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# Differential effects of ammonium and nitrate deposition on fen phanerogams and bryophytes

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Atmospheric N deposition; Botanical diversity; Mesotrophic fens; Nutrient limitation; Productivity

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## Abstract

**Question:** High atmospheric nitrogen (N) deposition has been shown to affect productivity and species composition of terrestrial ecosystems. This study focused on the differential effects of the two inorganic N forms in atmospheric deposition (i.e. ammonium and nitrate).

**Methods and location:** Nutrient addition experiments were carried out during 4 years in a mesotrophic fen in a low-deposition area in Ireland. In a factorial design, plots were fertilized with ammonium and/or nitrate, in two doses comparable with 35 and 70 kg N ha$^{-1}$ y$^{-1}$ and compared with an unfertilized control.

**Results:** Vascular plant biomass as well as bryophyte biomass were not affected by N dose but showed significantly different responses to the N form. In the ammonium-fertilized plots, vascular plant biomass was higher and moss biomass was lower than the control, while nitrate additions had no effect. Vascular plant species density was high (16 species per 0.49 m$^2$) and was not affected by any of the treatments; bryophyte species density was also high (seven species per 0.04 m$^2$) but showed a significant decrease upon ammonium fertilization.

**Conclusion:** The vulnerability of the mesotrophic vegetation to enhanced atmospheric N deposition depends strongly on the N form. If N would be mainly deposited as $NO_x$, no detrimental effects on the vegetation will occur. If, however, the deposition is mainly in the form of $NH_y$, the bryophyte vegetation will be seriously damaged, while the vascular plant vegetation will show an increased biomass production with possible shifts in dominance from *Carex* and herb species to grasses and shrubs.

## Introduction

Atmospheric deposition is a major source of nitrogen (N) for terrestrial ecosystems. As N is a macronutrient and limits plant and microbe growth in many natural and semi-natural systems (Vitousek & Howarth 1991; Gruber & Galloway 2008), the size of the annual N input through atmospheric deposition directly influences ecosystem functioning. Atmospheric N deposition has been rising in the large industrial and agricultural regions of the world since the onset of the industrial revolution (Galloway et al. 2004; Bobbink et al. 2010). Particularly since the 1950s, the effects of the enlarged N inputs on terrestrial ecosystems have been reported to be quite dramatic (Morris 1991; Bobbink & Roelofs 1995; Bobbink et al. 1998, 2010). In nutrient-poor ecosystems, such as heathlands, bogs and fens, the high N deposition has led to enhanced primary production with shifts in the dominance of plant species, often associated with loss of plant diversity (Berendse & Aerts 1984; Bobbink & Willems 1987; Aerts et al. 1992; Bobbink et al. 1992; De Kroon & Bobbink 1997). Critical loads of N have been estimated for different types of terrestrial ecosystems, taking into account differences in vulnerability, to help formulate effective and realistic targets for emissions in environmental policies (Bobbink et al. 2003). In addition to the fertilizing effect of elevated atmospheric N deposition, with its stimulating effect on plant biomass production, there are also other, more direct effects of the inorganic N compounds on the health and vitality of plants. Of the two main inorganic N species that have polluted the environment, nitrate originates mostly from $NO_x$ produced during fossil fuel combustion, whereas ammonium is derived from $NH_y$ compounds that evaporate from manure and dung in agricultural practice (Hosker & Lindberg 1982). While the enrichment of terrestrial systems with nitrate mostly results in increases of primary production and associated vegetation changes, the enrichment with ammonium has also direct toxic effects on plants. In the canopy of trees, high ammonium deposition causes a disturbance of the ionic balance in the leaves, with drastic consequences for leaf longevity and whole-plant vitality (Roelofs et al. 1985; Zottl 1990). Similar toxic effects of high ammonium have been found for heathlands (Roelofs 1986; Bobbink et al. 1992) and grasslands (Heil et al. 1988). In addition to the direct effects on plant leaves, high ammonium concentrations in soils and sediments also has been shown to negatively affect the growth of plants in terrestrial systems (Heil et al. 1988; Dorland et al. 2003; van den Berg et al. 2005; Lucassen et al. 2003).

