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A positive feedback: herbivory, plant growth, salinity, and the desertification of an Arctic salt-marsh

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Summary

1 A 2-year study is described which suggests that a positive feedback process results in the destruction of salt-marsh swards and the exposure of bare sediments at La Pérouse Bay, Manitoba, Canada. Lesser snow geese initiate the process by grubbing for roots and rhizomes of salt-marsh graminoids (*Puccinellia phryganodes* and *Carex subspathacea*) in spring. The increased rates of evaporation from sediments beneath disturbed or destroyed swards in summer result in high soil salinities that adversely affect the growth of the remaining grazed plants.

2 Above-ground biomass and soil salinity differed between sites in the salt marsh. Soil salinity was inversely related to above-ground biomass and shoot density of *Puccinellia phryganodes*. Increased biomass led to reduced soil salinity at sites where exclosures were erected.

3 Plant growth, measured as the rate of leaf births on *Puccinellia* shoots, was reduced by high soil salinities at sites where exclosures were erected.

4 Leaf demography of transplanted experimental plants of *Puccinellia* differed in 1992, but not 1991, between plants transplanted into sites with different amounts of above-ground biomass. Leaf births and deaths were highest for plants grown in sites where above-ground biomass was high and lowest for plants transplanted into bare sites. Grazing had no effect on leaf demography in 1991 and only marginally increased the rate of leaf deaths in 1992.

5 Growth of transplanted individuals of *Carex subspathacea* was similarly highest at sites where the standing crop of *Puccinellia* and *Carex* was high and was lowest in bare sites.

6 Algal crusts, which formed on bare or poorly vegetated sites, also reduced the growth of *Puccinellia* plants.

7 The effects of this deleterious positive feedback on plant growth are discussed in relation to changes occurring in the lesser snow goose colonies at La Pérouse Bay and elsewhere.

Keywords: geese, graminoids, grazing, halophytes, Hudson Bay, shoot and leaf demography, standing crop

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Introduction

Changes in the abundance of a keystone species may result in abrupt and rapid changes in plant populations, species assemblages and ecosystem processes (Paine 1980; Mann 1982; Bertness 1984; Power 1990; Kerbes *et al.* 1990; Strong 1992). Positive feedback processes frequently bring about these changes

(DeAngelis *et al.* 1986; Power 1992; Wilson & Agnew 1992). This study examines the effects of intensive foraging by a keystone herbivore, the lesser snow goose (*Anser caerulescens caerulescens* L.), which results in the progressive destruction of salt-marsh vegetation via a positive feedback that produces soil conditions inimical for plant growth.

Lesser snow geese, which use the North American Central and Mississippi flyways and breed in the eastern Canadian Arctic, have increased from 1.2 million to almost two million birds between 1973 and 1989 (Boyd *et al.* 1982; Cooch *et al.* 1989). At La Pérouse

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Bay, Manitoba, a colony of lesser snow geese has grown from 2000 breeding pairs in 1968 (Cooke *et al.* 1982) to 23 000 breeding pairs in 1992 (R.H. Kerbes unpublished aerial photographic census data) and has expanded its geographical range on the Cape Churchill peninsula (Cooch *et al.* 1993). Other snow goose colonies on the west coast of Hudson Bay (Kerbes *et al.* 1990) and at Cape Henrietta Maria in Ontario (K.R. Abraham, unpublished data) have shown a comparable increase in numbers and in the geographical extent of the colonies. The rapid expansion in numbers of the greater snow goose (*Anser caerulescens atlantica* L.) also has considerably increased grazing pressure on arctic vegetation (Gauthier *et al.* 1995).

A consequence of increased numbers of birds in the region is that foraging on salt-marsh vegetation has intensified over the last decade (Jefferies 1988a,b; Iacobelli & Jefferies 1991). Faecal densities on salt-marsh swards at La Pérouse Bay, which are an index of the intensity of foraging, have increased between 1982 and 1990 from $< 1 \text{ m}^{-2} \text{ week}^{-1}$ to about $10 \text{ m}^{-2} \text{ week}^{-1}$ during the snow-free season (R. L. Jefferies, unpublished data). The foraging includes both grubbing and grazing by the geese. Grubbing for roots and rhizomes of graminoid species by both staging birds and the local population of breeding geese in spring results in the destruction of salt marsh swards (Jefferies 1988b).

Both the area of salt marsh covered by intact graminoid swards and the above-ground biomass of these swards have decreased over the last decade at La Pérouse Bay. Between 1985 and 1989, the area covered by intact swards decreased by 50% along permanent transects totalling 800 m in length (R. L. Jefferies, unpublished data). Between 1979 and 1991, above-ground biomass of intact swards decreased from about 50 g m^{-2} to about 25 g m^{-2} (Williams *et al.* 1993). Similar decreases in vegetational cover have been documented for other salt-marshes grazed by lesser snow geese on the west coast of Hudson Bay (Kerbes *et al.* 1990).

Inland from the salt marsh at La Pérouse Bay, extensive grubbing by geese around *Salix* bushes in spring has led to exposure of dark peaty soil, increased surface soil temperatures and increased soil salinity (Iacobelli & Jefferies 1991). The high soil salinities have then caused the death of the *Salix* bushes (Iacobelli & Jefferies 1991). High goose numbers not only reduce graminoid biomass of the salt-marsh swards by intensive foraging, but also may trigger long-term edaphic processes responsible for the decline in salt-marsh graminoid vegetation via a positive feedback process.

A positive feedback occurs 'when the response of a system to an initial deviation of a system acts to reinforce the direction of change' (DeAngelis *et al.* 1986). Intense grazing and extensive grubbing by geese appear to trigger salt-marsh destruction. The

decreased above-ground biomass results in increased soil evaporation rates, and the deposition of salts in the upper layers of sediment. The resultant high salinities can limit the growth and survival of plants, thereby further reducing above-ground biomass and exposing more soil surface which lead to further increases in evaporation and soil salinity. Other processes, such as the formation of thick algal crusts on the surface of sediments and soil erosion may also reduce plant growth and survival, and contribute to this positive feedback cycle.

Validation of this positive feedback between soil salinity and the salt-marsh graminoid vegetation at La Pérouse Bay requires that: (1) a reduction of the graminoid sward should result in an increase in soil salinity and (2) increased soil salinity leads to reduced graminoid growth. Together, these lead to a third proposal, that graminoid growth per shoot system will be lower in areas of reduced biomass. These predictions were tested, by experimental manipulations in the field at La Pérouse Bay during the summers of 1991 and 1992.

