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# Response of enchytraeid worm populations to different forms of nitrogen (ammonia, ammonium, and nitrate) deposition

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## Abstract

The changes to ecosystems and ecosystem functioning induced by anthropogenic reactive nitrogen deposition continue to be studied in a range of habitats. In semi-natural habitats, these effects can be pronounced, often with negative impacts on the native flora. An experimental site established on an ombrotrophic bog provides a unique opportunity for the study of the effect of long-term simulated N deposition. The response of enchytraeid worms to different forms of nitrogen deposition (as ammonia, ammonium or nitrate) was assessed at this site, which has been receiving N treatments since 2002: previous studies on the site have shown that high N deposition (64 kg N ha$^{-1}$ yr$^{-1}$) has changed the above-ground vegetation. In this study, the below-ground response of enchytraeids to N treatment was shown to be dependent on site wetness. Under favourable site conditions, i.e. when the peat moisture content was high, enchytraeid abundance was negatively affected by N deposition in the form of ammonia or nitrate, whereas addition of ammonium, ammonium plus PK (=$K_2HPO_4$), and to a lesser extent, nitrate plus PK, appeared to increase enchytraeid abundance. However, when the bog was drier, enchytraeid numbers were similar across all treatments and appeared to be insensitive to N.

**Keywords:** Oligochaeta, enchytraeids, ombrotrophic bog, oxidised N, reduced N

## 1. Introduction

Atmospheric nitrogen (N) deposition in various forms (oxidised and reduced, wet and dry) to semi-natural habitats, such as ombrotrophic bogs, continues to affect vegetation cover, plant species diversity and ecosystem functioning, often resulting in negative effects on the more N-sensitive plant species (Aerts et al. 1992, Bobbink et al. 1998, Lamers et al. 2000, Galloway et al. 2008). Ombrotrophic bogs are characterised by specialised plant communities that are adapted to low nutrient conditions, and as these habitats rely solely on atmospheric nutrient inputs, they are particularly sensitive to increased N deposition.

Enchytraeid worms are found in a wide range of habitats. Together with their high abundance and species diversity, they could provide a sensitive barometer for assessing the effects of anthropogenic activities on soil (Didden & Römbke 2001). In acidic, peaty soils, the enchytraeids are important organisms, making up 75 % of the total mesofauna. The enchytraeids are the keystone species in these soils, responsible for organic matter decomposition and nutrient cycling (Standen 1978, Laakso & Setälä 1999, Cole et al. 2000, Cole et al. 2002, van Vliet et al. 2004). The effect of increased N on enchytraeids has been studied in grasslands and upland peats, often following the application of N to small plots (e.g. Coulson & Butterfield 1978, Yesmin et al. 1995, Thompson 2003). However, the effect of N on enchytraeids has not been fully investigated in simulations of N deposition processes under 'real world' conditions, where N additions reflect UK-wide N deposition and where application rates are coupled to local meteorological conditions (e.g. rainfall and wind speed and direction). The main mechanism controlling the enchytraeid response is still uncertain due to contrasting and variable results, where high N deposition has been shown to both increase (Coulson & Butterfield 1978) and reduce enchytraeid numbers (Yesmin et al. 1995). Enchytraeids are likely to respond to N deposition via indirect effects to their food source (e.g. decomposing litter, bacteria and fungi) and soil pH (Standen 1982).

A previous study conducted in 2005 on an ombrotrophic bog (Prendergast-Miller et al. 2008) investigated the effect of the dry N deposition treatments (as ammonia gas) on enchytraeid abundance at an experimental site. The study found that within three years of exposure to dry N deposition, there were decreasing gradients in peat N content (as ammonium and nitrate concentrations) and peat pH, with increasing distance from the ammonia source. Above-ground, *Calluna* N concentrations were significantly increased, and within 8 m of the point source *Calluna* was more susceptible to frost damage (Sheppard et al. 2008). In contrast, enchytraeid abundance showed no response to increased N deposition and was highly variable. This lack of response was attributed to the relatively longer time (> 3 yr) required for above-ground foliar N to become incorporated into the litter layer (Thompson 2003). Here we report on an assessment of enchytraeid abundance made after six years of N treatment of different forms (as ammonium, nitrate or ammonia), to examine the effect of both wet and dry deposition on the enchytraeids. In order to detect whether any change was occurring in the enchytraeids, we compared abundance in control plots (receiving ambient N deposition, ~ 8 kg N $ha^{-1}$ $yr^{-1}$) with that from plots receiving the highest N deposition as ammonium, nitrate or ammonia. This was to test the hypothesis that the enchytraeids would show a positive response to N deposition mediated through the changes in leaf and litter N content which would be expected after six years.