The differential effects of nitrate and ammonium enrichment complicate the evaluation of the effects of enhanced atmospheric N deposition. In naturally oligotrophic or mesotrophic ecosystems in particular, there may be a response of higher productivity and associated species shifts, as well as a direct toxic effect, which may inhibit some sensitive species more than others. Both effects may result in shifts in species dominance and local extinctions of rare species. Mesotrophic fens are an example of an ecosystem type that is very species-rich and, because of its nutrient-poor conditions potentially vulnerable to the effects of high atmospheric N deposition. Earlier studies have indicated that many fens are limited by either N or P, with often a co-limitation by both elements (Beltman et al. 1992; Verhoeven et al. 1993, 1996a, 1996b; Beltman et al. 1996; Vitousek et al. 2010). As these systems are characterized by a well-developed bryophyte layer, the effects may also result in a different degree of dominance of the vascular plant layer versus the bryophyte layer. Initial experiments in the laboratory have shown that several characteristic bryophyte species from fens are sensitive to high ammonium concentrations (Paulissen et al. 2004, 2005). However, experimental work in fens has so far not enabled a full evaluation of the differential effects of ammonium versus nitrate enrichment on biomass production and vegetation structure.

To test the effects of atmospheric N deposition on species-rich, mesotrophic fens, we carried out a field experiment in a fen in central Ireland, where atmospheric deposition is low (4-8 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$) and more or less equally composed of oxidized and reduced N (Beltman et al. 1993; Aherne & Farrell 2002). More specifically, we asked three research questions: (1) What is the effect of N additions on the biomass production and species density of the vascular plants and bryophytes in the fen?; (2) What is the difference between adding the extra N as nitrate or as ammonium? (3) Are there any signs of toxic effects of ammonium on certain plant functional groups? Our approach was to carry out a 4-year nutrient addition experiment in the field with a full factorial design to test the effects of N dose (addition of 0, 35 and 70 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$) and N form (nitrate versus ammonium) on the vegetation response.

## Methods and location

### Site description

Scragh Bog is situated in County Westmeath, Ireland at ca. 10 km north of Mullingar near Lough Owel (53°5′N 8°5′W; National Irish grid N 420,590) (Fig. 1). It is situated in an oval-shaped depression in between glacially deposited ridges (eskers), consisting of sand, gravel and clay. The agricultural areas around Scragh Bog are used as meadows (O'Connell 1980). Scragh Bog covers 23 ha and mostly consists of a raft with plant communities floating on water and is thus characterized ecologically as a fen rather than a bog. The fen plant communities (Fig. 1) contain many rare species and some red list species (O'Connell 1981; Beltman et al. 2002). The species density is generally high, with 15 species of vascular plants and six species of bryophytes per 40 cm × 40 cm plot (Dorland et al. 1996).

Scragh Bog is fed by springs near the south-east end, by precipitation, groundwater flow and run off from the fields. The basin discharges its surplus water via a drain in the north-western corner (O'Connell 1981). The calcium-rich surface water originates from the springs and from diffuse groundwater inflow with a pH between 6 and 7. Nutrient availability is low (Beltman et al. 2002). Occasionally, the fen is flooded, up to 50 cm above the raft, which prevents the natural succession of the fen vegetation towards the ombrotrophic bog stage, because the typical bog-forming bryophytes are negatively affected by these floods. The eskers are grazed and fertilized with manure and artificial fertilizers and this might cause eutrophication; traces of eutrophication were detected in the marginal zones bordering the agricultural land (unpubl. data). The Department for Wildlife has reached agreements with most local farmers via Rural Environmental Protection schemes, so they receive a financial compensation in return for low-level application of fertilizers and reduced bank management. Scragh Bog is owned by the Irish Peatland Conservation Council (IPCC)