Methods

STUDY SITE AND SPECIES

The eastern salt marsh at La Pérouse Bay ($58^{\circ}04'N$, $94^{\circ}03'W$), Manitoba, is dominated by swards of two short (*c.* 2 cm tall) non seed-setting graminoids, *Puccinellia phryganodes* (Trin.) Scribn. & Merr and *Carex subspatheae* Wormsk. *Puccinellia* is both the more abundant and the more salt tolerant (Srivastava & Jefferies 1995a,b) of the two species. Both species undergo extensive clonal growth, with *Puccinellia* producing stolons from axillary shoots and *Carex* tillers from underground rhizomes.

DEMOGRAPHY OF *Puccinellia* PLANTS IN AREAS OF HIGH AND LOW BIOMASS IN 1991

Field methods

Growth of *Puccinellia phryganodes* was examined at sites differing in the amount of above-ground biomass and in soil salinity in a *c.* 300-m \times 400-m area of salt-marsh on the eastern shore of the bay. This area was inundated by tides only in late August after the experiment was complete. Sites were divided into two categories of biomass subjectively (Srivastava & Jefferies 1995b): low biomass ($\approx 25 \text{ g dry matter m}^{-2}$ in mid-summer) and high biomass ($\approx 50 \text{ g dry matter m}^{-2}$ in mid-summer), and into three categories of salinity which formed a continuum of increasing salinity.

In early June 1991 after snow melt, 1-m \times 1-m plots were established in high biomass and low biomass areas and the salinity of the water in the top 1 cm of soil in each area was measured on 15 August 1991 (cf. Srivastava & Jefferies 1995b) using an automated flame emission spectrophotometer (Perkin

Elmer Model 3110). Four categories of plots were recognized *a posteriori* based on the sodium concentration in extracted soil water: high biomass with 0–2 g L⁻¹ Na⁺, low biomass with 0–2 g L⁻¹ Na⁺, low biomass where the sodium concentration was 2–4 g L⁻¹ Na⁺, and low biomass with 4–8 g L⁻¹ Na⁺. Seven plots of each type were monitored. In addition, shoot density (shoots cm⁻²), above-ground biomass (g m⁻²) of *Puccinellia*, and gravimetric water content (g_{water} g_{dry soil}⁻¹) were also measured on one randomly selected grazed turf from each category (Srivastava & Jefferies 1995b).

Although the effects of soil salinity and biomass on plant growth was the primary focus of this study, results from previous investigations indicated that grazing (Bazely & Jefferies 1989) and plant origin (Sadul 1987) were important determinants of *Puccinellia* growth. A multifactorial design was used to examine the relative importance of all of these factors, and their interactions. Two plants originating from a high biomass and two from a low biomass sward were transplanted into each of the 28 plots to determine whether plants from a certain biomass type were adapted to local conditions characteristic of the site where that biomass type was present. At each plot, one plant of each biomass type was exclosed from goose grazing by poultry netting (50 cm × 50 cm; 2.5 cm mesh). Each of the 28 plots (four categories × seven replicates) therefore had four plants representing one of each possible combination of origin (high biomass, low biomass) and grazing level (grazed, exclosed). All plants (*c.* 2.5 cm in length) were transplanted on 6 June 1991 and were identified by colour-coded toothpicks inserted in the soil adjacent to the transplant.

Plant growth was assessed using a nondestructive demographic method. Leaves (*c.* 8 mm in length), each identified by a code of one to three small Indian ink dots, were individually monitored during the growing season. At each census, the condition (alive, senescing or dead), size (emergent or full sized), and grazing history (intact or grazed) of existing leaves and the birth of new leaves and shoots were recorded. Leaves with noticeable yellowing of 30–70% of the surface area were classed as senescing, and those less than 2 mm long as emergent. The demography of plants was scored on the following five census dates: 11–13 June, 25–28 June, 9–10 July, 24–25 July, and 7–9 August. Plants in plots were examined in the same randomized order on all census dates.

Leaf birth rates (number of leaves produced during the study period divided by days of the study) and death rates were calculated for the main shoot of each plant, the combined axillary shoots of each plant, and the total shoots of each plant (main + axillary shoots). Senescent leaves present at the end of the study period were scored as equivalent to half a leaf death, and emergent leaves as equivalent to half a leaf birth. These values were summed as appropriate.

The calculated demographic parameters included data from plants that died, otherwise estimates would be biased towards healthy plants. Mortality values are presented for comparison.

Statistical analysis

The demographic (Kirk 1982; Day & Quinn 1989) experiment was analysed with a three-way ANOVA. The experiment was designed with seven plots nested within four treatment levels, and with each plot crossed with two grazing levels and two plant origins. Each possible grazing and origin combination within a plot were represented by four plants; demographic data were averaged over these plants to avoid the possibility of pseudoreplication. The dependent variables for the ANOVA analysis are the six demographic variables: main shoot leaf births, main shoot leaf deaths, axillary shoot leaf births, axillary shoot leaf deaths, and total (main + axillary shoots) leaf births and deaths (note that count data were used for this analysis because of expectations of a Poisson error structure, although in the figures we present rate data to enable comparison with the 1992 results). The main shoot leaf birth and death data were normally distributed with homogeneous variances (Shapiro–Wilks test, Bartlett's test, $P > 0.05$), so ANOVA analyses were straightforward. The axillary shoot, and hence total plant demography data, contained numerous zero values, and so we used log-linear models to relate the values of the dependent variables to their linear predictors in an ANOVA with Poisson errors and a log link (Crawley 1993). Planned comparisons used the F statistic for data with normal errors, and the χ^2 statistic for data with Poisson errors. The above analyses were performed using GLIM software (version 4.0, NAG Ltd, Oxford).

The effect on soil salinity of exclosure from geese was examined for each biomass category separately using a two-way (grazing treatment × time since exclosure) ANOVA. Salinity data (g Na⁺ L⁻¹) were log-transformed to reduce correlations between means and variances.

DEMOGRAPHY OF *Puccinellia* PLANTS IN HIGH BIOMASS, LOW BIOMASS AND BARE AREAS IN 1992

Field methods

Analysis of the 1991 results led us to change some procedures for 1992. Plant growth was examined in sites which included unvegetated 'bare' sites, as well as high biomass and low biomass sites. In addition, biomass, soil salinity, and other soil variables at sites were examined throughout the season rather than only at the end of the season.