## 2. Materials and methods

### 2.1 Site description

Whim Moss in the Scottish Borders (3° 16′W and 55° 46′N) is an experimental site established in 2002 on an ombrotrophic bog, as part of the UK Natural Environment Research Council's GANE (Global Atmospheric Nitrogen Enrichment) programme. The manipulation experiment was established to study the long-term effects of simulated N deposition as ammonia, ammonium or nitrate to a semi-natural habitat. The Whim Moss vegetation is classified as M19 (*Calluna vulgaris – Eriophorum vaginatum* mire) (Rodwell 1991). The vegetation is a mosaic of *Sphagnum* mosses, with *Calluna vulgaris* (L.) Hull, *Eriophorum vaginatum* (L.), and some *Cladonia* lichen species. The site is unmanaged, but is impacted by rabbits.

The N treatments are applied to the site in real-time depending on the local meteorological conditions, as the automated release system ensures that the treatments are only applied when certain threshold parameters are met, such as wind speed and direction. This provides a unique opportunity to observe and compare the effects of different forms of N deposition (wet vs. dry, oxidised vs. reduced) above- and below-ground. The site is divided into two areas to study the effects of (1) wet deposition as ammonium or nitrate sprayed in solutions (made from rainwater collected at the site) over circular plots (4 m diameter), and (2) dry deposition, as ammonia gas ($NH_3$) released over a 60 m transect. Full descriptions of the treatments and manipulations are given in Sheppard et al. (2004) and Leith et al. (2004). The wet treatments (reduced ($NH_4Cl$) or oxidised N ($NaNO_3$)) are provided as a fine spray of rainwater mixed with three doses of N (8, 24 or 56 kg N $ha^{-1}$ $yr^{-1}$), with and without phosphorus (P) and potassium (K). The control plots receive only ambient N deposition, with no additional rainwater (~ 8 kg N $ha^{-1}$ $yr^{-1}$). The treatments are applied over the plots when the wind speed is < 5 m $s^{-1}$, and not when the ground is frozen (Sheppard et al. 2004). At the dry deposition area, which simulates N deposition from a point source such as a large poultry farm, the ammonia gas release system is activated whenever the wind speed is > 2.5 m $s^{-1}$ and within the 180–215° designated sector of the transect (Leith et al. 2004). Therefore, the frequency of N addition to the respective plots varies between the different forms of N, and application may be more than once a day, or even none at all over a dry summer or during winter.

The study presented here focused on the high N treatments from the wet deposition plots (receiving 64 kg N $ha^{-1}$ $yr^{-1}$ as ammonium or nitrate) and the dry deposition transect (8 m from the ammonia release pipe, where deposition is 64 kg N $ha^{-1}$ $yr^{-1}$), in order to identify if any effect on the enchytraeids was occurring. Samples were taken in June 2008 from the selected N treatments shown in Tab. 1. Samples were taken again in October from the same plots to determine if the effects shown earlier in the year were still present.

Tab. 1 Selected treatments (Control, wet and dry N deposition) sampled at Whim Moss for assessment of enchytraeid abundance.

| **Treatment** | **Number of plots** | **Annual deposition (kg N $ha^{-1}$ $yr^{-1}$)** |
|---|---|---|
| **Control (no added nutrients)** | 4 | 8 (ambient) |
| **Wet deposition plots** | | |
| Ammonium ($NH_4Cl$) | 4 | 64 (ambient + 56) |
| Ammonium + PK ($NH_4Cl + K_2HPO_4$) | 4 | 64 (ambient + 56) |
| Nitrate ($NaNO_3$) | 4 | 64 (ambient + 56) |
| Nitrate + PK ($NaNO_3 + K_4HPO_4$) | 4 | 64 (ambient + 56) |
| **Dry deposition transect** | | |
| Ammonia ($NH_3$) gas<br>(8 m from point source) | 1 | 64 (ambient + 56) |

