtestijn, R.S.P., 1996. Denitrification in grassland soils in the Netherlands in relation to irrigation, N-application rate, soil water content and soil temperature. *Soil Biology and Biochemistry* 28, 231–237.
- Dijk, E., Eck, N., 1995. Ammonium toxicity and nitrate response of axenically grown *Dactylorhiza incarnata* seedlings. *New Phytologist* 131, 361–367.
- Dorland, E., Bobbink, R., Messelink, J.H., Verhoeven, J.T.A., 2003. Soil ammonium accumulation after sod cutting hampers the restoration of degraded wet heathlands. *Journal of Applied Ecology* 40, 804–814.
- Dorland, E., van den Berg, L.J.L., van de Berg, A.J., Vermeer, M.L., Roelofs, J.G.M., Bobbink, R., 2004. The effects of sod cutting and additional liming on potential net nitrification in heathland soils. *Plant and Soil* 265, 267–277.
- Dorland, E., Hart, M.A.C., Vermeer, M.L., Bobbink, R., 2005a. Assessing the success of wet heath restoration by combined sod cutting and liming. *Applied Vegetation Science* 8, 209–218.
- Dorland, E., van den Berg, L.J.L., Brouwer, E., Roelofs, J.G.M., Bobbink, R., 2005b. Catchment liming to restore degraded, acidified heathlands and moorland pools. *Restoration Ecology* 13, 302–311.
- Dupré, C., Stevens, C.J., Ranke, T., Bleeker, A., Peppeler-Lisbach, C., Gowing, D.J.G., Dise, N.B., Dorland, E., Bobbink, R., Diekmann, M., 2010. Changes in species richness and composition in European acidic grasslands over the past 70 years: the contribution of cumulative atmospheric nitrogen deposition. *Global Change Biology* 16, 344–357.
- Eschen, R., Mortimer, S.M., Lawson, C.S., Edwards, A.R., Brook, A.J., Igual, J.M., Hedlund, K., Schaffner, U., 2007. Carbon addition alters vegetation composition on ex-arable fields. *Journal of Applied Ecology* 44, 95–104.
- Fagerli, H., Aas, W., 2008. Trends of nitrogen in air and precipitation: model results and observations at EMEP sites in Europe, 1980–2003. *Environmental Pollution* 154, 448–461.
- Fangmeier, A., Hadwiger-Fangmeier, A., Van der Eerden, L., Jager, H.J., 1994. Effects of atmospheric ammonia on vegetation: a review. *Environmental Pollution* 86, 43–82.
- Falkengren-Grerup, U., 1995. Interspecies differences in the preference of ammonium and nitrate in vascular plants. *Oecologia* 102, 305–311.
- Fenn, M.E., Baron, J.S., Allen, E.B., Rueth, H.M., Nydick, K.R., Geiser, L., Bowman, W.D., Sickman, J.O., Meixner, T., Johnson, D.W., Neitlich, P., 2003. Ecological effects of nitrogen deposition in the Western United States. *BioScience* 53, 404–420.
- Forde, B.G., Clarkson, D.T., 1999. NO_3^- and NH_4^+ nutrition of plants: physiological and molecular perspectives. *Advances in Botanical Research* 30, 1–90.
- Fowler, D., O'Donoghue, M., Muller, J.B.A., Smith, R.I., Dragosits, U., Skiba, U., Sutton, M.A., Brimblecombe, P., 2004. A chronology of nitrogen deposition in the UK between 1900 and 2000. *Water, Air and Soil Pollution Focus* 4, 9–23.
- Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P., Asner, G.P., Cleveland, C.C., Green, P.A., Holland, E.A., Karl, D.M., Michaels, A.F., Porter, J.H., Townsend, A.R., Vörösmarty, C.J., 2004. Nitrogen cycles: past, present and future. *Biogeochemistry* 70, 153–226.
- Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L.A., Seitzinger, S.P., Sutton, M.A., 2008. Transformation of the nitrogen cycle: recent trends, questions and potential solutions. *Science* 320, 889–892.
- Garten, J.R., Hanson, P.J., 1990. Foliar retention of 15-NO_3^- and 15-NH_4^+ by red maple (*Acer rubrum*) and White oak (*Quercus alba*) leaves from simulated rain. *Environmental and Experimental Botany* 30, 333–342.
- Gerendas, J., Ratcliffe, R.G., 2000. Intracellular pH regulation in maize root tips exposed to ammonium at high external pH. *Journal of Experimental Botany* 51, 207–219.
