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Reduced nitrogen has a greater effect than oxidised nitrogen on dry heathland vegetation

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Reduced nitrogen and high NH_4^+/NO_3^- ratios in deposition are responsible for a decline of forbs in Western European heathlands.

Abstract

We investigated the effects of different ratios of reduced (NH_4^+) versus oxidised (NO_3^-) nitrogen in deposition on heathland and species-rich grassland vegetation at high nitrogen deposition levels in large mesocosms filled with nutrient-poor soils to which different NH_4^+/NO_3^- ratios were applied. The response of the forbs, *Antennaria dioica*, *Arnica montana*, *Gentiana pneumonanthe*, *Thymus serpyllum*, the grasses *Danthonia decumbens*, *Deschampsia flexuosa*, *Nardus stricta* and the shrub *Calluna vulgaris* was recorded. The forb *A. dioica* and the grass *D.decumbens* preferred low NH_4^+/NO_3^- ratios and were characterised by a negative correlation between NH_4^+/NO_3^- ratios and biomass and survival, whereas the grasses *N. stricta* and *D. flexuosa* showed no correlation with NH_4^+/NO_3^- ratios. Lime addition eliminated the negative effects of high NH_4^+ concentrations in deposition for *A. dioica* and the grass *D. decumbens*. The implications of these findings for heathland vegetations are discussed.

Keywords: Amino acids; Grass encroachment; Herbaceous species; Mesocosms; N enrichment; NH_4^+/NO_3^- ratios

1. Introduction

Heathlands and species-rich grasslands are vegetation types characterised by poor soil fertility and low productivity (Gimingham et al., 1979). These vegetation types can be found in various parts of the world, especially in mountainous habitats, and are common in the Atlantic and sub-Atlantic regions of Western Europe. Lowland heathlands and species-rich grasslands were once a common semi-natural vegetation type in the temperate regions of Western Europe, maintained by mowing, sheep grazing, burning and sod removal, which prevented succession towards woodlands (Heil and Aerts, 1993). From the beginning of the 20th century, however, heathlands and species-rich grasslands in Western Europe started to decline, mainly as a result of changes in land use, urbanisation and conversion to agricultural land (De Smidt, 1975, 1979; Webb, 2002). Despite many conservation programmes and the incorporation of these vegetation types into nature reserves, their decline has continued over the last 50 years. This has mainly been attributed to habitat fragmentation, changes in hydrology and an increased atmospheric deposition of nitrogen (N) and sulphur (S) compounds, resulting in eutrophication and acidification of the soil (Heil and Diemont, 1983; Galloway, 1995; Roelofs et al., 1996; Bobbink et al., 1998).

From the early 1980s, it became clear that N deposition was a major determining factor in the species composition of these vegetation types. It was suggested that atmospheric N deposition results in grasses becoming dominant and species-rich grasslands and dwarf shrub vegetations, dominated by *Calluna vulgaris*, developing into species-poor vegetations dominated by grasses such as *Molinia caerulea* and *Deschampsia flexuosa* (Heil and Diemont, 1983; Roelofs, 1986; Aerts and Heil, 1993; Swertz et al., 1996). Results of many N enrichment studies on species-rich grasslands (Morecroft et al., 1994;

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Carroll et al., 2003), heathlands and bogs (Aerts et al., 1990; Tomassen et al., 2003), and coniferous forests (Kellner and Redbo-Torstensson, 1995), for example, support this view and generally show an increased growth of grasses with increased N load, at the expense of forb species.

Atmospheric N deposition consists largely of reduced N (NH_x), mainly originating from agricultural sources, and oxidised N (NO_y), mainly originating from fuel combustion (Galloway, 1995). In large parts of Western Europe (e.g. Germany, the Netherlands, and large parts of Great Britain), N is mostly deposited in the reduced form, whereas in other regions (e.g. parts of Great Britain and Scandinavia) it is oxidised N which dominates (Bobbink et al., 1992; Eerens et al., 2001; Galloway and Cowling, 2002). In the UK, deposition of reduced N, but not of oxidised N, was spatially correlated with vegetation changes over recent decades in species-rich grasslands, heaths and bogs (Smart et al., 2004). Detailed field studies carried out in oak forests in southern Scandinavia have shown that changes in the species composition of ground flora are closely correlated to the dominant N form in the soils, and to soil processes such as nitrification and mineralisation, both of which are related to soil acidity (Diekmann and Falkengren-Grerup, 1998, 2002; Falkengren-Grerup and Schöttelndreier, 2004).

