Biogeochemistry **45:** 285–302, 1999.

Seasonal dynamics of N in two *Sphagnum* moss species and the underlying peat treated with $^{15}NH_4{}^{15}NO_3$

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Accepted 18 September 1998

Key words: ammonium, dissolved organic N, ^{15}N, peat, *Sphagnum* moss

Abstract. Uptake of ^{15}N labelled NH_4NO_3 by two *Sphagnum* mosses on a raised bog in north east Scotland was measured at different times of the year. In a field experiment, fortnightly additions of NH_4NO_3 at natural abundance, equivalent to 3 g N m^{-2} yr^{-1}, were made over 14 months to cores of *Sphagnum capillifolium* occupying hummocks and *S. recurvum* colonizing hollows. Pre-harvested cores were treated with $^{15}NH_4{}^{15}NO_3$ two weeks before harvesting and ^{15}N abundance determined for the total N in the moss, inorganic and dissolved organic N (DON) in the moss water and extractable inorganic, organic and microbial N in the underlying peat. The proportion of added ^{15}N taken up by the mosses two weeks after each addition averaged 72% and ranged between 11 and 100%, tending to be least during October when the rising water table reached the surface, particularly for *S. recurvum*. A small proportion of the ^{15}N was detected in the moss water as $NH_4{}^+$ (0.01%) and as DON (0.03%) and on occasions a large proportion remained unaccounted for. In waters from *S. capillifolium*, DON was proportional to the amount of inorganic N added, but this was not the case for *S. recurvum*. Little or no ^{15}N was detected in the underlying peat partly because of the large size and variability of the $NH_4{}^+$, DON and microbial N pools.

Introduction

Raised bogs are generally considered to be nutrient poor environments supporting vegetation that has adapted to the acid conditions and the supply of nitrogen (N) and other nutrients from precipitation (van Breemen 1995). The trend for increasing N deposition from the atmosphere has important implications for peatland ecosystems (INDITE 1995). Williams et al. (1998) compared the growth and response of *Sphagnum magellanicum* to added N at five sites across Europe and reported that water-table depth was an important factor influencing growth of *Sphagnum magellanicum* and, indirectly, the response to added N. Aerts et al. (1992) suggested that the capacity of *Sphagnum* mosses to assimilate N was influenced by the phosphorus (P) nutrition of the site. Nitrogen assimilation without concomitant growth leads to moss

tissues with decreased C:N ratios which will enhance their decomposition at senesence (Aerts et al. 1992). The greater turnover of C and nutrients in the surface peat horizons which could result would increase nutrient availability. In this case, indigenous vegetation adapted to low N inputs would be unable to compete with those utilizing greater amounts of N (Baxter et al. 1992), which could eventually lead to reduced rates of peat accumulation.

Atmospheric deposition is the main source of inorganic N reaching raised bogs, but there is little information about the sizes and activities of different N pools in peatland ecosystems and their fluctuations in relation to the magnitude of the incoming N. The capture of N in deposition by the moss vegetation can be extremely variable between sites (Williams et al. 1998) and information about the penetration of inorganic N into the underlying peat is scarce. Peat bogs in general have been regarded as sinks for inorganic N though the accumulation of N in different bogs over long periods of time has shown variations in the degree of immobilization of N which has been attributed to the availability of other nutrients such as P (Damman 1988).

Williams and Silcock (1997) applied NH_4NO_3 to *S. magellanicum* at different rates between 1 and 10 g N m^{-2} yr^{-1}, but detection of the retained N in the moss and peat was difficult at lower rates of application because of the variability in plant biomass. The same experiment, repeated at other European sites showed that there was a strong relationship between moss growth and the depth of the water table which appeared to influence N concentration in the moss (Williams et al. 1998). In this paper, we describe an experiment in which ^{15}N labelled NH_4NO_3 has been added to peat cores, *in situ*, supporting two *Sphagnum* moss species in contrasting habitats, in pools and hummocks, on a raised bog in northeast Scotland. The experiment was designed to test the hypothesis that atmospheric N deposition that enters the moss vegetation also influences N dynamics in the underlying peat and that the effects vary with time of year and are influenced by water table depth.

Materials and methods

Experimental site

The site used for this study is a raised bog, the Moidach More (National Grid Reference NJ 030420) in the north-east of Scotland, at an altitude of 275 m above sea level. The mean annual rainfall is approximately 800 mm and the mean annual temperature 8 °C. The average depth of the peat is 2.1 m, and peat more than 0.5 m thick extends to 760 ha. The vegetation comprises *Sphagnum* species, *Erica tetralix* L. and *Trichophorum cespitosum* (L.) Hartm.. *Calluna vulgaris* (L.) Hull occupy areas where there has been

disturbance from peat cutting or burning. The experiment was carried out on carpets of *Sphagnum capillifolium* (Ehrh.) Hedw. and *S. recurvum* (P. Beauv.) where relatively undecomposed moss extended to 20 cm depth.

