

## LESSER SNOW GEESE AND THE NITROGEN ECONOMY OF A GRAZED SALT MARSH

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### SUMMARY

(1) The acetylene-reduction technique was used to measure nitrogenase activity of surface sediments of a subarctic salt marsh, in order to estimate whether at least some of the nitrogen of forage plants that is incorporated into body tissues of a herbivore (lesser snow goose, *Chen caerulescens caerulescens*) is replaced by nitrogen fixation.

(2) Nitrogenase activity was consistently higher in grazed plots compared with rates in ungrazed plots. Estimates of total amounts of nitrogen fixed in grazed plots between June and September ('melt to freeze-up') were approximately  $1 \text{ g N m}^{-2}$ . Unlike ungrazed swards, where plant litter accumulated, mats of cyanobacteria were present on the surface of sediments between individual plants.

(3) Levels of exchangeable and soluble ammonium and nitrate ions were measured in sediments, in order to determine amounts of inorganic nitrogen available for plant growth. Levels of exchangeable and soluble ammonium ions were low (e.g.  $< 6 \mu\text{g}$  exchangeable  $\text{N-NH}_4 \text{ g dry wt}^{-1}$  sediment) throughout most of the growing season, but higher levels were detected in early spring and fall, particularly in grazed plots. Only trace amounts of nitrate ions were present in sediment extracts.

(4) A feedback model involving different aspects of the nitrogen cycle describes the strong interaction between the herbivore and salt marsh vegetation. The intense cropping of vegetation results in little accumulation of plant litter. Patches of sediment (c. 0.5 cm in diameter) are colonized by cyanobacteria that maintain the long-term input of nitrogen.

### INTRODUCTION

Shoots of graminoid plants usually contain between 0.9% and 4% of their dry weight as nitrogen. In contrast, animals not only have a higher nitrogen content (8–14% of body weight), but also excrete a significant fraction of their intake (Mattson 1980). Thus, obtaining adequate supplies of nitrogen and essential amino acids is a major problem for herbivores (McNeill & Southwood 1978). In addition, certain smaller herbivores, such as geese, require more nutritious and digestible foods than large herbivores, because of their limited ability to digest fibre (Demment & Van Soest 1983). The digestive strategy of geese eating graminoid plants is to ingest large amounts of forage without extracting most of the nutrients and energy from the food (Owen 1972, 1975; Sibly 1981). For example, the digestion by geese of total organic matter averaged 37% in the brant goose (*Branta bernicla* L.) and the Canada goose (*B. canadensis* L.), although the digestion of protein was between 61% and 80% (Buchsbau, Wilson & Valiela 1986). The lesser snow goose (*Chen caerulescens caerulescens* L.) digested approximately 64% of the total nitrogen in forage (Cargill & Jefferies 1984b).

A breeding colony of lesser snow geese feeds intensively on the salt marsh flats at La Pérouse Bay, Manitoba, Canada. The growth of vegetation is nitrogen-limited (Cargill &

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Jefferies 1984a). It is estimated that the maximum amount of nitrogen removed annually by the geese is about  $2.2 \text{ g m}^{-2}$ , most of which is incorporated in to the bodies of geese that fly south (Cargill & Jefferies 1984b). The export of nitrogen each year depletes the reservoir of this element in the salt marsh. The activities of the geese result in the accumulation of low amounts of plant litter (*c.*  $20 \text{ g m}^{-2}$ ), so that sediment is often visible between individual shoots of the two important forage species, *Puccinellia phryganodes* (Trin.) Scribn. and Merr and *Carex subspathacea* Wormsk (Cargill & Jefferies 1984a; Bazely & Jefferies 1986). Unlike ungrazed swards where plant litter accumulates, mats of cyanobacteria and green algae develop on the surface of the sediments, particularly in early spring. Certain species of cyanobacteria are known to fix atmospheric nitrogen (Sprent 1979; Postgate 1982).