Each of three biomass categories (high biomass, low biomass, bare sediment) was represented by four sites widely placed within the same study area as used

in 1991. Each site contained 22 *Puccinellia* plants transplanted in 50-cm × 50-cm areas in each of two adjacent plots; one plot of which was exclosed by poultry netting (1 m × 1 m) to exclude geese. The centres of the adjacent areas were at most 90 cm apart, so all plants within a site experienced similar edaphic conditions. Unlike the design in 1991 which had a few plants at many sites, this design had many plants at a few sites. Since plant origin was found to have a minor contribution to variance in 1991, all plants had the same origin, a 1-m² area of a high biomass *Puccinellia*-*Carex* sward.

The plots for each biomass category were selected to represent the average soil salinity of that biomass category (determined from independent sites, see Srivastava & Jefferies 1995b). Since soil-water salinity is uniform between sites in the early spring, plants were transplanted into six plots per biomass category. Four plots per biomass category were selected from these six plots on 12 July, when salinity differences between biomass categories were evident. The salinity of the soil water in the upper 1 cm of a 10-cm × 10-cm block of soil was measured with a salinity/conductivity meter (Yellow Springs Instrument Co., OH, model 33).

Plants were transplanted on 20–22 June 1992. The very late spring precluded earlier planting. The demography of the transplanted plants was examined, using methods described earlier, on three census dates about 17 days apart: 30 June–2 July, 16–19 July, and 3–4 August. Most plants did not produce axillary shoots. Therefore, leaf birth and death rates of axillary shoots were not calculated. Total leaf birth and death rates were calculated, and are similar in value to corresponding values for the main shoot. Uneven sample size, caused by the removal of a few plants by geese, was corrected by randomly selecting 18 plants per plot for analysis.

A block of soil (c. 8 cm × 8 cm × 4 cm deep) was removed from each of the exclosed and grazed plots at all sites on 26 June, 12 July, 21 July and 30 July. Care was taken not to disturb or affect transplanted plants by soil removal. From each soil block, above-ground biomass ($g_{\text{dry wt}} m^{-2}$), sodium concentration of extracted soil-water ($g L^{-1}$), gravimetric water content ($g_{\text{water}} g_{\text{dry soil}}^{-1}$), bulk density ($g_{\text{dry soil}} cm^{-3}$), and redox potential (Eh values) were determined, as described elsewhere (Srivastava & Jefferies 1995b). Plots were exclosed from 26 June, the first date of soil sampling, so this date represents pre-exclosure conditions.

Statistical analysis

The experiment was designed to be analysed by a three-way ANOVA, with four plots nested in each of three biomass categories, all crossed by two grazing treatments (grazed, exclosed). The seasonal demographic data of total leaf births and deaths, however, had unequal variances and were not normally dis-

tributed, even after numerous transformations. This was largely due to extensive mortality in low biomass and bare sites. On many plants no new leaves were produced and all the original (2–3) leaves died, both of which led to low variances in the data. Data were therefore analysed by the nonparametric Friedman's test (version for replicated designs, chi-squared statistic; Gibbons 1985). Since Friedman's test is appropriate only for two-way designs, sites of all three biomass categories were examined together in a site ($k = 12$) by grazing treatment design. Once a significant plot effect was established, the effect of biomass category could be examined by a planned comparison between plots of each biomass category.

DEMOGRAPHY OF *Carex* PLANTS IN HIGH BIOMASS AND BARE AREAS IN 1992

Given that *Carex* is more sensitive to salinity than *Puccinellia* (Srivastava & Jefferies 1995a), it was expected that its growth would be at least as reduced between high biomass and bare sites as that of *Puccinellia*. *Carex* plants, originating from a 1-m² area of sward, were transplanted into the grazed area of each of the high biomass and bare sites ($n = 25$ per site): they were interspersed among the previously described *Puccinellia* plants. Growth was measured using the same methods as for *Puccinellia*.

DEMOGRAPHY OF *Puccinellia* IN BARE AREAS WITH AND WITHOUT ALGAL CRUSTS IN 1992

Three 1-m × 2-m sites were selected with a uniform, thick, blistering and dry algal crust on the sediment surface. Sites were ≈ 100 m apart and were exclosed from grazing with poultry netting. At each site, the algal crust was carefully removed with a scalpel from 28 circles of 10 cm diameter. The distance between the centres of adjacent circles was at least 22 cm.

A total of 150 individual *Puccinellia phryganodes* plants of similar size were isolated from a 15-cm × 20-cm turf, in order to minimize genetic variability among *Puccinellia phryganodes* plants (cf. Sadul 1987). On 6 July 1992, one *Puccinellia* plant was transplanted into the centre of each circle from which the crust was removed, save three circles per site which were reserved for soil sampling (described below). In addition, a total of 25 plants per site were planted in an intact algal crust between the circles and at least 15 cm from the centre of the nearest circle ($n = 25$ plants per treatment per site).

Growth of the transplanted *Puccinellia* plants was measured using demographic techniques described earlier. Census dates were 13 days apart, on 7 July, 20 July, and 2 August 1992. Since virtually no plants produced axillary shoots, only the demographic parameters of total leaf birth and total leaf death rate were calculated. Non-parametric statistical analyses were used for data of leaf birth and death rates, since

these data were both non-normally distributed (Shapiro–Wilks test, $P < 0.01$) and had heterogeneous variances (Bartlett's test, $P < 0.05$).

On 27 July, 7-cm \times 7-cm \times 4-cm-deep blocks of soil were collected from each of the three remaining circles per site and under the adjacent intact algal crusts. Redox potentials (Eh values), from just below the subsurface to a depth of 2 cm, were determined by the use of a platinum electrode for each soil sample. The top 1 cm of soil of each sample was used for soil salinity, soil bulk density and gravimetric water content measurements as described earlier.

Results

SOIL SALINITY IN SITES OF DIFFERENT BIOMASS

The soil salinity of sites was inversely related to the amount of graminoid vegetation (measured as above-ground biomass or shoot density) in both 1991 and 1992 (Fig. 1). High biomass plots were thus less saline than low biomass plots, which in turn were less saline