### 2.2 Peat sampling

From the wet deposition site, 2–3 cores were taken from each plot. On the ammonia transect, 4 cores were taken within 8 m of the ammonia release pipe. An additional 4 cores were taken from the control plots, which receive ambient N deposition with no additional nutrients or water. The cores were taken using a 3 cm diameter corer, and the peat was sampled to a depth of 10 cm. Samples were bagged in the field and returned to the laboratory where they were stored at 4 °C. The cores were cut vertically in half: one portion was used for pH (1:2 ratio of peat:deionised water) and dry weight determination (oven-dried overnight at 105 °C); the other half was used for enchytraeid extraction. Cores from the same plots were pooled together. The enchytraeids were extracted for 3 hr using Baerman funnels which were set up under a bank of lights (O’Connor 1957). Enchytraeids were collected in small glass vials attached to the end of the funnels and immediately counted. As an indication of whether nutrient addition had altered litter and peat quality within the assumed enchytraeid feeding depth, oven-dried surface litter and peat (0–10 cm depth) samples from the control, ammonium and nitrate plots were analysed on a CN analyser for total carbon and nitrogen. Data on precipitation and peat temperature (at a depth of 10 cm) are measured automatically at the site, and these were used to calculate monthly means between May and October 2008.

### 2.3 Statistical analysis

To test for differences between treatments in moisture content, pH and C:N ratios, data were analysed by one-way ANOVA; significant differences ($P < 0.05$) were determined using post-hoc Tukey’s honestly significant difference tests. T-tests were performed to test for differences between months within the same treatment. Non-parametric tests were used to compare treatments in each month for enchytraeid abundance as the data did not meet the requirements for equal variance and normality. All analyses were performed on Minitab v.15.

## 3. Results

### 3.1 Moisture content

The samples taken in June were significantly wetter (mean gravimetric water content 9.2 g $g^{-1}$ dwt) than the October samples (mean gravimetric water content 1.9 g $g^{-1}$ dwt) (Fig. 1; $P < 0.001$). This was despite significantly more rain falling in the month preceding October compared to June (Fig. 2). The mean monthly rainfall, measured daily at the site, was actually higher ($P < 0.001$) in October (5.45 mm) compared to June (3.16 mm), and the mean monthly

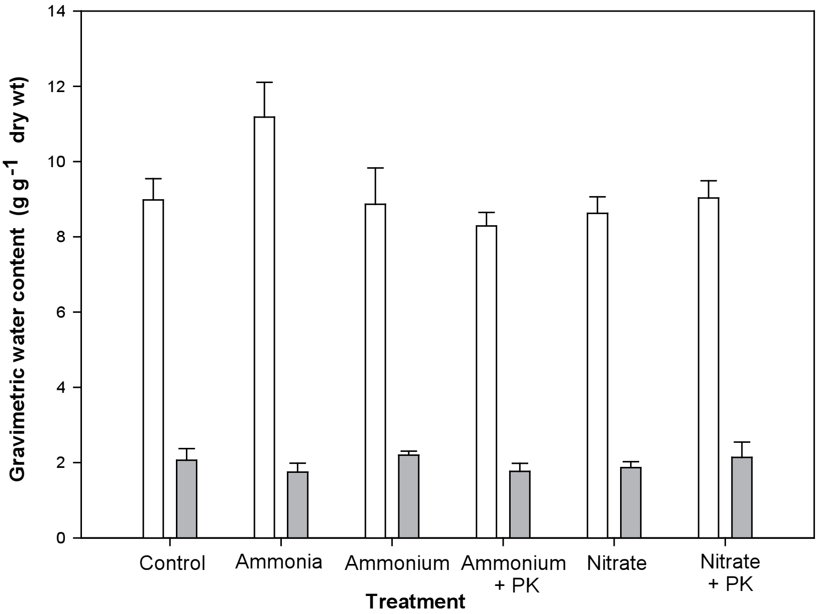

Fig. 1 Peat gravimetric water content (mean + s.e.m.) from cores sampled in June (open bars) and October (shaded bars) 2008 (n = 4 per treatment). Refer to Tab. 1 for details of the different treatments.