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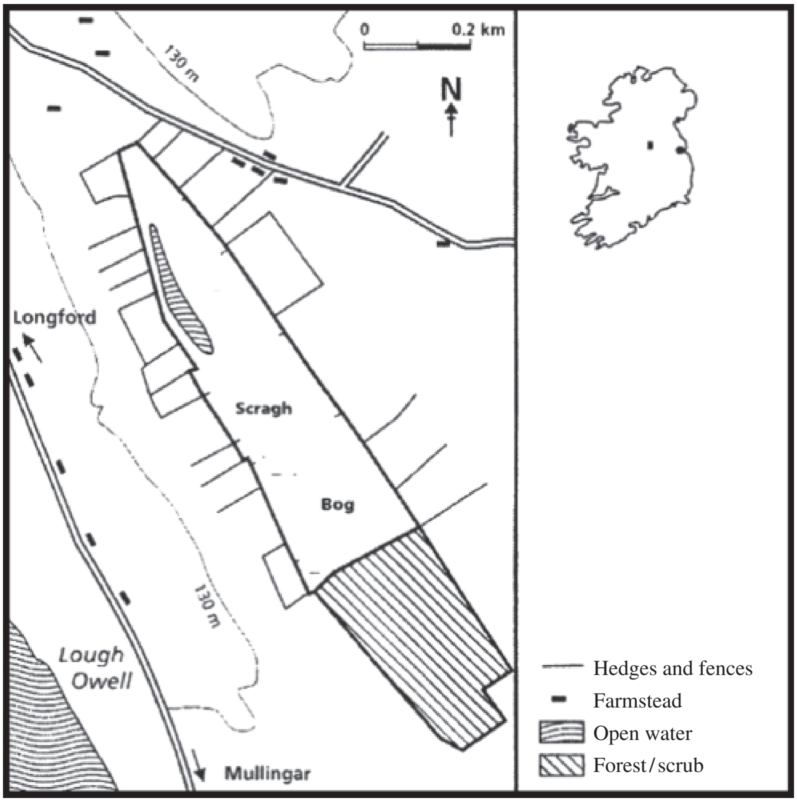

**Fig. 1.** Location of Scragh Bog in Ireland. The site is a mesotrophic fen with a small catchment with mostly agricultural land use (O'Connell 1980, 1981).

and has been designated as a nature reserve since 1992 [IPCC (Irish Peatland Conservation Council) 2005].

The first fen inventory was not carried out in Ireland until 2000 (Crushell 2000), which indicated the presence of 67 fens. The IPCC estimated that originally there was ca. 100 000 ha of fen wetland in Ireland of which 78% has been lost and damaged, and called for protection and conservation of remaining intact sites such as Scragh Bog.

## Experimental design

The experiment was set up in a factorial design with three doses of N application (0, 35 and 70 kg N $ha^{-1}$ $yr^{-1}$; N-0, N-35 and N-70, respectively) and two different forms of inorganic N ($NH_4$ and $NO_3$; see Table 1). The resulting three levels of N application represent environments with low N deposition (control, the ambient N deposition in Mullingar is estimated to be 4-8 kg N $ha^{-1}$ $yr^{-1}$, with equal molar contributions of reduced and oxidized nitrogen; Beltman et al. 1993; Aherne & Farrell 2002), high deposition (35 kg N $ha^{-1}$ $yr^{-1}$ added) and very high deposition (70 kg $ha^{-1}$ $yr^{-1}$ added). These higher levels are based on historical and present-day levels of N deposition in areas with intensive agriculture and industrial activities in Western Europe (e.g. The Netherlands and Germany). In addition, two treatments involved the application of phosphorus (P), to exclude the possibility of a strong control of biomass production by this element.