Field experiment

S. capillifolium and *S. recurvum* were chosen for the experiment because they colonised contrasting sites, *S. capillifolium* is a hummock forming species whereas *S. recurvum* occupies hollows and pools (Daniels & Eddy 1985). Three replicate areas of each species were selected where each species was common. During June 1994, hollow pvc cylinders, (length 30 cm, internal diam. 7.5 cm) were inserted into the moss carpet at 216 points (108 for each moss species) on the bog surface. The core top was level with the surface of the moss carpet and vascular plants removed from each core. The cores, set out in the three replicated blocks for each species, were numbered and the treatments and sample times randomized between the cores in each replicate block. At fortnightly intervals, aqueous solutions of NH_4NO_3 were applied to half of the cores and deionised water to the controls. The N addition every two weeks was 0.51 mg N $core^{-1}$ (115 mg N m^{-2}: 3 g N m^{-2} yr^{-1}) applied in 200 cm^3 aliquots using a syringe modified to include 6 needle outlet ports to simulate the dropwise addition of rain. To avoid edge effects, solutions were applied evenly over a quadrat, 20 × 20 cm, that contained the core at its centre. Regular N additions were postponed if cores became waterlogged or iced-over during the winter and additional amounts added later when conditions allowed. This occurred in both moss species. Initially, the cores were harvested monthly and then less regularly between October and March. Two weeks before each harvest the N treated cores received $^{15}NH_4{}^{15}NO_3$ (99.8 atom% ^{15}N) at the same rate of addition as the unlabelled N; the controls received the same volume of deionized water. On two occasions in December and March, cores were removed from the bog to an open area adjacent to the laboratory for treatment with ^{15}N labelled NH_4NO_3 and incubation. The bottoms of these cores were covered with nylon mesh and the cylinders placed inside tall 1 dm^3 beakers with an artificial water table maintained at the surface of the core as it had been in the field by addition of deionised water. Labelled N was added and the cores incubated in the open for two weeks prior to sampling. Cores were harvested on nine different occasions between July 1994 and August 1995, the date referring to the month of harvest.

The water-table depth was monitored at two week intervals at a central point in each of the three blocks for each species. Rainwater was collected every two weeks at three locations at the field site adjacent to the cores. Samples were filtered through Millipore filters (0.45 μm) and stored at 4 °C prior to analysis.

Core analysis

Each peat core was removed from the pvc cylinder in the laboratory and sliced transversely into 5 cm sections for analysis. Some cores were incomplete after excavation, but in all cases the cores extended to 25 cm depth. Each section was weighed and stored at 4 °C prior to subsampling. The surface 5 cm of each core containing the live moss was filtered under suction on a glass fibre filter (Whatman GFA) and the plant material freeze-dried and ball-milled for total-N and ^{15}N abundance determinations by mass spectrometry (Finnegan MAT). Filtrates were then filtered through membrane filters (0.45 μm) under suction and made up to volume with deionised H_2O.

Moisture contents of the cores were determined by drying weighed subsamples at 105 °C. Bulk density was expressed as the weight of dry matter per unit volume. The degree of decomposition of samples was assessed using the method of von Post (1929). Acidity was measured as the pH of suspensions of peat in 0.01M $CaCl_2$ at a sample: solution ratio of 1:5 (w/v).

For inorganic and dissolved organic nitrogen (DON) in the peat below 5 cm depth, fresh samples (10 g) were shaken for 2 hr with 50 cm^3 0.5 M K_2SO_4 and filtered through glass fibre filters (Whatman GFA) under suction. The peat was washed with a further 50 cm^3 of extractant and made up to 100 cm^3.

Microbial N was determined by the fumigation-extraction (FE) method after fumigation for 18 hr with chloroform vapour (Williams & Sparling 1984) and extraction with 0.5 M K_2SO_4.

Microbial N was calculated from the total N flush using the value 0.54 for k_N (Brookes et al. 1985).

Chemical analyses

Total N in samples of moss and peat was determined at the same time as the ^{15}N abundance by mass spectrometry. Total P was measured for cores harvested in August 1994, by dissolving the ash of ignited samples in 5 M HCl and measuring total P as PO_4 colorimetrically (Murphy & Riley 1962).

Total N in water extracted from the moss and in 0.5 M K_2SO_4 extracts of fresh and fumigated peat was analysed colorimetrically as NO_3 after oxidation with alkaline potassium persulphate (Williams et al. 1995). Ammonium in 0.5 M K_2SO_4 extracts was diffused into 0.01 M H_2SO_4 after treatment of the extract with magnesium oxide (Bremner 1965) and the trapped NH_4^+ determined colorimetrically (Crooke & Simpson 1971). Nitrate in water and 0.5 M K_2SO_4 extracts in oxidized solutions was analyzed as NO_2^- after reduction with copperized cadmium (Henriksen & Selmer-Olsen 1970).

Table 1. Description of the organic material in profiles from the two habitats and the degree of decomposition H (1–10) on the von Post scale (von Post 1929).

Depth, cm	*Sphagnum capillifolium*	*Sphagnum recurvum*
0–5	Stems and leaves of *S. capillifolium*	Stems and leaves of *S. recurvum*
5–10	Compressed light-brown *Sphagnum* leaves and stems, *Eriophorum vaginatum*, H2/3	Compressed light to dark brown leaves and stems of *Sphagnum* H3/4
10–15	*Sphagnum* leaves, black peat, pseudo-fibrous H4	Medium brown *Sphagnum* leaves, *Eriophorum vaginatum* stems, black peat H3/4
15–20	Medium to dark brown *Sphagnum*, H4/5	Medium to dark brown *Sphagnum* leaves H3/4
20–25	*Sphagnum* moss peat, H5	*Sphagnum* moss peat H5