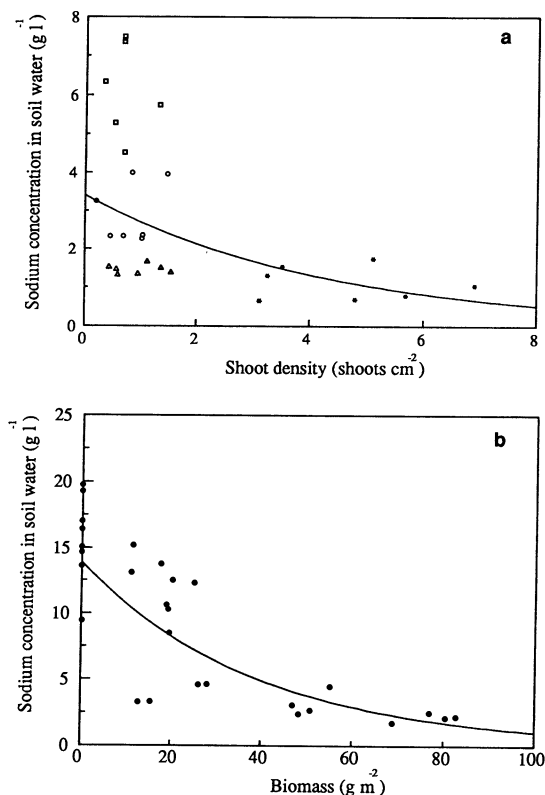


Fig. 1 (a) Sodium concentration in soil water as a function of shoot density of sites on 15 August 1991. Sites were divided into four treatment categories for analysis: The regression line ($r = -0.61$) was calculated for a logarithmic form of sodium concentration. Low biomass sites had a soil-water salinity of either 0–2 (Δ), 2–4 (\circ) or 4–8 (\square) $\text{g L}^{-1} \text{Na}^+$, and high biomass sites ($*$) had a soil-water salinity of 0–2 $\text{g L}^{-1} \text{Na}^+$. (b) Sodium concentration (\bullet) in soil water as a function of site biomass for sites in 1992 (average data for season used). The regression line ($r = -0.85$) was calculated for a logarithmic form of sodium concentration.

than bare plots (Table 1; a more detailed analysis is in Srivastava & Jefferies 1995b). These differences in soil salinity between biomass categories are maintained over most of the growing season (Srivastava & Jefferies 1995b).

Such a correlation between soil salinity and biomass does not necessitate a causal link. To test if biomass reduces soil salinity, we used goose grazing to manipulate above-ground biomass: geese were allowed to graze one half of high biomass, low biomass, and bare plots ($n = 4$ plots per biomass category) while the other half of each plot was excluded from geese. Before enclosure, the grazed and excluded areas had similar values of biomass and soil salinity (Fig. 2). One month after the enclosures were erected, the excluded areas of high biomass plots had $\approx 40 \text{ g m}^{-2}$ more biomass than grazed areas (Fig. 2d). This was associated with a substantial reduction (33% on average) in the soil salinity of excluded areas relative to grazed areas (Fig. 2a; ANOVA on postenclosure dates, $P < 0.02$). Low biomass and bare areas where grazing had no effect on biomass (Fig. 2d) serve as a control, and no effect on soil salinity was detected (Fig. 2; ANOVAs with salinity data, $P > 0.05$). In all plots, soil salinity increased during the growing season (date effect in above ANOVAs, $P < 0.01$), with no interaction with treatment (ANOVAs, $P > 0.05$). It is difficult to imagine what other aspects of grazing might have caused this outcome and it therefore appears that biomass removal increases soil salinity.

Puccinellia GROWTH IN SITES DIFFERING IN SALINITY AND BIOMASS

The positive feedback hypothesis requires that plant growth is reduced by increasing salinity and consequently is lower in areas of reduced biomass. We tested these requirements by examining the leaf demography of transplanted plants in sites differing in biomass and salinity.

In 1991, sites were divided into four treatment categories based on site biomass and soil salinity as described earlier. For each *Puccinellia* plant, leaf births and deaths were counted for the main shoot and axillary shoots separately, and then summed for the whole plant, resulting in six related demographic measures (see Methods). The treatment effect was significant for all the demographic variables (ANOVAs, $P < 0.05$) except main shoot deaths (ANOVA, $P = 0.065$). All other effects, including the effects of grazing and plant origin and all possible interactions, were not significant (ANOVA, $P > 0.05$).

This treatment effect does not reflect differences between high biomass and low biomass plots *per se*. If plant performance in all low biomass plots, irrespective of soil salinity, is compared to that in high biomass plots, there is no significant difference in any demographic variable (planned comparison, using an

Table 1 Vegetation and soil characteristics of sites, and *Puccinellia* performance in sites in (a) 1991 and (b) 1992. Data on shoot density, vegetation biomass, sodium concentration in soil water and soil water content, were collected on (a) 15 August 1991 ($n = 7$ sites) and (b) 30 July 1992 ($n = 4$ sites). Data for these four variables are presented for grazed areas only, as these variables were affected by enclosure (see text). Data on *Puccinellia* mortality, axillary shoot production, and total leaf birth rate were collected over the growing season and are for grazed and exclosed areas combined, as enclosure did not affect these variables (see text). For these three variables, $n = 56$ in 1991 (a) and $n = 144$ in 1992 (b). Error bars are ± 1 SE

	Shoot density (shoots cm^{-2})	Biomass (g m^{-2})	Sodium in soil water (g L^{-1})	Soil water content ($\frac{\text{g}_{\text{water}}}{\text{g}_{\text{soil}}}$)	<i>Puccinellia</i> plants which died (%)	<i>Puccinellia</i> plants which produced axillary shoots (%)	Total leaf births per <i>Puccinellia</i> plant per day
1991							
High biomass	4.64 ± 0.49		1.11 ± 0.15	1.18 ± 0.08	4%	41%	0.135 ± 0.008
Low biomass							
0–2 $\text{g Na}^+ \text{L}^{-1}$	0.95 ± 0.15		1.46 ± 0.23	1.45 ± 0.11	7%	73%	0.189 ± 0.016
2–4 $\text{g Na}^+ \text{L}^{-1}$	0.82 ± 0.15		2.93 ± 0.28	1.11 ± 0.09	7%	61%	0.184 ± 0.017
4–8 $\text{g Na}^+ \text{L}^{-1}$	0.71 ± 0.11		5.90 ± 0.43	1.22 ± 0.12	14%	39%	0.108 ± 0.010
all sites	0.83 ± 0.08		3.43 ± 0.44	0.26 ± 0.07	9%	58%	0.160 ± 0.009
1992							
High biomass		60.4 ± 2.1	4.4 ± 0.5	0.65 ± 0.02	3%	10%	0.135 ± 0.008
Low biomass		21.9 ± 4.5	20.3 ± 1.7	0.55 ± 0.02	86%	1%	0.189 ± 0.016
Bare		0.2 ± 0.1	21.7 ± 1.7	0.49 ± 0.04	94%	0%	0.184 ± 0.017

empirical scale parameter where appropriate, $P > 0.05$), contrary to the positive feedback hypothesis.