**Table 1.** Fertilizer application at the sampling sites in Scragh Bog. The experiment ran from August 2003 until July 2007. Fertilizer was applied in three equal doses in May, Aug and Oct of each year.

| Code | | Treatment |
|---|---|---|
| Control | Control | Only water |
| $35NH_4$ | Single-ammonium | 35 kg N $ha^{-1}$ $yr^{-1}$ applied as $NH_4Cl$ |
| $70NH_4$ | Double-ammonium | 70 kg N $ha^{-1}$ $yr^{-1}$ applied as $NH_4Cl$ |
| $35NO_3$ | Single-nitrate | 35 kg N $ha^{-1}$ $yr^{-1}$ applied as $NaNO_3$ |
| $70NO_3$ | Double-nitrate | 70 kg N $ha^{-1}$ $yr^{-1}$ applied as $NaNO_3$ |
| 10P | Phosphate | 10 kg P $ha^{-1}$ $yr^{-1}$ applied as $NaH_2PO_4 \cdot H_2O$ |
| 70N+P | All nitrogen and phosphate | $35NH_4+35NO_3+10P$ |

Five blocks of seven sampling plots were laid out at the north-eastern side of the fen in the zone dominated by *Carex lasiocarpa* (Fig. 1). Each sampling plot measured 1 m × 1 m and was separated from the adjacent plot by a buffer strip of 1 m. The sampling plots per cluster received one of seven randomized treatments with fertilizer, as

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indicated in Table 1. Nutrients were dissolved in tap water, which contained less than 0.14 mg $N\text{-}NH_4\,l^{-1}$, 0.14 mg $N\text{-}NO_3\,l^{-1}$ and 0.02 mg $P\,l^{-1}$ (average values over 4 years), and sprayed over the surface.

The fen was visited three times a year to apply portions of the annual fertilizer dose, to sample soil pore water and make photographs of the plots. The frequent applications were meant to avoid unnatural peak nutrient inputs while still maintaining a significantly enhanced input. The experiment ran from August 2003 until July 2007. In 2007 the vegetation in the sampling plots was harvested by clipping quadrats of 70 cm × 70 cm for phanerogams and 20 cm × 20 cm for bryophytes. The biomass was sorted to species level and weighed. Species samples were pooled to functional groups (herbs, graminoids, dwarf shrubs, trees, dead vascular plant material and moss), ground and digested using a modified Kjeldahl method (Bremner & Mulvaney 1982). The N and P concentrations were determined colorimetrically and potassium (K) concentration flame-photometrically, using a Skalar SA-40 continuous-flow analyzer (Skalar BV, Breda, The Netherlands).

The results for vascular plant and bryophyte biomass and for nutrient concentrations in plant material and litter were analysed with two-way ANOVA's, with N dose and N form as factors. Skewed data were transformed by taking the logarithm or square-root. Mean values were compared by using Tukey's *post-hoc* tests. All treatments (including those with P applications) were also compared with the control treatment by using one-way ANOVA and Dunnett's *post hoc* tests. All statistical procedures were carried out with SPSS 11.5 for Windows (SPSS Inc., Chicago, IL, USA).

## Results

### Biomass and species density

Two-way ANOVA showed that total vascular plant biomass as well as bryophyte biomass were not affected by N dose but showed significant differences among treatments with different N forms (Table 2). The interaction terms were not significant. More specifically, vascular plant biomass did not differ between the N-0, N-35 and N-70 treatments, whereas it was significantly higher than the control in the $NH_4$ treatments only (Fig. 2). The moss biomass showed almost a reversed picture, with a significant decrease compared with the control in the $NH_4$ treatments only, while N dose did not show any significant effects (Fig. 2). The species density of higher plants was high, 16 species per 0.49 $m^2$, and was not influenced by the N-dose or by the N-form treatments. The species density of mosses measured about seven species per 0.04 $m^2$ and showed a significant decrease compared with the control in the $NH_4$ treatment only (Table 2, Fig. 3).

