Patterns of vegetation change and the recovery potential of degraded areas in a coastal marsh system of the Hudson Bay lowlands

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Summary

1 In recent decades, foraging by increasing numbers of lesser snow geese has led to loss of vegetation and changes in soil conditions in marshes on the Hudson Bay coast.

2 Changes in species composition were recorded in areas unprotected from goose foraging and in exclosures of varying age (5–15 years) erected in intact swards and on bare sediments where foraging had occurred at La Pérouse Bay, Manitoba.

3 In the supratidal marsh, plants failed to establish naturally in either open or exclosed (15 years) plots in bare areas. In moist intertidal soils, vegetative fragments of the asexual species *Puccinellia phryganodes* readily established and formed a mat in exclosures (5 years).

4 Changes in species assemblages occurred over 11 years in exclosed and adjacent open plots in intertidal and supratidal marshes. Loss of vegetation cover and species richness, particularly dicotyledonous species, and the reversion of later successional plant assemblages to earlier successional assemblages occurred in open plots. In the absence of foraging, late successional graminoids and willow species replaced early successional graminoids.

5 Late successional grasses of the upper intertidal marsh died when transplanted into degraded soils but still survived after one season in control plots, suggesting that an early successional template is needed for establishment.

6 In the absence of goose foraging, natural re-vegetation by clonal propagation can occur only where edaphic conditions are suitable. Within exclosures, vegetation changes resemble those in undamaged areas where goose foraging pressure is still moderate. We propose a state and transition model for vegetation change in the system based on succession patterns, alternative vegetation states and geomorphological events.

Key-words: alternate stable states, Arctic, habitat degradation, lesser snow geese

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Introduction

Grazing intensity of herbivores can exert a strong influence on vegetation dynamics within terrestrial systems (Holling 1973; Noy-Meir 1975; May 1977). Herbivores may retard or promote succession depending on the species composition of plant assemblages and patterns of herbivory (Bakker 1985; Pastor *et al.* 1988; Dublin *et al.* 1990; Prins & Van der Jeugd 1993; Ungar 1998; Dormann *et al.* 2000; Zacheis *et al.* 2000). When a dominant species is the preferred forage, species richness and evenness may increase (McBrien *et al.* 1983; Furbish & Albano 1994). In contrast, when grazing is intensive and non-selective, competition patterns observed under moderate grazing pressure may disappear (Taylor *et al.* 1997). In some instances, when consumption rate of forage plants exceeds their growth rate, herbivores may trigger rapid, non-linear shifts of species assemblages towards alternate states, often characterized by either temporary or permanent loss of vegetation and by low species richness (Ludwig & Tongway 1995; Milton & Dean 1995; Whiteford *et al.* 1995; Magnússon 1997; Van de Koppel *et al.* 1997).

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Vegetational loss and soil degradation have occurred as a result of herbivory in coastal marshes of the Hudson Bay lowlands, one of the breeding grounds of the lesser snow goose, *Chen caerulescens caerulescens* L., a keystone species in this system (Hik *et al*. 1992; Jefferies 1997). In recent decades, this mid-continent population has increased in numbers at 7% per year, probably as a result of the high quality, agricultural food subsidy available on the wintering grounds and along migration routes (Abraham *et al*. 1996; Jefferies *et al*. 2002). In the early 1980s when the goose population at La Pérouse Bay, Manitoba (58°44′ N, 94°28′ W) was an estimated 5000 pairs of birds (Cooke *et al*. 1995), changes over 5 years in species composition in intertidal exclosures indicated that grazing slowed vegetational change (Bazely & Jefferies 1986). By 1997 the population had increased to an estimated 44 500 pairs (Abraham, Ross & Rockwell, unpublished aerial survey) and grubbing by adult birds in spring, together with intense grazing by family groups in summer, had led to the destruction of salt-marsh swards and exposure of sediments (Srivastava & Jefferies 1996). In 1993 (the latest available information) over 2500 ha of coastal habitats at La Pérouse Bay showed a decline in vegetation cover compared with that 20 years earlier (Jano *et al*. 1998). Loss of vegetation cover and increased soil evaporation rates have resulted in hypersaline soils that have limited re-establishment of plants (Iacobelli & Jefferies 1991; Srivastava & Jefferies 1996).

