Nutrient limitation of plant growth and forage quality in Arctic coastal marshes

JACQUELINE T. NGAI* and ROBERT L. JEFFERIES

Department of Botany, University of Toronto, 25 Willcocks Street, Toronto, Ontario, Canada, M5S 3B2

Summary

1 Foraging by geese has led to vegetation loss in salt marshes along the Hudson Bay coast and lesser snow geese are increasingly grazing inland freshwater marshes. We determined whether different nutrients limit the growth of forage plants in the two habitats, and whether these differences affect the nutritional quality of vegetation available to geese at La Pérouse Bay, Manitoba.

2 Results from fertilization experiments indicate that primary productivity in the salt marsh is both nitrogen and phosphorus limited, whereas the freshwater marsh is phosphorus limited. Total amounts of calcium, magnesium and potassium in above-ground biomass per unit area showed similar differences in limitation.

3 Leaves of preferred forage species have higher nutrient concentrations (nitrogen, phosphorus, calcium, potassium, magnesium, sodium) and lower C : N and C : P ratios than alternative forage. The main forage species in the salt marsh (*Puccinellia phryganodes*) has higher nutrient content per unit mass, for nitrogen, magnesium, calcium and sodium, than the major freshwater marsh species(*Carex aquatilis*). The difference in nutritional quality of forage between the marshes is likely to have had consequences for goose fitness, and may have contributed to the reported declines in gosling survivorship and size.

4 At moderate grazing intensities, seasonal growth of salt-marsh forage is maintained by addition of nitrogen and, to a lesser extent, phosphorus from high numbers of goose faeces to swards. In contrast, the low densities and low phosphorus content of goose faeces in the phosphorus-limited freshwater marsh mean that plants are unlikely to recover rapidly from the effects of grazing. As a consequence, the freshwater marsh is likely to become increasingly less productive as foraging intensifies.

5 Nutrient gradients in vegetation across an ecotone and changes in foraging behaviour have resulted in adverse effects on both the growth rates of individuals and the population structure of a herbivore.

Key-words: geese, mineral nutrients, nitrogen, nutrient stoichiometry, phosphorus, wetland

Journal of Ecology (2004) **92**, 1001–1010

Introduction

Nutrient availability for plant growth is an important factor influencing primary production (Aerts & Chapin 2000) and the nutritional quality of forage for herbivores. Because of the variation in nutrient concentrations in plant tissues, herbivores forage selectively to meet their nutritional requirements (White 1993), and

Correspondence: R.L. Jefferies (fax +1 416 978 5878; e-mail jefferie@botany.utoronto.ca).
*Present address: Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, Canada V6T 1Z4.

forage quality has consequences for the survival and reproductive success of herbivores (Awmack & Leather 2002; Frost & Elser 2002; Sterner & Elser 2002). At a landscape level, selective foraging can take the form of differential habitat use (Frank *et al.* 1998; Augustine *et al.* 2003), in order to utilize pulses of food availability or patches of nutrient-rich foods. When habitat change occurs, herbivores may be forced to alter foraging patterns, which can be detrimental to their fitness. The effects are mediated by trophic linkages between nutrients, forage plants and herbivores.

At La Pérouse Bay and on the Cape Churchill Peninsula, Manitoba, a colony of lesser snow geese (*Chen caerulescens caerulescens* A.O.U.) breeds each summer.

Traditionally, these birds nested and fed in salt marshes on the shores of the Bay (Cooke *et al.* 1995). In recent decades, however, the lesser snow goose population has increased dramatically, largely in response to changes in agricultural practices on their wintering grounds and along their migration routes (Jefferies *et al.* 2003). These changes have allowed the birds to feed increasingly on agricultural products that are readily available and are of high nutritional quality (Jefferies *et al.* 2003). The mid-winter index counts of the mid-continent population of lesser snow geese, to which the population at La Pérouse Bay belongs, has increased from an estimated 0.78 million birds in 1970 to 2.7 million in 2002 (Canadian Wildlife Service Waterfowl Committee 2002; Kruse & Sharp 2002).

Foraging activities by this increasingly large population of birds has led to a substantial reduction in salt-marsh vegetation (Jefferies & Rockwell 2002) and to changes in soil properties that make re-vegetation increasingly difficult (Srivastava & Jefferies 1996; Handa *et al.* 2002). Consequently, forage has become scarce, forcing the birds to move inland to nearby freshwater marshes to nest and feed during the post-hatch period. Aquatic-based studies have suggested that primary production in freshwater and marine ecosystems may be limited by different nutrients, with freshwater primary productivity limited by phosphorus (P) and that in marine systems limited by nitrogen (N) (Vitousek & Howarth 1991). We use data on the differences in N : P stoichiometry in plant tissues (Koerselman & Meuleman 1996) and the results from fertilization experiments to examine the nutrient limitation of plant growth, and thus forage availability, in the salt and freshwater marshes, and to determine whether a switch in nutrient limitation exists between the marshes.

The declines in gosling survivorship and size that have been recorded at La Pérouse Bay in recent decades (Cooch *et al.* 1991b; Francis *et al.* 1992; Williams *et al.* 1993) are probably caused by a reduction in the amount of food available in the salt marsh (Cooch *et al.* 1991a,b; Williams *et al.* 1993). However, the quality of forage may also affect gosling size (Gadallah & Jefferies 1995b; Lepage *et al.* 1998), and this is especially important for herbivores with low digestion efficiency, such as geese, which depend on nutrient-rich forage in order to maximize their nutrient intake (Sedinger 1992). Hence, we first determined whether the geese preferentially foraged on plants possessing high nutrient concentrations and favourable C : N : P stoichiometry (Elser *et al.* 2000; Sterner & Elser 2002) by comparing these nutritional characteristics in preferred vs. less grazed (alternative) species, as well as in non-forage plants, in the two marsh types. The classification of species into preferred and alternative forage is based on long-term observations since 1978 of goose foraging behaviour during the post-hatch period and is not simply a reflection of the abundance of species. We then compared the nutritional quality of the main forage plant in the salt marsh with that in the freshwater marsh to determine

whether, with the shift in habitat use, the birds are receiving forage of lower quality. Because the availability of one nutrient can affect the uptake of another (e.g. Epstein 1972; Sheard 1974; Treseder & Vitousek 2001), we also examined whether N or P additions influence amounts of other nutrients in the standing crop. Finally, we consider whether nutrient limitation for both the herbivores and their forage plants has implications for the sustainability of increased foraging in freshwater habitats.