**Table 2.** Two-way ANOVAS for vascular plant and moss biomass as well as species numbers against inorganic nitrogen (N) dose and inorganic N form.

| Dependent variable | Source | *df* | *F* | *P* |
|---|---|---|---|---|
| Vascular plant biomass | Corrected model | 4 | 2.514 | 0.074 |
| | Intercept | 1 | 162.264 | 0.000 |
| | N dose | 1 | 0.977 | 0.335 |
| | N form | 1 | 4.889 | 0.039 |
| | N dose × N form | 1 | 0.566 | 0.461 |
| Moss biomass | Corrected Model | 4 | 5.397 | 0.004 |
| | Intercept | 1 | 357.938 | 0.000 |
| | N dose | 1 | 0.540 | 0.471 |
| | N form | 1 | 13.206 | 0.002 |
| | N dose × N form | 1 | 0.010 | 0.921 |
| Number of vasc ular plant species | Corrected model | 4 | 0.202 | 0.934 |
| | Intercept | 1 | 599.131 | 0.000 |
| | N dose | 1 | 0.019 | 0.893 |
| | N form | 1 | 0.468 | 0.502 |
| | N dose × N form | 1 | 0.019 | 0.893 |
| Number of moss species | Corrected model | 4 | 3.475 | 0.026 |
| | Intercept | 1 | 170.126 | 0.000 |
| | N dose | 1 | 0.684 | 0.418 |
| | N form | 1 | 6.159 | 0.022 |
| | N dose × N form | 1 | 0.349 | 0.561 |

In the one-way ANOVAS the positive and negative effects of $NH_4$ addition on plant and moss biomass, respectively, are clearly shown (Fig. 4). Nitrate additions did not have any effect at all. The P treatment also did not affect either vascular plant or moss biomass, although the combined N+P treatment resulted in higher vascular plant and lower moss biomass than the control (Fig. 4). The various plant functional type groups showed no significant biomass responses to N-dose or N-form (data not shown). Biomass of the grasses and the dwarf shrubs (mostly *Oxycoccus palustris)* showed a significant increase in the N+P treatment only.

### Nutrient concentrations in plant material

The N concentrations in the total vascular plant vegetation were not affected by the treatments (Fig. 5). All values for N are below the critical value that is generally accepted as indicative of N limitation (14 mg $g^{-1}$; De Wit et al. 1963). The P concentrations show significant increases compared with the control in the two treatments with P addition. All other values are close to the critical value of 0.7 mg $g^{-1}$. The K concentrations are also mostly lower than the critical concentration of 8 mg $g^{-1}$. All three nutrients, N, P and K, are in quite short supply in this fen, while N appears the most limiting. The N:P ratio of

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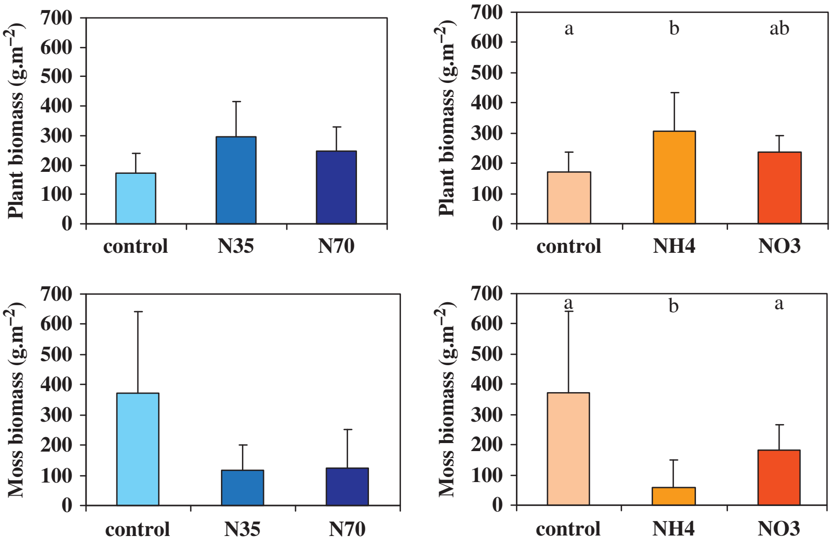

**Fig. 2.** Biomass of vascular plants (top) and mosses (bottom) in relation to nitrogen (N) fertilization. Error bars are SD. Left, effect of N dose (0, 35 and 70 kg N ha$^{-1}$ y$^{-1}$), regardless of inorganic N form.; right, effect of inorganic N form (0, $NH_4^+$ and $NO_3^-$), regardless of dose. Bars with different letters are statistically different ($P < 0.05$).

