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Soil nitrogen transformations on a subantarctic island

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Abstract: The vascular vegetation of a mire-grassland community on Marion Island (47°S, 38°E) takes up *c.* 158 mg N m^{-2} d^{-1} in summer. Bryophytes take up *c.* 36 mg N m^{-2} d^{-1} during their peak growth period. Since inputs of N through precipitation and biological fixation are negligible, mineralization of organic N must have supplied the bulk of this N. From changes in peat inorganic N levels and rates of uptake by the vegetation we estimate mean mineralization rates of 178 mg N m^{-2} d^{-1} in summer and 55 mg N m^{-2} d^{-1} in winter. *In situ* incubation of peat give a maximum mineralization rate of 48 mg N m^{-2} d^{-1}. At this rate the small (700 mg m^{-2}) pool of available N in the upper 25 cm of peat would be depleted by the vascular vegetation in about seven days and bryophytes would deplete the available N pool in the top 25 mm in two days. Hence the rate of N mineralization measured by incubation is much too low to account for the fluctuations in concentrations of inorganic N in the peat and the amounts taken up by the vegetation. This may be due to losses through denitrification or to the fact that soil macroinvertebrates were excluded from the incubation.

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Introduction

Annual net primary production (ANP) of Marion Island (47°S, 38°E) vegetation can be very high. For example, Smith (1987a) reported a total (above- plus below ground) ANP of 2178 g m^{-2} y^{-1} for a mire-grassland. This is considerably higher than values found for any of the 52 Northern Hemisphere tundra and tundra-like sites investigated during the the International Biological Programme (IBP) (Wielgolaski *et al.* 1981). It is also higher than the maximum production found for the ten North American IBP Grassland Biome sites (1425 g m^{-2} y^{-1}; Sims & Singh 1978) or for a range of temperate sedge wetlands (max. 1741 g m^{-2} y^{-1}; Bernard & Gorham 1978) and bog marshes (max. 1539 g m^{-2} y^{-1}; Reader 1978). Large ANP's have also been reported for other Marion Island communities (Smith 1978, 1987b) and for other subantarctic islands (Jenkin 1975, Lewis Smith & Walton 1975, Lewis Smith 1984).

The large ANP results in a substantial annual uptake of nutrients by the vegetation because the island plants are not particularly efficient in conserving nutrients through back translocation from senescing tissue (Smith 1988), and N is the element required in largest quantities. For example, the mire-grassland vegetation annually takes up 24.8 g N m^{-2} (Smith 1988). The pool of "available" N in the underlying peat (*c.* 0.7 g m^{-2}, to 25 cm depth) is amongst the lowest measured for any ecosystem (Smith 1987c) and must be replenished about 36 times during the year to supply the needs of the vegetation. The site was not directly influenced by seal or seabird manuring, and other inputs of N (precipitation, biological fixation and chemical weathering) together provided only about 1% of the vegetation's requirements. It was therefore suggested (Smith 1988) that the bulk of the N (also P, K and Ca) required was provided by net mineralization during peat decomposition and that decomposition/mineralization processes in the peat and nutrient uptake by the vegetation are probably closely coupled. A need was recognized for investigations into soil nutrient transformations on the island.

In this paper we describe the changes in inorganic N concentrations in the mire-grassland peat over a year and report the results of a study of *in situ* N transformation rates and an investigation of inorganic N transformations by peat extracts. We compare measured mineralization rates with the quantities of N required by the vegetation.

Materials and methods

The mire-grassland site is approximately 300 m west of the meteorological station on the island's eastern coastal plain. The vegetation (described under "study mire 1" in Smith 1987a) consists of short graminoids and bryophytes. Soil temperature was measured using maximum and minimum thermometers pressed into the top 10 cm of peat.

Temporal changes in peat inorganic N concentrations

Eight cores were taken to a depth of 25 cm with a 4 cm diameter corer at approximately fortnightly (September–May) or monthly (May–September) intervals. Each was taken at a 0.25 m^2 quadrat from which plant material had been removed for standing crop analysis. The quadrats selected were of a homogenous composition and were estimated visually as being representative of the stand type as a whole (Smith 1987a

provides details of the sampling strategy).

Each core was divided into three longitudinal subsamples. One was weighed, dried at 105°C and reweighed to assess water content. Another was air-dried and used for determination of organic C, "Kjeldahl" N (taken to equal total N since NO_3^- levels were low), total P, "available" P, cation exchange capacity and exchangeable cations, using methods described by Smith (1987d). The third subsample was stored at 4-6°C and used within 8 h of collection to determine NH_4^+-N (on 0.5 M NaCl extracts by the phenolhypochlorite reaction; Solorzano 1969), NO_2^--N and NO_3^--N (Greiss-Ilosvay reaction on the same extracts, NO_3^- being reduced to NO_2^- with spongy cadmium, Mackereth *et al.* 1978) and pH (combination electrode immersed in a slurry of 10 g peat : 20 ml water).

In situ N transformation rates

A pit was dug in the mire-grassland peat and large, horizontal samples removed from one wall, representing five depths (0–25, 25–75, 75–125, 125–175 and 175–225 mm). Larger roots were removed and each sample was mixed in a cake mixer and subdivided into four 400 g subsamples. Forty ml of one of the following solutions ("treatments") was added to each subsample:

distilled water (unamended treatment),
100 mg l^{-1} glucose solution (+G),
100 mg l^{-1} NH_4^+-N solution (as NH_4 Cl) (+N)
100 mg l^{-1} glucose plus 100 mg l^{-1} NH_4^+-N solution (G+N).

Each subsample was thoroughly mixed and then divided into twenty, approximately equal, portions. Four portions were used immediately to determine NH_4^+-N, NO_3^--N and NO_2^--N concentrations and pH (time 0). Another four were used to determine water content (drying at 105°C to constant mass). The rest were placed in 10 x 7 cm bags made of 25 μm thick, low-density polyethylene. The peat in the bags was pressed into a *c.* 5 mm thick layer, air bubbles smoothed out and the bags sealed with a hot wire. The bags were inserted horizontally into the opposite wall of the pit from which they had been collected, at depths corresponding to those from which they were removed. After 7, 14 and 21 days four bags of each treatment were removed from each depth and analysed for inorganic forms of N, pH and water content. Sampling regime for the study was thus: 5 depths x 4 treatments x 4 sampling dates x 4 replicates.