An objective of this study was to determine whether rates of nitrogen fixation were higher in grazed than in ungrazed swards. A higher rate of fixation in grazed swards may compensate for nitrogen removed by the geese. Nitrogenase activity, an indicator of nitrogen fixation, was examined in grazed areas and in exclosures (ungrazed areas), with the use of the acetylene-reduction technique (Stewart, Fitzgerald & Burris 1967; Hardy *et al.* 1968). This method has been used to detect nitrogenase activity in temperate salt marshes (Jones 1974; Carpenter, Van Raalte & Valiela 1978; Patriquin & Keddy 1978; Patriquin & McClung 1978; Aziz & Nedwell 1979) and in arctic sites (Granhall & Selander 1973; Stutz & Bliss 1975; Stutz 1977; Alexander, Billington & Schnell 1978; Jordan, McNicol & Marshall 1978; Henry & Svoboda 1986).

Although certain species of cyanobacteria contribute to the input of nitrogen into salt marshes, the availability of this element for higher plant growth depends on its subsequent release in sediments as inorganic nitrogen. In the absence of  $^{15}\text{N}$  studies to detect the movement of this fixed nitrogen into higher plants, levels of exchangeable and soluble ammonium and nitrate ions were measured in sediments beneath grazed and ungrazed swards in order to determine amounts of inorganic nitrogen available for plant growth. The C/N ratios of the upper layers of sediment were also measured as they are known to affect rates of net mineralization of organic nitrogen (Alexander 1977; Atlas & Bartha 1981; Haynes 1986).

## MATERIALS AND METHODS

### *The site*

The tidal flats at La Pérouse Bay ( $58^{\circ} 04' \text{N}$ ,  $94^{\circ} 03' \text{W}$ ), 25 km east of Churchill, are colonized by *Puccinellia phryganodes* and *Carex subspathacea*, together with *Potentilla egedii* Wormsk., *Plantago maritima* L., *Ranunculus cymbalaria* Pursh. and *Stellaria humifusa* Rottb. (Jefferies, Jensen & Abraham 1979; Jefferies 1988). Approximately 7000 pairs of adult lesser snow geese and more than 15000 gosling graze intensively on the tidal flats and the adjacent sedge meadows during daylight hours from late June to mid-August when they begin their southward migration (Cooke *et al.* 1982). The demand for forage is high; goslings increase in weight from about 80 g when they hatch to 1500 g when fully fledged about seven weeks later.

### *Measurement of nitrogenase activity*

In 1984 nitrogenase activity of surface sediments was measured in grazed and ungrazed areas using the acetylene-reduction technique (Stewart, Fitzgerald & Burris 1967; Hardy *et al.* 1968). Round tubes (10 cm in diameter, 1.5 cm in depth) were cut and immediately

placed in inverted glass Mason jars, so that the lid rested on the sediment. From the upturned glass base a small glass tube protruded through which gases were introduced, or taken. The volume of air space inside a sealed jar was approximately 800 ml.

Experiments were conducted at two sites. The first site was situated on an island in a tidal lagoon where a four-year-old enclosure (5 m × 5 m, ungrazed plot) and an adjacent grazed plot were used. At the second site paired plots were located on the open tidal flats where an enclosure had been erected in 1981. The heavily grazed graminoid swards at both sites were dominated by *Puccinellia phryganodes*. The positions of selected turves and the placing of chambers were chosen at random.

Using copper-constantan thermocouples the difference between temperatures inside the chambers or jars and ambient air temperatures did not exceed 2°C. The Mason jars were placed in the shadow of a wooden board.

At the start of each incubation appropriate amounts of acetylene generated from calcium carbide were injected into a jar. Immediately following the addition of acetylene a sample of the vessel gas was taken in a 5-ml vacutainer (Becton-Dickinson Red Stopper, no additive; tubes no. 6434). Turves were incubated in jars for 3.5 hours before a sample was taken. Over this period a linear relationship between the amount of ethylene produced and the length of the incubation period was observed. Precautions taken included the incubation of turves and the collection of gas samples in the absence of acetylene, and the determination of background levels of ethylene in vacutainer tubes.

Vacutainers were returned to the field station. Samples of gas were withdrawn from each and injected into a portable field gas chromatograph (L & D Instruments, Melbourne, Australia) in order to determine the amounts of ethylene present. Using the appropriate corrections, nitrogenase activity was expressed as the amount of acetylene reduced  $\text{m}^{-2} \text{min}^{-1}$ , based on the difference between the initial and final amounts of ethylene in the incubation vessels.

