

Diagnostic indicators of elevated nitrogen deposition

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Moss tissue N is a good indicator of enhanced N deposition at sites close to point sources of NH₃, but of limited diagnostic value in wet deposition dominated areas.

Abstract

Tissue N content of mosses, which has been shown to be an indicator of enhanced N, was studied at a range of locations dominated either by wet or dry deposited and oxidised and reduced forms of N. Tissue N responded differently to wet and dry deposited N. For a 1 kg ha⁻¹ y⁻¹ increase in N deposition, tissue N increased by 0.01% at wet deposition sites but by 0.03% at sites dominated by dry deposited NH₃. Tissue N at wet deposition sites responded more to concentrations of NO₃⁻ and NH₄⁺ in precipitation (r^2 0.63) than to total N deposition (r^2 0.27), concentration explaining 66% of the variation in tissue N, wet deposition 33%. The study clearly concludes that tissue N concentration in mosses provides a good indication of N deposition at sites where deposition is dominated by NH₃, and is also valuable in identifying vegetation exposed to large concentrations of NH₄⁺ or NO₃⁻, in wet deposition dominated areas, such as hilltops and wind exposed woodland edges.

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1. Introduction

Increased deposition of atmospheric N, largely from intensive agriculture is affecting biodiversity and the composition of natural and semi-natural vegetation in Europe (Bobbink et al., 1993; Falkengren-Grerup, 1986; Pitcairn et al., 1998, 1991; Haines-Young et al., 2000). Critical loads for N as kg N ha⁻¹ y⁻¹ set for a range of ecosystems are currently exceeded in many areas of Western Europe. The accurate description and mapping of the atmospheric deposition of N is important for the determination of current critical loads (Bobbink et al., 2002), essential for the protection of sensitive vegetation.

Atmospheric N deposition includes a wide range of compounds in the gas phase, in aerosols and in precipitation.

The main compounds include nitrogen oxides, nitric oxide, NO, and nitrogen dioxide, NO₂, nitric acid (HNO₃), ammonia (NH₃), particulate nitrate (NO₃⁻), particulate ammonium (NH₄⁺), and nitrate (NO₃⁻), ammonium (NH₄⁺) and organic N in rain. The dry and wet deposition maps for the UK produced from the work of CEH Edinburgh and NETCEN (AEA Technology) rely on a combination of monitoring networks and deposition models. Current methods for production of the maps are described in NEGTAP (2001) and NH₃ deposition modelling is described by Smith et al. (2000).

The spatial resolution of deposition maps is currently 5 km × 5 km, and maps are produced using a combination of land class and land cover data to provide deposition weighted by the proportions of the land uses within the grid square. However, atmospheric nitrogen input to the countryside is very patchy as a consequence of local sources of NH₃ (Sutton et al., 1998), variations in the aerodynamic roughness of vegetation (Fowler et al., 1998) especially the presence of small areas of trees in an otherwise short

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vegetation landscape, and orographic effects, especially on wet deposition (Fowler et al., 1988). As a result, some areas receive very large inputs of N relative to the mean annual deposition, which for the UK averages about 17 kg N ha^{-1} (Fig. 1). The magnitude of the peaks in deposition varies greatly, but values between 50 kg N ha^{-1} and 100 kg N ha^{-1} annually are not uncommon (Pitcairn et al., 1998; Crossley et al., 1992). It would therefore be very useful if indicators of elevated nitrogen deposition could be identified and used to confirm the likely spatial scale of exceedance of the critical load values, which are currently being applied throughout Europe (Hornung et al., 1995).

A wide range of indicators of elevated nitrogen deposition and critical loads exceedance have been described and evaluated (Pitcairn et al., 1998, 2001, 2003; Sutton et al., 2004, 2001). Of these, tissue N content of selected plant species has probably been the most extensively researched indicator of N deposition. Species vary in their growth requirements for N.

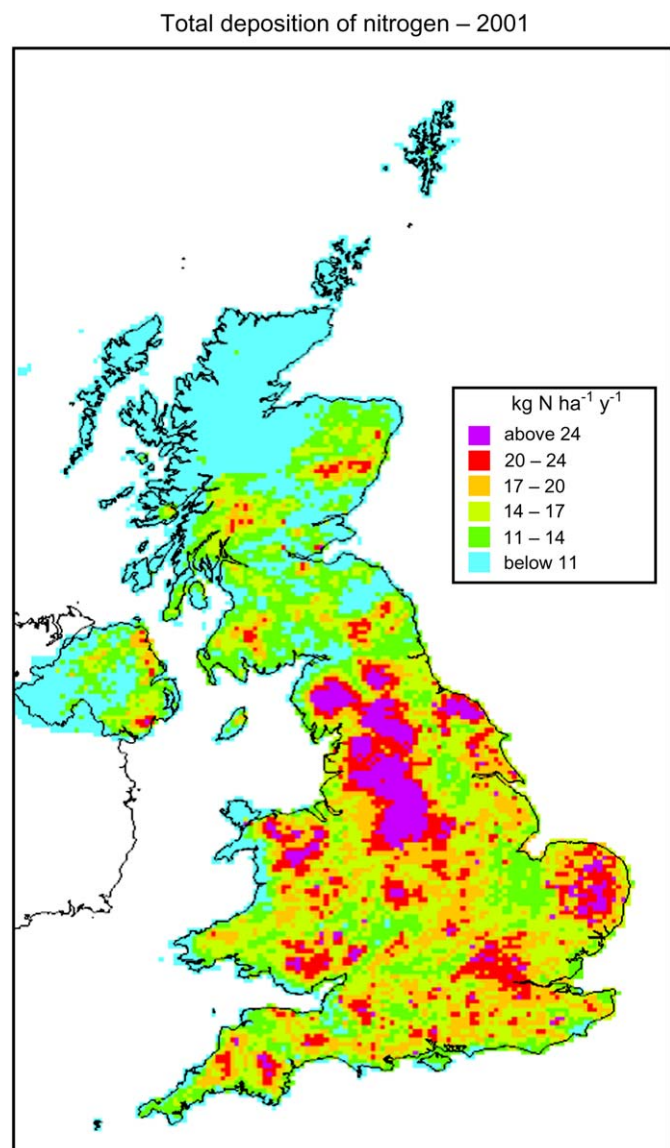


Fig. 1. Total nitrogen deposition ($\text{kg N ha}^{-1} \text{ y}^{-1}$) in the UK for 2000–2002.