For measurement of ^{15}N abundance in NH_4^+ and NO_3^-, extracts and water samples were treated first with MgO and NH_3 diffused into 0.01 M H_2SO_4 at 30 °C. After 3 days the acid trap was replaced and Devarda's alloy added to the suspension to reduce NO_3^- to NH_4^+ and diffusion allowed to occur for a further 3 days. For total N in extracts of fumigated and unfumigated samples, the N was first converted to NO_3^- by alkaline oxidation with potassium persulphate (Williams et al. 1995). The oxidised extracts were then treated with Devarda's alloy and 0.1 M NaOH and NH_3 diffused into 0.01 M H_2SO_4 during 3 days at 30 °C. The resulting $(NH_4)_2SO_4$ solutions were then dried and submitted for determination of the $^{15}N/^{14}N$ ratio by mass spectrometry. Samples for $^{15}NH_4^+$ determination contained small quantities of N and the amounts were increased by the addition of 25 μg N as $(NH_4)_2SO_4$ at natural abundance and redried before ^{15}N abundance measurements. The concentrations and ^{15}N abundance of organic N in the extracts were calculated as the difference between total and the sum of NH_4^+ and NO_3^-.

Calculation of ^{15}N uptake

Uptake of added ^{15}N by the moss in each core was expressed as the total weight of ^{15}N in the moss less that in the untreated moss (mg N m^{-2}). The quantity of added ^{15}N recovered in each N pool was calculated from the pool size and the ^{15}N abundance (atom%) less the amount of ^{15}N in the untreated control cores and expressed as a percentage of added N.

Table 2. Physical and chemical characteristics of the peat profiles beneath *S. capillifolium* and *S. recurvum*. Values in parentheses are standard errors of difference between species means.

Depth cm	Bulk density g dm^{-3} (n = 54)		pH (0.01 M $CaCl_2$) (n = 54)		Ash % dry mass (n = 6)	
	S. capillifolium	*S. recurvum*	*S. capillifolium*	*S. recurvum*	*S. capillifolium*	*S. recurvum*
5–10	57.7	50.2 (5.3)	3.15	3.33 (0.01)	2.9	2.1 (0.15)
10–15	78.2	61.8 (6.8)	3.09	3.23 (0.02)	2.8	2.7 (0.27)
15–20	91.9	69.5 (9.9)	3.08	3.21 (0.02)	3.0	2.0 (0.58)
20–25	101.4	87.1 (17.4)	3.09	3.19 (0.02)	3.1	2.6 (0.53)

Statistical analysis

The results were expressed on an area (g or mg N m^{-2} per 5 cm thick layer) and on a dry weight basis (mg kg^{-1} dry matter) for statistical analysis. A comparison of the two N treatments and two species over nine sampling times was carried out at each depth by analysis of variance. For skewed distributions, values were transformed to the natural logarithm, but for clarity, untransformed means and standard errors of difference between means from the ANOVA of untransformed data are presented. All statistical analyses were performed using the Genstat package (Genstat 5 Committee 1993).

Results

Site characteristics

The visual characteristics of the peats from beneath the two *Sphagnum* species were very similar in the surface 25 cm (Table 1). The bulk density was marginally greater under *S. capillifolium* than *S. recurvum* (Table 2), but these differences were not significantly ($P < 0.05$) different. Water table levels at both site types were equally low during the summer months, increased in September and remained close to the surface until June (Figure 1). From September until June the water table was at a significantly ($P < 0.001$) lower depth beneath *S. capillifolium* than *S. recurvum*. The pH of the peat was significantly ($P < 0.01$) greater beneath *S. recurvum* than *S. capillifolium* to 25 cm depth though the differences were relatively small (Table 2).

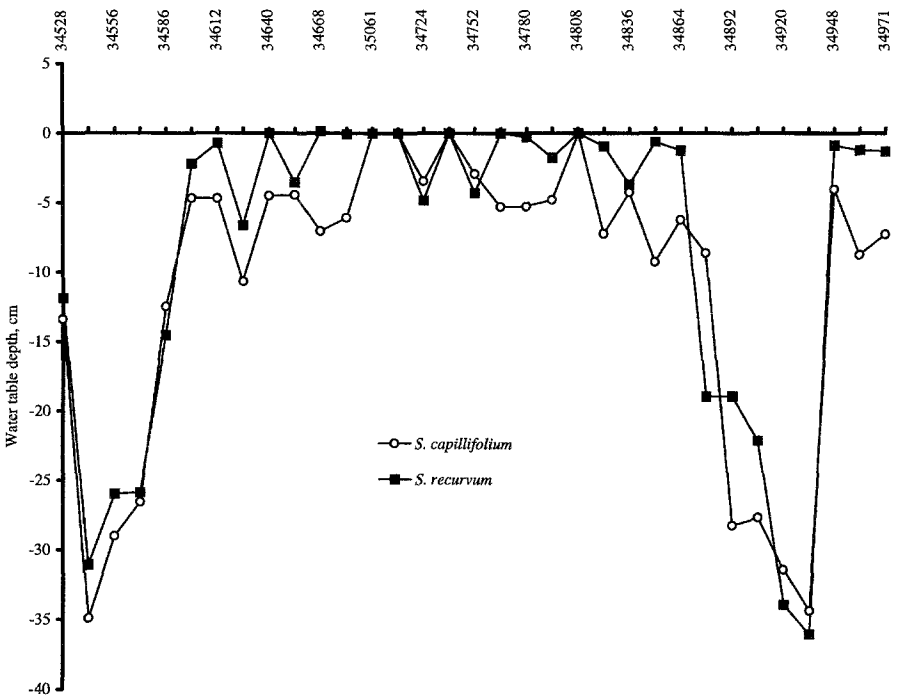

Figure 1. Rainfall (cm), and water table depth (cm) at *S. capillifolium* ○ and *S. recurvum* ■ sites during the experiment.