High concentrations of NH_4^+ have been found to be toxic to many herbaceous plants, whereas increased concentrations of NO_3^- have been found to stimulate growth (Gigon and Rorison, 1972; De Graaf et al., 1998). Several studies found that herbaceous plant species from species-rich grasslands preferred NO_3^-, whereas many grasses and ericoid species preferred NH_4^+ as their main N source (De Graaf et al., 1998; Falkengren-Grerup and Schöttelndreier, 2004). The vulnerability of herbaceous plant species to elevated NH_4^+ concentrations has been attributed to a reduced base cation uptake, leading to cation deficiency (Bennet and Adams, 1969; Polle et al., 1994; De Graaf et al., 1998). Recent studies using hydroponics found that the herbaceous species *Gentiana pneumonanthe*, *Antennaria dioica*, *Succisa pratensis* and *Cirsium dissectum* were sensitive to high NH_4^+ concentrations in combination with low pH (3.5–4) levels (Lucassen et al., 2003; van den Berg et al., 2005). In contrast, acid-tolerant grasses such as *D. flexuosa* did not respond to elevated NH_4^+, indicating that the acid-intolerant species from slightly buffered ecosystems in particular, might be dramatically affected by a shift from an NO_3^- dominated system towards an NH_4^+ dominated ecosystem in combination with acidification (van den Berg et al., 2005).

Although the effects of atmospheric N deposition on vegetation development have been extensively investigated (see, e.g. Bobbink and Heil, 1993; Power et al., 1998; Carroll et al., 2003), there have been few reports on the effects of atmospheric deposition of reduced (NH_4^+) versus oxidised (NO_3^-) nitrogen, i.e., of different NH_4^+/NO_3^- ratios, on (semi)-natural vegetation and all of the studies focussed upon aquatic plants and *Sphagnum* species rather than vascular terrestrial plant species. In field or mesocosm N manipulation experiments, Schuurkens et al. (1987), LütkeTwenhöven (1992) and Paulissen et al. (2004) have examined the effects of both reduced and oxidised N on soft waters and bogs. All three studies concluded that NH_4^+ was the more detrimental form of N in these ecosystems. Moreover, until now no report investigated the effects of different NH_4^+/NO_3^- ratios at fixed total N loads and different levels of acidification.

Current risk assessment and dynamic modelling of the impacts of N deposition in Europe do not consider the differential effects of NH_4^+ and NO_3^- and the interaction with soil acidity. In many regions of Europe, NO_3^- emissions are decreasing more rapidly than those of NH_4^+ and therefore NH_4^+/NO_3^- ratios in deposition may increase even if total N deposition falls. For this reason, understanding the effects of NH_4^+/NO_3^- ratios, independently of N deposition, and in combination with soil acidification, is very important.

To investigate the effect of different NH_4^+/NO_3^- ratios on species-rich grasslands and heathlands, we used mesocosms, filled with mineral soil from a heathland, to which artificial rain with different NH_4^+/NO_3^- deposition ratios was applied whilst the total N deposition was kept at a fixed rate of $40\ kg\ N\ ha^{-1}\ yr^{-1}$. Lime was added to half of the mesocosms in order to investigate the interaction between pH of the soil pore water, NH_4^+/NO_3^- ratios and plant growth responses. In order to investigate responses to $40\ kg\ N\ ha^{-1}\ yr^{-1}$ on our mesocosms, we compared these with controls with a very low N application rate of $3\ kg\ N\ ha^{-1}\ yr^{-1}$; this was done only for the high NH_4^+/NO_3^- ratio, as this was the treatment for which the biggest effects were expected.

The effects were investigated using large mesocosms into which four herbaceous species (*A. dioica*, *Arnica montana*, *G. pneumonanthe*, *T. serpyllum*), three grasses (*Danthonia decumbens*, *D. flexuosa*, *Nardus stricta*) and one shrub (*C. vulgaris*) were planted, to represent species-rich lowland heath vegetation. Biomass, mortality and the chemical composition of the plants were measured to assess fitness and survival. We hypothesised that acidification and high NH_4^+/NO_3^- ratios would negatively affect the survival and fitness of the herbaceous species *A. dioica*, *A. montana*, *G. pneumonanthe* and *T. serpyllum* and the grass *D. decumbens*, as these are characteristic species of weakly buffered conditions and are regarded as acid-sensitive species. The dwarf shrub *C. vulgaris* and the grasses *D. flexuosa* and *N. stricta* can occur in eutrophied and acidified heathlands and are therefore thought to be acid-tolerant as well as tolerant to high NH_4^+/NO_3^- ratios. We also hypothesised that lime addition would reduce the negative effects of high NH_4^+/NO_3^- deposition ratios on the growth and survival of herbaceous species, as acidification would be diminished and nitrification would be increased, thus decreasing NH_4^+/NO_3^- ratios in the soil.

2. Materials and methods

2.1. Experimental design and plant species

In October 2000, mineral sand ($12\ m^3$) was collected from a dry heathland at the De Hamert nature reserve in the south of the Netherlands (51°32′N, 6°11′E). The sand was collected from a depth of 0 cm down to approx. 30 cm, after removal of the plant material and the organic top layer. The heathland was relatively poor in species, was dominated by *C. vulgaris* and suffered