While annual crops require large amounts of added N to maximise production, many native plant species require very much less. Increased inputs of atmospheric N can lead to loss of biodiversity when slow growing species with low N requirements are out competed by more vigorous species able to respond to increased N inputs. Lower plants species, particularly bryophytes and lichens, which obtain N largely from rainfall and other atmospheric inputs, are most at risk from enhanced N deposition. Early studies with *Sphagnum* species showed that tissue N and nitrate reductase concentrations were closely linked to atmospheric N inputs (Woodin et al., 1985; Press et al., 1986; Woodin and Lee, 1987). Early field studies (Pitcairn et al., 1995; Baddeley et al., 1994) on a regional scale showed that tissue N content of selected species was related to atmospheric nitrogen deposition. Tissue N concentrations of mosses and *Calluna vulgaris* collected from the North West of Scotland where N deposition was low ($6 \text{ kg N ha}^{-1} \text{ y}^{-1}$), were smaller than those of mosses collected from Cumbria, North West England, where N deposition was much larger (Pitcairn et al., 1995). Similarly, Baddeley et al. (1994) found that altitude enhanced N deposition to upland areas was reflected in tissue N concentrations of *Racomitrium lanuginosum*. Atmospheric N deposition increases with altitude due to increased precipitation with altitude, frequent cover by orographic cloud (containing 3–5 times the NO_3^- and NH_4^+ concentrations present in rain) and orographically enhanced deposition according to the “seeder-feeder effect” (Fowler et al., 1988). Altitude enhanced tissue N concentrations were also demonstrated for *Calluna vulgaris* by Pitcairn et al. (1995) and for *Nardus stricta*, *Deschampsia flexuosa*, *Calluna vulgaris*, *Erica cinerea*, and *Hylocomium splendens* by Hicks et al. (2000) along transects of increasing altitude in North-West Scotland.

Recent work has shown tissue N content of bryophytes, herbs and trees to be a particularly useful indicator of livestock farm emissions of NH_3 and their effects (Pitcairn et al., 1998, 2001, 2003). Data from these livestock studies and the earlier regional study were used to derive a model relating moss tissue N with atmospheric N deposition (Pitcairn et al., 1998). The resulting curve showed that the relationship was not linear and that foliar N increased rapidly with increasing inputs of atmospheric N up to 20 kg y^{-1} . At larger inputs the foliar N increases became progressively smaller, suggesting that physiological saturation may have occurred, including for example the potential for a larger compensation point in vegetation exposed to large NH_3 concentrations.

In the earlier regional study (focussed mainly on upland areas dominated by wet deposition in the west of the UK) the maximum tissue N concentration was 1.6%, despite relatively large inputs of N, whereas in the gradient studies around livestock farms, dominated by dry deposition, tissue N values of up to 4% were measured. There is therefore a need to further examine the relationship between tissue N and N deposition in a range of sites to explore the effects of different forms of deposition. In areas of wet deposition, the usefulness of tissue N, to indicate enhanced N deposition in areas where there is large variability in wet deposition of N can be fully explored.

The objective of the study described in this paper is to evaluate the diagnostic value of tissue N as an indicator of enhanced N deposition, by investigating the underlying reasons for the differences in moss tissue N concentrations observed between wet and dry deposition dominated sites. Moss tissue N was measured in a number of transects in wet upland areas where wet deposition of N dominates (6 transects), and lowland areas dominated by dry deposition of NH_3 from intensive livestock farms (2 transects in East Anglia and 3 transects from Eastern Scotland). Differences in moss tissue N content between the wet and dry deposition sites are discussed, and possible reasons for the differences are reviewed.

2. Methods

2.1. Field sampling

Samples of ectohydric mosses were collected at 6 sites in high wet deposition areas (2000–2002) and 6 sites in areas with large dry deposition of nitrogen, including areas adjacent to intensive livestock farms (1995–2001). Where possible, samples were collected along a gradient of N deposition (along an altitudinal gradient at wet deposition sites; along a gradient from a possible NH_3 source at dry deposition sites). The sites were chosen to represent a range of pollution climates in the UK, from Slioch in North West Scotland, a relatively unpolluted site, to Thetford in East Anglia, an area of large NH_3 concentrations. At least 2 species of moss were collected at each site, chosen on the basis of distribution, and availability of tissue N data from previous studies.

Three composite samples of each species were collected from each location (Table 1). The upper 3–5 cm of shoot tissue were selected, washed briefly in deionised water, dried at 70 °C and ground. Ground samples were analysed for total N by combustion (CNS Analyser, Elementar Model: Vario EL; Burkard Scientific Ltd, Uxbridge, UK). Mean tissue N contents (\pm standard deviation) were obtained for each species. Where results for each species were close, tissue N results for each site are expressed as % tissue N per g dry weight of ectohydric moss. Where there was large, interspecific variation, results are given for each species sampled.