Measurements of nitrogenase activity were made on six occasions between June and September on both the island and on the open tidal flats. Incubations were run in series between 08.00 and 20.00 h C.S.T. There were four replicate incubation jars for each treatment (grazed or ungrazed plots), as well as a jar to which no acetylene was added.

#### *Exchangeable and soluble levels of ammonium and nitrate ions in sediments and carbon/nitrogen ratios of sediments*

In 1983, amounts of exchangeable ammonium and nitrate ions in sediments were measured on a number of occasions between 20 June and 15 October for an ungrazed site (enclosure erected in 1981) and an adjacent grazed site on the open tidal flats. On each sampling date six blocks of sediment (2 cm × 2 cm × 7 cm) were cut at random from the surface layers of each of the two sites. After the fresh weights of the samples were determined in the field laboratory, they were incubated in 50 ml of 1 M potassium chloride for three 3 h (ratio 1:5 w/v). The solutions were filtered and the concentrations of ammonium ions in the extracts determined colorimetrically using the phenol-nitroprusside method (Solarzano 1969). Amounts of nitrate ions were also determined colorimetrically after reduction of nitrate to nitrite (Morris & Riley 1963). Additional samples of sediment were taken in order to obtain the fresh weight/dry weight ratio, as described above. The results were expressed as  $\mu\text{g N}$  of ammonium or nitrate ions per g dry weight of soil.

On the same dates, two water samples were squeezed from similar sediment blocks as described above. They were analysed for soluble ammonium and nitrate ions according to the methods described previously.

Five sediment blocks (10 cm × 10 cm × 10 cm) were taken at random from grazed and ungrazed swards (exclosures) dominated by *Puccinellia phryganodes* in July 1983. Layers of each block of sediment were cut every 2 cm down the profile, dried at 80°C and ground to a fine powder. A LECO analyser was used to determine percentages of carbon and nitrogen in a sample of powder from each layer of a block.

## RESULTS

### *Rates of acetylene reduction*

Nitrogenase activity, as measured by the rate of acetylene reduction, was higher in grazed sites (Fig. 1a, b). Overall, results from the island and marsh sites were similar, as were measurements made at different times of a day. In the grazed sites rates were between 0.5 and 1.0  $\mu\text{mol C}_2\text{H}_2$  reduced  $\text{m}^{-2} \text{min}^{-1}$ , except in early September when rates fell to less than 0.3  $\mu\text{mol C}_2\text{H}_2$  reduced  $\text{m}^{-2} \text{min}^{-1}$ . Nitrogenase activity was very much lower in ungrazed plots, especially in the exclosure on the tidal flats. With the exception of the dates mentioned above, rates were between 0.1 and 0.2 and 0.05 and 0.1  $\mu\text{mol C}_2\text{H}_2$  reduced  $\text{m}^{-2} \text{min}^{-1}$ , respectively, for the island exclosure and the exclosure on the tidal flats. At the end of July and the beginning of August, when high activities were recorded at the island site, air temperatures approached 30°C. Although day temperatures in September were comparable with temperatures that prevailed for much of the season, minimum air temperatures during the night fell sharply to 0°C with frequent ground frosts, and rates of ethylene production were considerably reduced.

Cyanobacteria were visible on the surface of sediments collected from grazed sites. *Oscillatoria* and *Lyngbya* species were common. Turves from the exclosure were examined, no mats of cyanobacteria were observed. A quantitative study of numbers of cyanobacteria in grazed plots and exclosures was not made.

### *Levels of exchangeable and soluble ammonium ions in sediments*

In 1983, initial amounts of exchangeable ammonium were significantly higher in the grazed site, at 13  $\mu\text{g}$  of N-NH<sub>4</sub> g dry wt<sup>-1</sup> of sediment, compared with 1.3  $\mu\text{g}$  N-NH<sub>4</sub> g dry wt<sup>-1</sup> in the sediments of the three-year-old exclosure (Fig. 2). However, from late June until early September, values for both plots were between 1 and 5.5  $\mu\text{g}$  of N-NH<sub>4</sub> g dry wt<sup>-1</sup> of sediment. A rise in the levels of exchangeable ammonium ions to 9.6 and 12.8  $\mu\text{g}$  of N-NH<sub>4</sub> g dry wt<sup>-1</sup>, respectively, in ungrazed and grazed sites occurred late in the season.