By contrast, there is evidence for a negative effect of salinity on plant growth, another requirement of the positive feedback hypothesis. Among low biomass plots, plants in the most saline sites (4–8 $\text{g L}^{-1} \text{Na}^+$ in extracted soil water) had substantially lower values for all demographic variables than those for plants

grown in less saline sites (0–2 and 2–4 $\text{g L}^{-1} \text{Na}^+$; planned comparison, using an empirical scale parameter where appropriate, $P < 0.05$; Fig. 3). As a consequence, more plants died and fewer produced axillary shoots in the more saline sites (Table 1). In pot experiments, *Puccinellia* plants characteristically reduce the production of axillary shoot leaves more than those on main shoots when salinity increases

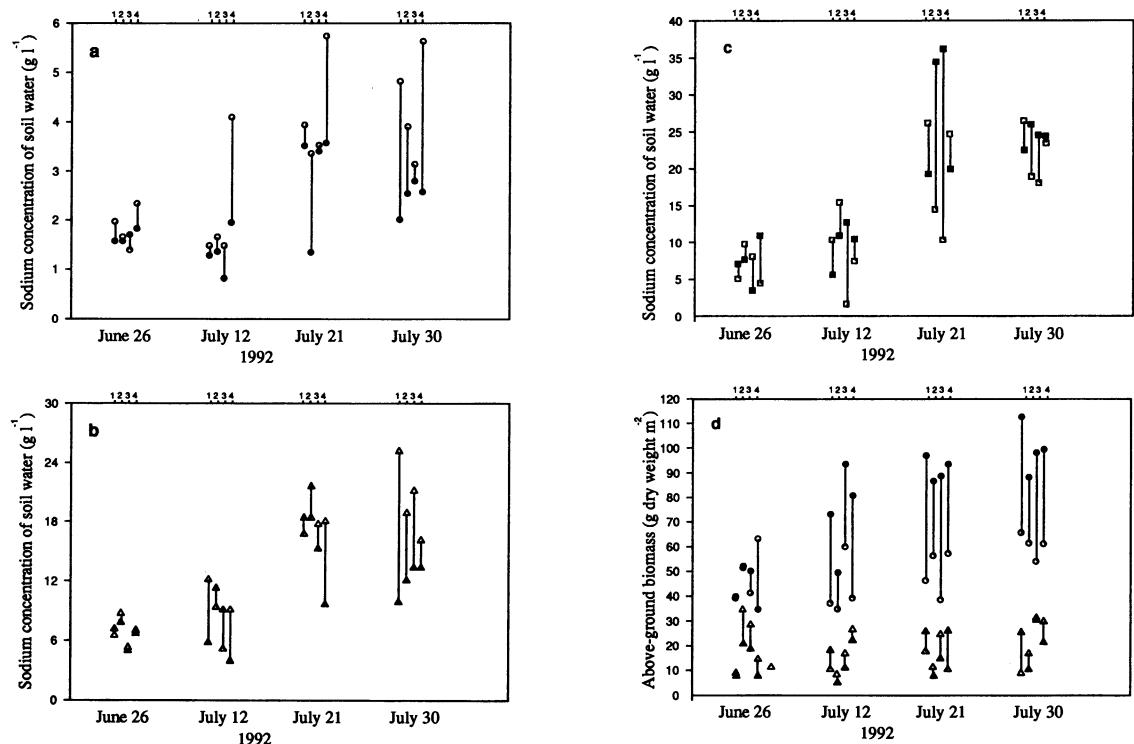
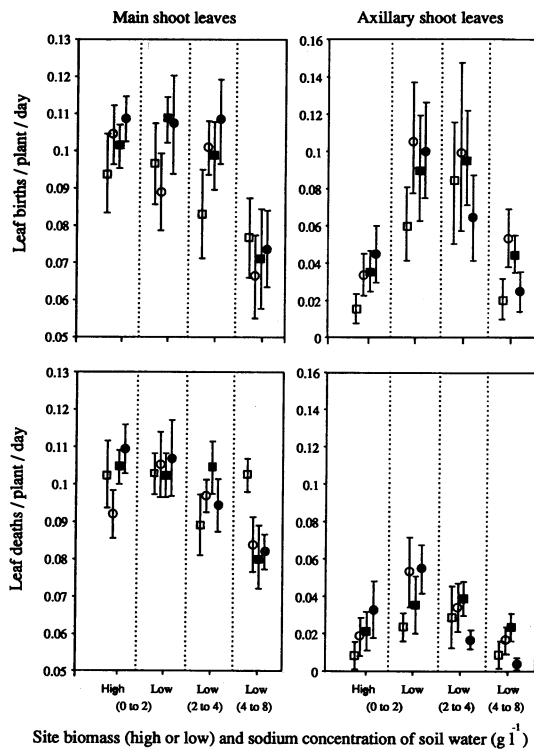


Fig. 2 Sodium concentration in soil water at numbered sites with high biomass (a), low biomass (b), or which are bare (c), with (open symbols) or without (closed symbols) grazing. Plots were exclosed on 26 June 1992. Note that the vertical axes differ between (a), (b) and (c). (d) Above-ground biomass of high biomass (circles) and low biomass (triangles) numbered sites. Open and closed symbols as above. The biomass of bare sites was negligible and so is not shown.



Site biomass (high or low) and sodium concentration of soil water (g L^{-1})

Fig. 3 Seasonal changes in leaf demography for *Puccinellia* plants of high biomass origin (\square , \blacksquare) and low biomass origin (\circ , \bullet), in grazed (\square , \bullet) and excluded (\blacksquare , \circ) areas of sites in 1991. Dotted lines separate sites in different treatment categories (based on site biomass and the sodium concentration of soil water). Demographic parameters were calculated for the period 11 June–9 August 1992. Error bars are ± 1 SE (untransformed data). Note that the vertical axes differ between the graphs of main shoot and axillary shoot demography.

(Srivastava & Jefferies 1995a). The same pattern is evident among the low biomass plots: the ratio of axillary shoot to main shoot leaf births decreased from 1.21 in sites of low salinity ($0\text{--}2 \text{ g L}^{-1} \text{ Na}^+$) to 0.69 in sites of high salinity ($4\text{--}8 \text{ g L}^{-1} \text{ Na}^+$).