2.2. N deposition estimates

Estimates of N wet deposition were obtained from the 5 × 5 km UK maps of nitrate and ammonium deposition and from field measurements. Estimates of dry deposited N were obtained by applying a deposition velocity to measured NH_3 concentrations (obtained from the UK Ammonia National

Table 1
Sampling transects

Site	Region	Grid Reference
<i>Wet deposition areas</i>		
Slioch	Ross and Cromarty, N W Scotland	NG00 68
Cairnwell	Glen Shee, Perthshire	NO13 77
Dunslair Heights	Scottish Borders	NT28 43
Great Dun Fell	Cumbria	NY71 33
Snowdonia	N Wales	SH
Plynlimon	Mid Wales	SN79 87
<i>Dry deposition sites</i>		
Sites in NH_3 National Monitoring Network	East Anglia	Various
Thetford sites	East Anglia	TL92 89
Earlston Poultry Farm	Scottish Borders	NT58413
Livingston Poultry Farm	Central Scotland	NS087704
Fettercairn Pig Farm	N E Scotland	NO67 76

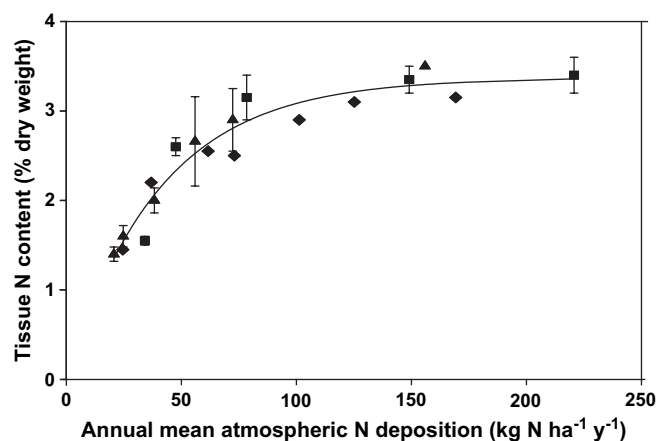


Fig. 2. Relationship between moss tissue N (% dry weight) and atmospheric N deposition downwind of 3 intensive livestock farms.

Monitoring Network and experimental sites). Flux measurement studies at Auchencorth Moss (Flechard and Fowler, 1998) showed that canopy resistance to deposition is affected by NH_3 concentration. The canopy resistances for the moorland vegetation obtained at Auchencorth moss were originally assumed appropriate for woodland vegetation studies in the vicinity of livestock farms (Pitcairn et al., 1998, 2002), although concentrations measured close to livestock farms were much larger than ambient concentrations measured at Auchencorth Moss. Recent studies (Leith et al., 2004) using a NH_3 flux chamber system allowed the relationships between NH_3 concentrations and canopy resistances to be quantified for a range of NH_3 concentrations for moorland vegetation. These studies provided more appropriate deposition velocities for the concentrations measured around livestock farms. Although the dry deposition sites described in this paper are woodland rather than moorland sites, the Leith et al. (2004) relationship has been used for estimating NH_3 deposition at the East Anglian sites and the livestock sites.

3. Results

3.1. Dry deposition sites

3.1.1. Intensive livestock sites

The impact of NH_3 emissions from intensive livestock farms, on species composition and tissue N content of a range of vegetation types was investigated at 3 sites in the late 1990s. A brief summary of the sites is given in Table 2. For further details see (Pitcairn et al., 1998, 2001, 2003). Concentrations of NH_3 close to the livestock buildings were very large (annual mean 24–59 $\mu\text{g m}^{-3}$) and declined with distance to reach upwind background values (1.6–5 $\mu\text{g m}^{-3}$) in 1 km. The N deposition values were calculated using the relationship between canopy resistance (r_c) and ambient NH_3 concentration from Leith et al. (2004). Foliar N concentrations of sampled mosses (*Brachythecium rutabulum*, *Eurynchium praelongum*, *Hylocomium splendens*, *Rhytidiadelphus squarrosus*, *Rhytidiadelphus triquetrus*) were also large ($\sim 4\%$ N) close to the livestock farms and declined with distance ($<1.4\%$ N). A very close relationship was found (Pitcairn et al., 1998) between ammonia concentrations or atmospheric N deposition and tissue N content of ectohydric mosses at each farm (Fig. 2) and the livestock farm studies show conclusively that total tissue N content of mosses is an excellent

Table 2
Livestock Sites Descriptions, (taken from Pitcairn et al., 1998)

Farm	Livestock	Estimated emission	Landscape	Vegetation
Earlston Poultry Farm	120,000 broilers (farmed on a 44 day cycle)	4800 kg N y ⁻¹	Mixed agriculture	30 year old <i>Pinus sylvestris</i> plantation with some <i>Betula pubescens</i> and a ground flora of fern, herbs and mosses
Livingston Poultry Farm	210,000 broilers (farmed on a 44 day cycle)	14,000 kg N y ⁻¹	Mixed agriculture	Coniferous shelter belt, mixed deciduous and birch woodland. Ground flora of ferns, grasses, <i>Rubus</i> spp.
Fettercairn Pig Farm	2000 animals including 200 breeding sows	4200 kg N y ⁻¹	Mixed agriculture	Mature deciduous woodland. Ground flora dominated by <i>Luzula sylvatica</i> and <i>Petastites hybridus</i>

indicator of N deposition where deposition is dominated by dry deposition and where a gradient of N deposition exists.

3.2. East Anglian sites

Further studies took place in East Anglia, UK, an area dominated by dry deposited N and where background NH₃ concentrations are large (>3 µg m⁻³). Sites were selected from the National UK Ammonia Monitoring Network and from a large-scale ammonia project operating in the Thetford area of East Anglia. Species sampled included *Pseudoscleropodium purum*, *Rhytidiadelphus squarrosus*, *Brachythecium rutabulum* and *Eurynchium praelongum*.