Materials and methods

SITE DESCRIPTION

The study sites are located at La Pérouse Bay (58°43′ N, 94°26′ W), Wapusk National Park, about 30 km east of Churchill, Manitoba. The intertidal salt marsh is on the shore of La Pérouse Bay, while the freshwater marsh is approximately 1.8 km further inland, beyond the high-water mark of spring tides. The dominant plant species in the salt marsh are *Puccinellia phryganodes* and *Carex subspathacea*, although dicotyledonous species such as *Potentilla egedii*, *Plantago juncoides* and *Ranunculus cymbalaria* colonize established swards of *P. phryganodes*. Nomenclature follows Porsild & Cody (1980). The vegetation in low-lying areas of the freshwater marsh consists of moss (mainly *Drepanocladus* spp. and *Scorpidium scorpioides*) and stands of *Carex* species, dominated by *Carex aquatilis*. On the higher hummocks, *Scirpus caespitosus* and *Dryas integrifolia* grow, as well as the low shrubs that include *Salix arctophila*, *S. reticulata*, *Rhododendron lapponicum* and *Empetrum nigrum*.

The salt marsh soil is classified as a Regosolic Static Cryosol, while the soil of the freshwater marsh is a Lithic-mesic Organic Cryosol (Agriculture Canada Expert Committee on Soil Survey 1987). In the upper 5 cm of the salt-marsh soil below the litter layer, total soil nitrogen and total soil phosphorus per unit soil volume are 3.72 ± 0.32 g N cm^{-3} (mean $\pm$ SEM) and 0.27 ± 0.15 g P cm^{-3}, respectively, under intact vegetation. Both total soil nitrogen and phosphorus are lower in the freshwater marsh ($N = 0.989 \pm 0.114$ g N cm^{-3}, $P = 0.031 \pm 0.008$ g P cm^{-3}, Ngai 2003).

EXPERIMENTAL DESIGN AND PLANT SAMPLING

A field factorial fertilization experiment was conducted, with three levels each of nitrogen and phosphorus. Nitrogen was added to plots as NH$_4$Cl and treatment levels were called 0N (0 g N m^{-2}), 1N (8.5 g N m^{-2}) and 2N (17 g N m^{-2}). Phosphorus was added as a mixture of the two salts, Na$_2$HPO$_4$·2H$_2$O and NaH$_2$PO$_4$·H$_2$O in equal amounts with respect to P, and the treatments were labelled 0P (0 g P m^{-2}), 1P (6 g P m^{-2}) and 2P (12 g P m^{-2}). The pH of a solution of the two phosphates was similar to that of the soil solution (about

pH 7). The above amounts of salts were applied twice during the growing season, in mid-June and mid-July, to appropriate areas. Herbivore exclosures, separated by 100 m, were established on *Puccinellia* swards in the salt marsh (*n* = 6) and in stands of *Carex aquatilis* in the freshwater marsh (*n* = 5). Within each exclosure, nine subplots were marked out and randomly assigned to one of the nine treatments. Freshwater marsh exclosures and subplots were 3 × 3 m and 80 × 80 cm, respectively, while in the salt marsh, exclosures were 2 × 2 m and treatment subplots were 50 × 50 cm. The sizes of exclosures and subplots were based on the different growth forms and densities of *Puccinellia phryganodes* and *Carex aquatilis* in the two marshes. A corridor of 10–20 cm was left between subplots to minimize treatment contamination between neighbouring subplots.

Above-ground plant biomass was sampled at the end of the growing season for both the salt marsh and the freshwater marsh fertilization experiments. In the salt marsh, a representative 7.5 × 7.5 cm turf was taken from each subplot, and the above-ground plant tissue removed at ground level, washed in deionized water and dried at 50 °C for a week. In the freshwater marsh, above-ground plant tissue was sampled by removing all tissue at ground level from a 20 × 20 cm section of each subplot. Live tissue was separated by species and then washed and dried as described above. Shoot densities of *Carex aquatilis* are lower than those of *Puccinellia phryganodes* so larger plot sizes were used for sampling in the freshwater marsh in order to obtain a more representative sample of the vegetation. All samples were transported to the University of Toronto for analysis. The growth response of mosses in the freshwater marsh to fertilization also was determined by taking a representative 10 × 10 cm turf from each subplot to ensure that any lack of response by the higher plants was not due to competition from mosses for added nutrients (Kotanen 2002). All samples of above-ground biomass were re-dried in Toronto and weighed to the nearest milligram.

In order to compare the N : P ratios of the leaf tissue of plants from the salt and freshwater marshes, plants of the primary forage species (*Puccinellia phryganodes*, *n* = 17, and *Carex aquatilis*, *n* = 19, respectively) were collected from early June to early August. These collections were independent of the experiment described above and of a comparison of preferred and alternative forage species, for which plants were collected approximately every 2 weeks over an area of about 5.7 km², between the beginning of June and the beginning of August, as plant phenology and their availability allowed. This sampling was restricted to ungrazed, live above-ground tissue and, whenever possible, three samples were taken at each collection. In total, seven alternative (*Calamagrostis deschampsioides*, *Carex aquatilis*, *Eriophorum angustifolium*, *Festuca rubra*, *Leymus mollis*, *Parnassia palustris* and *Potentilla egedii*) and eight preferred forage species (*Carex subspathacea*, *Chrysanthe-*

mum arcticum, *Dupontia fisheri*, *Plantago juncoides*, *Puccinellia phryganodes*, *Ranunculus cymbalaria*, *Triglochin maritima* and *Triglochin palustris*) were sampled. In addition, eight species not eaten by the geese in the post-hatch period (*Achillea nigrescens*, *Castilleja raupii*, *Hippuris tetraphylla*, *Menyanthes trifoliata*, *Potentilla palustris*, *Salicornia borealis*, *Scirpus caespitosus* and *Senecio congestus*) were collected. As with the samples from the experimental plots, plant tissue was washed in deionized water, dried and transported to Toronto for nutrient analysis.

NUTRIENT ANALYSIS

Before nutrient analysis, dried samples of live plant tissue were ground in a Wiley mill (mesh size 40, model A, Thomas Scientific, Swedesboro, USA). Carbon (C) and nitrogen concentrations in plant tissues were measured with the use of a CHN elemental analyser (Costech International S.l.r., Milan, Italy), while phosphorus concentrations (as phosphate) were determined using the molybdenum blue method (Ames 1966) following Kjeldahl digestion of tissue (Allen 1989). Calcium (Ca), sodium (Na), potassium (K) and magnesium (Mg) concentrations were measured using an atomic absorption spectrophotometer (model 3110, Perkin-Elmer, Rexdale, Ontario, Canada), in either the atomic-absorption or flame-emission mode.

DATA ANALYSIS

Biomass and nutrient data from the fertilization experiment were tested to ensure that assumptions of normality (Shapiro-Wilk test, $\alpha > 0.05$) and homogeneity of variance (Bartlett's test, $\alpha > 0.05$) were met, and data were transformed as needed. If data remained non-normal despite transformations, non-parametric tests were used. Biomass results were compared between the treatments using Tukey-Kramer tests (Sokal & Rohlf 1995). Full factorial two-way analyses of variance were run, with nitrogen and phosphorus treatments as fixed factors and exclosures as random blocks, to examine the effects of the treatments on biomass, as well as on the nutrient concentrations of the plant tissues (Sokal & Rohlf 1995). Stoichiometric differences between the two sites were examined using a Wilcoxon rank-sum test, as N : P data were non-normal. Similarly, two-way ANOVAs were performed to test for the effects of N or P availability on the quantity of other nutrients (Ca, Mg and K) present in the above-ground biomass. This quantity was calculated by multiplying the concentration of nutrients in plant tissue (g nutrient g^{-1} dry weight tissue) by the amount of biomass present per unit area (g dry weight m^{-2}).