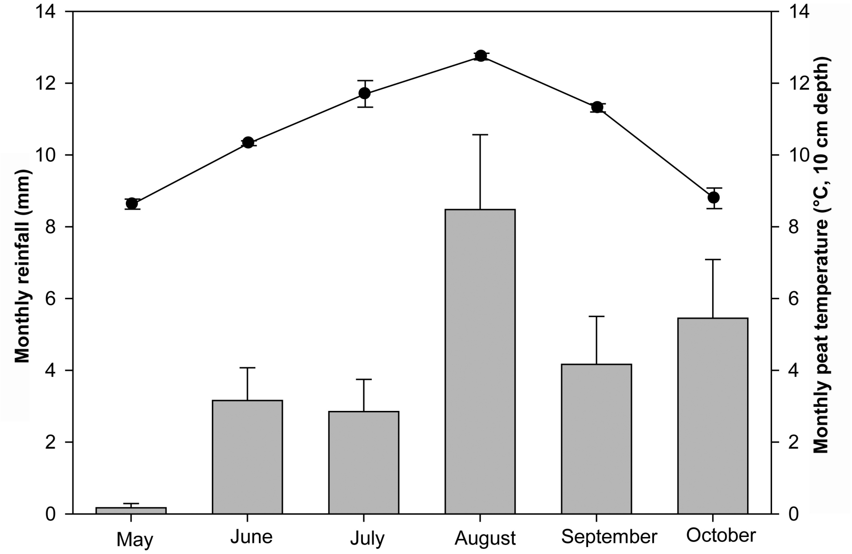

Fig. 2 Monthly rainfall (mean + s.e.m.; shaded bar) and peat temperature at 10 cm depth (mean ± s.e.m.) measured at the site between May and October 2008.

peat temperature was lower (P < 0.001) in October (Fig. 2). There were no difference in moisture content between the different treatments in June or October.

### 3.2 Peat pH

The pH from peat samples in June was generally higher than the pH from the samples taken in October (P < 0.001). For the ammonium and nitrate plots pH did not change between sampling time. In both months, there was a treatment effect on peat pH (P < 0.001 for each month; Fig. 3): in June, the pH from the ammonia and nitrate + PK treatments was higher than the control and both ammonium treatments; in October, the pH of the control and ammonium + PK plots was significantly lower than the ammonia and both nitrate treatments. There was a significant correlation between peat pH and gravimetric water content in June (r = 0.474, P < 0.05) but not in October (r = –0.006, P > 0.05).

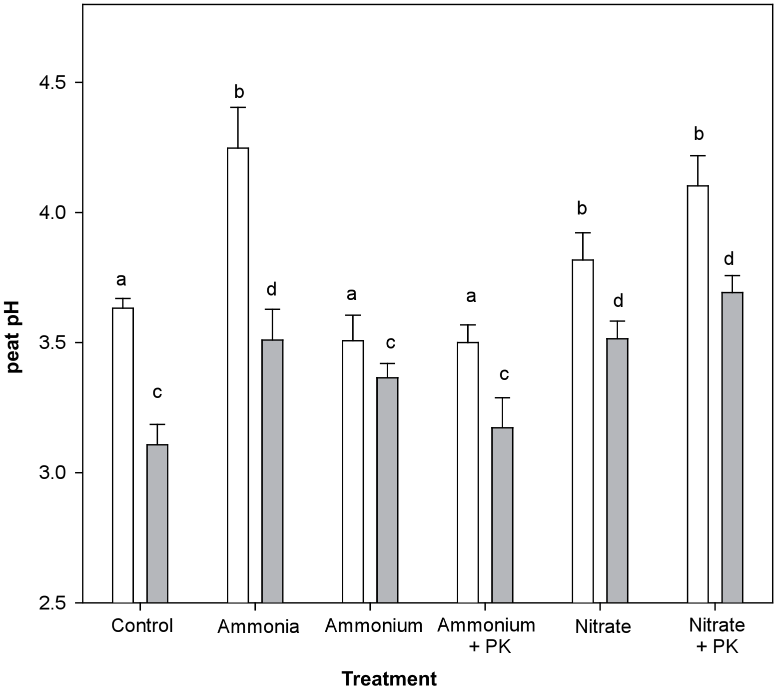

Fig. 3 Peat pH (mean + s.e.m.) from cores sampled in June (open bars) and October (shaded bars) 2008 (n = 4 per treatment.). Bars with the same letters in June or October are not significantly different (P > 0.05). Refer to Tab. 1 for details of the different treatments.