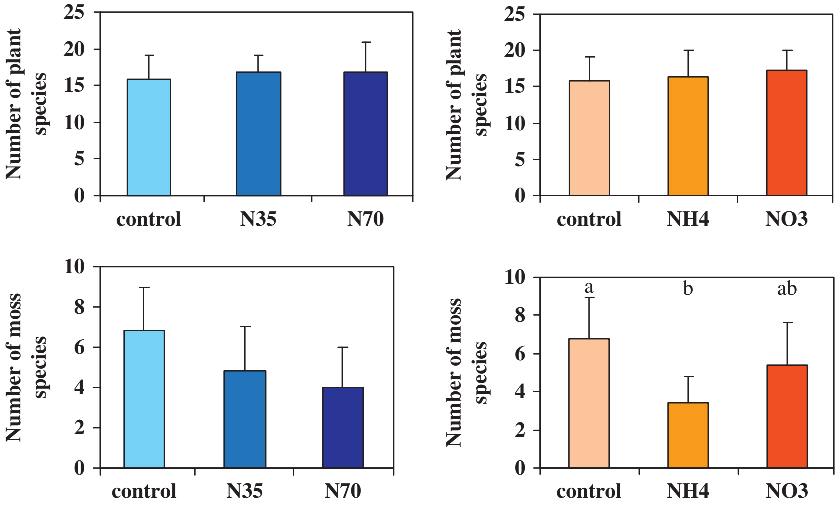

**Fig. 3.** Number of vascular plant species per 0.49 m$^2$ (top) and moss species per 0.04 m$^2$ (bottom) in relation to nitrogen (N) fertilization. Error bars are SD Left, effect of N dose; right, effect of inorganic N form. Bars with different letters are statistically different ($P < 0.05$).

the vegetation in the control treatment indicates a co-limitation by N and P (Koerselman & Meuleman 1996), while the N:K ratio indicates co-limitation by N and K (Venterink et al. 2003) (Table 3). The N:P ratios clearly show that the N limitation is lifted and turns into P limitation in all four treatments with N-only additions. Conversely, N assumed a limiting role in the two treatments with P addition.

Plant N, P and K concentrations in plant functional types hardly responded to the N-dose or N-form treatments (data not shown). The P concentrations of grasses and dwarf shrubs were significantly higher than the control in the treatments with P addition, which is commonly found in fertilization experiments (Verhoeven et al. 1996b).

## Discussion

Our long-term field experiment shows that mesotrophic fens do not necessarily react to N fertilization with an increased overall biomass production or decrease in plant diversity. The most striking result of the experiment is that enrichment with only nitrate did not result in any significant biomass or species diversity response of