Figure 3 shows the concentrations of ammonium ions in interstitial water in sediments in grazed and ungrazed sites between June and mid-October 1983. The results have been expressed as  $\mu\text{g}$  N-NH<sub>4</sub> in soil water g<sup>-1</sup> of dried sediment, in order to compare the data with amounts of exchangeable ammonium ions in sediments. Seasonal trends follow results given in Fig. 2, although values are lower. In the exclosure, levels of ammonium ions in the water fluctuated between 0 and 2.0  $\mu\text{g}$  N-NH<sub>4</sub> g dry wt<sup>-1</sup> of sediment between June and September. Initial amounts in the grazed plot were 4–6  $\mu\text{g}$  N-NH<sub>4</sub> g dry wt of sediment; however, these fell rapidly in late June to values similar to those in ungrazed plots. In October levels increased again, reaching 5  $\mu\text{g}$  and 3.8  $\mu\text{g}$  N-NH<sub>4</sub> g dry wt<sup>-1</sup> of sediment, respectively, in grazed and ungrazed plots.

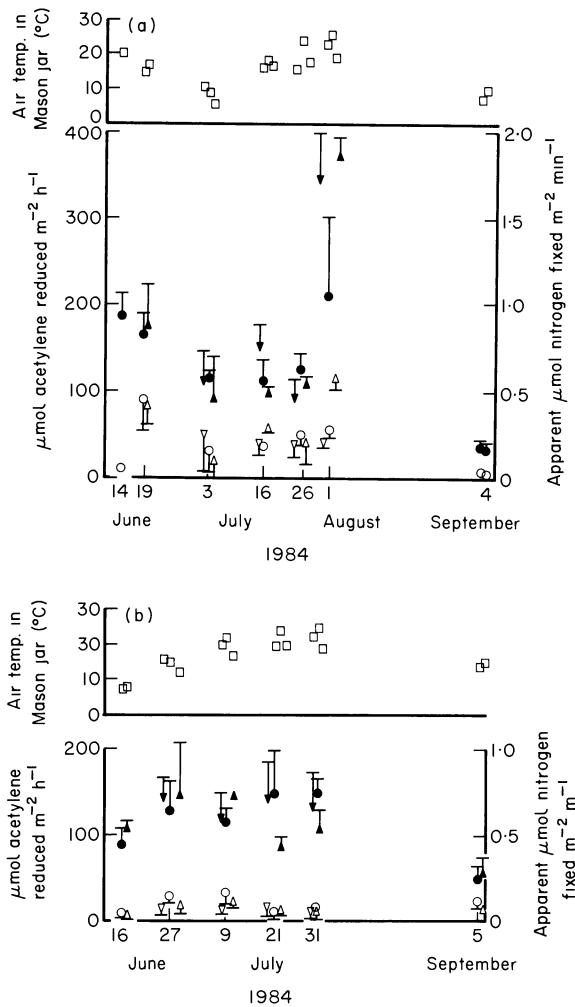


FIG. 1. Nitrogenase activity measured as rate of acetylene reduction ( $\mu\text{mol C}_2\text{H}_2$  reduced  $\text{m}^{-2} \text{ h}^{-1}$ ) and apparent rates of nitrogen fixation ( $\mu\text{mol N}_2$  fixed  $\text{m}^{-2} \text{ min}^{-1}$ ), of grazed (closed symbols) and ungrazed (open symbols) swards dominated by *Puccinellia phryganodes* on a tidal lagoon island (a) and a tidal salt marsh (b) at La Pérouse Bay, Manitoba in 1984. ( $\nabla, \nabla$ ), incubations from 08.00 to 11.30 h; ( $\bullet, \circ$ ), incubation from 12.00 to 15.30 h; ( $\blacktriangle, \triangle$ ), incubations from 16.00 to 19.30 h. Values are means  $\pm 1$  S.E.,  $n=4$ . Calculation of apparent rates of nitrogen fixation assumes a theoretical ratio between rates of acetylene reduction and nitrogen fixation of 3:1. Mean air temperature ( $n=8$ ) within incubation (Mason) jar is show in °C.