The recovery potential of these degraded systems is largely unknown. Shifts in ecosystem structure caused by herbivores often tend to be asymmetric, such that restoration of the system is seldom as simple as lowering levels of herbivory (Bradshaw 1997). Vegetation transitions may be coupled with discontinuities in abiotic conditions that cannot be easily reversed (Westoby *et al*. 1989; Bazely & Jefferies 1996; Rietkerk & Van de Koppel 1997). When vegetation change is a non-linear process with apparent discontinuities (Rose & Harmsen 1981), or a series of threshold responses between meta-stable states (Westoby *et al*. 1989; Rietkerk & Van de Koppel 1997), restoration efforts require knowledge of the various variables that need to be manipulated in order to achieve state transitions (Hobbs 1994; Hobbs & Norton 1996).

We have examined the pattern and rate of natural re-vegetation at La Pérouse Bay in intertidal and supratidal marshes where loss of vegetation had occurred, in order to determine whether recovery was possible in plots from which geese were excluded. In addition, changes in early and later successional assemblages of species were documented over 11 years both in the presence and absence of grazing, in order to evaluate longer term changes in species assemblages. Lastly, experimental transplants were made to test whether later successional species (*Festuca rubra* and *Calamagrostis deschampsioides*) could establish directly in degraded sediments, or whether the early successional vegetation template was a necessary precursor. The results have been synthesized with our previous knowledge of the system in a proposed state and transition model of vegetation dynamics.

DESCRIPTION OF SITE

Salt-marshes develop on exposed coastal flats at La Pérouse Bay (Jefferies *et al*. 1979) in a region where isostatic uplift is occurring at a rate of about 0.8 cm per year (Andrews 1973). Primary colonizers of estuarine brackish soft sediments are *Hippuris tetraphylla*, *Hippuris vulgaris*, *Ranunculus cymbalaria* and *Myriophyllum exalbescens*. Nomenclature follows Porsild & Cody (1980). On tidal flats, following colonization of bare sediments by diatoms and cyanobacteria, *Puccinellia phryganodes* is the initial vascular plant to establish, followed by *Carex subspathacea* and *Ranunculus cymbalaria*. The early presence of the latter two species is largely dependent on the availability of brackish water from shallow drainage channels. Once *Puccinellia-Carex* swards are well developed, dicotyledenous plants such as *Potentilla egedii*, *Stellaria humifusa* and *Plantago maritima* var. *juncoides* establish. As the elevation of the ground increases as a result of isostatic uplift, sediment accumulation and frost-heave, soils become better drained (less saline) and an organic soil layer develops (Jefferies *et al*. 1979). In the absence of destructive foraging, a relatively species-rich willow-grassland establishes in the rarely flooded supratidal marsh (< 2 times every 3 years) in which *Festuca rubra*, *Calamagrostis deschampsioides*, *Salix brachycarpa* and *Salix myrtillifolia* are dominant. At more inland sites, where sediments are less well drained, sedge meadows dominated by *Carex aquatilis* replace the salt-marsh vegetation (Kerbes *et al*. 1990; Kotanen & Jefferies 1997).

Hik *et al*. (1992) have argued that the *Puccinellia-Carex* and *Festuca-Calamagrostis* plant assemblages are examples of stable vegetation states that shift asymmetrically in response to low to moderate grazing pressure resulting in a standing crop of *Puccinellia-Carex* swards of *c*. 40 g m^{-2} and an increase in ground elevation. In areas of higher elevation in intertidal salt-marshes, when grazing declines or is stopped by erection of exclosures, *Puccinellia-Carex* swards shift towards the *Festuca-Calamagrostis* state, but at lower elevation a similar vegetational change fails to occur in the short term (< 5 years) (Bazely & Jefferies 1986). When swards of *Festuca-Calamagrostis* are moderately grazed, the vegetation does not easily revert to a *Puccinellia-Carex* sward. However, if foraging pressure is high (standing crop of *Puccinellia-Carex* swards < 20 g m^{-2}), grubbing and hypersalinity trigger shifts of both *Puccinellia-Carex* swards and *Festuca-Calamagrostis*-willow assemblages to a third stable state where the soil is essentially devoid of vegetation (Iacobelli & Jefferies 1991; Srivastava & Jefferies 1996). The transition, which is rapid, creates a mosaic of sediment and vegetation where patches are irregular in distribution and of varying size (1–30 m^2).