Table 3. Quantities of NH_4^+, NO_3^- and DON in rain water collected at the field site during the period of the experiment and on an annual basis.

	g N m^{-2} ± se* (n = 3)		g N m^{-2} yr^{-1} ± se (n = 3)	
NH_4^+	0.51	0.05	0.41	0.04
NO_3^-	0.17	0.01	0.14	0.01
DON	0.28	0.04	0.24	0.04
Total	0.96		0.79	

*se = standard error of the mean.

Nitrogen inputs in rainwater

The quantities of NH_4^+, NO_3^- and DON in rainwater fluctuated with season and tended to be lower during the winter and early spring between mid-November and late April. With one exception during July, NH_4^+ predominated over NO_3^- throughout and the NH_4:NO_3 ratio ranged from 0.4 to 92 mainly because of variations in the concentrations of NO_3^-. The quantity of DON also varied between the sampling occasions. The total fluxes of N in

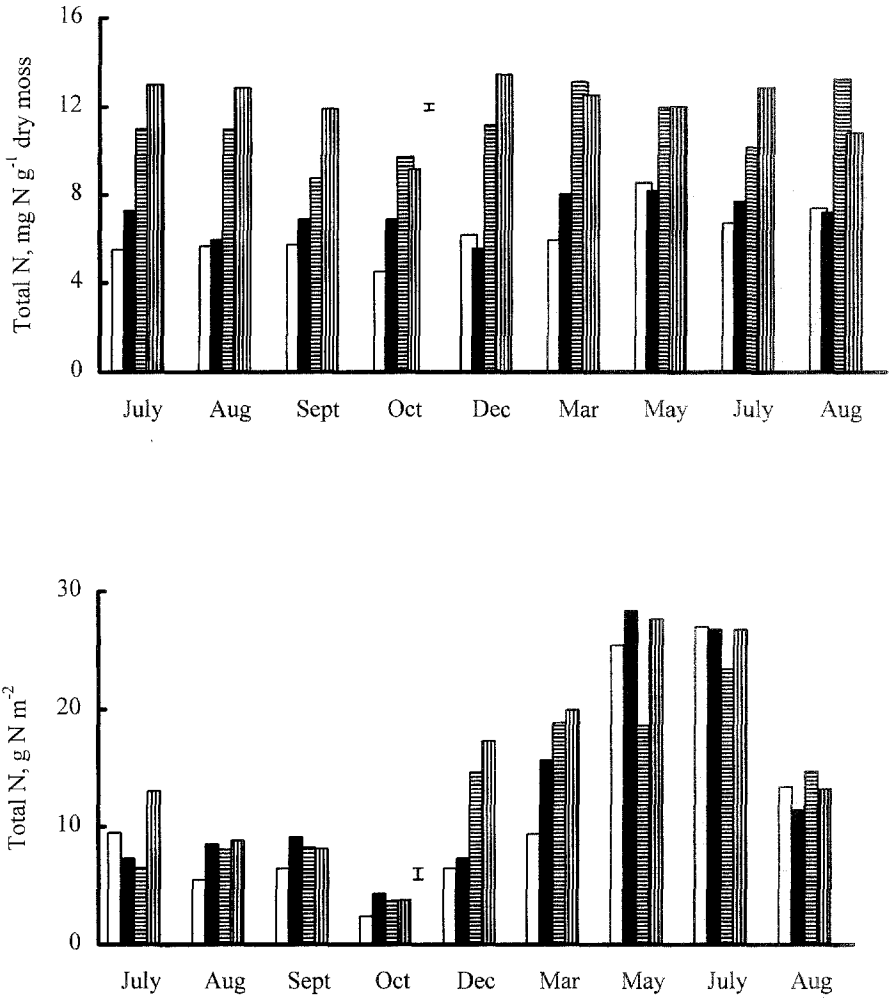

Figure 2. (2A) Concentration of total N (mg g^{-1}dry moss) in the surface 5 cm moss of *S. capillifolium* (control) □ and treated ■ with 0.115 g N m^{-2} as NH_4NO_3 applied every two weeks (3 g N $m^{-2}yr^{-1}$) and of *S. recurvum* control ▤ and N treated ▦. Error bars show the standard error of difference between the control and N treatment means averaged over species and time (n = 54). (2B) Total N contents (g N m^{-2}) of the surface 5 cm moss in *S. capillifolium* □ control and N treated ■ and *S. recurvum* control ▤ and N treated ▦. Error bars show the standard error of difference between the control and N treatment means averaged over species and time (n = 54).

rainwater over the experimental period was calculated as 0.8 g N $m^{-2}yr^{-1}$ in wet deposition (Table 3).

Total N in mosses

The concentration of total N in the mosses was consistently greater in *S. recurvum* than *S. capillifolium* at each sample date (Figure 2A) and averaged over all dates the mean was significantly ($P < 0.001$) greater for *S. recurvum* than *S. capillifolium*, 11.6 mg N g^{-1} compared with 6.6 mg N g^{-1} dry moss (standard error of difference (sed) = 0.6). The total N concentrations in the moss tissues, averaged over the two species and nine sampling occasions were increased significantly ($P < 0.001$) by the addition of N compared with the control, 9.6 compared with 8.7 mg N g^{-1} dry moss (sed = 0.32). Nitrogen concentrations averaged over both species and N treatments changed with time, being significantly ($P < 0.001$) lower during October 1994 than in the summer months of 1995.