Concentrations of nitrate ions in the potassium chloride extracts and in the samples of interstitial water were extremely low. On most occasions the ion was not detected; in late summer and fall, concentrations barely rose above background levels but the differences were not significant.

The mean nitrogen contents of the sediments were less than 1% by weight (Table 1). In both grazed and ungrazed sites the percentages declined from 0.6 to 0.7 in the upper 2 cm to between 0.27 and 0.29 at a depth of 8–10 cm. There was a corresponding rise in the C/N

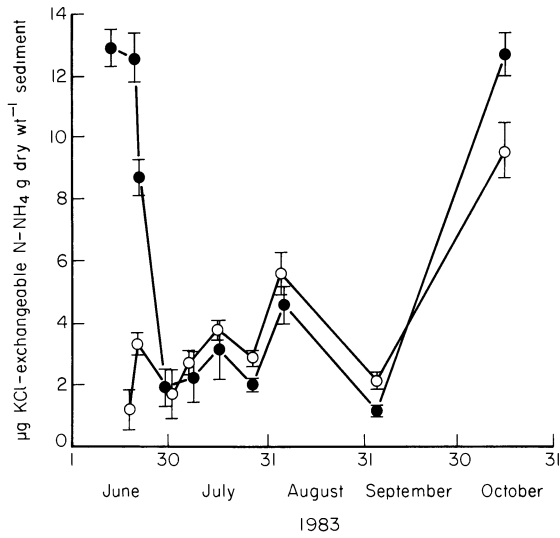


FIG. 2. Seasonal trends in levels of exchangeable ammonium ions ( $\mu\text{g N-NH}_4$  per g of dried sediment) beneath grazed (●) and ungrazed (○) swards of *Puccinellia phryganodes* in a salt marsh at La Pérouse Bay, Manitoba in 1983. Values are means  $\pm$  1 S.E.,  $n = 5$ . The ungrazed plot had not been grazed for three years.

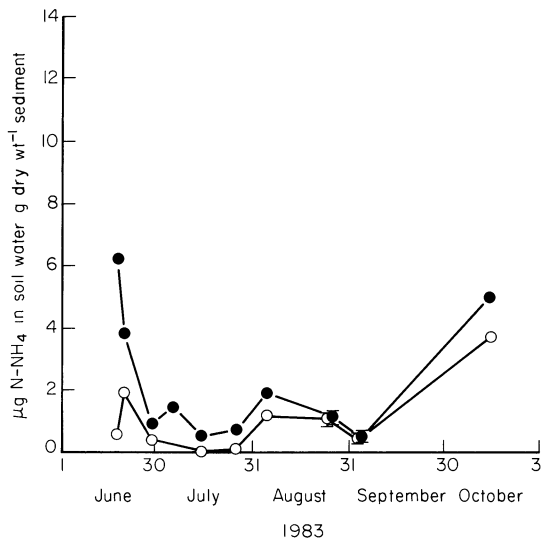


FIG. 3. Seasonal trends in levels of soluble ammonium ions in interstitial water of sediments ( $\mu\text{g N-NH}_4$  per g of dried soil) beneath grazed (●) and ungrazed (○) swards of *Puccinellia phryganodes* in a salt marsh at La Pérouse Bay, Manitoba in 1983. Values are means of two or three replicates. The ungrazed plot had not been grazed for three years.

TABLE 1. Mean C/N ratios and percentage nitrogen contents of sediments collected in July 1983 at different depths (cm) beneath grazed and ungrazed swards of *Puccinellia phryganodes* on the tidal flats at La Pérouse Bay, Manitoba (all values as means  $\pm$  1 S.E.,  $n=5$ ).

Depth (cm)	Ungrazed sward		Grazed sward	
	C/N ratio	% N	C/N ratio	% N
0-2	16.9 $\pm$ 0.2	0.7 $\pm$ 0.03	18.7 $\pm$ 1.0	0.6 $\pm$ 0.04
2-4	32.0 $\pm$ 0.9	0.4 $\pm$ 0.02	24.3 $\pm$ 1.8	0.4 $\pm$ 0.04
4-6	29.6 $\pm$ 1.2	0.3 $\pm$ 0.01	27.1 $\pm$ 1.7	0.3 $\pm$ 0.03
6-8	28.3 $\pm$ 1.3	0.3 $\pm$ 0.02	30.8 $\pm$ 1.9	0.3 $\pm$ 0.02
8-10	19.5 $\pm$ 1.8	0.3 $\pm$ 0.02	36.8 $\pm$ 5.1	0.3 $\pm$ 0.05

ratio of organic litter from 17-18:1 at the surface to a value greater than 29:1 at the base of the profile.