N transformations in sand columns

Swimming pool filter sand ("silica sand"; bulk density 1.5 g cm^{-3}) was rinsed in distilled water until it appeared clean. It was air-dried and 100 g added to each of nine, open-ended glass tubes (18 cm long and 2.4 cm diameter). The ends of the tubes were loosely plugged with glasswool and fitted with rubber stoppers containing a 10 mm diameter glass tube cut flush with the stopper surfaces. A 200 ml conical flask was fitted to the free ends of both stoppers, forming a reservoir on either end of the sand column. The flasks had two side-arms, one capped with a silicone rubber serum stopper and the other with non-absorbent cotton wool and aluminium foil. The sand columns plus reservoirs were autoclaved and allowed to cool. The mean moisture content of the sand then was 8.3% (oven-dry basis, measured by sacrificing two of the columns). For two columns 100 ml distilled water was added to one of the reservoirs and the sand leached by inverting the column reservoir systems. No NH_4^+-N, NO_3^--N or NO_2^--N could be detected in the leachate. To one reservoir of each of the other five columns, 100 ml of filtered (0.2 μm), autoclaved distilled water containing one of the following was added: 10 mg NH_4^+-N (as NH_4 Cl), 10 mg NH_4^+-N plus 13 mg glucose, 10 mg NO_3^--N (as Na NO_3), 10 mg NO_3^--N plus 13 mg glucose or 10 mg NH_4^+-N plus 10 mg NO_3^--N. Each solution also contained 0.1 mg P (as K_2HPO_4), a trace of yeast extract ("marmite") and 0.5 ml of a slurry of the mire peat collected from 50 mm depth. The columns were leached six times by repeatedly inverting the column/reservoir systems and the leachate then sampled aseptically (0.5 ml removed through the serum stopper with a flamed hollow needle). Concentrations of NH_4^+-N, NO_3^--N and NO_2^--N and bacterial counts (epifluorescence microscopy of acridine-orange stained subsamples) were determined on dilutions of the removed sample (time 0). The errors in inorganic N determinations associated with this procedure (sample removal, dilution, colour development and measurement) were determined by analysing ten 0.5 ml subsamples from the column reservoir containing the NH_4^+-N plus NO_3^--N solution. Coefficients of variation across the ten replicates were 1.9% for NH_4^+-N and 3.1% for NO_3^--N. This column was then discarded. The other four were placed in a dark incubator at 10°C for 24 days. Every 48 hours they were leached by inverting three times and 0.5 ml of the leachate removed for inorganic N determinations and bacterial counts. After 16 days 10 ml of the leachate from each column was placed in stoppered sterile test tubes and degassed by bubbling argon through it. The tubes were placed in an anaerobic desiccator (GasPak^R Anaerobic Systems, BBL,Cockeysville, USA) at 10°C. Every 48h 0.5 ml was removed for inorganic N analyses.

Statistical treatment of data

The significances of variations in concentrations of the three forms of inorganic nitrogen across depth, time and treatment found in the plastic bag experiment were tested by multifactor analysis of variance (AOV). Differences between specific levels of these individual factors, and the effects of their interactions, were examined using a (Tukey) multiple range test. For the sand column experiment, the rates of changes in NH_4^+ or NO_3^- were compared across treatments by testing (student *t*) the differences between the simple regression slopes of the concentration versus time data for the periods when the concentrations were changing.

Results

Peat chemical composition

Some chemical characteristics (ranges of within-sampling date means) of the mire-grassland peat are given in Table I. Except for pH, NH_4^+-N, and NO_3^--N there were no conspicuous or consistent seasonal variations. Water contents reflected the intensity of precipitation just before sampling but the peats were always very wet. Organic C contents were high, corresponding to between 80 and 90% loss on ignition and up to 98% organic matter content. Because of this, Kjeldahl N contents were large; between 3000 and 5000 times greater than the combined concentrations of NH_4^+-N, NO_3^--N and NO_2^--N. Similarly, substantial total P concentrations occurred but plant-available levels of P were fairly low, especially if considered on a soil volume basis (0.6–7 μg cm^{-3}). Cation exchange capacities were high, probably also related to the high organic matter concentrations. Ca and Mg were the dominant exchangeable cations but their concentrations as a percentage of the CEC were low. Mg:Ca ratios in the cation exchange suite were substantially higher than those usually found in peats from cold-temperate and subpolar sites (Brown & Veum 1974), reflecting the influence of seaspray on peat chemistry at the island. For the same reason, the amount of exchangeable Na always exceeded that of K. Monthly minimum peat temperature (0–10 cm depth) at the site varied from 3.5°C in July and August to 8.7°C in February. Maximum peat temperatures varied between 5.2°C (July) and 11.9°C (February).

Peat pH increased steadily from a mean of 4.7 in September to 5.3 in February, remained approximately constant until June and then declined slowly until late August.

Throughout the year NH_4^+ was the predominant form of inorganic N and concentrations were relatively consistent within, but varied markedly between, sampling dates (Fig. 1). They increased significantly (P<0.001) from low values during three periods; early November to mid-December, early January to early March and mid-April to late June. Highest NH_4^+-N concentrations occurred during late June, but values then decreased five-fold by August. NO_3^--N concentrations were less consistent within sampling dates but also varied quite markedly between dates, with most increases occurring during periods when NH_4^+-N values were either low or were decreasing from high levels (Fig. 1). Small (max. 8 μg g^{-1}.) quantities of nitrite-N occurred in the peats early in summer but from December to August NO_2^- was detected in only one sample.