Multivariate analyses of variance (MANOVA) were conducted to test for any effect of species (independent variable) on nutrient concentrations (dependent variables: N, P, K, Ca, Mg and Na), because multiple measurements (i.e. concentrations of several mineral nutrients)

were taken on one sample (Stevens 2002). Monocotyledons and dicotyledons were analysed separately because of the known differences in the nutrient concentrations of tissues of these two groups of plants (Aerts 1996). We have included data on the amounts of sodium in plant tissues, partly because some plants were collected from a saline environment, and partly because we were able to compare the data with an existing data base for some of the species (Gadallah & Jefferies 1995a). However, because C was considered a structural element rather than a nutrient, and there was little variation in the total amount of carbon per unit mass of plant tissue (44% to 46% of the dry weight), results for C were not included in the analyses. Nonstructural carbon is important in goose nutrition, but this component was not analysed separately. Although we later consider variation between species in C : N : P stoichiometry, differences in C : N and C : P ratios are largely due to variation in N and P concentrations and there is a non-significant effect of species on variation in C concentrations. When there was a significant effect of species on nutrient concentrations, linear contrasts were conducted to compare preferred vs. alternative forage species. Univariate analyses of variance (ANOVA) also were run for each nutrient, and for C : N and C : P ratios to determine if there was an effect of species on the nutritional characteristics of the tissues. Again, in the case of significant species effects, linear contrasts were conducted. Nutrient differences between field-collected plants of *Puccinellia phryganodes* and *Carex aquatilis* were tested separately for each nutrient using either a Student's *t*-test or Wilcoxon rank-sum test (Sokal & Rohlf 1995). All analyses were performed using JMP version 4.0.2 (SAS Institute, Cary, North Carolina).

Results

In the salt marsh, additions of either N or P alone significantly increased above-ground biomass levels above that of the control (Fig. 1a, Tukey-Kramer test, $\alpha = 0.05$). However, while the biomass in the N-alone treatments was slightly higher than that in the P-alone plots, the difference between these treatments was non-significant. When nutrients were added together, the resulting above-ground biomass was significantly higher than the biomass in any of the control, N-alone or P-alone treatments, with N being the most important element determining this response. A two-way ANOVA revealed that there was a significant effect of nitrogen treatments ($F_{2,40} = 119.30$, $P < 0.0001$), as well as a significant effect of the phosphorus treatments ($F_{2,40} = 64.78$, $P < 0.0001$). A significant N × P interaction also was observed ($F_{4,40} = 3.93$, $P = 0.01$).

In the freshwater marsh, in contrast, the above-ground plant biomass from N-alone plots (1N0P and 2N0P) was not different from the biomass of control plots, but when P was added, there was an increase in vascular plant biomass, irrespective of whether N was added as well (Fig. 1b). A two-way ANOVA showed that
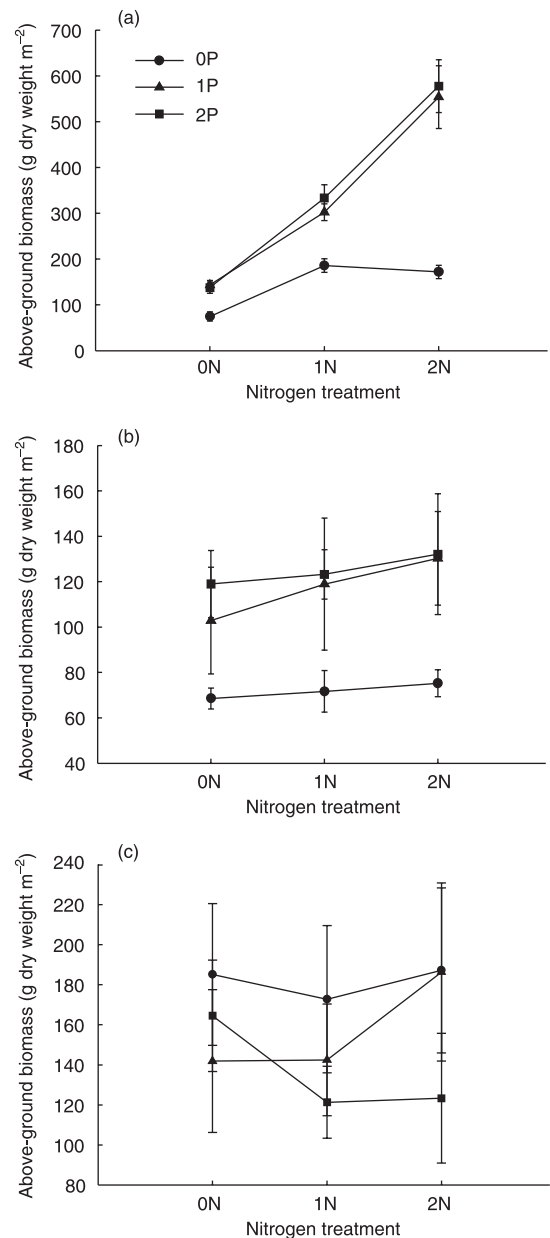

Fig. 1 (a) The main effects (nitrogen and phosphorus) plotted for the above-ground biomass of vascular plants in the salt marsh in response to additions of these fertilizers ($n = 6$, 50 days after the initial nutrient addition). (b) The response of the vascular plants and (c) moss in the freshwater marsh ($n = 5$, 40 days after the initial nutrient addition). Zero, one unit of N or P, or two units of these elements were added to field plots in a factorial design (see text for amounts added). The experiments were conducted at La Pérouse Bay, Manitoba.

there was a significant effect only for the P treatments ($F_{2,32} = 16.47$, $P < 0.0001$), while the N effect ($F_{2,32} = 1.01$, $P = 0.38$) and N × P interaction ($F_{4,32} = 0.22$, $P = 0.92$) were non-significant. Similar results were obtained for moss biomass (Fig. 1c), except that the trend for the P treatments was non-significant (P, $F_{2,32} = 2.69$, $P = 0.08$; N, $F_{2,32} = 0.64$, $P = 0.53$; N × P, $F_{4,32} = 0.81$, $P = 0.53$).