- Ghnaya, T., Slama, I., Messedi, D., Grignon, C., Ghorbel, M.H., Abdely, C., 2007. Effects of Cd^{2+} on K^+ , Ca^{2+} and N uptake in two halophytes *Sesuvium portulacastrum* and *Mesembryanthemum crystallinum*: consequences on growth. *Chemosphere* 67, 72–79.
- Gloser, V., Gloser, J., 2000. Nitrogen and base cation uptake in seedlings of *Acer pseudoplatanus* and *Calamagrostis villosa* exposed to an acidified environment. *Plant and Soil* 226, 71–77.

- Hauck, M., 2010. Ammonium and nitrate tolerance in lichens. *Environmental Pollution* 158, 1127–1133.
- Hautier, Y., Niklaus, P.A., Hector, A., 2009. Competition for light causes plant biodiversity loss after eutrophication. *Science* 324, 636–638.
- Hogan, E.J., Minnullina, G., Sheppard, L.J., Leith, I.D., Crittenden, P.D., 2010. Response of phosphomonoesterase activity in the lichen *Cladonia portentosa* to N and P enrichment in a field manipulation experiment. *New Phytologist*, 911–925.
- Holland, E.A., Braswell, B.H., Sulzman, J., Lamarque, J.F., 2005. Nitrogen deposition onto the United States and Western Europe: synthesis of observations and models. *Ecological Applications* 15, 38–57.
- Houdijk, A.L.F.M., Verbeek, P.J.M., van Dijk, H.F.G., Roelofs, J.G.M., 1993. Distribution and decline of endangered herbaceous heathland species in relation to the chemical composition of the soil. *Plant and Soil* 148, 137–143.
- Jansen, A.J.M., Roelofs, J.G.M., 1996. Restoration of *Cirsio-Molinietum* wet meadows by sod cutting. *Ecological Engineering* 7, 279–298.
- Keeler, B.L., Hobbie, S.E., Kellogg, L.E., 2009. Effects of long-term nitrogen addition on microbial enzyme activity in eight forested and grassland sites: implications for litter and soil organic matter decomposition. *Ecosystems* 12, 1–15.
- Klap, J.M., Schmidt, P., 1995. Measures to counter effects of eutrophication and acidification in forests with special values of nature: description of the initial situation and the implementation of the measures under controlled field conditions on six sites in the Netherlands. Hinkeloord Report No. 13183. Departments of Forestry, Agricultural University Wageningen, Wageningen, The Netherlands.
- Kleijn, D., Bekker, R.M., Bobbink, R., De Graaf, M.C., Roelofs, J.G.M., 2008. In search for key biogeochemical factors affecting plant species persistence in heathland and acidic grasslands: a comparison of common and rare species. *Journal of Applied Ecology* 45, 680–687.
- Knorr, W., Prentice, I.C., House, J.J., Holland, E.A., 2005. Long-term sensitivity of soil carbon turnover to warming. *Nature* 433, 298–302.
- Koyama, L., Tokuchi, N., 2003. Effects of NO₃ availability on NO₃ use in seedlings of three woody shrub species. *Tree Physiology* 23, 281–288.
- Lamers, L.P.M., Bobbink, R., Roelofs, J.G.M., 2000. Natural nitrogen filter fails polluted raised bogs. *Global Change Biology* 6, 583–586.
- Lazof, D.B., Rincon, M., Rufty, T.W., MacKown, C.T., Carter, T.E., 1994. Aluminium accumulation and associated effects on ¹⁵NO₃ influx in roots of two soybean genotypes differing in Al tolerance. *Plant and Soil* 164, 291–297.
- LeBauer, D.S., Treseder, K.K., 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* 89, 371–379.
- Limpens, J., Berendse, F., 2003. How litter quality affects mass loss and N loss from decomposing *Sphagnum*. *Oikos* 103, 537–547.
- Limpens, J., Berendse, F., Klees, H., 2003. N deposition affects N availability in interstitial water, growth of *Sphagnum* and invasion of vascular plants in bog vegetation. *New Phytologist* 157, 339–347.
- Löfgren, S., Cory, N., Zetterberg, T., Larsson, P., Kronnäs, V., 2009. The long-term effects of catchment liming and reduced sulphur deposition on forest soils and runoff chemistry in southwest Sweden. *Forest Ecology and Management* 258, 567–578.