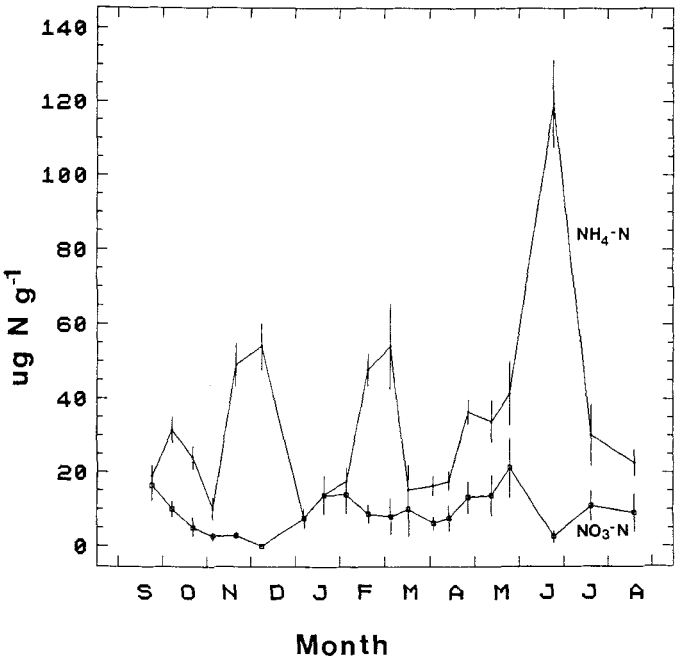

Fig. 1. Temporal variations in soil inorganic N concentrations (μg N per g oven-dry peat) in the 0–25 cm layer of peat at the mire-grassland.

Peat N transformations in buried plastic bags

Inorganic N concentration changes in peat in plastic bags buried at different depths for 21 days are shown in Fig. 2. Details of the NH_4^+-N data for day 0, i.e. the initial endogenous concentrations, the quantities added and those recovered soon (1–2 hours) after addition are given in Table II. For the +N and G+N treatments, the amounts of NH_4^+-N recovered were less than the endogenous plus added amounts and the greatest discrepancies were for the 0–25 mm depth.

Interestingly, at both levels of N treatment, glucose-treated peats mostly possessed higher extractable NH_4^+-N concentrations than did peats to which glucose had not been added (Fig. 2). Although there were exceptions (e.g. for all depths on day 0 and throughout the sampling period in the 25–75 mm layer; Fig. 2b) and in some cases the differences were small (e.g. between unamended and +G samples at the two lowermost depths; Figs 2d & e), across depths, sampling dates and levels of added N the effect of glucose addition was significant at P=0.05. Overall, +G samples contained 29% more NH_4^+-N than did unamended ones and N+G samples 18% more than +N samples. Possible causes of this are discussed below.

Table I. Chemical composition and monthly mean minimum and mean maxiumum temperatures of the mire-grassland peat. Concentrations are on a peat dry mass basis and represent the range of 19 sampling date means found over one year.

	% of dry mass				μg g^{-1}			milli-equivalents 100 g^{-1}					°C	
pH	moisture	Dichromate oxidized C	Kjeldahl N	Total P	NH_4-N	NO_3-N	Avail. P	C.E.C	Exchangeable Ca	Mg	Na	K	Monthly min	Monthly max
4.6–5.3	1050–1750	31–37	1.6–2.7	0.08–0.15	7–120	0–22	9–99	79–91	4.7–9.1	4.9–6.4	0.8–1.9	0.4–1.4	3.5–8.7	5.2–11.9

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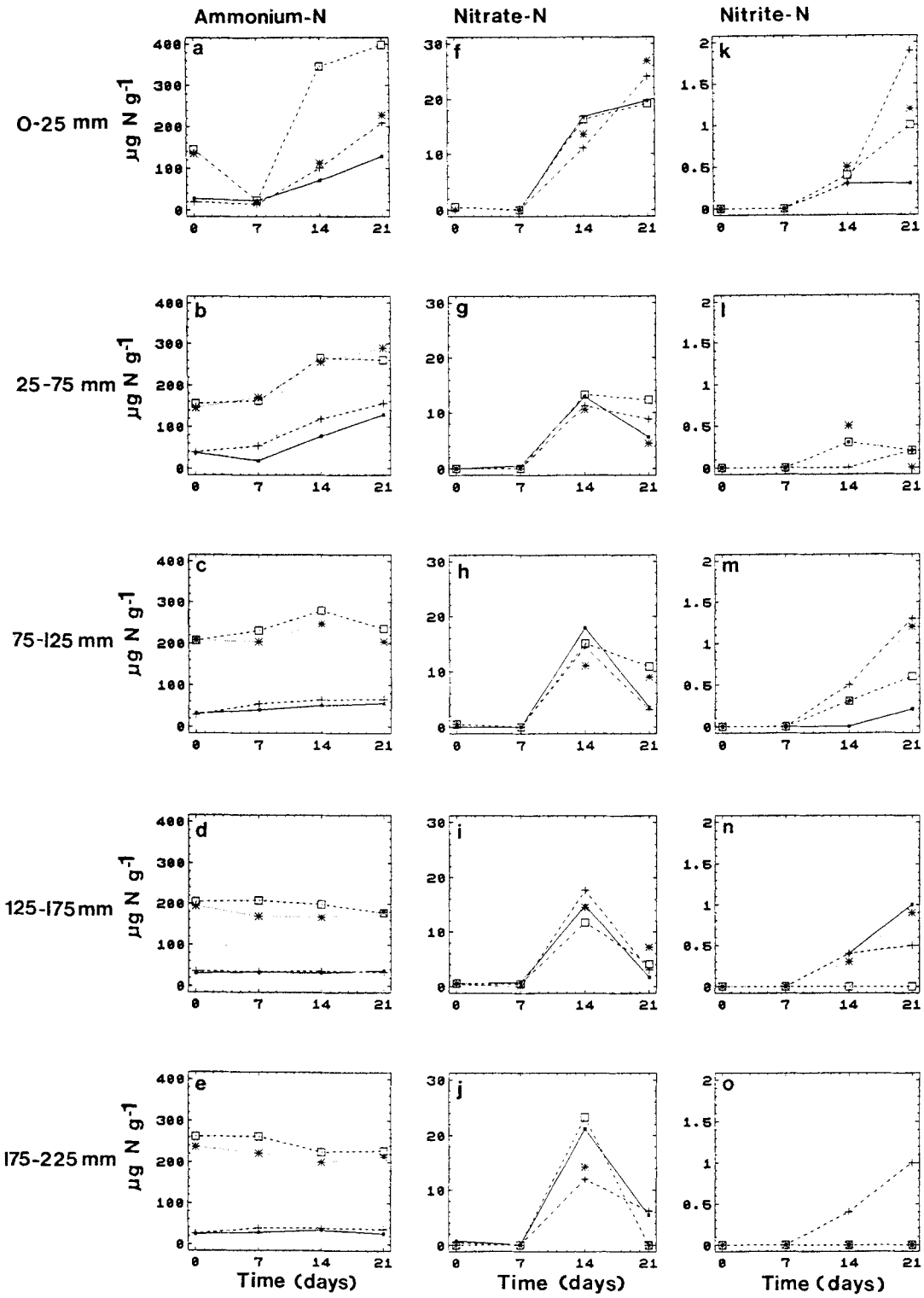