In the salt marsh, both N and P treatments significantly increased amounts of other nutrients (Ca, K, Mg)

Table 1 Statistical analysis of the effects of nitrogen and phosphorus additions on the total amounts of calcium, potassium and magnesium in above-ground biomass of *Puccinellia phryganodes* (salt marsh) and *Carex aquatilis* (freshwater marsh) expressed on a per unit area basis. ***$P < 0.0001$, **$P < 0.01$, *$P < 0.05$ (two-way ANOVA with N and P as fixed factors and exclosure as a random factor)

	Nutrient	Factor	d.f.	*F* ratio	Significance level
Salt marsh	Ca	N	2,40	42.45	***
		P	2,40	31.53	***
		N × P	4,40	4.35	**
		Exclosure	5,40	3.08	
	K	N	2,38	56.13	***
		P	2,38	56.84	***
		N × P	4,38	6.78	**
		Exclosure	5,38	1.56	
	Mg	N	2,40	70.61	***
		P	2,40	45.42	***
		N × P	4,40	2.12	
		Exclosure	5,40	1.56	
Freshwater marsh	Ca	N	2,32	0.59	
		P	2,32	12.67	***
		N × P	4,32	2.49	
		Exclosure	4,32	2.74	
	K	N	2,32	0.10	
		P	2,32	19.07	***
		N × P	4,32	0.34	
		Exclosure	4,32	1.48	
	Mg	N	2,32	3.24	
		P	2,32	17.12	***
		N × P	4,32	0.51	
		Exclosure	4,32	5.70	**

in shoots of *Puccinellia phryganodes* when expressed on a per unit area basis (Table 1). In the case of Ca and K, there were also significant N × P interactions. Only P treatments significantly increased the amounts of Ca, K and Mg held in the above-ground biomass of *Carex aquatilis* in the freshwater marsh.

For the survey of forage and non-forage species, there was a significant effect of species on nutrient concentrations in leaf tissue of plants collected from the salt and freshwater marshes, both for monocotyledons ($F_{50,240.52} = 4.96$, $P < 0.0001$) and dicotyledons ($F_{55,332.23} = 11.10$, $P < 0.0001$). There also was a significant difference between alternative and preferred forage species (Fig. 2; monocotyledons, $F_{5,52} = 7.71$, $P < 0.0001$; dicotyledons, $F_{5,71} = 12.66$, $P < 0.0001$). In monocotyledons, preferred forage species had higher P, K and Na concentrations (Table 2), and in dicotyledons, concentrations were higher in the preferred forage species for N, P, Mg, K and Na compared with alternative species. Preferred dicotyledonous forage species had significantly higher concentrations of Ca, Mg and Na than non-forage species ($F_{5,71} = 11.17$, $P < 0.0001$). Because only one non-forage monocotyledon was collected, statistical comparisons between preferred and non-forage monocotyledons were not possible.

Leaf tissue of unfertilized *Puccinellia* plants collected from the control plots in the salt marsh had higher amounts of N, Mg, Na and Ca per unit tissue weight than comparable values for leaves of *Carex aquatilis*

(Fig. 3; Student's *t*-test, $\alpha = 0.01$). *Carex aquatilis* had significantly higher K concentrations (Student's *t*-test, $P = 0.019$), but P concentrations were not significantly different from those in leaves of *Puccinellia phryganodes* (Wilcoxon rank-sum test, $P = 0.37$). Similarly, carbon amounts per unit mass of tissue were slightly higher in *Carex aquatilis* (458.65 ± 0.84 mg C g^{-1} dry weight tissue vs. 452.25 ± 3.42) but this difference was non-significant (Student's *t*-test, $P = 0.16$).

Differences between species were found for both C : N and C : P ratios (Table 3, Fig. 4) in monocotyledons ($F_{10,103} = 6.28$, $P < 0.0001$ and $F_{10,100} = 7.40$, $P < 0.0001$, respectively) and dicotyledons ($F_{11,83} = 3.80$, $P = 0.0002$ and $F_{11,83} = 3.74$, $P = 0.0002$, respectively). Preferred forage species had lower C : N and C : P ratios than alternative species for both monocotyledons (C : N, $F_{1,103} = 18.68$, $P < 0.0001$; C : P, $F_{1,100} = 20.14$, $P < 0.0001$) and dicotyledons (C : N, $F_{1,83} = 11.82$, $P = 0.0009$; C : P, $F_{1,83} = 11.73$, $P = 0.0009$). Although there was a significant effect of species on N : P ratios (monocotyledons, $F_{10,100} = 6.54$, $P < 0.0001$; dicotyledons, $F_{11,83} = 4.49$, $P < 0.0001$), overall, preferred and alternative forage species did not differ significantly in their N : P ratios, either for monocotyledons ($F_{1,100} = 0.96$, $P = 0.33$) or dicotyledons ($F_{1,20} = 1.29$, $P = 0.26$). Non-forage dicotyledons did not differ from preferred dicotyledons in any of the nutrient ratios (N : P, $F_{1,83} = 0.30$, $P = 0.59$; C : N, $F_{1,83} = 0.0015$, $P = 0.97$; C : P; $F_{1,83} = 0.12$, $P = 0.75$).

Table 2 Results of univariate ANOVAs and linear contrasts comparing nutrient concentrations in leaf tissue in preferred vs. alternative, or non-forage species collected from salt and freshwater marshes in the coastal zone of La Pérouse Bay, Manitoba

|			N	P	Ca	Mg	K	Na
Monocotyledons	Species	d.f.	11,83	11,83	11,75	11,75	11,75	11,75
		F ratio	5.21	2.94	13.53	14.09	5.21	47.92
		P	< 0.0001	0.0025	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Contrasts	Preferred vs. alternative	d.f.	1,83	1,83	1,75	1,75	1,75	1,75
		F ratio	2.81	4.07	0.37	2.89	4.15	29.61
		P	0.098	0.0047	0.54	0.091	0.042	< 0.0001
Dicotyledons	Species	d.f.	11,83	11,83	11,75	11,75	11,75	11,75
		F ratio	3.54	2.94	13.53	14.09	5.21	47.93
		P	0.00040	0.0025	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Contrasts	Preferred vs. alternative	d.f.	1,83	1,83	1,75	1,75	1,75	1,75
		F ratio	5.28	7.05	0.24	15.81	7.72	72.26
		P	0.024	0.0095	0.62	0.00016	0.0069	< 0.0001
	Preferred vs. non-forage	d.f.	1,83	1,83	1,75	1,75	1,75	1,75
		F ratio	0.0091	0.30	10.54	9.39	0.74	62.44
		P	0.92	0.58	0.0017	0.0030	0.39	< 0.0001
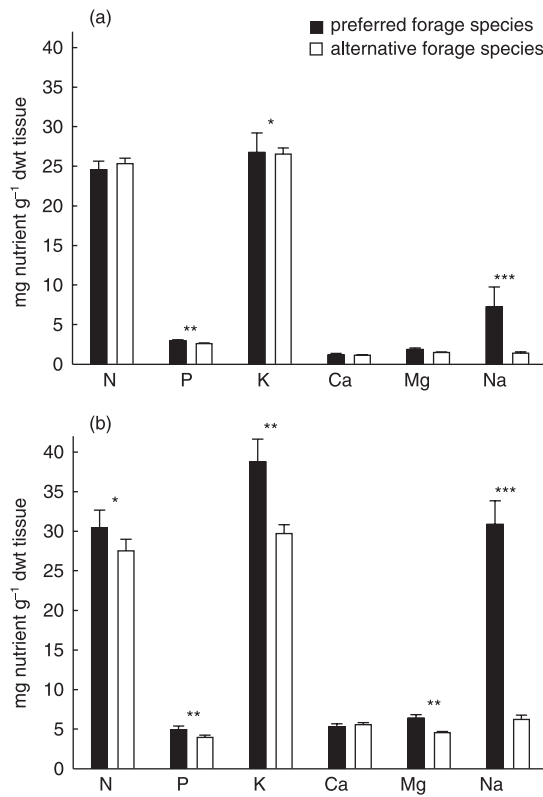
Fig. 2 Nutrient concentrations in leaf tissue (means ± SE) of preferred and alternative (a) monocotyledonous forage species (*n* = 43 and 66 for preferred and alternative species, respectively) and (b) dicotyledonous forage species (*n* = 22 and 20 for preferred and alternative species, respectively). ***P < 0.0001, **P < 0.01, *P < 0.05 (linear contrasts following ANOVA). Shoot tissue was collected from early June to early August from plants growing in the salt and adjacent freshwater marshes in the coastal zone of La Pérouse Bay, Manitoba.