- Lucassen, E.C.H.E., Bobbink, R., Smolders, A.J.P., Van der Ven, P.J.M., Lamers, L.P.M., Roelofs, J.G.M., 2003. Interactive effects of low pH and high ammonium levels responsible for the decline of *Cirsium dissectum* (L.) Hill. *Plant Ecology* 165, 45–52.
- Lumme, I., 1994. Nitrogen uptake of Norway spruce (*Picea abies* Karst.) seedlings from simulated wet deposition. *Forest Ecology and Management* 63, 87–96.
- Luna, B., Moreno, J.M., 2009. Light and nitrate effects on seed germination of Mediterranean plant species of several functional groups. *Plant Ecology* 203, 123–135.
- Manning, P., Newington, J.E., Robson, H.R., Sauners, M., Eggers, T., Bradford, M.A., Bardgett, R.D., Bonkowski, M., Ellis, R.J., Grange, A.C., Grayston, S.J., Kandeler, E., Marhan, S., Reid, E., Tscherko, D., Godfray, H.C.J., Rees, M., 2006. Decoupling the direct and indirect effects of nitrogen deposition on ecosystem function. *Ecology Letters* 9, 1015–1024.
- Manning, P., Houston, K., Evans, T., 2009. Shifts in seed size across experimental nitrogen enrichment and plant density gradients. *Basic and Applied Ecology* 10, 300–308.
- Marschner, H., 1995. Mineral Nutrition of Higher Plants. Academic Press, London.
- Maskell, L.C., Smart, S.M., Bullock, J.M., Thompson, K., Stevens, C.J., 2010. Nitrogen deposition causes widespread species loss in British habitats. *Global Change Biology* 16, 671–679.
- Mountford, J.O., Lakhani, K.H., Kirkham, F.W., 1993. Experimental assessment of the effects of nitrogen addition under hay-cutting and aftermath grazing on the vegetation of meadows on a Somerset peat moor. *Journal of Applied Ecology* 30, 321–332.
- Nordin, A., Högberg, P., Näsholm, T., 2001. Soil nitrogen form and plant nitrogen uptake along a boreal forest productivity gradient. *Oecologia* 129, 125–132.
- Paavolainen, L., Smolander, A., 1998. Nitrification and denitrification in soil from a clear-cut Norway spruce (*Picea abies*) stand. *Soil Biology and Biochemistry* 30, 775–781.
- Palmqvist, K., Dahlman, L., 2006. Responses of the green algal foliose lichen *Platismatia glauca* to increased nitrogen supply. *New Phytologist* 171, 343–356.
- Paulissen, M.P.C.P., Van der Ven, P.J.M., Dees, A.J., Bobbink, R., 2004. Differential effects of nitrate and ammonium on three fen bryophyte species in relation to pollutant nitrogen input. *New Phytologist* 164, 451–458.
- Pearce, I.S.K., Woodin, S.J., van der Wal, R., 2003. Physiological and growth responses of the montane bryophyte *Racomitrium lanuginosum* to atmospheric nitrogen deposition. *New Phytologist* 160, 145–155.
- Pearson, J., Stewart, G.R., 1993. The deposition of atmospheric ammonia and its effects on plants. *New Phytologist* 125, 283–305.
- Pearson, J., Soares, A., 1995. A hypothesis of plant susceptibility to atmospheric pollution based on intrinsic nitrogen metabolism: why acidity really is the problem. *Water, Air and Soil Pollution* 85, 1227–1232.
- Pérez-Soba, M., van der Eerden, L.J.M., 1993. Nitrogen uptake in needles of Scots pine (*Pinus sylvestris* L.) when exposed to gaseous ammonia and NH₄ fertilizer in the soil. *Plant and Soil* 153, 231–242.
- Persson, J., Högberg, P., Ekbal, A., Högberg, M., Nordgren, A., Näsholm, T., 2003. Nitrogen acquisition from inorganic and organic sources by boreal forest plants in the field. *Oecologia* 137, 252–257.
- Peuke, A.D., Jeschke, W.D., Dietz, K.J., Schreiber, L., Hartung, W., 1998. Foliar application of nitrate or ammonium as sole nitrogen supply in *Ricinus communis* – I. Carbon and nitrogen uptake and inflows. *New Phytologist* 138, 675–687.
- Prober, S.M., Thiele, K.R., Lunt, I.D., Koen, T.B., 2005. Restoring ecological function in temperate grassy woodlands: manipulating soil nutrients, exotic annuals and native perennial grasses through carbon supplements and spring burns. *Journal of Applied Ecology* 42, 1073–1085.