In summary, in 1991 leaf birth rates did not differ

between high and low biomass plots, despite low biomass plots being more saline and salinity reducing plant growth (Fig. 3). This apparent contradiction may be resolved by considering the effects of intra-specific competition. If high and low biomass plots of the same salinity ($0\text{--}2 \text{ g L}^{-1} \text{ Na}^+$) are compared, the low biomass plots have more leaf births (in total; Table 1), presumably because the lower plant density of such plots leads to the reduced intraspecific competition. In 1992, leaf demography was examined in plants from the four representative sites for each biomass category. Since axillary shoot production was very low, only total (main shoot + axillary shoot) leaf demography was examined. Total leaf birth and death rates both varied considerably between sites (Friedman test, sites not differentiated by biomass category, $P < 0.001$). However, both rates were strikingly higher in high biomass plots than in low biomass and bare plots, and the leaf birth rate was slightly, but significantly, higher in low biomass plots than in bare plots (Wilcoxon rank sum, Z-statistic, $P < 0.05$; Fig. 4). Leaf death rates were similar between low biomass and bare plots (Wilcoxon rank sum, Z-statistic, $P > 0.05$). These results support the positive feedback hypothesis: plant growth is greater in plots with more vegetation. This may reflect the low soil salinity of the more vegetated plots. Indeed, the salinity of plots was a much better predictor of plant mortality (logarithmic form of Na^+ ; $r^2 = 0.89$) and total leaf birth rate (logarithmic form of Na^+ ; $r^2 = 0.94$) than plot biomass, or for that matter soil water content, redox potential, or bulk density (Fig. 5). Specifically, in stepwise regressions, no linear or logarithmic form of these site variables was significant after $\log \text{Na}^+$ had been entered.

Grazing did not influence the leaf birth rate of plants (Friedman test, $P > 0.05$). By contrast, the leaf death rate of plants was slightly but significantly higher in excluded areas (Friedman test, sites not differentiated by biomass category, $P < 0.01$).

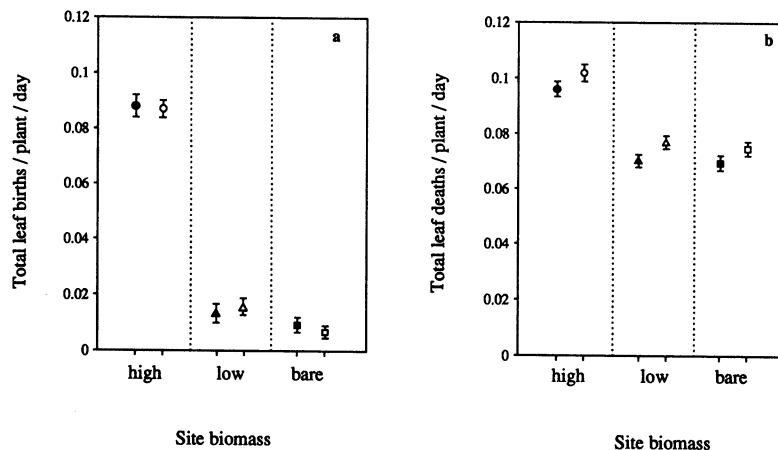


Fig. 4 Leaf birth rates (a) and death rates (b) of *Puccinellia* plants in 1992 as a function of site biomass (high biomass, low biomass, bare) and grazing pressure (solid symbols refer to grazed plants; open symbols refer to excluded plants). Error bars are ± 1 SE (untransformed data).

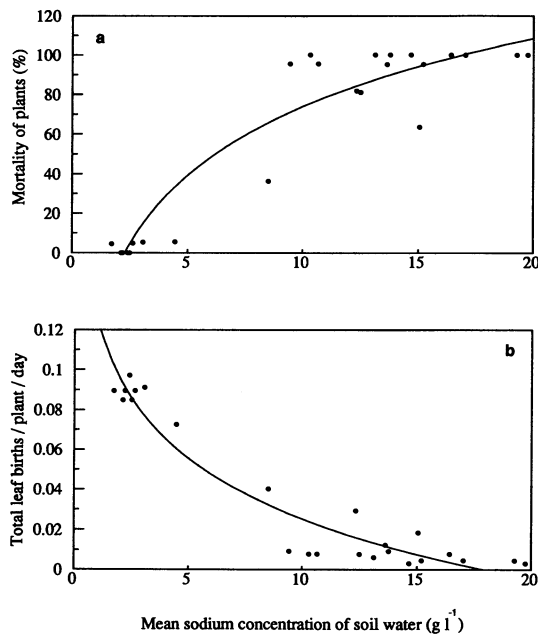


Fig. 5 Relationships between the sodium concentration in soil water in 1992 (mean of data of 26 June and of 30 July) and (a) deaths of *Puccinellia* plants as a percentage of total plants ($r^2 = 0.89$; $n = 24$) and (b) total leaf birth rate ($r^2 = 0.93$; $n = 24$). Each symbol represents a percentage value (a) or a mean value (b) for 18 plants in either grazed or enclosed areas of sites. Regression lines are calculated using a logarithmic form of sodium concentration.

THE GROWTH OF PLANTS OF *Carex* SUBSPATHACEA AT DIFFERENT SITES

All plants of *Carex* died in bare sites, compared with 17–37% deaths in the high biomass sites. Like *Puccinellia* in 1992, *Carex* growth was less in areas of reduced biomass.

Although all *Carex* plants in bare sites had died by the end of the first sampling interval, *Puccinellia* plants were still alive in three of the four bare sites. Similarly, in grazed plots at high biomass sites, *Puccinellia* deaths at the end of the study period were consistently lower than those of *Carex* (0% vs. 17%, 5% vs. 29%, 0% vs. 24% and 6% vs. 37% for high-biomass sites 1, 2, 3 and 4, respectively).

THE EFFECT OF ALGAL CRUSTS ON THE GROWTH OF *Puccinellia* IN BARE SITES

Plants grown in algal crusts, compared to those grown without crusts, had far fewer leaf births and more leaf

deaths (Friedman tests, $P < 0.001$; Table 2). Almost all leaf births occurred on main shoots (main and axillary shoot leaves are therefore not examined separately). By the end of the study, leaf deaths had exceeded leaf births to such an extent on some plants that no living leaves remained; these plants were declared dead. More plants died in areas with intact algal crusts (64–92% of plants died, depending on site) than in areas without algal crusts (24–64% of plants died; G -test, $G_3 = 21.2$, $P < 0.005$; Table 2).

Plants grown at different sites differed significantly in the rate of leaf births (Friedman test, $P < 0.001$) but not deaths (Friedman test, $P > 0.10$). Differences in plant growth between sites are linked to spatial variation in salinity. Site C, with the lowest rate of leaf births and axillary shoot production, was more saline (mean = 19.1 g Na⁺ L⁻¹ soil water) than site A (mean = 11.8 g Na⁺ L⁻¹ soil water) or site B (mean = 16.4 g Na⁺ L⁻¹ soil water). The sites differed significantly in soil salinity (ANOVA, $P < 0.05$, following overall effect of site on soil variables in MANOVA, Wilks Lambda, $P < 0.05$) but not soil water content, redox potential or bulk density (ANOVAs, $P > 0.05$).