Fig. 2. Ammonium-N (**a–e**), nitrate-N (**f–j**) and nitrite-N (**k–o**) concentrations (μg per g dry peat) in peat in plastic bags buried at different depths for 21 days. Treatments are: small dots with solid line, unamended; plus sign with dashed line, glucose added; asterisk with dotted line, NH_4^+ added; open square with dashed/dotted line, glucose plus NH_4^+ added.

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Table II. Endogenous NH_4^+-N concentrations (μg N g^{-1} dry peat)in peats from different depths, the amounts added and those recovered after 1–2 hours.

	Treatment	Depth mm 0–25	25–75	75–125	125–175	175–225
Endogenous NH_4^+-N*	-	23	38	30	33	25
NH_4^+-N added	-	168	141	192	195	246
NH_4^+-N recovered after 1–2 hours	+N	135	145	208	195	237
	G+N	145	155	207	205	262
NH_4^+-N "lost"	+N	56	34	14	33	34
	G+N	46	24	15	23	9

*Mean of the eight unamended and +G replicates at time 0

The greatest change in NH_4^+-N concentration with time occurred in the 0–25 mm depth layer (Fig. 2a). For unamended and +G peats, the concentration did not change from day 0 to day 7 but then increased sharply, especially in the +G samples. For the +N and G+N treatments, NH_4^+-N concentrations declined very markedly so that by day seven all of the added NH_4^+ had disappeared. Nitrification can probably be ruled out as causing this disappearance since NO_3^- levels remained constant over the first seven days. It was most likely due to bacterial uptake. From day seven NH_4^+ concentrations increased, and more so in the N+G than the +N samples.

Endogenous NH_4^+-N levels in the 25–75 mm depth peats were nearly double those in the top 25 mm. In unamended samples the concentration decreased to about half of the original value in the first week and then increased (Fig. 2b). For the other three treatments NH_4^+-N concentrations increased steadily over the 21 days. Similarly, at 75–125 mm depth (Fig. 2c), NH_4^+-N concentrations in unamended and +G samples increased over the 21 days. Those in the +N and G+N peats increased between days 0 and 14 and then declined.

Thus, excepting for the striking disappearance of added NH_4^+-N from the +N and G+N treatments in the top 25 mm during the first 7 days, the overall patterns of NH_4^+ concentration changes in the upper three depths were fairly consistent, i.e. they increased overall from day 0 to day 21. The general pattern was thus one of net N mineralization. What differed markedly were the amounts of NH_4^+-N produced at the different depths. Across all four treatments the mean amount produced in the 25–75 mm layer was 66%, and that in the 75–125 mm layer only 14%, of the amount produced in the top 25 mm. Considering only unamended peats the values at 25–75 mm were 91%, and at 75–125 mm 24%, of those in the top layer.

Temporal variations in NH_4^+-N concentrations at depths below 125 mm (Figs 2 d & e) differed from those in the top three depths in that, overall, either the concentrations did not change significantly (unamended, +G) or they decreased (N, G+N). This continued the pattern noted above of decreasing mineralization rates with increasing depth. The average amount of NH_4^+-N lost in the N and G+N treatments below 125 mm depth was 25 μg NH_4^+-N g^{-1}, slightly more than the concomitant increases in NO_3^- and NO_2^-.

Initial NO_3^--N concentrations were low and at all depths either remained so or declined to even lower values during the first week of burial (Figs 2f–j). For all depths and treatments they increased markedly between day 7 and 14. Thereafter they declined, except at 0–25 mm where they continued to increase. The variations in NO_3^--N levels across both depth and time were significant at $P < 0.001$, as was also the depth x time interaction. Most of the depth effect was due to the top 25 mm having a mean (i.e. across treatments and sampling dates) concentration about double those for the other depths. Since initial concentrations were zero (or close to zero) this suggests either a greater rate of nitrification or a lower rate of denitrification in the 0–25 mm layer than deeper in the profile. Overall then, as was the case for NH_4^+, the greatest changes in NO_3^- occurred in the 0–25 mm layer.

No endogenous nitrite occurred in the peats and none had appeared after the first seven days in plastic bags (Figs 2k–o). However, time of burial was the most significant "main effect" and accounted for 77% of the overall variation in NO_2^- concentrations, so that by day 21 the overall mean concentration was 0.6 μg NO_2^--N g^{-1}. The time x depth interaction was also highly significant ($P = 0.004$), mainly due to higher rates of NO_2^--N appearance in the top 25 mm. In general, rates of NO_2^--N appearance tended to decrease with depth but the 25–75 mm layer (Fig. 2l) was anomalous in this respect.