- Prosser, J.I., 1989. Autotrophic nitrification in bacteria. *Advances in Microbial Physiology* 30, 125–181.
- Raven, J.A., Smith, F.A., 1976. Nitrogen assimilation and transport in vascular plants in relation to intracellular pH regulation. *New Phytologist* 76, 415–431.
- Roelofs, J.G.M., Kempers, A.J., Houdijk, A.L.F.M., Jansen, J., 1985. The effect of airborne ammonium sulphate on *Pinus nigra* var. *maritima* in the Netherlands. *Plant and Soil* 84, 45–56.
- Roelofs, J.G.M., Boxman, A.W., Van Dijk, H.F.G., 1987. Effects of airborne NH₄ on natural vegetation and forests. In: Asman, W.A.H., Diederik, H.S.M.A. (Eds.), *Ammonia and Acidification*, Symposium EURASAP, Bilthoven, The Netherlands, 13–15 April 1987. RIVM/TNO, Bilthoven, pp. 266–276.
- Sanchez-Hoyos, M.A., Manrique, E., 1995. Effect of nitrate and ammonium ions on the pigment content (xanthophylls, carotenoids and chlorophylls) of *Ramalina capitata*. *Lichenologist* 27, 155–160.
- Sanchez-Martin, L., Vallejo, A., Dick, J., Skiba, U.M., 2008. The influence of soluble carbon and fertilizer nitrogen on nitric oxide and nitrous oxide emissions from two contrasting agricultural soils. *Soil Biology and Biochemistry* 40, 142–151.
- Sanger, L.J., Billett, M.F., Cresser, M.S., 1993. Assessment by laboratory simulation of approaches to ameliorate peat acidification. *Environmental Pollution* 81, 21–29.
- Schojerring, J.K., Husted, S., Mäck, G., Mattsson, M., 2002. The regulation of NH₄ translocation in plants. *Journal of Experimental Botany* 53, 883–890.
- Schortemeyer, M., Stamp, P., Feil, B., 1997. Ammonium tolerance and carbohydrate status in maize cultivars. *Annals of Botany* 79, 25–30.
- Sievering, H., Tomaszewski, T., Torizzo, J., 2007. Canopy uptake of atmospheric N deposition at a conifer forest: part I – canopy N budget, photosynthetic efficiency and net ecosystem exchange. *Tellus Series B – Chemical and Physical Meteorology* 59B, 483–492.
- Silver, W.L., Herman, D.J., Firestone, M.K., 2001. Dissimilatory nitrate reduction to ammonium in upland tropical forest soils. *Ecology* 82, 2410–2416.
- Singh, B., Amrithale, D., 1992. Effect of light and its interaction with nitrate and ammonium ions in seed germination of *Caesulia axillaris*. *Physiologia Plantarum* 85, 43–48.
- Stevens, R.J., Laughlin, R.J., Malone, J.P., 1998. Soil pH affects the processes reducing nitrate to nitrous oxide and di-nitrogen. *Soil Biology and Biochemistry* 30, 1119–1126.
- Stevens, C.J., Dise, N.B., Mountford, J.O., Gowing, D.J., 2004. Impact of nitrogen deposition on the species richness of grasslands. *Science* 303, 1876–1879.
- Stevens, C.J., Dise, N.B., Gowing, D.J., 2009. Regional trends in soil acidification and metal mobilisation related to acid deposition. *Environmental Pollution* 157, 313–319.
- Stevens, C.J., Tilman, D., 2010. Point source ammonia emissions are having a detrimental impact on prairie grasslands. *Water, Air and Soil Pollution* 211, 435–441.
- Suding, K., Collins, S., Clark, C., Cleland, E., Gough, L., Gross, K., Milchunas, D., Pennings, S., 2005. Functional and abundance-based mechanisms explain diversity loss due to nitrogen fertilization. *Proceedings of the National Academy of Science* 102, 4387–4392.
- Sutton, M.A., Milford, C., Dragosits, U., Place, C.J., Singles, R.J., Smith, R.I., Pitcairn, C.E.R., Fowler, D., Hill, J., ApSimon, H.M., Ross, C., Hill, R., Jarvis, S.C., Pain, B.F., Phillips, R., Harrison, R., Moss, D., Webb, J., Espenhahn, S.E., Lee, D.S., Hornung, M., Ullyett, J., Bull, K.R., Emmett, B.A., Lowe, J., Wyers, G.P., 1998. Dispersion, deposition and impacts of atmospheric ammonia: quantifying local budgets and spatial variability. *Environmental Pollution* 102, 349–361.