The total N content of the moss in the surface 5 cm of core, expressed as g N m^{-2}, followed a marked seasonal pattern in both species and in the control as well as N treated cores (Figure 2B). This was largely determined by the dry matter content of the surface 5 cm core and less by the total N concentration which, apart from the October values, was almost constant by comparison (Figure 2A). Total N contents in both species reached a minimum during October and increased steadily to a maximum in May and July before decreasing again. Averaged over sample dates and N treatments the total N content was significantly ($P < 0.05$) greater in *S. recurvum* than *S. capillifolium*, 14.2 g N m^{-2} compared with 12.4 g N m^{-2} (sed = 0.99). The differences between the species changed significantly ($P < 0.05$) with time and in May and July 1995 the N content of *S. capillifolium* became comparable with that of *S. recurvum*. Averaged over all sampling dates, total N content was significantly ($P < 0.05$) greater in N treated moss than in the control, 14.3 compared with 12.3 g N m^{-2} (sed = 0.97). There was no indication that N accumulated in the mosses in relation to the amounts added.

The weight of ^{15}N in the mosses per unit area was similar in both species, and followed the same significant ($P < 0.001$) pattern with time which decreased in October (Table 4). The addition of N increased significantly ($P < 0.001$) the ^{15}N content, and this effect did not alter significantly with time. The uptake of added ^{15}N, i.e. the difference between the ^{15}N content of the N treated moss and that of the control expressed as a percentage of added ^{15}N, ranged from 11% for *S. recurvum* during October 1994 to >100% during July 1995. This uptake value varied with the weight of the core and became less variable when expressed per weight of dry matter in the core (not shown) such that the differences between times were not significant.

Table 4. Content of ^{15}N, mg $^{15}N\ m^{-2}$, in the moss tissues of control and N treated cores two weeks after the addition of 115 mg ^{15}N as $^{15}NH_4{}^{15}NO_3$ at 99.8 atom%. Values in parentheses expressed as percentage of added ^{15}N.

Sample date	*S. capillifolium*			*S. recurvum*		
	Control	N+	Difference	Control	N+	Difference
July 1994	34.7	85.3	50.7 (44.1)	23.9	123.4	99.3 (86.4)
August	20.0	99.7	79.7 (69.3)	29.4	75.7	46.2 (40.2)
September	23.5	79.5	55.9 (48.6)	30.0	71.9	41.9 (36.4)
October	8.7	54.6	45.7 (39.8)	13.5	24.6	12.7 (11.0)
December	23.5	99.6	76.0 (66.1)	53.4	166.3	112.9 (98.2)
March 1995	33.9	113.5	79.4 (69.1)	68.1	145.5	77.4 (67.3)
May	91.4	226.0	134.6 (117)	66.9	168.6	101.6 (88.4)
July	97.0	219.2	122.3 (106)	84.1	218.7	134.6 (117)
August	48.3	139.6	91.2 (79.3)	52.6	181.4	128.8 (112)
Mean	42.3	124.1	81.7 (71.1)	46.9	130.7	83.9 (73.0)
sed* species	2.6 (n = 54)					
N trt	5.4 (n = 54)					
time × N	16.5 (n = 6)					

*sed = standard error of difference between the species or the N treatment means.

Table 5. Mean contents, averaged over 9 sample dates of $^{14+15}N$ and ^{15}N in $NH_4{}^+$, $NO_3{}^-$ and DON in water, extracted from the control and N treated (N+) mosses by suction two weeks after treatment. Values in parentheses are the differences between N+ and control expressed as a percentages of added ^{15}N (115 mg $^{15}N\ m^{-2}$).

	S. capillifolium		*S. recurvum*		
	N0	N+	N0	N+	sed* (n = 27)
$NH_4{}^+$, mg N m^{-2}	1.6	1.9	3.1	4.6	0.64
$^{15}NH_4{}^+$, μg N m^{-2}	5.9	8.8 (< 0.01)	11.5	28.0 (0.02)	6.7
$NO_3{}^-$, mg N m^{-2}	0.29	0.28	0.35	0.59	0.09
$^{15}NO_3{}^-$	ND†	ND	ND	ND	ND
DON, mg N m^{-2}	9.7	11.6	9.8	12.8	1.12
^{15}DON, μg N m^{-2}	34	51 (0.01)	30	85 (0.05)	31.8

†ND = not determined.
sed = standard error of difference between the control and N treatment means.