### 3.3. Surface litter and peat C:N ratios

Surface litter and peat samples (0–10 cm depth) from the control and treatments receiving the highest nutrient additions (without PK) were analysed for total carbon and nitrogen to provide an indication of whether high nutrient input had altered litter and peat quality. Lower C:N ratios compared to the control, due to the higher N content, would suggest improved substrate quality. Although the surface litter C:N ratios appeared to be lower in the ammonium

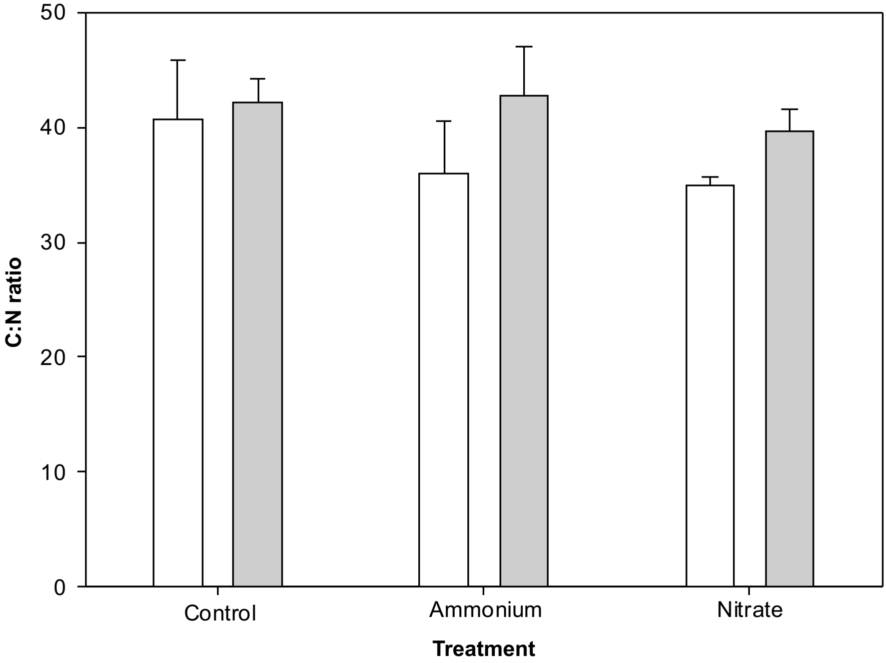

Fig. 4 C:N ratios (mean + s.e.m.) of surface litter (open bars) and peat (0–10 cm depth; shaded bars) sampled from the control, ammonium and nitrate plots (n = 4). Refer to Tab. 1 for details of the different treatments..

and nitrate plots, this was not significantly different compared to the C:N ratio of the control plots (Fig. 4). Peat C:N ratios (0–10 cm) were also similar between treatments. There were no significant differences between surface litter and peat C:N ratios for each treatment.

### 3.4 Enchytraeid abundance

Overall enchytraeid abundance was greater in samples taken in June compared to October, $P < 0.005$ (Fig. 5A). In the samples taken in June, ammonium + PK addition increased enchytraeid abundance compared to the control ($P < 0.05$). In contrast, ammonia and nitrate additions appeared to lower enchytraeid abundance. In October, no enchytraeids were found in the ammonia treated plots and there was no difference in abundance between the control and other treatments ($P > 0.05$). There were significant negative correlations between peat pH and enchytraeid abundance ($r = -0.475$, $P < 0.05$) and water content and enchytraeid abundance ($r = -0.519$, $P < 0.01$) in June. There were no correlations between these variables and enchytraeids in October (pH: $r = -0.343$, $P > 0.05$; moisture content: $r = -0.063$, $P > 0.05$).

Enchytraeid abundance was also calculated per g dry wt of the peat samples (Fig. 5B) to reflect the difference in moisture content measured in June and October. Here, there was no