There was no overall effect of either the presence of algal crusts, or a site by algal crust interaction for the above soil variables (MANOVA, Wilks Lambda, $P > 0.05$).

Discussion

The three predictions arising from a positive feedback between poor plant growth and high soil salinity (Fig. 6a) were: (1) a decrease in above-ground biomass is associated with an increase in soil salinity; (2) high soil salinities reduce plant growth and as a result (3) plant growth is less at sites with reduced above-ground biomass. The evidence summarized below gives considerable support for the first two predictions and some support for the last prediction.

Soil salinity appears to be substantially influenced by the amount of above-ground biomass. Reductions in biomass, such as that caused by heavy grazing, result in increased soil salinity (Fig. 2). Localized areas of bare sediment, usually caused by goose foraging, are thus hypersaline in mid-summer, while nearby patches of intact vegetation are associated with less saline soils (Fig. 1; Srivastava & Jefferies 1995b). The

Table 2 Growth of transplanted *Puccinellia phryganodes* plants in three sites, with and without algal crusts (mean \pm SE, $n = 25$)

	Site A		Site B		Site C	
	no crust	crust	no crust	crust	no crust	crust
TLB (leaves plant ⁻¹ day ⁻¹)	1.18 \pm 0.20	0.32 \pm 0.09	1.24 \pm 0.23	0.48 \pm 0.12	0.36 \pm 0.10	0.20 \pm 0.07
ASLB (leaves plant ⁻¹ day ⁻¹)	0.12 \pm 0.09	0.00	0.12 \pm 0.09	0.00	0.00	0.00
TLD (leaves plant ⁻¹ day ⁻¹)	2.36 \pm 0.14	2.6 \pm 0.13	2.1 \pm 0.11	2.82 \pm 0.14	2.24 \pm 0.14	2.58 \pm 0.11
Plant deaths (%)	0.28	0.64	0.24	0.64	0.64	0.92

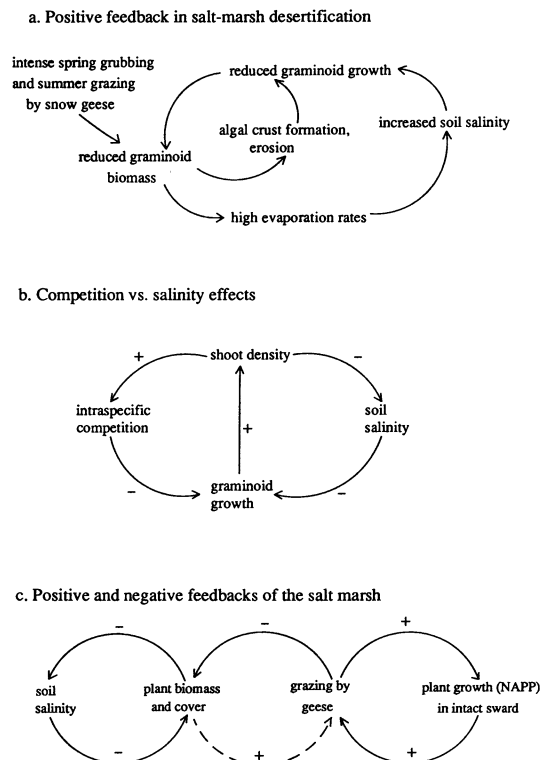


Fig. 6 Diagrams of the interrelationships between feedback processes, and plant competition for the grazed salt-marsh swards at La Pérouse Bay. (a) A positive feedback between soil salinity and graminoid growth, triggered by intense goose foraging and resulting in loss of salt-marsh vegetation. (b) This positive feedback between soil salinity and graminoid growth is opposed by a negative feedback between intraspecific competition and graminoid growth. The positive and negative signs represent the type of correlation between the factors linked by arrows, and the direction of the arrows indicates causality in both (b) and (c). (c) The positive feedback between soil salinity and graminoid cover in the salt marsh is linked to a positive feedback between goose grazing and primary productivity in patches of intact swards (described in text). Arrows connecting two variables in both directions with the same sign indicate a positive feedback. A negative feedback occurs where the signs above the two arrows are different. Note that the effect of plant biomass on the size of the goose colony will only be evident over more than one season (dotted arrows), as opposed to the other interactions (solid arrows), so a time lag is expected in this potentially regulatory negative feedback.

salinity of the La Pérouse Bay soils is derived not directly from tidal sources, but rather from buried marine sediments which underlie much of the Hudson Bay Lowlands (Price & Woo 1988). Vegetation reduces the evaporative water loss from surface sediments, as shown by experiments we report elsewhere (Iacobelli & Jefferies 1991; Srivastava & Jefferies 1995b), thus slowing the upward movement of salts through the soil. Similar results from New England salt marshes have been reported by Bertness *et al.* (1992). Exposure of marsh soil to direct solar radiation resulted in elevated soil salinity in bare patches. At both locations, the intact swards maintained conditions conducive for plant growth by restricting evaporation and the build up of salinity.

At La Pérouse Bay the growth of graminoids was depressed by high soil salinities. This is evident in the leaf demography of plants in low biomass sites in 1991 (Fig. 3), and in the plant mortality data of 1992 (Fig. 5). Similar decreases in growth of these graminoids can be generated by watering potted plants, grown in the field, with saline solutions (Srivastava & Jefferies 1995a).

In both years therefore the first two predictions of the positive feedback hypothesis were supported: biomass reduced salinity, and salinity reduced plant growth. In 1992, the final prediction held: leaf birth rates of plants were greatest at high biomass sites, intermediate at low biomass sites, and lowest in bare sites. In 1991, by contrast, leaf birth rates did not differ between high and low biomass sites, despite low biomass sites being more saline and salinity reducing plant growth. It is possible that, in terms of plant growth, the less intense intraspecific competition of low biomass sites compensated for the greater salinity of such sites in 1991 but not 1992 (Fig. 6b). Similar interactions between intraspecific competition and salinity tolerance are evident in the demography of a *Hordeum jubatum* L. population (Badger & Ungar 1991).

This difference in results between years could be due to differences in experimental design or meteorological factors. Given that plants grown separately at La Pérouse Bay, as part of other experiments, also showed much greater salt tolerance and axillary shoot production in 1991 than in 1992 (Srivastava & Jefferies 1995a), it seems likely that weather differences between years are responsible. Indeed, the weather in 1991 and 1992 differed dramatically: 1991 was one of the warmest and wettest years on record, whereas 1992 was one of the coldest and driest (Churchill Weather Office Monthly Reports, Environment Canada). On most days between May and August, the difference in temperature between the two years exceeded 5 °C. Soil salinity was similar between years (Srivastava & Jefferies 1995b), but it may be that salinity stress was exacerbated by the cold temperatures and dry winds that characterized 1992.