3.3. Sites from the National UK Ammonia Monitoring Network

The network sites were carefully chosen to provide background concentrations (Sutton et al., 1998) and therefore are not situated close to any known NH₃ sources. Results do not show a clear relationship between moss tissue N concentrations and atmospheric N deposition and values tend to be smaller (0.8–1.6% N) than those reported for livestock sites.

3.3.1. Thetford sites

An intensive ammonia study in Thetford (part of the GANE Research Programme, Theobald et al., 2004) provided a network of NH₃ monitoring masts within the Thetford area of East Anglia, which encompasses several large NH₃ sources. N deposition estimates ranged from 16.6 to 95 kg N ha⁻¹ y⁻¹. However, moss tissue N concentrations (0.8–2.3% N) were again not as large as might be expected at the high N deposition sites, especially when compared with the livestock sites in Scotland. The largest tissue N values were found in mosses collected beneath forest canopies. At these sites NH₃ deposition to tree canopies and the resulting throughfall is likely to enhance N deposition to the woodland floor above that estimated from NH₃ concentrations measured 1.5 m above ground.

Data from all East Anglian sites sampled are plotted in Fig. 3, which shows weak evidence of a trend between N deposition and moss tissue N. Despite dry deposition estimates of up to 95 kg N ha⁻¹ y⁻¹, maximum tissue N concentrations were only 2.3%, whereas similar deposition estimates close to intensive livestock farms resulted in much larger tissue N

values. Although surprising, similar discrepancies have been observed elsewhere. In the Netherlands, for example, despite the large deposition of N recorded, foliar N concentrations in *Calluna vulgaris* from Dutch heathlands are not always large. These differences may reflect local variability in NH₃ emissions and concentrations that is characteristic of agricultural areas in the Netherlands (Sutton et al., 2004). Many small and large sources of ammonia in East Anglia contribute to a large background concentration of atmospheric N which could raise the amount of NH_x in the plant tissues, thereby increasing the NH₃ 'compensation point', which would provide a feedback tending to limit net nitrogen deposition (Sutton et al., 1993, 1995; Sutton and Fowler, 1995). This feedback and the low rainfall in East Anglia, may have contributed to the very variable tissue N values at these sites. It is clear that even in regions with very large NH₃ emissions, tissue N concentrations are not significantly enhanced generally. The data show large values only very close to large sources or in woodland.

3.4. Wet deposition sites

Four major transects were surveyed: Slioch in North West Scotland, Dunslair Heights in South East Scotland; Great

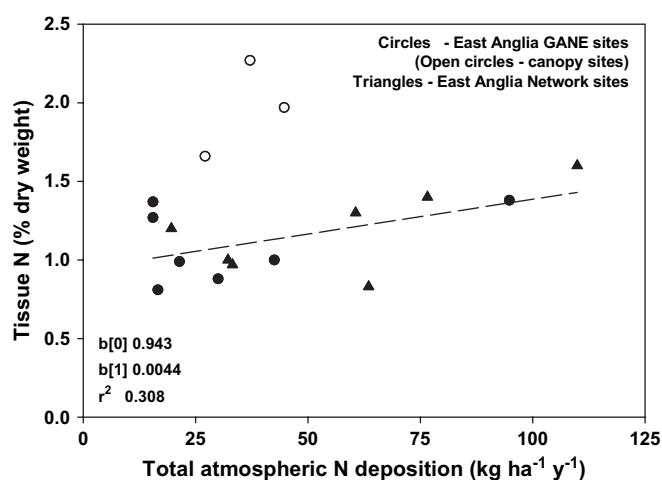


Fig. 3. Relationship between tissue N of selected mosses and atmospheric N deposition (kg N ha⁻¹ y⁻¹) at sites in East Anglia, UK, in May 2000 and 2001. Open circles denote GANE collection sites under forest canopies. These have been included in the figure for information, but were excluded from the regression analysis.

Dun Fell in Cumbria, England and Snowdonia in Wales. Two smaller surveys took place in Glen Shee in East Central Scotland, and Plinlimon in West Wales.

3.4.1. Slioch transect, Wester Ross

Slioch is a 980 m mountain in the North West highlands of Scotland, 26 km east and 13 km south east of the Wester Ross coast. Deposition of N ranged from 22 kg N ha⁻¹ y⁻¹ at the summit to 6 kg N ha⁻¹ y⁻¹ at sea level. Tissue N content of *Sphagnum capillifolium* (0.8% N) collected at 800 m was significantly larger (at 5% level) than that collected at 100 m (0.63% N) with half the annual mean N deposition. For *Racomitrium lanuginosum*, no significant differences in tissue N were found between sites although concentrations tended to be larger above 500 m (0.55% N) than at 100 m (0.45% N).

3.4.2. Dunslair heights transect, South East Scotland

Atmospheric deposition has been intensively monitored at Dunslair Heights near Peebles in South East Scotland. This transect has been afforested in areas, allowing a comparison between N deposition effects in open largely heather moorland and on the edge of conifer plantation. N deposition ranged from 17.6 kg N ha⁻¹ y⁻¹ at the valley floor to 24.6 kg N ha⁻¹ y⁻¹ on the open summit (600 m asl), and 30.7 kg N ha⁻¹ y⁻¹ on the afforested summit (600 m asl). Tissue N content in the 2 species sampled (*Pleurozium schreberi* and *Rhytidiadelphus squarrosus*) did not show an increase with altitude enhanced deposition but was increased significantly (at 1% level) by canopy enhanced deposition in the 'under trees' samples.