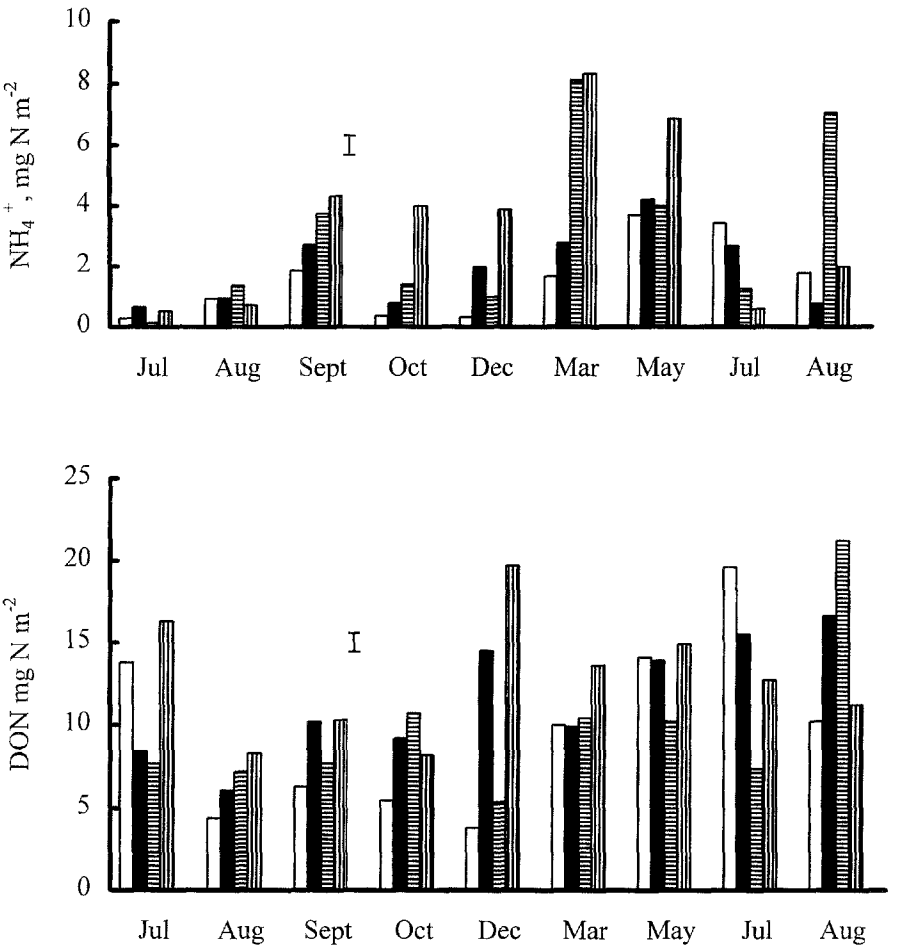

Figure 3. Quantities of (A) NH_4^+ (mg N m^{-2}) and (B) dissolved organic N (DON) (mg N m^{-2}) in the water extracted by suction from *S capillifolium*, control □ and N treated ■ with 0.115 g N m^{-2} as NH_4NO_3 every two weeks (3 g N $m^{-2}yr^{-1}$) and *S. recurvum*, control ▤ and N treated ▦. Error bars show standard error of difference between the control and N treatment means averaged over species and time (n = 54).

Nitrogen in moss water

Analysis of the water extracted by suction from the fresh moss indicated very low concentrations of NH_4^+ and NO_3^-, the latter barely above the lower limit of detection of 0.01 ppm N. The quantities of NH_4^+ although marginally greater in *S. recurvum* than *S. capillifolium* (Table 5) were not significantly ($P < 0.05$) different between the species and there was no effect of NH_4NO_3 addition. Amounts of NH_4^+ changed significantly ($P < 0.001$) with time and reached peak values in September and May for *S. capillifolium* and in

September and March for *S. recurvum* (Figure 3). The greater September values coincided with the rising water table, whereas in March and May the water table had not fallen appreciably. The isotope ratio of $^{15}NH_4^+$, averaged over the nine sampling occasions and the two species, was significantly ($P < 0.001$) greater in N treated than in control cores, 0.536 atom% compared with 0.367 atom% in the control. This difference changed significantly with time ($P < 0.01$) and was greatest during October (0.536 atom%) and December (1.022 atom%). Averaged over all the sampling dates, labelling in *S. recurvum* (0.609 atom%) was significantly ($P < 0.05$) greater than in *S. capillifolium* (0.464 atom%). The detection of $^{15}NH_4^+$ in the moss water occurred at times when concentrations in the untreated cores were also high, indicating that uptake was limited at this time. The mean quantities of $^{15}NH_4^+$ in the waters were significantly ($P < 0.05$) greater in N treated cores than in the control and the calculated recoveries were less than 0.01% of the ^{15}N applied (Table 5). The amounts of N as NO_3^- in the moss water were almost ten times smaller than those of NH_4^+ (Table 5) and were not subject to isotope ratio measurements because of the small quantities.

Dissolved organic N (DON) was present in the water in greater concentrations than the inorganic fraction and the amounts changed significantly ($P < 0.001$) with season (Figure 3). The trend in mean values suggested a general increase in DON with time and, therefore, with additions of NH_4NO_3. Linear regressions of DON in the moss water against the cumulative amounts of N added to *S. capillifolium* showed a significant ($P < 0.01$) positive linear regression (DON (mg m^{-2}) = 32.2 + 0.013 x added N (mg m^{-2}), $R^2 = 0.754$, $P < 0.01$), but no such relationship was detected in *S. recurvum* or in the untreated cores. The addition of NH_4NO_3 significantly ($P < 0.05$) increased the amounts of DON in the moss water, averaged over all sampling occasions (Table 5), but on two sampling times, in July 1994 and 1995 for *S. capillifolium* and in October 1994 and August 1995 for *S. recurvum*, the quantity of DON was decreased by N addition. These decreases occurred when the DON in the untreated cores was already high, > 10 mg m^{-2}.

The mean calculated ^{15}N abundance of the DON fraction averaged over all sampling dates was significantly ($P < 0.001$) greater in N treated samples (0.554 atom%) than in the control (0.367 atom%). Labelling changed significantly ($P < 0.05$) with time and was greater in October (0.613 atom%), December (1.104 atom%) and March (0.765 atom%) than other months.

The mean ^{15}N labelling of DON tended to be greater ($P = 0.052$) in *S. recurvum* (0.667 atom%) than in *S. capillifolium* (0.441 atom%). Thus NH_4NO_3 addition had contributed to DON, but the mean calculated recoveries of added ^{15}N in the DON pool were all below 0.1% (Table 5).