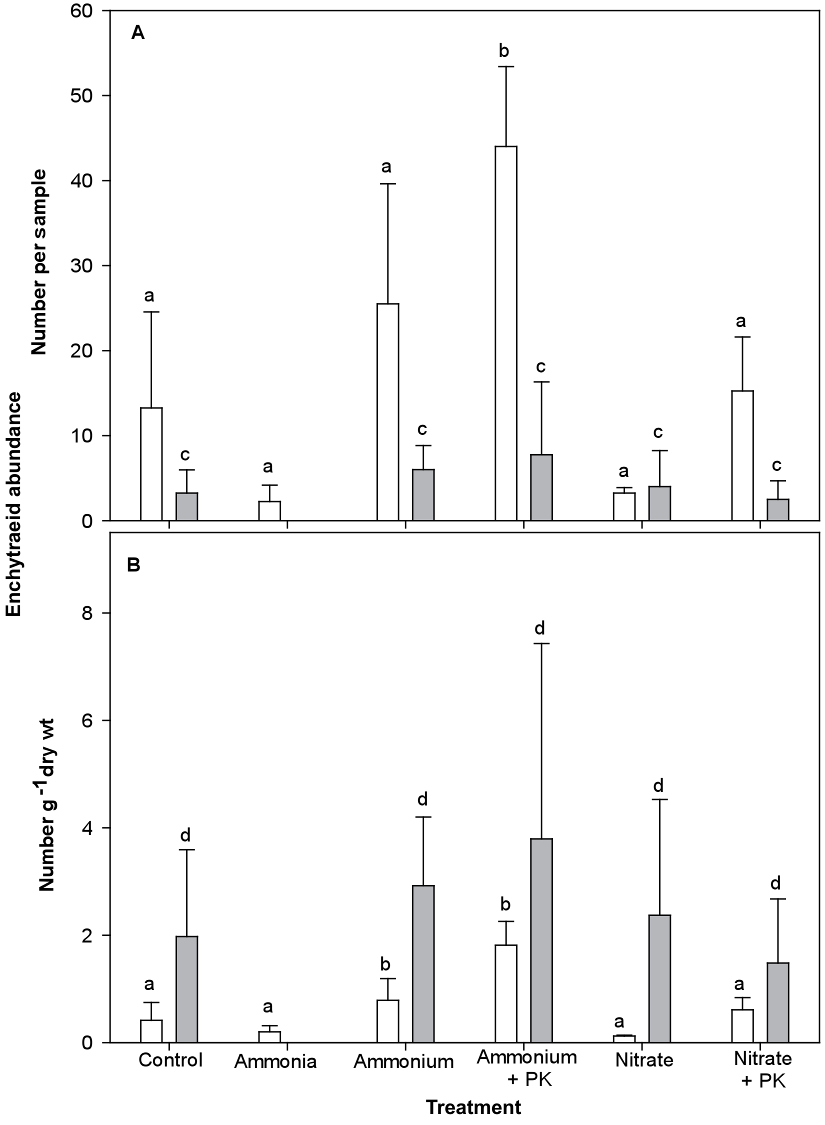

Fig. 5 Enchytraeid abundance (mean + s.e.m.) extracted from peat cores at each treatment in June (open bars) and October (shaded bars) 2008; n = 4 per treatment. Enchytraeid abundance is represented as number per sample (A) and number per g dry peat (B). Bars with the same letters in June or October are not significantly different (P > 0.05). Refer to Tab. 1 for details of the different treatments.

significant difference in enchytraeid abundance between the two sampling times. N treatment had no effect on abundance in October, but in June, the number of enchytraieds was highest in the ammonium and ammonium + PK treatments ($P < 0.05$).

## 4. Discussion

This paper has addressed the question of enchytraeid sensitivity (abundance) to N form and other drivers, using a N manipulation experiment on an ombrotrophic peat bog, Whim Moss, to determine if high N deposition (in the form of reduced and oxidised, wet and dry N) has affected the enchytraeids. The results, with lower numbers in October when the peat was drier, indicate that peat moisture content is the main factor controlling enchytraeid abundance. Under wetter conditions, enchytraeids responded to addition of N as ammonium + PK and the results suggest that enchytraeids were negatively affected by ammonia, nitrate, and to a lesser extent by nitrate + PK. Additions of the different N forms had a significant effect on soil pH and it seems likely that the enchytraeid response to the different N additions reflects these pH changes, rather than changes in litter or peat N status.

### 4.1 Site conditions

Peat moisture and temperature are important factors controlling enchytraeid abundance, and in the UK, enchytraeids are most abundant during the summer months with numbers declining in winter (Peachey 1963, Cole et al. 2002). Here also, enchytraeid abundance was highest in June, implying more favourable environmental conditions than in October when peat temperature was lower. However, peat samples were only taken to a depth of 10 cm, and it is possible that the enchytraeids had migrated deeper into the peat prior to the October sampling to avoid desiccation (Springett et al. 1970). The weak correlation between peat moisture and pH suggests that lower peat moisture may also have affected the peat pH, which was lower in October compared to June. This means that site wetness, as an important regulator of enchytraeid abundance, will determine whether any response to habitat perturbation can be discerned; this highlights the need for regular sampling.