3.4.3. Great Dun Fell/Cumbria transect

This transect ran from Corney Fell on the Cumbrian coast to Great Dun Fell (GDF) in the Pennines and eastward to Moorhouse National Nature Reserve. All the sites along the transect were open. Species sampled included *Sphagnum capillifolium*, *S. papillosum*, *Pleurozium schreberi*, *Hylocomium splendens*, *Rhytidiadelphus squarrosus* and *Brachythecium albicans*.

Atmospheric deposition has been extensively studied at GDF for many years and excellent estimates of N deposition were available (Choularton et al., 1988; Fowler et al., 1988). Total atmospheric N deposition ranged from 18 kg N ha⁻¹ y⁻¹ at the coast, to 40 kg N ha⁻¹ y⁻¹ on GDF summit. Despite this large deposition range, tissue N values tended to be fairly uniform (1.0–1.2%) with a small increase in the samples from GDF summit where N deposition was largest.

3.4.4. Snowdonia transect, North Wales

This transect (which combined both wet and dry deposition dominated sites) included Llyn Llydaw (430 m asl) on Snowdon, with a high wet N deposition, 2 sites close to a poultry farm with large NH₃ dry deposition and 2 coastal sites, including one where the contribution of NH₃ from grazing to deposition may be poorly estimated. Species sampled included *Sphagnum capillifolium*, *S. papillosum*, *Pleurozium schreberi*, *Rhytidiadelphus squarrosus* and *Racomitrium lanuginosum* at Llyn Llydaw; *Brachythecium rutabulum* near the poultry

farm and *Pleurozium schreberi*, *Pseudoscleropodium purum* and *Hylocomium splendens* at Newborough Warren and Llyn peninsula.

As expected, tissue N content of samples collected close to the poultry farm, was very large (3.1% N). At Llyn Llydaw, where N deposition was estimated to be 44 kg N ha⁻¹ y⁻¹, tissue N content was modest (0.95% N) and only 15% larger than that measured in the Llyn coastal samples (0.80% N) where estimated N deposition was 63% smaller.

3.4.5. Cairnwell transect, Glen Shee

Sampling took place at 3 altitudes on Cairnwell, a 915 m mountain in Glen Shee in the East Central Scottish Highlands, where good N deposition estimates have been obtained. Different species were sampled at each height, *Racomitrium lanuginosum* at 900 m, *Pleurozium schreberi* at 750 m and *Sphagnum capillifolium* at 600 m. Concentrations of tissue N were largest (1.23%) at the 750 m site, and smallest (0.81%) in *R. lanuginosum* collected from the highest N deposition site. *R. lanuginosum* tends to contain smaller concentrations of tissue N than other species, and while 0.81% is small relative to other values at Glen Shee, it is a fairly large concentration for *R. lanuginosum* relative to other sites (cf Slioch, Table 12).

3.4.6. Plinlimon transect, Mid Wales

This transect in Mid Wales ran from the west coast to Plinlimon summit (650 m asl) and beyond. The area encompassed a range of woodlands, rough grassland and moorland. Samples were collected from open ground at each altitude. A large range of species (*Hypnum jutlandicum*, *Hylocomium splendens*, *Sphagnum papillosum*, *Sphagnum capillifolium*, *Pleurozium schreberi* and *Rhytidiadelphus loreus*) was collected due to the wide ecological range, thus making comparisons difficult. No trend in tissue N concentrations in relation to altitude enhanced N deposition was observed.

The data from the 6 wet deposition transects are plotted in Fig. 4. The slope of the line indicates a fairly small range of tissue N content (0.6–1.6% N) for a wide range of atmospheric N deposition (7–44 kg N ha⁻¹ y⁻¹). However there is a reasonable relationship between tissue N and N deposition with a linear regression of r^2 0.243. When the deposition data for total N are split into reduced and oxidised (Fig. 4b,c), it is clear that while tissue N responds to both forms, the relationship is stronger for reduced N (r^2 0.266) compared with oxidised N (r^2 0.131).

4. Discussion

In the following discussion, the focus is on the different responses of tissue N to the chemical climate and form of deposited N.

4.1. Wet versus dry deposition

Results have shown that tissue N concentrations are smaller at wet deposition sites than at dry deposition sites with the same estimated annual N deposition. In Fig. 5, data from 6