Fig. 3 Comparison between the foliar nutrient concentrations (means ± SE) of the main salt marsh forage species (*Puccinellia phryganodes*, *n* = 17) and the main freshwater marsh forage species (*Carex aquatilis*, *n* = 19) in the coastal zone of La Pérouse Bay, Manitoba. Results are from field-collected plants. ***P < 0.0001, **P < 0.01, *P < 0.05 (Student's *t*-tests for N, K, Ca, Mg and Na, and Wilcoxon rank-sum test for P).

marsh (N : P ratios of 29.33 ± 1.74 and 18.27 ± 0.52, respectively; Wilcoxon rank-sum test, *U* = 180, *P* < 0.0001).

Discussion

The salt and freshwater marshes were found to differ in the responses of the vegetation to additions of nitrogen and phosphorus and in the elemental concentrations of the above-ground plant tissues. In addition, they differ in the overall nutritional quality of forage present at each site. The fertilization experiments indicated that both N and P limit plant growth in the salt marsh, although the system is closer to P saturation than to N saturation. In contrast, plant growth in the freshwater marsh is constrained by phosphorus availability, with added nitrogen having little effect on plant growth. This pattern of greater N limitation in the salt marsh

Based on nutrient data from field-collected plants, *Carex aquatilis*, the major forage species from the freshwater marsh, had a significantly higher N : P ratio (by atom) than *Puccinellia phryganodes* from the salt
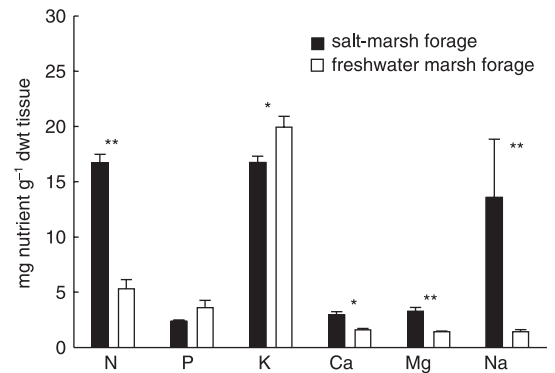
Table 3 C : N : P ratios for above-ground biomass of forage and non-forage plants (mean ± SE). Ratios are given by atom. The habitat in which the species is found is also indicated: intertidal salt marsh (I), supratidal salt marsh (ST) and freshwater marsh (FW). Plant tissues were collected from early June to early August from salt and freshwater marshes at La Pérouse Bay, Manitoba

		C : N		C : P		N : P	
	Habitat	Mean	SE	Mean	SE	Mean	SE
Achillea nigrescens	ST	16.89	2.86	265.30	43.67	15.72	0.08
Calamagrostis deschampsioides	ST	26.94	3.92	823.51	187.67	34.51	9.24
Carex aquatilis	FW	20.03	0.63	501.24	20.89	25.89	1.41
Carex subspathacea	I	18.80	2.10	405.61	52.38	21.88	2.10
Castilleja raupii	ST	18.13	1.59	188.50	13.05	10.91	0.85
Chrysanthemum arcticum	I	17.46	1.15	218.99	15.39	12.64	0.58
Dupontia fisheri	FW	27.45	5.29	335.18	51.60	12.58	1.03
Eriophorum angustifolium	FW	22.55	1.71	385.73	27.43	18.22	1.77
Festuca rubra	ST	24.62	1.64	490.31	49.67	19.87	1.40
Hippuris tetraphylla	ST	14.58	0.53	303.48	26.27	20.85	1.68
Leymus mollis	ST	24.81	1.61	491.07	37.09	19.85	0.92
Menyanthes trifoliata	FW	13.69	0.74	234.99	31.84	16.88	1.41
Parnassia palustris	ST	21.07	1.40	360.58	45.63	17.07	1.86
Plantago juncoides	I	18.64	1.40	322.08	38.44	16.95	1.49
Potentilla egedii	I	19.71	1.47	316.20	31.50	15.98	0.94
Potentilla palustris	I	15.32	0.62	239.36	14.94	15.52	0.54
Puccinellia phryganodes	I	23.38	0.84	430.98	15.20	18.57	0.54
Ranunculus cymbalaria	I	10.51	1.21	171.57	33.69	16.00	1.76
Salicornia borealis	I	10.70	1.49	150.26	19.39	14.11	0.51
Scirpus caespitosus	FW	24.93	0.23	1347.16	28.23	54.06	1.61
Senecio congestus	I	18.33	1.97	288.13	35.00	16.11	1.23
Triglochin maritima	ST	13.25	1.24	239.18	22.18	18.13	0.75
Triglochin palustris	I	16.03	1.93	460.81	112.41	27.32	3.96

and P limitation in the freshwater marsh is supported by the results of the N : P ratios for the plant tissue collected as part of the field survey, with shoots of the freshwater *Carex aquatilis* having significantly higher N : P ratios than those of *Puccinellia phryganodes* in the salt marsh.

Both N and P limitation have been observed in salt marshes (e.g., N, Pigott 1969; Valiela & Teal 1974; Kiehl *et al*. 1997; P, Tyler 1967), while freshwater meadows dominated by *Carex* species have shown varying degrees of N- and P-limited plant growth (Shaver & Chapin 1980; Verhoeven & Schmitz 1991; Bowman *et al*. 1993; Shaver *et al*. 1998). Our findings are consistent with a switch from N-limited plant growth in marine-influenced sites to P limitation in freshwater areas, as has been found in lake fertilization experiments (Hecky & Kilham 1988). Although Kotanen (2002) and Malmer *et al*. (2003) have found that mosses can compete with plants for added nutrients, we found only a non-significant biomass response by the freshwater mosses to P addition and no response to N. This suggests that the lack of response by *Carex aquatilis* to N fertilization does not reflect the unavailability of nitrogen due to its competitive uptake by mosses.