### 4.2 Effect of N deposition on enchytraeids

High N deposition in different forms (ammonia vs. ammonium or nitrate) has had variable effects on the vegetation at Whim Moss (Carfrae et al. 2005, Sheppard et al. 2008). After four years of treatment (2002–2006), high N deposition as dry ammonia deposition, has had a marked effect on the dominant ericoid *Calluna*; foliar N concentrations have increased and the plants are more sensitive to stresses from drought, frost and pathogens (Sheppard et al. 2008). The distribution of sensitive moss and lichen species has also been negatively affected at high ammonia concentrations. The effect on the vegetation is clearly seen close to the point source, where the *Calluna* has been bleached. However, on the wet deposition plots, reduced N (as ammonium) and oxidised N (as nitrate) at equivalent N doses have produced only small increases in foliar N concentrations and increased *Calluna* cover (Sheppard et al. 2008). Analysis of surface litter and peat samples from the control and wet deposition plots (Fig. 4) showed no significant effect of N deposition, suggesting the response shown by the enchytraeids in these plots to N treatment was not mediated via substrate quality.

Below-ground, high N deposition has affected peat chemistry. Compared to the ambient (control) site, ammonia and nitrate deposition have increased the peat pH, and these trends did not change with drier peat conditions. In contrast, there has been no significant change in the pH of the ammonium plots. At the high ammonia site, the higher pH (pH 4.2), compared to the control plot (pH 3.6), now exceeds the range tolerated by *Cognettia sphagnetorum* (pH 2.7 to 3.8 (Yesmin et al. 1995)), and this could explain the very low numbers recorded from this plot, even though the peat moisture content here was high in June. On the wet deposition plots, the form of N has had contrasting effects: deposition as ammonium increased enchytraeid numbers, whereas numbers are lower on the nitrate plots, which have a higher pH (pH 3.8). These observations strongly suggest that the different N forms are affecting enchytraeid abundance via soil pH. In order to test the effect of N form alone, we would need to counteract the pH effect.

The inclusion of additional nutrients (phosphorus and potassium) has slightly increased enchytraeid abundance in both the ammonium and nitrate PK treatments. The higher abundance from the nitrate + PK treatment suggests that the extra nutrients can ameliorate the negative effect of nitrate on its own. Therefore, these essential elements may be limiting enchytraeid abundance at the site, as the enchytraeids appear to need PK to increase their abundance.

### 4.3 Long-term N deposition reduces species diversity

Despite the increase in enchytraeid numbers from the ammonium plots, the species diversity at the site has been lowered. In April 2002, a survey of enchytraeids from across the site found five enchytraeid species, dominated by *C. sphagnetorum* with 83 % abundance (V. Standen pers. comm.). Other species found were *Mesenchytraeus sanguineus*, *M. flavus*, *Cernosvitoviella* spp., and *Marionina clavata*. In the 2005 study, only three species were identified: *C. sphagnetorum*, *M. sanguineus*, and *Cernosvitoviella* spp. (Prendergast-Miller et al. 2008). In this study, only *C. sphagnetorum* was identified. Thompson (2003) suggested that an improvement in N conditions would result in the replacement of *C. sphagnetorum* with other enchytraeid species that prefer less acidic conditions. Our results from samples taken after six years of elevated N deposition suggest that high N deposition is having a negative impact on species diversity. However, given the control plots also had only one species, it is possible that other environmental factors have contributed to the loss of species diversity.

### 4.4. Conclusions

The results indicate that the form of N should be taken into account when investigating N deposition effects on enchytraeid abundance. The reason for this appears to be linked to the effect of N on peat pH, rather than through eutrophication effects. On the same site, ammonia, ammonium and nitrate are having contrasting effects on enchytraeid abundance. This observation points to the need to monitor more frequently to appreciate the significance of environmental influences (especially moisture content) on enchytraeid abundance in order to be able to separate these effects from those of anthropogenic influences. The significance of N deposition for enchytraeids is still not resolved, although this experiment suggests that in bogs PK availability may also be limiting, and thus modifying the N response.

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## 6. References

Aerts, R., B. Wallen & N. Malmer (1992): Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. – Journal of Ecology **80**: 131–140.

Bobbink, R., M. Hornung & J. G. M. Roelofs (1998): The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. – Journal of Ecology **86**: 717–738.

Carfrae, J. A., L. J. Sheppard, J. A. Raven, I. Leith, W. Stein, A. Crossley & M. Theobald (2005): Early effects of atmospheric ammonia deposition on *Calluna vulgaris* (L.) Hull growing on an ombrotrophic peat bog. – Water, Air, and Soil Pollution: Focus **4**: 229–239.