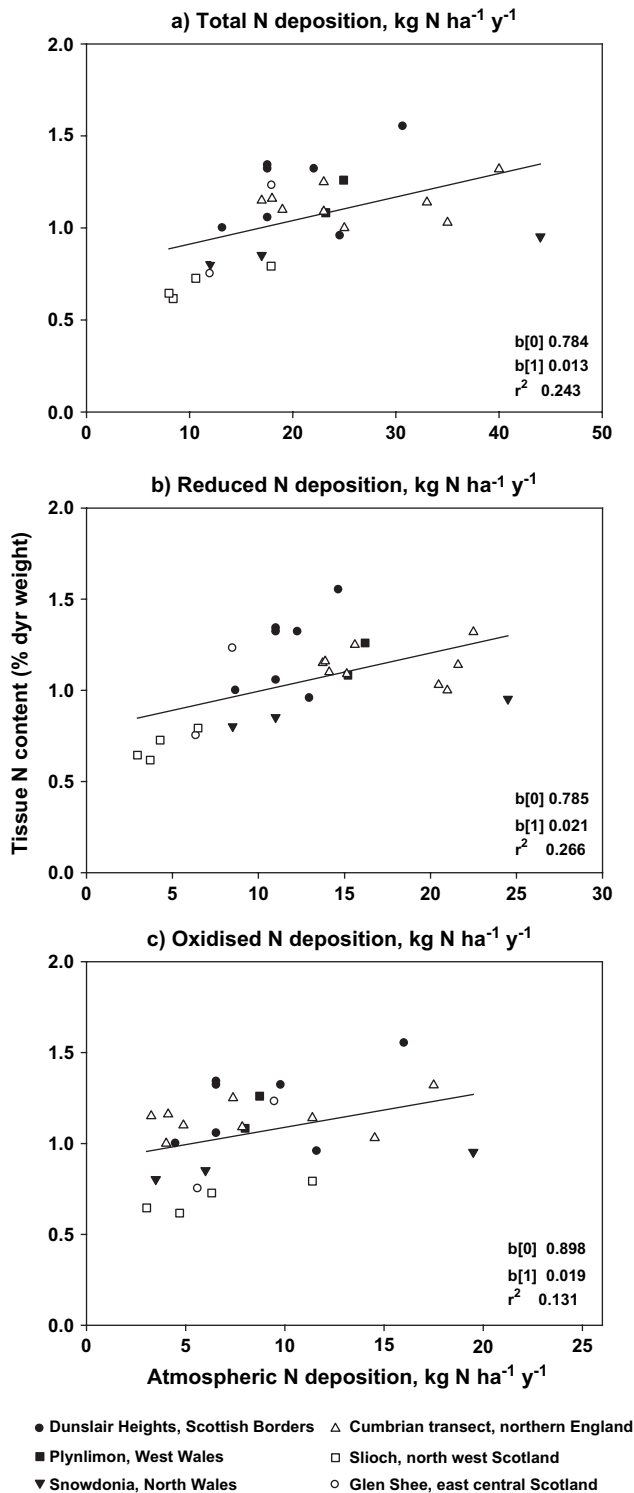


Fig. 4. Relationship between moss tissue N (% dry weight) and a) total N deposition, b) reduced N deposition and c) oxidised N deposition (kg N ha⁻¹ y⁻¹), at 6 wet deposition dominated transects in the UK.

wet deposition sites and from an early regional study (Pitcairn et al., 1995) have been added to the datasets from livestock sites and the East Anglian ‘high background’ sites. The results show that tissue N responds more to changes in deposited N along a gradient of dry deposited NH₃, than to changes in wet deposited NH₄⁺ + NO₃⁻ along altitudinal gradients. In areas

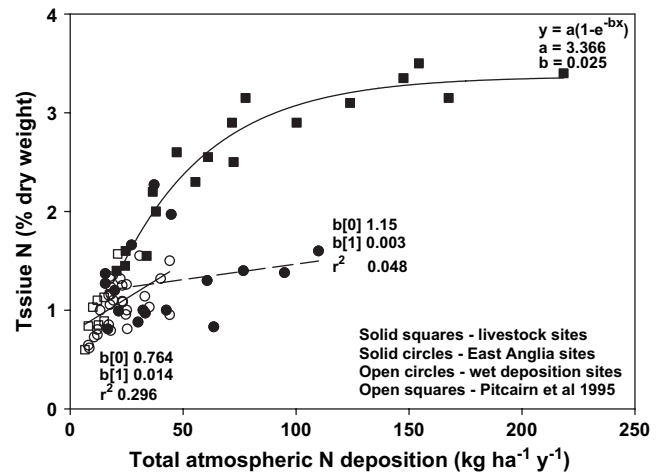


Fig. 5. Relationship between moss tissue N (% dry weight) and atmospheric N deposition (kg N ha⁻¹ y⁻¹) at all sites/transects sampled.

with large background NH₃ concentrations (>3 μg m⁻³), the response is less clear. Results confirm that larger concentrations of N (up to 4% N) occur in the tissues at sites where N deposition is dominated by dry deposited ammonia and where rainfall (and therefore leaching losses) is small, compared with sites where deposition is dominated by wet deposition (up to 1.6%N).

In Table 3, the increase in % tissue N for an increase of 1 kg N ha⁻¹ y⁻¹ above ‘background’ has been calculated for each site. For wet deposition sites, background was taken as the lowest altitude site where wet deposition has not been elevated orographically. For dry deposition sites, where deposition is estimated along a gradient, background deposition was taken as the upwind site or site furthest from the source and maximum elevation in tissue N was taken as the highest point on the curve before tissue N levels off. For the East Anglian sites, ‘background’ was taken as the site with the smallest estimated deposition although a mean value for sites remote from obvious

Table 3
% moss tissue N kg N⁻¹

Site	Region	% tissue N kg N ⁻¹
<i>Wet deposition sites</i>		
Slioch	N W Scotland	0.013
Cairnwell	East Central Scotland	0.005
Dunslair Heights (under canopy)	Scottish Borders	0.018
Great Dun Fell	Cumbria	0.011
Snowdonia	N Wales	0.013
Plynlimon	Mid Wales	—
Mean		0.012
<i>Dry deposition sites</i>		
<i>East Anglian Sites</i>		
Thetford sites	East Anglia	—
NH ₃ National Monitoring Network	East Anglia	0.008
<i>Intensive livestock sites</i>		
Earlston Poultry farm	Scottish Borders	0.027
Livingston Poultry Farm	Central Scotland	0.037
Fettercairn Pig Farm	N E Scotland	0.022
Mean		0.027

sources may be more appropriate. The table shows that for a $1 \text{ kg ha}^{-1} \text{ y}^{-1}$ increase in N deposition, tissue N increases by around 0.012% in wet deposition sites and 0.027% for dry deposition livestock sites. For the East Anglia sites, little or no obvious increase in tissue N can be observed above ‘background’ for an increase in N deposition. Many small and large sources of ammonia in East Anglia contribute to a large background concentration of atmospheric N. However, as emitted NH_3 is present in the gas phase for a very short time (<2–3 h) and is rapidly deposited to the surface, the exposure of vegetation to reduced N varies strongly with distance from sources. In general, highly elevated NH_3 concentrations are restricted to a zone <1 km from sources. At greater distances, the high ‘background’ consists of NH_4^+ in aerosol form, which is deposited only slowly onto short vegetation ($\text{vg} < 2\text{--}4 \text{ mm s}^{-1}$) but at much larger rates onto tall vegetation (woodland, hedgerows). Rates of aerosol deposition onto woodland are typically $10\text{--}20 \text{ mm s}^{-1}$ (Fowler et al., 2004). Thus the cause of the small tissue N values in East Anglia is simply that the tissue N response is to gas phase NH_3 concentrations, which, except very close to sources, are modest.