At high foraging intensities, a positive feedback involving increased evaporation from sediment exposed by heavy feeding by geese has led to increased soil salinity and loss of vegetation (Srivastava & Jefferies 1996). Before the large increase in the goose population, how-ever, the productivity of this plant-herbivore system was maintained by a different positive feedback in the salt marsh, whereby goose grazing increased plant productivity at low to moderate grazing pressures (Cargill & Jefferies 1984b). This enhancement of productivity was largely possible because faecal deposits left by the grazing birds greatly increased the amount of nitrogen that was readily available to the plants at a time when nitrogen supplies in the soil were reduced due to plant growth (Cargill & Jefferies 1984a; Bazely & Jefferies 1985; Hik & Jefferies 1990). This allowed *Puccinellia* to show compensatory growth following grazing, resulting in the greater availability of forage for the herbivores. However, a similar growth response of forage plants to faecal deposits from feeding geese has not been detected in freshwater marshes (Gauthier *et al*. 1995; Beaulieu *et al*. 1996). Gauthier *et al*. (1995) and Kotanen (2002) have suggested that this lack of response may be due to the effect of competition by mosses for nitrogen. In this study, we find that phosphorus, rather than nitrogen, limits primary productivity of vascular plants in the freshwater marsh, and this result may help to explain the poor response of *Carex* stands to deposits of nitrogen from geese.

Both nitrogen and phosphorus additions had significant effects on the total amounts of calcium, magnesium and potassium in above-ground biomass expressed on a unit area basis in the salt marsh. In contrast, only phosphorus treatments led to an increase in the
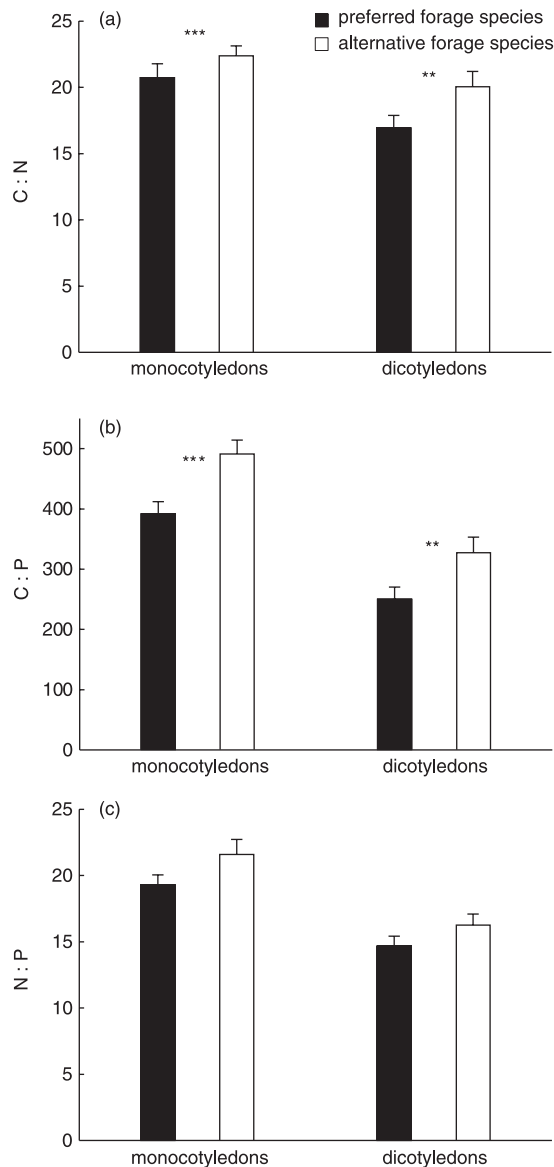
Fig. 4 (a) C : N, (b) C : P and (c) N : P ratios (by atom, means ± SE) in leaf tissue of preferred and alternative forage species collected from salt and freshwater marsh species at La Pérouse Bay, Manitoba. Data are given separately for monocotyledonous species ($n = 43$ for preferred, $n = 66$ for alternative) and dicotyledonous species ($n = 22$ for preferred, $n = 20$ for alternative). ***$P < 0.0001$, **$P < 0.01$, *$P < 0.05$ (linear contrasts following ANOVA).

amounts of these other nutrients in the standing crop per unit area in the freshwater marsh. This reflects the biomass response to nutrient additions at each site: treatments that stimulated plant growth also resulted in a greater amount of nutrients being held in the above-ground tissue because of the biomass increase.

Preferred forage species had similar or higher nutrient concentrations in tissue than did alternative forage species, as well as lower C : N and C : P ratios, suggesting that the nutritional quality of forage may influence goose foraging patterns. In contrast, although preferred forage had higher concentrations of some nutrients than those species that were not eaten by the geese,

C : N : P stoichiometries were similar, and the lack of clear trends suggests that other factors such as species abundance or plant secondary compounds may also play a role in determining foraging preferences. For example, the tissue of the non-forage species *Potentilla palustris* contains high concentrations of both tannins and alkaloids (Jung *et al*. 1979). The nutrient concentrations in the plant tissues are comparable with previous findings for northern graminoids (Chapin *et al*. 1975; Gadallah & Jefferies 1995a), and are generally higher than, or comparable with, those found in surveys of plant nutrient concentrations conducted in other geographical areas (e.g. Thompson *et al*. 1997; Fitter *et al*. 1998; Aerts & Chapin 2000; Ohlson & Staaland 2001). However, calcium and magnesium concentrations in plant tissue at La Pérouse Bay were substantially lower than those reported at an alpine site, although nitrogen, phosphorus and potassium concentrations were comparable (Körner 1989). The nutrient ratios found for the forage species at La Pérouse Bay were slightly below average values determined for a wide range of species (Fitter *et al*. 1998; Elser *et al*. 2000).

Puccinellia phryganodes, the main salt-marsh forage, has significantly higher concentrations of most nutrients in leaf tissues than does *Carex aquatilis* (Fig. 3, Gadallah & Jefferies 1995a). This means that, assuming a similar intake rate, herbivores are able to gain more nutrients per bite while grazing in the salt marsh. However, preliminary observations indicate a much lower peck rate on *Carex aquatilis* (10–20 per minute) than on *Puccinellia* (100–120 per minute) because of the low shoot density and the different plant growth forms. Shoots of the sedge can grow 50 cm high, whereas those of the grass are less than 5 cm in height. Hence, in spite of the larger bite size (two to three times greater), the intake rate appears to be lower when the geese are feeding on the poorer quality sedge leaves. Because egg reserves of lesser snow geese can only sustain newly hatched goslings for several days at the most (Ankney 1980), the birds must rely heavily on the local forage for their pre-fledging growth, and forage quality in the breeding grounds is critical in determining gosling size at the end of the growing season. Gosling size at the end of their first summer of life can substantially affect post-fledging survivorship (Owen & Black 1989; Van der Jeugd & Larsson 1998) and adult size, which in turn influences fecundity (Sedinger *et al*. 1995).