Cole, L., R. D. Bardgett & P. Ineson (2000): Enchytraeid worms (Oligochaeta) enhance mineralization of carbon in organic upland soils. – European Journal of Soil Science **51**: 185–192.

Cole, L., R. D. Bardgett, P. Ineson & J. K. Adamson (2002): Relationships between enchytraeid worms (Oligochaeta), climate change, and the release of dissolved organic carbon from blanket peat in northern England. – Soil Biology and Biochemistry **34**: 599–607.

Coulson, J. C. & J. Butterfield (1978): An investigation of the biotic factors determining the rates of plant decomposition on blanket bog. – Journal of Ecology **66**: 631–650.

Didden, W. & J. Römbke (2001): Enchytraeids as indicator organisms for chemical stress in terrestrial ecosystems. – Ecotoxicology and Environmental Safety **50**: 25–43.

Galloway, J. N., A. R. Townsend, J. W. Erisman, M. Bekunda, Z. Cai, J. R. Freney, L. A. Martinelli, S. P. Seitzinger & M. A. Sutton (2008): Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. – Science **320**: 889–892.

Laakso, J. & H. Setälä (1999): Sensitivity of primary production to changes in the architecture of belowground food webs. – Oikos **87**: 57–64.

Lamers, L. P. M., R. Bobbink & J. G. M. Roelofs (2000): Natural nitrogen filter fails in polluted raised bogs. – Global Change Biology **6**: 583–586.

Leith, I. D., L. J. Sheppard, D. Fowler, J. N. Cape, M. Jones, A. Crossley, K. J. Hargreaves, Y. S. Tang, M. Theobald & M. A. Sutton (2004): Quantifying dry $NH_3$ deposition to an ombrotrophic bog from an automated $NH_3$ field release system. – Water, Air, and Soil Pollution: Focus **4**: 207–218.

O'Connor, F. B. (1957): An ecological study of the enchytraeid worm population of a coniferous forest soil. – Oikos **8**: 161–199.

Peachey, J. E. (1963): Studies on the Enchytraeidae (Oligochaeta) of moorland soil. – Pedobiologia **2**: 81–95.

Prendergast-Miller, M., L. Cole, V. Standen, R. Rees, J. Parker, I. Leith & L. Sheppard (2008): Are enchytraeid worms (Oligochaeta) sensitive indicators of ammonia-N impacts on an ombrotrophic bog? – European Journal of Soil Biology **44**: 101–108.

Rodwell, J. S. (1991): British plant communities. Volume 2: mires and heaths. – Cambridge University Press, Cambridge, (England); New York: 640 pp.

Sheppard, L. J., A. Crossley, I. D. Leith, K. J. Hargreaves, J. A. Carfrae, N. van Dijk, J. N. Cape, D. Sleep, D. Fowler & J. A. Raven (2004): An automated wet deposition system to compare effects of reduced and oxidised N on ombrotrophic bog species: practical considerations. – Water, Air, and Soil Pollution: Focus **4**: 197–205.

Sheppard, L. J., I. D. Leith, A. Crossley, N. van Dijk, D. Fowler, M. A. Sutton & C. Woods (2008): Stress responses of *Calluna vulgaris* to reduced and oxidised N applied under 'real world conditions'. – Environmental Pollution **154**: 404–413.

Springett, J. A., J. E. Brittain, B. P. Springett (1970): Vertical movement of Enchytraeidae (Oligochaeta) in moorland soils. – Oikos **21**: 16–21.

Standen, V. (1978): The influence of soil fauna on decomposition by micro-organisms in blanket bog litter. – Journal of Animal Ecology **47**: 25–38.

Standen, V. (1982): Associations of Enchytraeidae (Oligochaeta) in experimentally fertilized grasslands. – Journal of Animal Ecology **51**: 501–522.

Thompson, A. (2003): Does nitrogen affect enchytraeids? – Newsletter on Enchytraeidae **8**: 81–88.

van Vliet, P. C. J., M. H. Beare, D. C. Coleman & P. F. Hendrix (2004): Effects of enchytraeids (Annelida: Oligochaeta) on soil carbon and nitrogen dynamics in laboratory incubations. – Applied Soil Ecology **25**: 147–160.

Yesmin, L., E. A. Fitzpatrick & M. S. Cresser (1995): Evidence for atmospheric deposition impacts on the enchytraeid worm population of UK upland ombrotrophic peats. – Chemistry & Ecology **11**: 193–205.

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