The observed differences in response at wet and dry deposition sites are supported by published results from open-top chamber experiments where ombrotrophic mire species were exposed to either a range of NH_3 concentrations or to NH_4^+ (applied as NH_4Cl solutions). Tissue N concentrations in *Calluna vulgaris*, and *Polytrichum commune* showed a significant response to increasing N additions and also to the form of N applied (Leith et al., 2002). Both species exhibited greater N uptake when N was supplied as NH_3 rather than as NH_4^+ on a per unit N basis. This is consistent with the findings of van der Eerden et al. (1990), who suggest that NH_3 taken up through the foliage is assimilated more quickly than NH_4^+ or NO_3^- absorbed via the cuticle or roots. However the pattern of exposure in open-top chamber experiments must also be taken into account, NH_3 being supplied continuously and NH_4^+ added 3 times per week for typically 1 h in each application.

The observed differences between tissue N concentration in wet and dry deposition dominated areas may partly be due to the washing of surface material through the plant canopy to the soil, during heavy rain in the wet areas. Whereas for dry deposition, a much longer contact time with the atmospheric N compounds is available for uptake and assimilation. The differences may also be influenced by concentration of N compounds on moss surfaces such that accumulation from wet deposition only occurs above a threshold concentration.

4.2. Tissue N response to concentration in high rainfall areas

In examining the impacts of N in rainfall on plants, it is clearly difficult to separate the effects of concentration from that of deposition. It is possible that at the ‘Wet Deposition’ study sites, tissue N responds more closely to rainfall concentrations of N ($\text{NO}_3^- + \text{NH}_4^+$) than to N deposition, and hence concentrations of nitrate and ammonium in rainfall in 2000

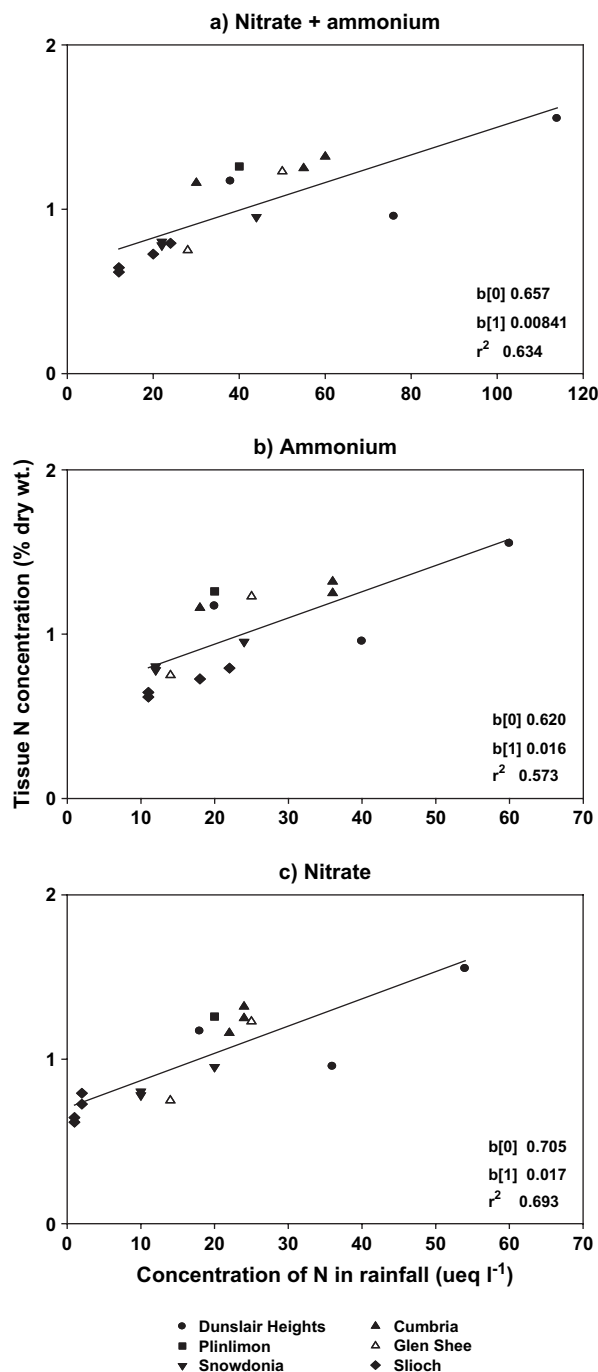


Fig. 6. Relationship between moss tissue N (% dry weight) and a) nitrate plus ammonium concentrations b) ammonium concentrations and c) nitrate concentrations ($\mu\text{eq l}^{-1}$) at 6 wet deposition dominated transects in the UK.

were obtained for most of the collection sites in the six transects. In Fig. 6a–c, tissue N from the 6 wet deposition transects is shown to be significantly related to concentrations of N ($\text{NO}_3^- + \text{NH}_4^+$) in rainfall ($r^2 0.63$). Little difference in tissue N response was observed between nitrate and ammonium concentrations in rainfall, although Paulissen et al. (2004) working with Dutch fen mosses found that the form of added N affected tissue nutrient concentrations including N.