Table 1 Summary of sites used for the long-term vegetation contrasts in the presence and absence of grazing at La Pérouse Bay, Manitoba

Code	Description	Year of establishment
SSE-1	Soft sediment estuarine	1982
FWG-1	Island, fresh-water, graminoid assemblage	1982
FWG-2	Island, fresh-water, graminoid assemblage	1983
FWW-1	Island, fresh-water, willow grassland	1986
STG-1	Supra-tidal, graminoid assemblage	1982
STG-2	Supra-tidal, graminoid assemblage	1982
STW-1	Supra-tidal, willow grassland	1982
STW-2	Supra-tidal, willow grassland	1982

Materials and methods

NATURAL REVEGETATION PATTERNS ON DEGRADED SITES

In 1984, a 5 × 5 m exclosure was erected on supratidal sediments that had been devoid of vegetation for at least 5 years, approximately 3 km inland from La Pérouse Bay. Similarly, in 1992, nine 2 × 2 m exclosures were erected on the west shore of La Pérouse Bay on the intertidal flats proximal to the braided estuary of the Mast river (although one exclosure was subsequently washed away). Relevés were done in August 1997 for all exclosures at both sites. In addition, on 27–29 July 1996 in the exclosures on the tidal flats, the basal cover of individual colonies of *Puccinellia phryganodes* was mapped using a 5 × 5 cm grid, and the total area of cover in each plot estimated. On 20–22 August 1997, 26 previously mapped colonies were re-measured. It was not possible to identify all colonies that were mapped in 1996, as those in plots close to drainage channels had become contiguous.

The unknown number of days that remained after 29 July in the 1996 growing season made it impossible to calculate relative growth rates for individual colonies. The ratio of the area of a colony in August 1997 relative to July 1996 was used as an alternative index of growth.

TRANSPLANTS OF *FESTUCA RUBRA* AND *CALAMAGROSTIS DESCHAMPSIOIDES*

Transplant material was cored from a patch of *Festuca-Calamagrostis* (2 × 2 m) in the eastern supratidal marsh at La Pérouse Bay. Cored plugs (22 mm diameter × 40 mm depth), that included both plant and soil material, were planted on 17 June 1997 into *Festuca-Calamagrostis* swards, proximal to donor patch (control) and into bare sediment. Three plots at each of two sites for each treatment were planted with 25 plugs (five columns × five rows) separated by 7 cm. The two sediment sites (*c.* 50 m apart, elevation difference < 5 cm) were located in the upper intertidal marsh where prior to degradation *Puccinellia-Carex* swards had been growing: exclusion of geese led to rapid establishment (< 5 years) of *Festuca* and *Calamagrostis* (Hik

et al. 1992). Transplants were scored for survival and senescence on 2, 14, 26 of July, and 7 and 17 of August 1997 using methods described by Handa & Jefferies (2000).

LONG-TERM VEGETATION RECORDS

Eight exclosures (5 × 5 m) were erected in the summers of 1982–86 in coastal marshes at La Pérouse Bay (Table 1) at sites across an apparent gradient of plant species assemblages from low (E, estuarine sediments, G, salt-marsh swards, of *Puccinellia* and *Carex*) to higher elevations (*c.* +60 cm) (W, willow-grassland assemblages) in the supratidal and riverine marshes. The soft sediment brackish estuarine marsh of the Mast river (SSE) was dominated by *Hippuris tetraphylla*, whereas an island brackish marsh in the Mast river delta (FW, freshwater sites), and a supratidal marsh on the western edge of the Bay (ST sites) were dominated by either willow-grassland or salt-marsh graminoids.

In 1986, 15 contiguous pairs of 50 × 50 cm plots were established inside and outside each exclosure (except FWG-1 and STG-1, which had only two pairs). Species composition in plots was scored in the summers of 1986, 1992 and 1997 by recording the plant rooted closest to each of 81 wire crosspoints in a 50 × 50 cm quadrat strung at 5-cm intervals. If no plant was rooted, the point was recorded as 'bare', or at the estuarine site as 'soft sediment' to differentiate unconsolidated sediment from consolidated sediment without vegetation. A percentage frequency for each species was calculated for each plot: species present in a plot, but not recorded at any of the 81 points, were assigned a percentage frequency of < 1%. In 1992 a severe winter storm damaged exclosure FWG-2 and several permanent plots were lost both inside and outside the exclosure. The exclosure was rebuilt around the undamaged plots; five (inside) and eight (outside) of the remaining plots were re-scored in 1997.

Although it would have been ideal to have greater replication of plots, it also would have been prohibitively expensive to do so considering time spent repairing exclosures each spring following ice, floodwater and tidal damage. In addition, the effects of polar bears, caribou and geese necessitated almost daily maintenance.