We show that the freshwater marsh has forage that is considerably lower in quality than the salt marsh forage, for most nutrients. This indicates that the quality of food obtained by the geese has been decreasing as the geese increasingly move from the salt marsh to the freshwater marshes. In particular, calcium and magnesium, which are important for skeletal formation (Robbins 1983), and nitrogen, which is critical for tissue production (Klasing 1998), are significantly lower in the new habitat. Even for nutrients, such as phosphorus, which are present in similar amounts in *Carex aquatilis* and *Puccinellia*, the lower peck rate of geese

on *Carex* also would result in reduced intake rates of this element. This lower intake of nutrients per bite may contribute to the decline in gosling size recorded at La Pérouse Bay (Cooch *et al*. 1991b). It is possible that the poorer nutritional quality of the freshwater forage may provide a negative feedback that limits the growth of the goose population. However, this seems unlikely given that the birds appear to be further expanding the area of habitat that they exploit, perhaps in order to maintain sufficient forage intake on the poorer quality forage in the freshwater marsh. Family groups have been observed feeding as far as the forest-tundra zone of the boreal forest, 15–20 km south of La Pérouse Bay.

The freshwater marshes of the Hudson Bay Lowlands are many orders of magnitude larger than the coastal salt marshes, hence much of the available forage is presently unexploited by the geese. However, it is probable that the local freshwater marshes adjacent to the degraded salt marsh will not be able to support the feeding activities of the increased numbers of geese in the long term. As indicated earlier, the P content of the soils is an order of magnitude lower than that of the salt marsh sediments. The deleterious effects of intensive snow goose feeding may be exacerbated by the minimal ability of the freshwater plants to respond to fertilization from faecal input. Given that these stands are P limited in terms of growth, any fertilizing effect of feeding geese will not be able to assist plants in recovering from biomass removal, as amounts of phosphorus in goose faeces are low and dropping densities are much less than those on intertidal swards (freshwater marsh, $0–10 \text{ m}^{-2}$ season^{-1}; salt marsh, $50–300 \text{ m}^{-2}$ season^{-1}). Values for the P content of faeces were only 1.5 ± 0.14 mg P (mean $\pm$ SEM) and 1.45 ± 0.18 mg P g^{-1} dwt of faeces, respectively ($n = 3$), when captive goslings were fed on a diet of either *Carex aquatilis* or *Puccinellia phryganodes* in feeding trials conducted in 1993 (see Gadallah & Jefferies 1995b for methods, protocol and sampling procedures). Hence, it is likely that the primary productivity of the grazed freshwater marshes will decrease with increased use by the geese as a consequence of nutrient depletion.

Acknowledgements

References

Aerts, R. (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology*, **84**, 597–608.

Aerts, R. & Chapin, F.S. III (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*, **30**, 1–67.

Agriculture Canada Expert Committee on Soil Survey (1987) *The Canadian System of Soil Classification*, 2nd edn. Agriculture Canada, Ottawa, Canada.

Allen, S.E. (1989) *Chemical Analysis of Ecological Materials*, 2nd edn. Blackwell Scientific, Oxford.

Ames, B.N. (1966) Assay of Inorganic Phosphate, Total Phosphate and Phosphatases. *Methods in Enzymology*. Volume 8: *Complex Carbohydrates* (eds E.F. Neufeld & V. Ginsburg), pp. 115–118. Academic Press, New York.

Ankney, C.D. (1980) Egg weight, survival, and growth of lesser snow goose goslings. *Journal of Wildlife Management*, **44**, 174–182.

Augustine, D.J., McNaughton, S.J. & Frank, D.A. (2003) Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecological Applications*, **13**, 1325–1337.

Awmack, C.S. & Leather, S.R. (2002) Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology*, **47**, 817–844.

Bazely, D.R. & Jefferies, R.L. (1985) Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. *Journal of Applied Ecology*, **22**, 693–703.

Beaulieu, J., Gauthier, G. & Rochefort, L. (1996) The growth response of graminoid plants to goose grazing in a High Arctic environment. *Journal of Ecology*, **84**, 905–914.

Bowman, W.D., Theodose, T.A., Schardt, J.C. & Conant, R.T. (1993) Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology*, **74**, 2085–2097.

Canadian Wildlife Service Waterfowl Committee (2002) *Population Status of Migratory Game Birds in Canada: November 2002*. Canadian Wildlife Service Migratory Birds Regulatory Report no. 7. Canadian Wildlife Service, Ottawa.

Cargill, S.M. & Jefferies, R.L. (1984a) Nutrient limitation of primary productivity in a sub-arctic salt marsh. *Journal of Applied Ecology*, **21**, 657–668.

Cargill, S.M. & Jefferies, R.L. (1984b) The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. *Journal of Applied Ecology*, **21**, 669–686.

Chapin, F.S. III, Van Cleve, K. & Tieszen, L.L. (1975) Seasonal nutrient dynamics of tundra vegetation at Barrow, Alaska. *Arctic and Alpine Research*, **7**, 209–226.

Cooch, E.G., Lank, D.B., Dzubin, A., Rockwell, R.F. & Cooke, F. (1991a) Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. *Ecology*, **72**, 503–512.

Cooch, E.G., Lank, D.B., Rockwell, R.F. & Cooke, F. (1991b) Long-term decline in body size in a snow goose population: evidence of environmental degradation? *Journal of Animal Ecology*, **60**, 483–496.

Cooke, F., Rockwell, R.F. & Lank, D.B. (1995) *The Snow Geese of La Pérouse Bay*. Oxford University Press, Oxford.

Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A. *et al.* (2000) Nutritional constraints in terrestrial and freshwater food webs. *Nature*, **408**, 578–580.

Epstein, E. (1972) *Mineral Nutrition of Plants*. John Wiley and Sons, New York.

Fitter, A.H., Wright, W.J., Williamson, L., Belshaw, M., Fairclough, J. & Meharg, A.A. (1998) The phosphorus nutrition of wild plants and the paradox of arsenate tolerance: does leaf phosphate concentration control flowering? *Phosphorus in Plant Biology* (eds J.P. Lynch & J. Deikman), pp. 39–51. American Society of Plant Physiologists, Rockville, Maryland.

Francis, C.M., Richards, M.H., Cooke, F. & Rockwell, R.F. (1992) Long-term changes in survival rates of lesser snow geese. *Ecology*, **73**, 1346–1362.

Frank, D.A., McNaughton, S.J. & Tracy, B.F. (1998) The ecology of the earth's grazing ecosystems. *Bioscience*, **48**, 513–521.

Frost, P.C. & Elser, J.J. (2002) Growth responses of littoral mayflies to the phosphorus content of their food. *Ecology Letters*, **5**, 232–240.

Gadallah, F.L. & Jefferies, R.L. (1995a) Comparison of the nutrient contents of the principal forage plants utilized by lesser snow geese on summer breeding grounds. *Journal of Applied Ecology*, **32**, 263–275.