From these field results, tissue N appears to be more closely linked to rainfall NO_3^- and NH_4^+ concentrations ($r^2 0.63$) than

to N deposition (r^2 0.27) although both undoubtedly affect N uptake. Concentration explains two thirds of the variation in foliar N while wet deposition explains less than one third. The importance of concentration in determining rates of N accumulation may also explain why different concentrations of tissue N were measured in mosses from sites where N deposition was similar. For example, *Racomitrium lanuginosum* tissue N concentrations in samples from Slioch summit were 60% smaller than those measured in samples from Cairwell summit in Glen Shee. While N deposition was only 14% smaller at Slioch, rainfall concentration of N was less than half that at Cairwell. Such an interpretation is consistent with the measurement of the largest tissue N values at sites frequently exposed to orographic cloud, which contains larger concentrations of NO_3^- and NH_4^+ concentrations than precipitation.

Further corroboratory evidence of the influence of both concentration and deposition of N in wet deposition, was provided in recent transplant experiments by Mitchell et al. (2004, 2005). They monitored N deposition to epiphytic moss communities in Atlantic woodlands in northern Britain for 12 months and measured tissue N in a range of moss species. The sites differed in the concentrations of ammonium and nitrate in stemflow and in stemflow flux of N. In Atlantic woodland sites in North-West Scotland, N concentrations in stemflow ranged from 6–9 μM and tissue N concentration tended to be around 1%. In contrast, in the more southern Atlantic woodland sites (southern Scotland and North West England) N concentrations ranged from 10–31 μM in stemflow, and tissue N concentrations of 1.24–1.92% were measured. While the stemflow concentrations of N in the Atlantic woodland study compare well with those measured in rainfall at sites in comparable locations in the study described here, the tissue N values tend to be larger. This is most likely due to a combination of the sampling of 'woodland' moss species, able to accumulate larger amounts of N than upland species, and exposure to concentrations of N on a more continuous basis in stemflow.

The current study thus underlines the importance of concentration of both gaseous NH_3 and $\text{NH}_4^+ + \text{NO}_3^-$ in rainfall in respect to N accumulation in mosses. At wet deposition sites, exposure to N deposition is episodic and concentrations in rainfall and cloud vary greatly with time. As there are roughly 200 rain day y^{-1} in the UK and precipitation falls at an area rate of 1 mm h^{-1} , with 1000 mm y^{-1} precipitation, surfaces are wet with precipitation only about 10% of the time. Pilot experimental studies suggest that tissue N accumulation does not occur at low concentrations of added N but only at concentrations commonly experienced in peak concentration events in rainfall.

If plants accumulation N only from the large concentration events (e.g. for argument, half of the distribution) the period of accumulation is restricted to 5% of the time. Hence, most of the time, mosses are exposed to small concentrations of N in rainfall, which are unlikely to lead to large tissue N concentrations even if the amounts of precipitation are large. Tissue N levels are consequently unlikely to reach high concentrations

in the field unless rainfall consistently contains large concentrations of N (as occurs in experimental conditions).

By comparison, at intensive livestock sites, bryophytes are exposed to fairly regular, large concentrations of NH_3 , resulting in the accumulation of large concentrations of N in the tissues. Breaks in the poultry cycles do not appear to affect tissue N close to the livestock buildings, as N is recycled from stores in the lower parts of the moss to the active growing tips (which are sampled) and there is no heavy rain to leach the NH_4^+ and organic N from foliage. At greater distances from the buildings, where tissue N is scarcely above background level, much of the N is used for growth and periods of low NH_3 concentrations do result in reduced tissue N.

Tissue N content of moss at sites in which N is mainly wet deposited, thus appears to be more closely related to concentration of nitrate and ammonium in rainfall than to total N deposition. Although the relationship is significant, it should be noted that several additional factors, including grazing pressure, site characteristics, interspecific variation and seasonal differences (Pitcairn et al., 2004) and growth rates and plant adaptation to climate and soil (Friend and Woodward, 1990) may influence foliar N concentrations.

5. Conclusions

- The livestock farm studies show that total tissue N content of mosses is an excellent indicator of N deposition where deposition is dominated by dry deposition of NH_3 . Tissue N increases by 0.027% per $\text{kg ha}^{-1} \text{y}^{-1}$ of deposited N in these areas.
- Responses of total tissue N to wet deposition are also observed but these show a weaker dependence on N deposition than at dry deposition dominated sites. In general, tissue N increases at 0.01% $\text{kg N ha}^{-1} \text{y}^{-1}$ for wet deposition dominated sites.
- Tissue N at wet deposition sites responds more to rainfall NO_3^- and NH_4^+ concentrations (r^2 0.63) than to N deposition (r^2 0.27).
- Spatial variability in tissue N in upland areas is related to cloud cover and concentrations of NO_3^- and NH_4^+ not to N deposition.
- In field conditions in the wetter areas of the UK, mosses are exposed to small concentrations of N in rainfall most of the time, with occasional peaks in concentration on hill-tops. Moss may accumulate N largely from the peak concentration events, rather than from all events in the distribution. This strategy would be unlikely to lead to large tissue N concentrations at wet deposition sites and may be the most likely reason for smaller responses to wet than to dry deposition.
- These results show that tissue N is a good indicator of enhanced N deposition at sites close to point source of NH_3 dominated by dry deposition, but of limited diagnostic value in wet deposition dominated sites.
- In wet deposition dominated sites, the indicator identifies areas subject to large concentrations of NO_3^- and NH_4^+ rather than large deposition of N.

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