N transformations in sand columns

Concentrations of inorganic N forms in sand columns over 24 days are shown in Fig. 3. Immediately after passing the solutions through the sand (day 0) concentrations of NO_3^--N in the column liquid contents were about 7% lower, and those of NH_4^+-N 17% lower, than in the added solutions. The decrease in NO_3^--N was almost exactly accounted for by dilution into the residual water contained by the sand after air-drying and autoclaving. The additional decrease in the case of NH_4^+-N was probably due to NH_4^+ adsorption onto the sand particles. No NH_4^+-N was ever detected in columns to which NO_3^- or NO_3^- plus G had been added (lower part of Fig. 3b) and, initially, no NO_3^--N could be detected in the columns to which NH_4^+ or NH_4^+ plus G were added (lower part of Fig. 3a). This suggests that no, or an undetectable amount, of NO_3^- was added via the yeast extract and peat slurry. Any NH_4^+-N from these two sources would have "disappeared" through adsorption onto the sand.

NH_4^+-N concentrations in columns which received NH_4^+ or NH_4^+ plus glucose (G) showed very similar patterns of change (Fig. 3a), decreasing over the first 10 days, increasing during the next eight days and then decreasing again. What differed significantly ($P < 0.001$) between the two treatments were the rates and absolute magnitudes of the initial disappearance of

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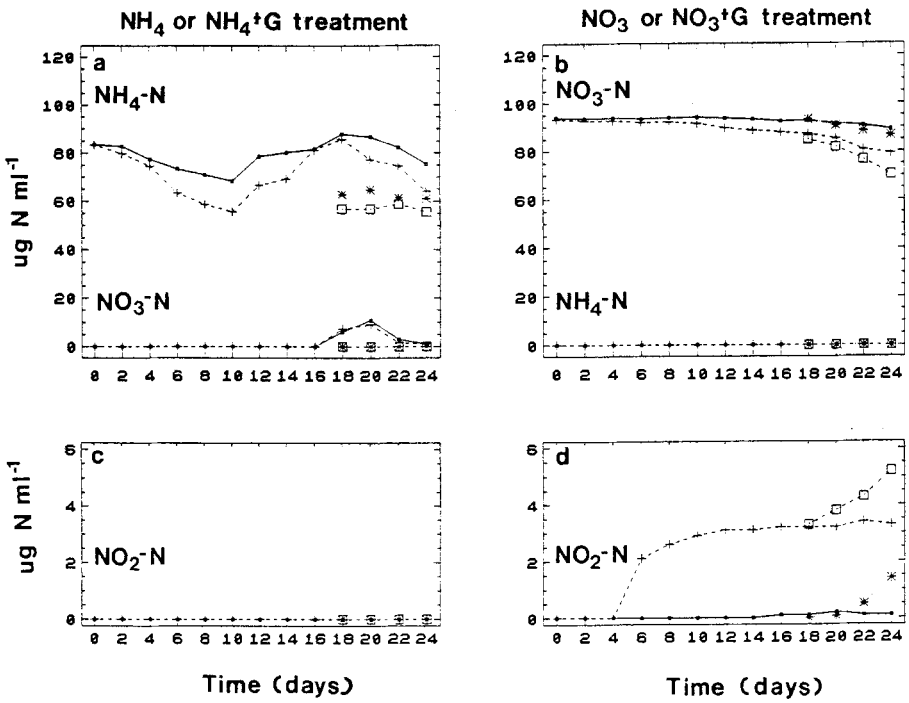

Fig. 3. Inorganic N concentrations (ug per ml) in sand column solutions to which NH_4^+ or NH_4^+ plus glucose (**a**, **c**) or to which NO_3^- or NO_3^- plus glucose (**b**, **d**) were added. Treatments were: For **a** & **c**; dots with solid line, NH_4^+ added; plus sign with dashed line, NH_4^+ plus glucose added; asterisk with dotted line, NH_4^+ added and solution held anoxic; open square with dashed/dotted line, NH_4^+ plus glucose added and solution held anoxic. For **b** & **d**; dots with solid line, NO_3^- added; plus sign with dashed line, NO_3^- plus glucose added; asterisk with dotted line, NO_3^- added and solution held anoxic; open square with dashed/dotted line, NO_3^- plus glucose added and solution held anoxic.

NH_4^+-N. By day 10, NH_4^+-N concentration in the NH_4^+ plus G column had decreased 83% more than in the column to which only NH_4^+ had been added. Making the column solution anoxic had a rapid effect on NH_4^+ concentrations in that for both treatments they had decreased by about 25% by the first time they were tested (day 18). This was probably due to loss of aerosolic NH_4^+ (or perhaps of NH_3) during the argon bubbling, rather than to transformation of NH_4^+-N or stimulation of bacterial uptake. No further changes in NH_4^+-N occurred under anoxic conditions.

Up to day 16, NO_3^--N did not occur in the columns to which NH_4^+ had been added (Fig. 3a). On day 18 small quantities were detected for both the $+NH_4^+$ and NH_4^+ plus G treatments. These increased to a mean of 10 μg NO_3^--N ml^{-1} for the two treatments on day 20 and then decreased. Anaerobiosis prevented the appearance of NO_3^- in both treatments.

NO_3^--N concentration changes in the columns fortified with NO_3^- and NO_3^- plus G were qualitatively similar but quantitatively greater in the latter (Fig. 3b). NO_3^--N declined, especially after day 10, and the rate of decline differed significantly between treatments (P <0.001). By day 24 concentrations for the $+NO_3^-$ treatment were 5% lower, and for the NO_3^- plus G treatment 15% lower, than they were on day 0. Anoxic conditions hastened the decline in NO_3^--N levels; again more so for the NO_3^- plus G than the $+NO_3^-$ treatment.

Nitrite was never detected in the $+NH_4^+$ or NH_4^+ plus G treatment columns, even under anoxic conditions (Fig. 3c). For the $+NO_3^-$ treatment, small quantities of NO_2^--N occurred after 16 days but concentrations remained low (<0.5 μg ml^{-1}, Fig. 3d). In the column which received both NO_3^- and glucose, NO_2^--N appeared on day 6, increased up to day 12 and remained fairly stable at about 3 μg ml^{-1}. For both the $+NO_3^-$ and the NO_3^- plus G treatments, making the solution anoxic caused a further increase (P < 0.001) in NO_2^--N and rates of increase were similar for the two treatments.