## DISCUSSION

Rates of acetylene reduction, particularly in grazed plots, were considerably higher than values recorded for high arctic sites (Stutz 1977; Alexander, Billington & Schnell 1978; Jordan, McNicol & Marshall 1978). They were in the same range as those recorded for algal mats in a subarctic mire in Sweden (Granhall & Selander 1973) and in the lower end of the range of values measured in temperate salt marshes (Jones 1974; Carpenter, Van Raalte & Valiela 1978; Patriquin & Keddy 1978; Patriquin & McClung 1978).

Rates of acetylene reduction discussed above are representative of sediment surfaces and not below-ground sediments. The surface of sediments in grazed sites at La Pérouse Bay is extensively colonized by species of *Oscillatoria* and *Lyngbya*. Some species of these genera are known to be diazotrophic under microaerophilic conditions (Sprent 1979; Postgate 1982) and in temperate salt marshes species of *Oscillatoria* and *Lyngbya* have been implicated as the main nitrogen-fixing organisms (Jones 1974; Patriquin & McClung 1978; Aziz & Nedwell 1979). Both Stutz (1977) and Jordan, McNicol & Marshall (1978) also reported the presence of members of the Oscillatoriaceae at Truelove lowland, Devon Island in the High Arctic in their investigations of nitrogen fixation.

Although there are obvious dangers in expressing the results of input of nitrogen (or rates of acetylene reduction) obtained from short-term incubations on a seasonal basis (Postgate 1982), such estimations have been attempted here for the period 14 June-30 September 1984 ('melt and spring run-off and freeze-up'). Results showed that there was little change in rates during each 12-hour period based on three consecutive incubations. In addition, when measurements were made over 24 h in early July, no significant differences were detected in rates for each incubation of four hours. Results of rates of acetylene reduction in grazed and ungrazed plots in 1983 were similar to those described for 1984, although fewer measurements were made during that season (Bazely 1984). The consistent pattern of results over the two years removes some of the uncertainties associated with extrapolations of this type. Estimates (June-September) of total amounts of nitrogen fixed are based on interpolation of the rates of acetylene reduction obtained on different occasions during the season. The estimates are also based on a 24-hour day, except they are adjusted for decreasing daylength in late August and September when darkness occurs, and when ground temperatures at night are close to or below 0 °C. Estimates of total amount of nitrogen fixed were 1.1 g (island) and 0.9 g (tidal flat) m<sup>-2</sup> for

grazed plots and 0.3 g (island) and 0.1 g (tidal flat)  $\text{m}^{-2}$  for ungrazed plots. The results indicate the higher input into grazed sites. Stewart (1965) estimated the annual nitrogen fixation on a rocky shore at  $2.5 \text{ g m}^{-2}$ . The value is similar to the estimate of Jones (1974) for a salt marsh in England, in which cyanobacteria are present for only part of the year. In the former case, desiccation limits algal growth on the rocky shore in summer and growth of higher plants in the salt marsh, such as *Puccinellia maritima*, restricts the development of algae. Estimates made by Jones (1974) are  $2.76 \text{ g N fixed m}^{-2}$  for *Salicornia* marsh and  $5.05 \text{ g N m}^{-2}$  for a *Puccinellia maritima* sward. The habitats are similar to La P erouse Bay in that growth of cyanobacteria is restricted to certain months of the year.