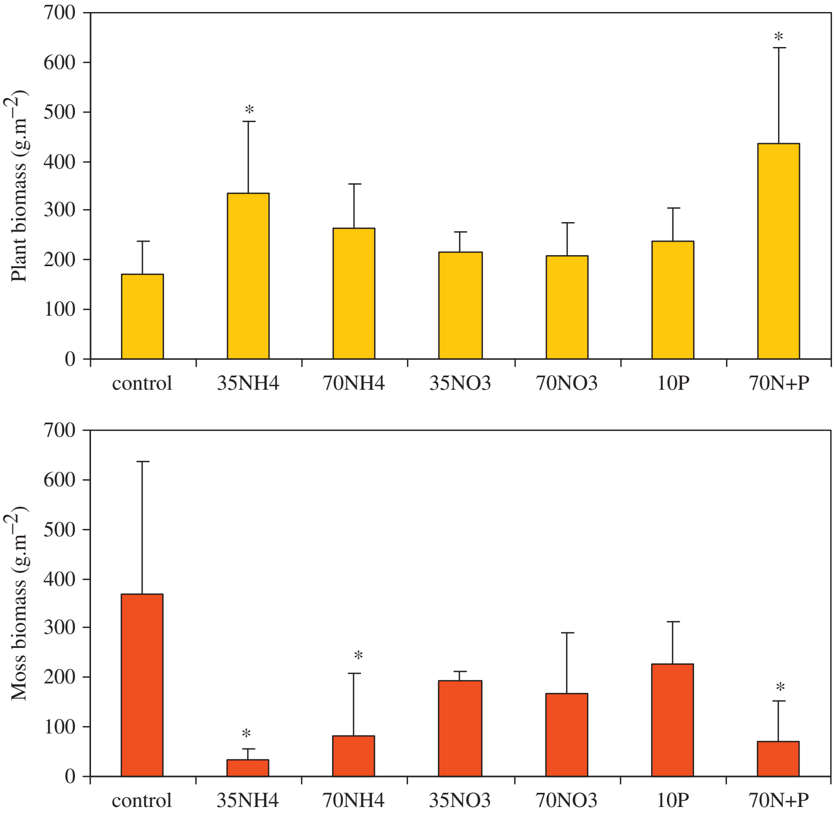

**Fig. 4.** Biomass of vascular plants and mosses in the individual treatments with SD. Means with an asterisk are significantly different from the control treatment (one-way ANOVA with Dunnet's *post hoc* test, bars with an asterisk are statistically different from the control, $P < 0.05$).

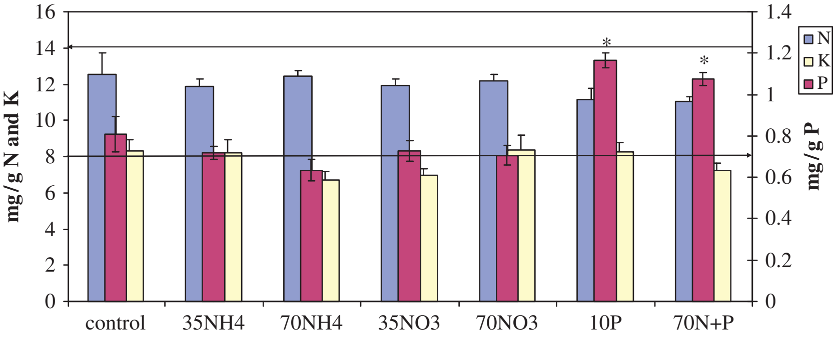

**Fig. 5.** Average nitrogen (N), phosphorus (P) and potassium (K) concentrations in vascular plant biomass in relation to the treatments. Bars with an asterisk are significantly different from the control. Arrows indicate the critical N and P concentrations for growth limitation (De Wit et al. 1963).

vascular plants or bryophytes, whereas the enrichment with only ammonium led to higher vascular plant biomass and lower bryophyte biomass accompanied by loss of bryophyte species diversity. To our knowledge, this is the first time that these differential effects of nitrate and ammonium in a mesotrophic ecosystem have been revealed through a field nutrient addition experiment.

The decline of the bryophyte layer after ammonium enrichment might have been caused by two mechanisms: (1) the simultaneous stimulation of the vascular plant growth leading to increased shading of the mosses; (2) a negative, toxic effect of the ammonium addition on the vitality of the bryophytes. Both mechanisms will probably have contributed to the negative effect. However, the seriousness of the bryophyte biomass decline (i.e. from an average of more than 350 g m$^{-2}$ to less than 60 g m$^{-2}$; Fig. 2) points in the direction of direct, toxic ammonium effects. The biomass increase of the vascular plant vegetation, from 170 g m$^{-2}$ to 340 g m$^{-2}$, was visible in the plots in the field, but did not lead to an excessively strong

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**Table 3.** Nutrient ratios in living tissues of vascular plant and moss material.