Bacterial numbers in the column solutions changed in a similar pattern across the four treatments, increasing over the first 8–12 days and then decreasing (Fig. 4). There were

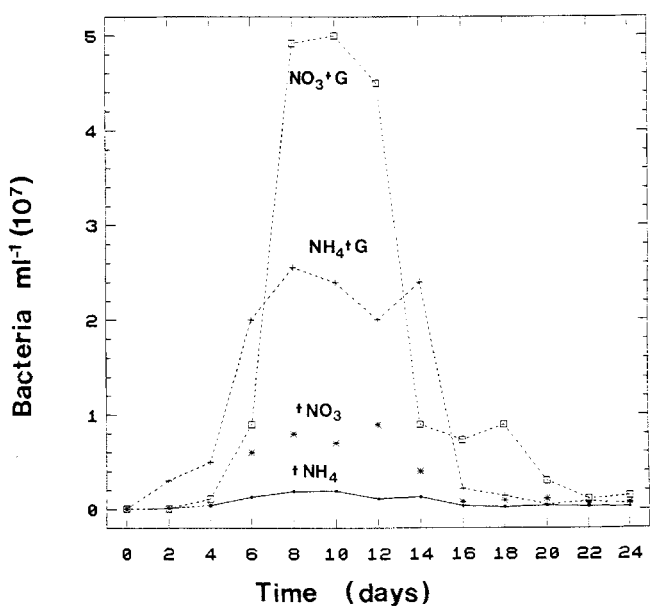

Fig. 4. Epifluorescence microscopy counts of bacteria in the solutions of columns which received NH_4^+ (solid line), NH_4^+ plus glucose (dashed line), NO_3^- (dotted line) or NO_3^- plus glucose (dashed/dotted line).

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marked differences between treatments in the magnitudes of the changes. Glucose addition was the most important factor determining both the rate of bacterial increase and the absolute number of cells attained, but at both levels of glucose higher numbers were reached in columns which received NO_3^- than in those which received NH_4^+.

Discussion

Incubations in plastic bags

The rapid "disappearance" of some of the NH_4^+ added to peat samples in the plastic bag experiment was not due to irreversible clay-lattice fixation of NH_4^+ since illitic clays do not occur on the island (Gribnitz *et al.* 1986). Some NH_4^+-N was probably adsorbed onto the peat colloids and subsequently not completely extracted. We displaced adsorbed NH_4^+ by shaking the peat samples seven times in fresh aliquots of 0.5 M NaCl and each time the extractant solution and peat were separated by centrifugation and filtration. For both unamended and NH_4^+-fortified samples no NH_4^+-N could be detected in the seventh filtrate. We therefore assumed that the procedure displaced all of the adsorbed NH_4^+ but possibly some of the NH_4^+-N was not recoverable.

The fact that the amounts of NH_4^+-N which "disappeared" soon after fortification were greatest for peats from 0–25 mm (presumably the most biologically-active layer) suggests rapid immobilization through bacterial uptake. It is unlikely that this could have accounted for all (46 or 56 μg N g^{-1}) of the NH_4^+-N which "disappeared". French & Smith (1986) reported a bacterial biovolume of 2.2 x 10^9 μm^3 g^{-1} dry peat in the top three cm of peat at the mire-grassland. Assuming a density of 1, a dry mass : fresh mass ratio of 0.2 and an N concentration of 5% of the dry mass for bacteria (Clarholm 1985), this biovolume corresponds to about 22 μg N in the bacterial biomass of 1 g dry peat. Hence, in two hours or less the bacteria must have taken up 2 to 2.5 times more N than the amount contained in their biomass, which seems improbable. However, that N immobilization can occur at an appreciable rate in the 0–25 mm layer is demonstrated by the fact that in the first seven days a further 117 to 122 μg NH_4^+-N g^{-1}, or about 5.5 times the amount initially in the biomass, had disappeared (Fig. 2a). Since there was no corresponding increase in NO_3^- during the same period this was unlikely to be due to nitrification.

The finding that glucose-treated samples generally possessed higher extractable NH_4^+-N concentrations than did peats which did not receive glucose seems opposite to what might be expected, i.e. glucose addition should increase C:N ratios and result in a net immobilization of N. However, the amount of C added represented < 0.03% of the endogenous C contents and would have had a negligible influence on C:N ratio. We offer two possible explanations for the higher NH_4^+-N concentrations in glucose treated peats. Glucose is a readily available, high energy substrate which has been shown to very markedly stimulate the growth (Lindeboom 1979) and activity (Grobler *et al.* 1987) of bacteria on the island. Normally, this would be expected to result in net N immobilization but C:N ratios in the mire-grassland peats are fairly low (15–18) so, at the relatively low levels of glucose amendment applied here, the overall effect of enhanced bacterial activity might be one of net N mineralization. The other possible explanation, which we favour, is that rates of bacterial N-fixation in the mire-grassland peats are increased by three orders of magnitude through glucose fortification (Smith 1984) and some of the fixed N may have been excreted as NH_4^+.

Sand column incubations

Quantitatively, the most striking changes in inorganic N concentrations found during the sand column incubations were for NH_4^+-N in columns to which NH_4^+ or NH_4^+ and glucose had been added. The decrease in NH_4^+-N over the first 10 days (greatest for the NH_4^+ plus G treatment) might have been due to continued adsorption of NH_4^+ onto the sand or to bacterial uptake, or both. The fact that bacterial counts in the column solutions increased markedly during the same period, and also much more so for the NH_4^+ plus G than for the $+NH_4^+$ treatment, suggests that at least some of the NH_4^+-N disappearance in the first 10 days was due to bacterial uptake. Similarly, the "reappearance" of NH_4^+-N over the next eight days was associated in both treatments with sharply declining bacterial counts and so could have been due to liberation of NH_4^+-N from senescing and dead cells. Against this, however, is the fact that the same pattern in bacterial numbers (increase followed by a decrease) occurred in the columns fortified with NO_3^- (indeed, within glucose treatments the changes in bacterial numbers were much more marked with NO_3^- than with NH_4^+), yet there were no cocomitant changes in NO_3^- concentrations (upper part of Fig. 3b). In fact, NO_3^- only started decreasing on day 12, after bacterial numbers had started to decline. We cannot explain why the initial increases in bacterial numbers were accompanied by disappearance of N when NH_4^+ was supplied but not when NO_3^-, which caused greater bacterial growth, was supplied. Similarly, we cannot say why a decrease in cell numbers (cell death) was associated with increasing NH_4^+-N levels in the $+NH_4^+$ treatments but not in the NO_3^- treatments where, again, absolute magnitudes of the changes in cell counts were significantly greater and one might have expected a substantial release of reduced N.