- Taylor, P.G., Townsend, A.R., 2010. Stoichiometric control of organic carbon–nitrate relationships from soils to the sea. *Nature* 464, 1178–1181.
- Teklemariam, T.A., Sparks, J.P., 2004. Gaseous fluxes of peroxyacetyl NO₃ (PAN) into plant leaves. *Plant, Cell and Environment* 27, 1149–1158.
- Theobald, M.R., Milford, K.J., Hargreaves, L.J., Sheppard, L.J., Nemitz, E., Tang, Y.S., 2001. Potential for ammonia recapture by farm woodlands: design and application of a new experimental facility. *The ScientificWorld* 1, 791–801.
- Török, K., Szili-Kovacs, T., Halassy, M., Toth, T., Hayek, Z., Paschke, M.W., Wardell, L.J., 2000. Immobilization of soil nitrogen as a possible method for the restoration of sandy grassland. *Applied Vegetation Science* 3, 7–14.
- Treseder, K.K., 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO₂ in field studies. *New Phytologist* 164, 347–355.
- Van den Berg, L.J.L., Dorland, E., Vergeer, P., Hart, M.A.C., Bobbink, R., Roelofs, J.G.M., 2003. Decline of acid-sensitive plant species in heathland can be attributed to ammonium toxicity in combination with low pH. *New Phytologist* 166, 551–564.

- Van den Berg, L.J.L., Dorland, E., Vergeer, P., Hart, M.A.C., Bobbink, R., Roelofs, J.G.M., 2005. Decline of acid-sensitive plant species in heathland can be attributed to ammonium toxicity in combination with low pH. *New Phytologist* 166, 551–564.
- Van den Berg, L.J., Peters, C.J., Ashmore, M.R., Roelofs, J.G., 2008. Reduced nitrogen has a greater effect than oxidised nitrogen on dry heathland vegetation. *Environmental Pollution* 154, 359–369.
- Van Leeuwen, E.P., Draaijers, G.P.J., Erisman, E.W., 1996. Mapping wet deposition of acidifying components and base cations over Europe using measurements. *Atmospheric Environment* 30, 2495–2511.
- Vergeer, P., van den Berg, L.J.L., Baar, J., Ouborg, N.J., Roelofs, J.G.M., 2006. The effect of turf cutting on plant and mycorrhizal spore recolonisation: implications for heathland restoration. *Biological Conservation* 129, 226–235.
- Vestgarden, L.S., Kjønaas, O.J., 2003. Potential nitrogen transformations in mineral soils of two coniferous forests exposed to different N inputs. *Forest Ecology and Management* 174, 191–202.
- Walker, K.J., Stevens, P.A., Stevens, D.P., Mountford, J.O., Manchester, S.J., Pywell, R.F., 2003. The restoration and re-creation of species rich lowland grassland on land formerly managed for intensive agriculture in the UK. *Biological Conservation* 119, 1–18.
- Wamelink, G.W.W., Goedhart, P.W., van Dobben, H.F., Berendse, F., 2005. Plant species as predictors of soil pH: replacing expert judgment by measurements. *Journal of Vegetation Science* 16, 461–470.
- Webster, G., Embley, T.M., Freitag, T.E., Smith, Z., Prosser, J.I., 2005. Links between ammonia oxidizer species composition, functional diversity and nitrification kinetics in grassland soils. *Environmental Microbiology* 7, 676–684.
- Wilson, E.J., Wells, T.C.E., Sparks, T.H., 1995. Are calcareous grasslands in the UK under threat from nitrogen deposition? – an experimental determination of a critical load. *Journal of Ecology* 83, 823–832.
- Wiedermann, M.M., Gunnarsson, U., Nilsson, M.B., Nordin, A., Ericson, L., 2009. Can small-scale experiments predict ecosystem responses? An example from peatlands. *Oikos* 118, 449–456.
- Wilson, E.J., 1992. Foliar uptake and release of inorganic nitrogen compounds in *Pinus sylvestris* L. and *Picea abies* (L.) Karst. *New Phytologist* 120, 407–416.
- Yoshida, L.C., Allen, E.B., 2001. Response to ammonium and nitrate by a mycorrhizal annual invasive grass and native shrub in southern California. *American Journal of Botany* 88, 1430–1436.