Table 6. Mean contents (mg N m^{-2}) of $^{14+15}N$ and ^{15}N in the NH_4^+, NO_3^-, DON microbial biomass (MBN) and flush, in the 5–10 cm peat layer of control and N treated (N^+) cores averaged over 9 sample dates.

	S. capillifolium		*S. recurvum*		
	Control	N+	Control	N+	sed* ($n = 27$)
NH_4^+	186	140	371	323	91
$^{15}NH_4^+$	0.7	0.5	1.4	1.3	0.17
NO_3^-	14.6	14.0	44.1	51.5	12.8
DON	437	380	710	760	114.5
^{15}N DON	1.6	1.6	2.5	3.1	0.19
MBN	1940	1910	1680	1840	321
^{15}N flush	3.7	4.0	3.4	3.6	0.4

*sed = standard error of difference between the means of the control and N treatment.
ND = not determined.

Nitrogen in the peat

The pool of NH_4^+ in the peat at 5–10 cm depth was greater than that in the moss water and values averaged over all sample dates were significantly ($P < 0.05$) greater in *S. recurvum* than in *S. capillifolium* (Table 6). The size of the NH_4^+ pool at this depth was not significantly altered by the addition of N, but ^{15}N abundance values suggested that $^{15}NH_4^+$ was present. Averaged over all dates, the ^{15}N abundance was significantly greater ($P < 0.001$) in N treated than control peat, 0.411 atom% compared with 0.367 atom%. Labelling of the NH_4^+ pool changed significantly ($P < 0.01$) with time and was greatest (0.595 atom%) during the first month (July) than on any other sampling occasion. The mean amounts of $^{15}NH_4^+$ for all dates and for the July treatment were not significantly different between control and N treated cores despite the increase in ^{15}N abundance indicative of the greater size and variability of the NH_4^+ pool in the underlying peat than in the surface waters (Table 6). Nitrate concentrations in extracts of peat were mostly at or below the level of detection and showed no differences between the moss species and no effects of added N (Table 6).

The average size of the DON pool was significantly greater under *S. capillifolium* than *S. recurvum*, but N addition had no effect on the content of ^{15}N (Table 6). Apart from July, the first month of the experiment, when the calculated ^{15}N abundance of the DON pool was 0.413 atom% and 0.427 atom% in *S. capillifolium* and *S. recurvum*, respectively, there was no evidence that

the K_2SO_4 extractable DON pool at 5–10 cm depth became labelled with ^{15}N on any of the other sampling occasions. The larger microbial biomass N pool failed to show any effects of added N and was not a sink for ^{15}N during the 2 week period on any occasion (Table 6).

There was no evidence of increased ^{15}N abundances at depths below 10 cm and the sizes of the various pools are not shown.

Total P

Total P concentrations in the surface 10 cm of the cores were significantly ($P < 0.001$) greater in *S. recurvum* than in *S. capillifolium*, 706 mg kg^{-1} and 354 mg kg^{-1}, respectively. A similar difference was present at 25 to 30 cm depth. Addition of N had had no significant effect on P concentration by the second month of treatment. The N:P ratios in the surface moss were 16 and 17 in the untreated *S. recurvum* and *S. capillifolium*, respectively, and 16 and 18, respectively, in the N treated mosses.

Discussion

With the exception of the October sampling date, *Sphagnum* moss in the surface 5 cm of the core accounted for most of the labelled N two weeks after application and the proportion increased to around 100 per cent in July 1995. Assimilation of more than 50% of the label by the moss confirmed uptake of both NH_4^+ and NO_3^- consistent with results of previous work under controlled conditions showing no preference by the moss for either NH_4^+ or NO_3^- (Silcock & Williams 1995). However, it was not clear whether one form or another was preferred when ^{15}N recoveries were < 50%. A decrease in ^{15}N uptake with the rising water table level in October was particularly noticeable in *S. recurvum*, though the reasons for this are not clear. The wetter hollows occupied by this species may have enabled label to diffuse into the surface waters. The more controlled additions of N in December and March gave better recoveries probably because conditions were not as wet as they were on the surface of the bog. The morphology of the moss plant also influences N capture by determining interception of rainwater and, whereas *S. capillifolium* forms a tight compact plant, *S. recurvum*, in contrast, is branched and elongated (Daniels & Eddy 1985) and may be less efficient at trapping rainwater than *S. capillifolium*. The addition of 3 g N m^{-2} yr^{-1} did increase the total N concentration in the mosses and therefore C:N ratios decreased, which is consistent with results obtained with *S. magellanicum* at applications of 10 g N m^{-2} yr^{-1} at the same site (Williams & Silcock 1997).

Thus, the circumstances described by Aerts et al. (1992) of increasing N concentrations and falling C:N ratio at increased levels of atmospheric deposition did occur to some extent though the calculated mean changes in C:N ratio, from 77 to 67 in *S. capillifolium* and from 43 to 40 in *S. recurvum*, were small.

The two *Sphagnum* habitats differed in their nutrient contents as well as moisture characteristics. Total P concentrations were greater in *S. recurvum* and the underlying peat than in *S. capillifolium* profiles, which could explain the greater concentration of N in *S. recurvum* as N:P ratios were very similar in both species. This suggests a better supply of P to the wetter hollows compared to the drier areas of the bog surface and both sites were close to the N:P ratio of 14 described by Aerts et al. (1992) as the threshold for P limiting conditions. However, this difference in P content did not appear to influence the uptake of ^{15}N, which averaged 71 and 73 per cent in *S. capillifolium* and *S. recurvum*, respectively.