Inorganic nitrogen status of the mire-grassland peat

Concentrations of NH_4^+-N and NO_3^--N in the mire-grassland peat seem fairly high when expressed on a dry peat-weight basis (up to *c.* 120 μg NH_4^+-N g^{-1} and up to *c.* 22 μg NO_3^--N g^{-1}; Fig. 1). However, as pointed out by Harmsen & Kolenbrander (1965), expressing inorganic N contents on a dry weight basis in peat soils of low bulk density and high water-holding capacity is unrealistic in terms of their availability for plant

growth . Bulk densities for the mire-grassland peats were 0.04–0.07 g cm^{-3}. On a peat volume basis, maximum inorganic N concentrations found at the mire-grassland were 8 μg NH_4^+-N cm^{-3} and 1.4 μg NO_3^--N cm^{-3} and mean values were less than a third of these maxima. Even the maximum values are much lower than those generally found for tundra or tundra-like ecosystems, even those considered to contain especially low levels of plant-available N; e.g. 17 μg N cm^{-3} in a tundra mire at Stordalen, Sweden (Rosswall & Granhall 1980) or 43 μg N cm^{-3} in a wet tundra meadow at Barrow, Alaska (Gersper *et al.* 1980). The Marion Island mire-grassland community is therefore particularly nutrient-poor with regards plant-available N and this is true of many of the island's plant communities. The low inorganic N status together with the other soil chemistry values in Table I presents a picture typical of peats from cool-temperate oceanic islands, i.e. acidic and waterlogged with an overwhelming predominance of organic rather than inorganic forms of N and P and a relatively greater importance of Mg and Na than of Ca amongst the exchangeable cations. Soil temperatures are low throughout the year, with little diurnal and seasonal variation.

Nitrogen transformations

The above considerations imply the following with regard to soil N transformation processes: mineralization rates may be expected to be low (consistently low temperatures and continual waterlogging, low pH and low soil Ca), nitrification rates should also be low (low pH, waterlogging, hence enhanced anaerobiosis) and denitrification may be important (acidity, substantial organic matter content, waterlogging/anaerobiosis).

The fact that nitrate is found in the mire-grassland peat, and the correspondence between increasing NO_3^--N levels during periods of declining NH_4^+-N (Fig. 1), indicate that nitrification does take place. The substantial increases, at all depths studied, of NO_3^--N concentrations in peat buried in plastic bags (Fig. 2f–j) shows that this may occur at least down to 225 mm. However, it is surprising that there were no conspicuous or consistent differences in rates of NO_3^--N appearance between peat samples which received NH_4^+-N and those which did not, since NH_4^+ availability is generally thought to be an important determinant of nitrification rate.

The results of the sand column experiment also afford evidence for nitrification. For the +NH_4^+ and NH_4^+ plus G columns the significant decrease in NH_4^+-N from day 18 under aerobic conditions was associated with the appearance of NO_3^--N (Fig. 3a). Anoxic conditions suppressed both these changes, which is what would be expected if they were caused by nitrification. NO_3^--N levels were always lower than the amounts of NH_4^+-N which disappeared, so possibly the NO_3^- formed was rapidly denitrified. Denitrifying conditions on the island (waterlogging, anoxia, acidity, high NO_3^- and organic matter contents) are generally associated with detectable quantities of nitrite. Although NO_2^- was never detected in columns treated with NH_4^+, only small quantities of NO_3^- occurred in them so perhaps the denitrification process was rapid and complete enough (i.e. leading to N_2O or N_2) to remove any NO_2^- being formed. In contrast, substantial quantities of NO_2^--N were found in the column which received NO_3^- plus G and some also occurred where NO_3^- alone was added. Anaerobic conditions enhanced the rates of both NO_3^- disappearance and NO_2^- appearance, suggesting that both were caused by denitrification. In the plastic bag experiment, NO_2^-N was formed as soon as NO_3^- built up to appreciable levels. Thus, the plastic bag and sand column experiments each yielded evidence of nitrification as well as of denitrification, and both nitrifying and denitrifying bacteria have been isolated from the mire-grassland peats (Steyn & Smith 1981). However, the greatest changes in inorganic N concentrations in both experiments, as well as in the mire-grassland peat during the year (Fig. 1), were for NH_4^+-N, indicating substantial rates of ammonification.

Nitrogen mineralization rates versus plant uptake

Considering the suggestion made in the introduction to this paper that nutrient uptake by the vegetation and nutrient mineralization rates in the peat are probably closely coupled, it is interesting to estimate N mineralization rates from the results presented here and to compare these with the amounts of N taken up by the mire-grassland vegetation. All calculations were based on the top 25 cm layer of peat, which contains almost all of the living roots in mire-grasslands (Smith 1985)

The fluctuations shown in Fig. 1 of inorganic N concentrations in the top 25 cm of peat were far too large to be accounted for by precipitation inputs (reported for the same period by Smith 1987e). Rather they must have been due to a shifting balance between mineralization and biological fixation on the one hand, and plant uptake, leaching and denitrification on the other. Smith (1988) showed that, together with the precipitation input, biological fixation and leaching account for only about 1% of N movement through the mire-grassland, so they are ignored here.