In the absence of  $^{15}\text{N}$  tracer studies, it was not possible to determine when the fixed nitrogen became available for plant growth. Jones (1974) demonstrated that a number of halophytic plants, including *Puccinellia maritima*, took up  $^{15}\text{N}$  which had been fixed initially by cyanobacteria. In the arctic and subarctic regions, the prevailing low temperatures restrict the activities of decomposers, so that plant litter tends to accumulate (Swift, Heal & Anderson 1979). However, not only were sediment temperatures between  $14^\circ\text{C}$  and  $25^\circ\text{C}$  at a depth of 1.0 cm in grazed sites for most of the summer (Bazely 1984), but also observations indicated that algal mats decomposed as the season progressed. It is likely that the high levels of exchangeable and soluble ammonium ions detected in sediments in spring and fall in grazed plots represent release of nitrogen from decomposing algae. The build-up of high levels in autumn associated with the input of ammonium nitrogen from organic nitrogenous substrates is maintained over the winter months when the sediments are frozen. In spring, additional mineralization may occur in the active layer, when warmer conditions allow the development of the appropriate microbial populations (Harmsen & van Schreven 1955). Both spring and autumn peaks in the levels of ammonium ions have been observed elsewhere (Davy & Taylor 1974). The depletion of exchangeable and soluble ions in the upper layers of sediment of grazed and ungrazed plots in summer is associated with the growth of higher plants.

The presence of nitrate ions in only trace amounts is probably related to depletion of exchangeable ammonium ions as a result of the uptake of this ion by plants. The  $K_m$  values for  $\text{NH}_4^+$  oxidation range from 1 to  $10 \text{ mg N l}^{-1}$  (Haynes 1986). The values are considerably greater than the concentration of ammonium ions in the sediments, hence *in situ* activities of populations of nitrifiers are likely to be limited by the low levels of ammonium ions (Haynes 1986). In addition, any nitrate ions produced are probably rapidly absorbed by plant roots. Net nitrification rates have been found to be high when the sediments were pulsed with ammonium ions in laboratory experiments (A. Jensen and R. L. Jefferies, unpublished data). Although rates of reduction of nitrate to ammonium ions were not measured, the rates were likely to be low as the soils were highly oxidized. Redox potentials were high in the upper layers of the sediments (Eh: 400–600 mV) in both grazed and ungrazed swards throughout the summer (Bazely 1984). Bohn (1971) indicates that at pH 7.0 nitrate is reduced in soils when the redox potential falls to about +225 mV. As indicated above, except for the very beginning of the season, corrected Eh measurements were considerably higher than this value.

The C/N ratio of organic material in the sediments is always greater than 16:1, and frequently above 25:1, and the total nitrogen content of the sediments is less than 0.7% by weight (Table 1). Harmsen & van Schreven (1955) and Campbell (1978) report that the generally accepted values for equilibrium between net rates of immobilization and mineralization of nitrogen are C/N ratios of 20–25:1 and a soil nitrogen content of



1.5–2.0%. Although there is a large range of variability in the critical percentages of nitrogen and in C/N ratios at which net immobilization gives way to net mineralization (Haynes 1986), the low nitrogen values, high C/N ratios and low levels of exchangeable ammonium ions taken together indicate that net immobilization predominates in the sediments.

Based on the growth response of *Puccinellia phryganodes* and *Carex subspathacea* to fertilizer, the production of the forage species appears to be nitrogen-limited (Cargill & Jefferies 1984a). Production of these species under the influence of grazing is sustained during the summer months by the input of soluble nitrogen, largely as ammonium ions, from faeces (Bazely & Jefferies 1985). The absence of any rise in the levels of exchangeable ammonium ions in sediments of grazed plots indicates that this additional source of soluble nitrogen is either being volatilized or taken up by the plants. Ruess & McNaughton (1987) also have suggested recently that increased rates of flow of nutrients in sediments via dung may be an important mechanism for maintaining high rates of nutrient cycling in the grazing food web on sites of low nutrient availability.

The geese therefore act on this ecosystem with high C/N ratios in the sediments by accelerating the breakdown and decomposition steps of the nitrogen cycle, thus providing a nitrogen source for forage species. Herbivory prevents the accumulation of litter which also allows cyanobacteria to colonize the sediment between grazed plants. These organisms fix an estimated 1.1 g of N m<sup>-2</sup> during the season, which replaces much of the nitrogen removed from the marsh by the geese (Cargill & Jefferies 1984b). The colonial foraging behaviour of the geese, which leads to intense cropping, is essential for maintenance of existing plant communities dominated by preferred forage species. This feedback system (Jefferies, Bazely & Cargill 1984) ensures that the supply of forage is adequate so that the geese can increase their body weight before the fall migration.

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