The presence of algal crusts reduced shoot survival and leaf production in bare sites. Similar dry and tough algal crusts are also found in low biomass sites, but not in high biomass sites (the soil surface beneath the vegetation mat is moist). It is unlikely, however, that the presence of algal crusts is entirely responsible for poor plant growth in low and bare sites compared to that in high biomass sites. If this was the case, differences in demography of plants between low biomass and bare sites (1992) and within low biomass sites (1991) would be minor (since all sites have algal crust) and would not be explained by variation in soil salinity (soil salinity was not correlated with algal crust presence in 1992).

Algal crusts are common in many salt-marshes (Golubić 1973; Adam 1990), and thick dried

algal crusts have been noted in nontidal saline areas (Ehrlich & Dor 1985). Blistering algal crusts, similar to those at La Pérouse Bay, are formed on well-drained sediments with prolonged exposure to drying conditions (Golubić 1973). Under these conditions, high rates of anaerobic decomposition occur and the consequent accumulation of CO₂ under the algal crust causes blistering (Golubić 1973). The anaerobic conditions coupled with the mechanical lifting of the drying algal crust, which may have exposed roots of *Puccinellia*, could have led to the death of plants. Although the presence of algal crusts did not appear to affect either soil water content or soil salinity significantly in this study, such effects have been shown in other studies (Golubić 1973; Price *et al.* 1989; Graetz 1991).

SALT-MARSH VEGETATION AND THE SNOW GOOSE COLONY

Over a period of years, a net decrease in the amount of salt-marsh vegetation is anticipated as a result of the positive feedback, with the rate being strongly influenced by yearly weather patterns. Since *Puccinellia* and *Carex* are the preferred forage for lesser snow geese, and goslings show poor growth when feeding on other types of forage (Gadallah & Jefferies 1995), this decrease in graminoid vegetation represents a decrease in the availability of quality forage for the goose population at La Pérouse Bay. Previous reductions of available forage over the last decade at La Pérouse Bay are thought to have caused a marked decline in gosling growth and survival (Cooch *et al.* 1991; Francis *et al.* 1992; Williams *et al.* 1993) and an increase in posthatch dispersal (Cooch *et al.* 1991; Cooch *et al.* 1993). Further loss of vegetation means that these trends can only be expected to continue.

Although posthatch dispersal is increasing, many breeding pairs show strong breeding-site fidelity (snow geese often live up to 8 years) and have not left the La Pérouse Bay salt marshes, despite low brood survival (Williams *et al.* 1993). The rate of reduction in vegetation may therefore exceed the rate of reduction in grazing pressure, and the predicted increase in desertification (see below) will exaggerate this asynchrony. Since goose grazing is concentrated in swards with high above-ground biomass, any reduction in grazing pressure will not necessarily affect low biomass and bare sites in any case (as shown by the enclosure experiment, cf. Fig. 2).

At La Pérouse Bay, between 1979 and 1983, grazing by geese was reported to increase substantially both the nitrogen content and the net above-ground primary production (NAPP) of graminoid swards (Cargill & Jefferies 1984; Bazely & Jefferies 1985, 1989). The increase in forage quantity and quality caused by grazing allowed for further goose grazing, creating a positive feedback between goose grazing and NAPP (Jefferies *et al.* 1986; Fig. 6c). This stimu-

lation of NAPP by grazing was reflected in a higher rate of total leaf births in graminoid plants (Kotanen & Jefferies 1987; Bazely & Jefferies 1989). In this study, however, total leaf births of *Puccinellia* in high biomass swards were not increased by grazing. This suggests that the positive feedback between NAPP and goose grazing is no longer dominating vegetation dynamics.

Experiments with captive goslings have shown that the enhancement of NAPP by goose grazing at La Pérouse Bay is greatest at intermediate levels of grazing pressure (Hik & Jefferies 1990; Hik *et al.* 1991). The grazing-NAPP positive feedback therefore becomes less effective as the grazing pressure increases (NAPP increases with grazing pressure at a decreasing rate). The salinity-biomass feedback, however, results in salinity increasing with grazing pressure, at an ever increasing rate, and so it becomes progressively more effective as the grazing level increases. There is a spatial component to these changes, as soil salinity increases with the size of a bare patch (Srivastava & Jefferies 1995b). A similar situation has been described for a New England salt-marsh, where the area of a bare patch is positively correlated with soil salinity and negatively correlated with plant growth (Bertness 1991; Bertness *et al.* 1992; Shumway & Bertness 1994). We suggest that the increase in goose densities, and hence grazing pressure over the last decade at La Pérouse Bay has resulted in the vegetation dynamics switching from being dominated by the grazing-NAPP positive feedback to being dominated by the salinity-biomass positive feedback. The alternative states of salt-marsh vegetation development at La Pérouse Bay have been discussed by Hik *et al.* (1992). Although this plant-herbivore interaction can maintain salt-marsh graminoid swards via a grazing-NAPP positive feedback, we do not regard this as a 'switch' process, as described by Wilson & Agnew (1992). The latter discuss processes where the plant community modifies the environment making it more suitable for that community. At La Pérouse Bay plant community development is strongly dependent on rates of isostatic uplift and patterns of foraging by geese. Ultimately uplift and the build up of soil organic material facilitate the establishment of a willow-grassland community in place of these salt-marsh graminoid swards.

Systems dominated by positive feedbacks often show threshold effects (DeAngelis 1992). Rapid changes in the state of the system occur when thresholds are crossed. As a result of increases in the intensity of foraging at La Pérouse Bay a vegetational threshold has been crossed leading to a decrease in the survival of goslings in recent years. In contrast, the cause of the increased adult lesser snow goose population over the last two decades is strongly linked to human activities elsewhere (use of agricultural crops by geese, refugia, decline in hunting) (Francis *et al.* 1992; Warren & Sutherland 1992). The

impoverishment of such terrestrial arctic coastal systems, which is ultimately a consequence of human activities, is leading to 'desertification' (Graetz 1991) of these systems. The processes resulting in the loss of vegetation on these coastal flats are similar to those that have led to destruction of vegetation by livestock in the Sahel region of Africa (Graetz 1991). In both cases weather patterns exacerbate the rate of destruction. Recovery of both systems is long-term, beyond the life expectancy of the present cohorts of the different herbivore species.

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