For the same period as in Fig. 1, Smith (1987c) assessed the temporal changes in nutrient standing stocks to a depth of 25 cm in the mire-grassland (study mire 1) and calculated the quantities of nutrients taken up by the vascular and bryophyte components of the vegetation. Over a 123 day period from mid-November to mid-March 19400 mg N m^{-2} (90% of the annual total) was taken up by the vascular vegetation, a mean rate of 158 mg N m^{-2} d^{-1}. Maximum rates during the period of peak growth (November to January) were double this. In November/December peat inorganic N levels in the top 25 cm increased by 44 μg g^{-1} (Fig. 1), equivalent to about 20 mg m^{-2} d^{-1}. Mineralization rates in this period must therefore have been at least 336 mg m^{-2} d^{-1}, a release of about 0.1% per day of the organic N contained in the peat. This is similar to a decomposition rate of 0.11% found for the mire-grassland community using a weight-loss technique (Smith 1987a). Mean mineralization rates in summer were therefore about

178 mg N m^{-2} d^{-1}.

Mineralization rates were probably lower in winter. The largest increase in peat inorganic N levels occurred from early April to late June, when in an 81 day period concentrations increased by 91 μg g^{-1} (Fig. 1) or 1570 mg N m^{-2}; a mean rate of increase of 19 mg N m^{-2} d^{-1}. Vascular plant uptake had virtually ceased by then, but there was a late summer/early winter flush of bryophyte growth during which 36 mg N m^{-2} d^{-1} was taken up into the bryomass (Smith 1987c). N mineralization rates in this period must therefore have been at least 55 mg N m^{-2} d^{-1}.

The changes in NH_4^+, NO_3^- and NO_2^- concentrations in the unamended peat samples in the buried plastic bags were used to estimate net mineralization/immobilization rates in the absence of plant uptake. The combined concentrations of these N forms were converted to an amount of N per m^2 in each depth. The lowermost layer was taken to be 75 mm thick so that the total depth was 25 cm, to bring it in line with the measurements leading to Fig. 1 and the nitrogen pools and budgets presented by Smith (1987c 1988). Summing the amounts for each depth yield a total quantity of inorganic N, in mg m^{-2} to 25 cm depth, at each sampling date.

During the first week of incubation there was a net immobilization of 36 mg N m^{-2} across the whole profile but over the next two weeks inorganic N increased by 670 mg m^{-2}. This represents an average mineralization rate of 48 mg N m^{-2} d^{-1}, or only 30% of the mean daily uptake of 158 mg m^{-2} d^{-1} for the vascular vegetation during summer. At this rate the pool of available N (0.7 g m^{-2}) would be depleted in about seven days. Mean mineralization rate in the 0-25 mm layer (from which the bryophytes probably take up nutrients) during the second two weeks in plastic bags was 13.5 mg m^{-2} d^{-1}. This corresponds to about 38% of the 36 mg N m^{-2} taken up daily by bryophytes. Since the available N pool in the 0–25 mm layer was 41 mg N m^{-2}, the shortfall between uptake and mineralization would deplete it in about two days.

We feel that the plastic bag incubation technique as it was used here maximized ammonification. Physical disturbance of the island peats almost invariably leads to a "flush" of NH_4^+, which may last up to a month (unpublished observations, V.R.S.). During sample preparation labile organic N would have been released through breaking and crushing fine roots and, initially at least, oxygen concentrations would be increased. Also, we calculated mineralization rates for the second two weeks of incubation, when rates of ammonium (and nitrate) appearance were greatest. Probably they could not have continued at such levels for much longer. Even so, it is obvious that the net mineralization rate of 48 mg N m^{-2} d^{-1} found during the second two weeks in plastic bags is too low to account for the fluctuations in peat inorganic N concentrations and the amounts of N taken up by the mire-grassland vegetation. Even if it were assumed to continue for a whole year it would account for only 70% of the vegetation's annual requirement for nitrogen.

We offer two reasons why rates of N mineralization measured by the plastic bag incubation technique are lower than those predicted from vegetation uptake and temporal changes in peat inorganic N concentrations. A substantial proportion of the nitrified NH_4^+ might have been rapidly denitrified so that it was not detected as NO_3^- (or NO_2^-) during the incubation. Denitrification losses are unknown but they would add to the amount of N which needs to be mineralized to meet the vegetation's requirements. In this sense the mineralization rates measured here, as well as those estimated as necessary to supply the needs of the vegetation, may be regarded as minimum estimates.

The other reason why the measured mineralization rates are lower than the observed rates of appearance of inorganic N in the peat and plant N uptake is that we considered nitrogen release mediated by microorganisms alone, whereas in the field other organisms assist in decomposition/mineralization processes. Very high densities (up to 19 g m^{-2}; Burger 1978) of soil macro- and mesofaunal species (mainly earthworms, Lepidopteran larvae and Coleopteran larvae and adults) occur in the mire-grassland communities. They are mainly detritus feeders and account for a substantial proportion of energy flow. For example, Crafford (1990) estimated that the larvae of one moth species alone consume about 150 g m^{-2} y^{-1} of plant litter and also process large quantities of peat. Such detritivores may stimulate rates of nutrient release by "short-circuiting" the slow decomposition of litter and peat by microorganisms and thus play an important role in nutrient cycling on the island.

Conclusions

The results presented here are limited by the usual ambiguities associated with simplistic N transformation studies in which the concentrations of a few inorganic N forms are monitored. Mainly, the ambiguities result from uncertainties regarding the sources and fates of the inorganic N forms which appeared or disappeared. For example, NO_2^- could have formed through nitrification or denitrification, NH_4^+ could have disappeared due to nitrification or bacterial uptake and decreasing NO_3^- concentrations could have been due to denitrification or assimilatory reduction by bacteria. These can only be resolved by ^{15}N tracer studies and by quantifying the gaseous products of denitrification. Our studies have shown that nitrification does occur in the acid, waterlogged peats of the island and suggest that denitrification leads to a subsequent loss of at least some of the formed nitrate.

Maximum N mineralization rates measured by the plastic bag technique were much too low to account for N uptake by the mire-grassland vegetation, even if inputs through biological fixation and precipitation are also considered. This may be due to unaccounted-for denitrification losses or because soil macroinvertebrates, which possibly play an important part in decomposition/nutrient cycling on the island, were excluded from the plastic bags. We are currently measuring N_2O and N_2 evolution from the peats and are assessing whether soil

macroinvertebrates enhance nutrient mineralization rates enough to meet the requirements of the vegetation.

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