The rapid disappearance of $^{15}NH_4{}^{15}NO_3$ was consistent with the report by Hemmond (1983) that additions of NH_4^+ and NO_3^- to the surface waters of an ombrogenous bog were removed in a matter of days. Assimilation of NH_4^+ and NO_3^- by the moss was the main process accounting for the added inorganic N. Extraction of *S. magellanicum* moss treated fortnightly with NH_4NO_3 at Moidach More failed to show retention of exchangeable NH_4^+ (Williams & Silcock 1997), which indicated that the residence time of added NH_4^+ in this pool was temporary and subject to more fluctuation than suggested by Hemmond (1983). The abundance of $^{15}NH_4^+$ in the moss water increased in winter months when recovery in the moss was low indicating that this was probably unassimilated ^{15}N. Nevertheless, a large portion of the added label remained unaccounted for during autumn and winter and was not detected in the relatively active N containing fractions, such as DON and microbial biomass N. The small amount of ^{15}N reaching the underlying peat and the relatively large size and variability of the NH_4^+, DON and microbial N pools prevented more precise calculations of ^{15}N recovery.

The acidity of the peat is considered sufficient to inhibit nitrification, which is generally inactive in nutrient poor bogs (Rosswall & Granhall 1980), and the absence of NO_3^- indicated more efficient removal of the anion compared to NH_4^+. Denitrification is also inhibited by acidity, yet peat (pH 3.8) from Thoreau's bog showed a potential to denitrify under controlled laboratory conditions (Hemmond 1983). Regina et al. (1996) reported that on nutrient poor ombrotrophic bogs, such as the Moidach More, fluxes of N_2O were either negative or small. On virgin undrained ombrotrophic bogs, mean N_2O fluxes were equivalent to 0.2 mg N m^{-2} for a 14 day period and comparable N_2O fluxes at Moidach More would only partly account for the 58 mg N m^{-2} added as NO_3^- every two weeks in the current study. However, these

measures of N_2O fluxes were made in Finland in areas of low N deposition, approximately 0.7 g N m^{-2} yr^{-1} (Williams et al. 1998), whereas the rate of addition of 3 g N m^{-2} yr^{-1} used in the current experiment could be expected to increase the rate of denitrification. The semi-aquatic conditions prevailing in the surface moss where the acidity of the water is less than that of the underlying peat and where there is an active microbial community (Gilbert et al. 1998) could be expected to favour denitrification.

Accumulation of amino acids in mosses receiving NH_4NO_3 has been reported (Baxter et al. 1992) and this is an obvious potential source of DON released into the water surrounding the moss (Silcock & Williams 1995). Indeed, the DON in the moss water associated with *S. capillifolium* was proportional to the quantity of added N. Failure to detect this relationship in *S. recurvum* may have been a consequence of its pool habitat where, during winter months, the surface waters on the bog could dilute the water associated with the moss in the core. The timing of the increased ^{15}N labelling of the DON fraction coincided with lower recovery of ^{15}N in the moss tissues and the decrease in moss N at the end of the summer when the contents of the plant cell are liable to leak (Gerdol 1990). The labelling of this DON confirmed that the applied ^{15}N was a source of DON and also indicated a tendency for the N rich *S. recurvum* to release more DON than *S. capillifolium*; confirming that the effect occurs in both species, though the linear relationship between DON and added N was only detected for *S. capillifolium*.

The unaccounted ^{15}N was greatest at the start of the experiment and the climatic conditions of the 1994 summer or the insertion of the plastic cylinders may have influenced moss growth and reduced N uptake. The unaccounted ^{15}N probably included a small quantity of NO_3^- denitrified in the surface waters, unassimilated NH_4^+ diffused to lower depths, where it would be rapidly transformed to organic forms, and DON either diffused or leached to the underlying *Sphagnum* litter and peat. If this did occur, the ^{15}N did not remain as DON or microbial N for very long even though the sizes of these N pools were appreciable. The mobility and rate of mineralization of DON in the peats will depend on its characteristics and more information about this N pool is required to better understand the dynamics of N in peats.

In conclusion, the two *Sphagnum* mosses accounted, on average, for 72 per cent of 3 g N m^{-2} yr^{-1} applied as NH_4NO_3 and a small proportion (0.03%) was detected as DON in the waters surrounding the moss. A smaller proportion of ^{15}N, $< 0.01\%$, present in the moss waters during winter months, was presumed to be unassimilated $^{15}NH_4^+$. The two mosses, *S. capillifolium* and *S. recurvum*, accumulated N and showed a slightly reduced C:N ratio that could enhance rates of organic matter decomposition and N mineralization

(Aerts et al. 1992). In relation to the amounts of total N in the living moss and in NH_4^+, DON and microbial N pools in the peat, the quantities of added N were small and not detectable by difference. Nevertheless, the use of ^{15}N label showed both temporal and spatial variations in the capacity of bog vegetation to assimilate atmospherically derived NH_4NO_3 and to release it as DON.

Acknowledgements

This work was jointly funded by the Scottish Office Agriculture, Environment and Fisheries Department and the European Community 3rd Framework Environment Programme (Environment Programme Contract No. EV5V-CT92-0099). Permission to use the Moidach More and access to the site were granted by Braemoray Estates and Scottish Natural Heritage. David Elston and Betty Duff, BIOSS, advised on statistical methods and Jenny Harthill carried out the ^{15}N analyses.

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