Gadallah, F.L. & Jefferies, R.L. (1995b) Forage quality in brood rearing areas of the lesser snow goose and the growth of captive goslings. *Journal of Applied Ecology*, **32**, 276–287.

Gauthier, G., Hughes, R.J., Reed, A., Beaulieu, J. & Rochefort, L. (1995) Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *Journal of Ecology*, **83**, 653–664.

Handa, I.T., Harmsen, R. & Jefferies, R.L. (2002) Patterns of vegetation change and the recovery potential of degraded areas in a coastal marsh system of the Hudson Bay lowlands. *Journal of Ecology*, **90**, 86–99.

Hecky, R.E. & Kilham, P. (1988) Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. *Limnology and Oceanography*, **33**, 796–822.

Hik, D.S. & Jefferies, R.L. (1990) Increases in the net aboveground primary production of a salt marsh forage grass: a test of the predictions of the herbivore optimization model. *Journal of Ecology*, **78**, 180–195.

Jefferies, R.L., Henry, H.A.L. & Abraham, K.F. (2003) Agricultural nutrient subsidies to migratory geese and ecological change to Arctic coastal habitats. *Food Webs at the Landscape Level* (eds G.A. Polis & M.A. Power). University of Chicago Press, Chicago, Illinois.

Jefferies, R.L. & Rockwell, R.F. (2002) Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science*, **5**, 7–16.

Jung, H.G., Batzli, G.O. & Seigler, D.S. (1979) Patterns in the phytochemistry of Arctic plants. *Biochemical Systematics and Ecology*, **7**, 203–209.

Kiehl, K., Esselink, P. & Bakker, J.P. (1997) Nutrient limitation and plant species composition in temperate salt marshes. *Oecologia*, **111**, 325–330.

Klasing, K.C. (1998) *Comparative Avian Nutrition*. CAB International, Wallingford.

Koerselman, W. & Meuleman, A.F.M. (1996) The vegetation N : P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology*, **33**, 1441–1450.

Körner, C. (1989) The nutritional status of plants from high altitudes. *Oecologia*, **81**, 379–391.

Kotanen, P.M. (2002) Fates of added nitrogen in freshwater arctic wetlands grazed by snow geese: the role of mosses. *Arctic, Antarctic and Alpine Research*, **34**, 219–225.

Kruse, K.L. & Sharp, D.E. (2002) *Central Flyway Population Survey Databook*. Office of Migratory Bird Management, US Fish and Wildlife Service, Denver, Colorado.

Lepage, D., Gauthier, G. & Reed, A. (1998) Seasonal variation in growth of greater snow goose goslings: the role of food supply. *Oecologia*, **114**, 226–235.

Malmer, N., Albinsson, C., Svensson, B.M. & Wallén, B. (2003) Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. *Oikos*, **100**, 469–482.

Ngai, J. (2003) *Nutrient limitation of plant growth and forage quality in Arctic coastal marshes*. MSc thesis, University of Toronto, Toronto.

Ohlson, M. & Staaland, H. (2001) Mineral diversity in wild plants: benefits and bane for moose. *Oikos*, **94**, 442–454.

Owen, M. & Black, J.M. (1989) Factors affecting the survival of barnacle geese on migration from the breeding grounds. *Journal of Animal Ecology*, **58**, 603–617.

Pigott, C.D. (1969) Influence of mineral nutrition on the zonation of flowering plants in coastal salt-marshes. *Ecological Aspects of the Mineral Nutrition of Plants* (eds I.H. Rorison, A.D. Bradshaw, M.J. Chadwick, R.L. Jefferies, D.H. Jennings & P.B. Tinker), pp. 25–35. Blackwell Scientific, Oxford.

Porsild, A.E. & Cody, W.J. (1980) *Vascular Plants of Continental Northwest Territories, Canada*. National Museum of Canada, Ottawa.

Robbins, C.T. (1983) *Wildlife Feeding and Nutrition*. Academic Press, New York.

Sedinger, J.S. (1992) Ecology of prefledging waterfowl. *Ecology and Management of Breeding Waterfowl* (eds B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec *et al.*), pp. 109–127. University of Minneapolis Press, Minneapolis, Minnesota.

Sedinger, J.S., Flint, P.L. & Lindberg, M.S. (1995) Environmental influence on life-history traits: growth, survival, and fecundity in black Brant (*Branta bernicla*). *Ecology*, **76**, 2404–2414.

Shaver, G.R. & Chapin, F.S. III (1980) Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. *Ecology*, **61**, 662–675.

Shaver, G.R., Johnson, L.C., Cades, D.H., Murray, G., Laundre, J.A., Rastetter, E.B. *et al.* (1998) Biomass and CO_2 flux in wet sedge tundras: responses to nutrients, temperature, and light. *Ecological Monographs*, **68**, 75–97.

Sheard, R.W. (1974) Nitrogen enhancement of surface applied fertilizer phosphorus uptake by forage species. *Canadian Journal of Soil Science*, **54**, 89–104.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. W.H. Freeman, New York.

Srivastava, D.S. & Jefferies, R.L. (1996) A positive feedback: herbivory, plant growth, salinity and the desertification of an Arctic salt-marsh. *Journal of Ecology*, **84**, 31–42.

Sterner, R.W. & Elser, J.J. (2002) *Ecological Stoichiometry*. Princeton University Press, Princeton, New Jersey.

Stevens, J.P. (2002) *Applied Multivariate Statistics for the Social Sciences*, 4th edn. Lawrence Erlbaum Associates, Mahwah, New Jersey.

Thompson, K., Parkinson, J.A., Band, S.R. & Spencer, R.E. (1997) A comparative study of leaf nutrient concentrations in a regional herbaceous flora. *New Phytologist*, **136**, 679–689.

Treseder, K.K. & Vitousek, P.M. (2001) Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests. *Ecology*, **82**, 946–954.

Tyler, G. (1967) On the effect of phosphorus and nitrogen, supplied to Baltic shore-meadow vegetation. *Botaniska Notiser*, **120**, 433–447.

Valiela, I. & Teal, J.M. (1974) Nutrient limitation in salt marsh vegetation. *Ecology of Halophytes* (eds R.J. Reimold & W.H. Queen), pp. 547–563. Academic Press, New York.

Van der Jeugd, H.P. & Larsson, K. (1998) Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. *Journal of Animal Ecology*, **67**, 953–966.

Verhoeven, J.T.A. & Schmitz, M.B. (1991) Control of plant growth by nitrogen and phosphorus in mesotrophic fens. *Biogeochemistry*, **12**, 135–148.

Vitousek, P.M. & Howarth, R.W. (1991) Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry*, **13**, 87–115.

White, T.C.R. (1993) *The Inadequate Environment*. Springer-Verlag, Berlin.

Williams, T.D., Cooch, E.G., Jefferies, R.L. & Cooke, F. (1993) Environmental degradation, food limitation and reproductive output: juvenile survival in lesser snow geese. *Journal of Animal Ecology*, **62**, 766–777.