| Treatment | Vascular plants | | Bryophytes | |
|---|---|---|---|---|
| | N:P | N:K | N:P | N:K |
| Control | 15.8 | 1.5 | 18.1 | 2.3 |
| $35NH_4$ | 16.6 | 1.5 | 20.9 | 3.7 |
| $70NH_4$ | 20.1 | 1.9 | 27.7 | 3.5 |
| $35NO_3$ | 16.7 | 1.7 | 18.2 | 2.5 |
| $70NO_3$ | 17.4 | 1.5 | 24.3 | 2.8 |
| 10P | 9.6 | 1.4 | 5.9 | 1.7 |
| 70N+P | 10.3 | 1.6 | 7.1 | 1.5 |

shading effect because parts of the bryophyte layer were still exposed to sunlight. The direct negative effects of ammonium on mosses have also been found in greenhouse experiments by (Paulissen et al. 2004, 2005) and by an ammonium addition experiment in a bog ecosystem (Sheppard et al. 2009). The negative effect of ammonium addition on moss species diversity meant an average decline from seven to four species per 0.04 $m^2$ (Fig. 3). The increased biomass in the vascular plant vegetation upon ammonium addition was accompanied by gradual changes in the dominance of species. Grasses (*Festuca rubra*, *Molinia caerulea*, *Agrostis stolonifera*) and some ericoids (*Oxycoccus palustris*) increased, while *Carex* species did not change and some herb species (*Menyanthes trifoliata* and *Potentilla palustris*) decreased. Such changes in species composition mostly only occur over intervals in the order of decades, while our experiment lasted for 4 years only, which is still too short to find significant changes in species composition. It should be stressed here that no changes or even trends in species density or dominance in either vascular plants or mosses occurred in the plots that had received only nitrate.

The absence of a biomass response either with increasing N addition or with P addition, in combination with the strong response to the combined addition of N and P, indicate that both elements are in short supply in this fen. It is most probable that there is a co-limitation of N and P for the vascular plant growth. The nutrient concentrations in the plant material lead to the same conclusion; even K concentrations in plant material are close to the critical value, indicating limitation. All three major plant nutrients, N, P and K, are scarce in this mesotrophic fen. Co-limitation by two nutrients is a phenomenon that is often found in low-productive herbaceous vegetation. Simultaneous limitation by N and P is common in fens and wet heathlands (Koerselman & Meuleman 1996; Verhoeven et al. 1996a, 1996b; Venterink et al. 2003), while N and K co-limitation is often found in Calthion wet meadows (Grootjans et al. 1996).

These overall nutrient-poor conditions could be an advantage in moderating the long-term effects of enhanced nutrient loading on the fen vegetation. The increase in atmospheric conditions from approximately 4 kg N $ha^{-1}$ $y^{-1}$ to approximately 8 kg N $ha^{-1}$ $y^{-1}$ that has occurred according to calculations based on data from Beltman et al. (1993) and Aherne & Farrell (2002), will not have raised the N availability in the fen so far. Even if N availability does rise, effects through increasing biomass production will only become drastic when N as well as P inputs are increased. Such enrichment would only be expected if run-off from the agriculturally used catchment became increasingly nutrient-rich. The current, rather extensive land use around the fen probably will not lead to such high inputs. If the atmospheric N deposition increases, the effect would be strongly dependent on the inorganic form of N. Our study shows that if N is mainly deposited as $NO_x$, no detrimental effects on the vegetation will occur. However, if the deposition is mainly in the form of $NH_y$, which is derived from ammonia volatilization in areas with intensive animal husbandry, the bryophyte vegetation will be seriously damaged, while the vascular plant vegetation will show an increased biomass production with possible shifts in dominance from *Carex* and herb species to grasses and shrubs. There are indications that the deposition of $NH_y$ has risen more than that of $NO_x$ in the central part of Ireland, where the fen is located.

The wider significance of this study is that mesotrophic fens in areas with enhanced N deposition would be particularly vulnerable with respect to the biomass production and diversity of the bryophyte layer if the deposition is mainly of the $NH_y$ type. Measures to reduce the agricultural sources of ammonia to the atmosphere include manure winter storage in combination with injection into the soil during the growing season. These measures have reduced the $NH_y$ deposition in The Netherlands by 35%, but current values there are still too high to exclude drastic effects on mesotrophic fen vegetation (Bobbink et al. 2010).

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