STATISTICAL METHODS

A suite of statistical techniques was used to analyse long-term vegetation records. Multivariate ordination analysis and rank order correlations enabled us to identify species assemblages and explore their direction and magnitude of change. While both analyses indicated a clear change in species assemblages over time and in response to grazing treatment, interpreting the direction of change was not as straightforward, given the substantial site-to-site variation (cf. Table 3). We subsequently performed a series of univariate tests on species (or lack of species) of interest that were recorded in plots. All analyses were limited to species that were recorded at least once at a frequency of > 5% in exclosures over the 11 years.

Detrended correspondence analysis (DCA) (Hill & Gauch 1980) was selected as an appropriate ordination method based on gradient length and preliminary correspondence analyses (Jongman *et al.* 1995). Data were prepared for analyses using ECOSURVEY (Carleton 1985), and analyses were performed using the program CANOCO (Ter Braak 1990). Values from all years for the grazed treatment at site STG-2 were omitted from the analysis due to death of plants by 1992. Pairwise comparisons of species assemblages between years, and between grazed and ungrazed treatments in each year, were made for each site using Kendall's rank correlation coefficient (τ), a non-parametric statistic (Sokal & Rohlf 1995). A conservative approach was taken with respect to pseudoreplication of plots (Hurlbert 1984). Although plots were likely to be biologically independent, we recognized that statistically they were not. Accordingly, each 'stand' in the ordination consisted of the mean percentage frequency of species calculated for each treatment, year and site (total: 45 stands). In the rank correlation, a mean percentage frequency was calculated for each treatment ($n = 15$, except at sites FWG-1 and STG-1 where $n = 2$).

In univariate tests, all plots were included in the analyses, and their lack of independence was acknowledged in the model: a repeated measures full factorial ANOVA (treatment × site × time). Treatment and site were treated as fixed factors (sites were selected *a priori* to represent different vegetation types). Time and plot were treated as non-independent and random factors. Analyses were done using S-PLUS (Mathsoft Inc., version 3.3, 1995). Given that species were frequently not present at all eight sites, not all records met the normality and homogeneity of variance assumptions. However, ANOVA is robust to departures from normality and unequal variances (Underwood 1997). Furthermore, our ANOVA results are supported by the more conservative non-parametric and multivariate analyses described above.

The pairing of our treatment plots at each site was based on the assumption that the plots within a site did not differ from each other in ways unrelated to the grazing treatment. As each combination (site × treatment) was unreplicated, it was impossible to test the validity of the assumption. Nonetheless, we believe the assumption to be fair given that plots within a site were carefully chosen to be similar with respect to vegetation composition, elevation and soil moisture and were within close spatial proximity (< 5 m) of one another.

Results

NATURAL RE-VEGETATION PATTERNS ON DEGRADED SITES

No plant cover established in the exclosure 3 km inland from the coast, except adjacent to the wire fence, where litter accumulated. Salinity of the soil solution at this site approaches 120 g of solutes litre^{-1} (Iacobelli & Jefferies 1991; Handa & Jefferies 2000). At the intertidal site on the western shore, that receives tidal and river water, however, vegetation established in all eight exclosures, predominantly plants of *Puccinellia phryganodes* (Table 2). Basal area of the grass colonies ranged from 1.3 to 586 cm^2 at the end of July 1996 to 13.8–973 cm^2 when re-measured in August 1997, giving an index of growth (see Methods) of 1.2–61. The large variance was restricted to plants less than 30 cm^2 in 1996; larger patches had growth indices of 1.2–10.5. By 1997 a continuous mat of *Puccinellia* was present on moist soils in exclosures adjacent to drainage channels, where the water content of these soils in late June and July is, on average, about 20% higher than those far from channels (Bazely 1984).

TRANSPLANTS OF *FESTUCA RUBRA* AND *CALAMAGROSTIS DESCHAMPSIOIDES*

Transplanted *Festuca-Calamagrostis* plants failed to establish in upper intertidal sediments. Within 2 weeks of planting, all plants were dead at site one and more than 50% at site two were dead: all died by 14 July 1997. In contrast, transplants in *Festuca-Calamagrostis* swards showed low mortality: in all plugs some plants survived

Table 2 The presence of species that have colonized bare sediments in eight exclosures (2×2 m) after 5 years at an intertidal site on the west shore of La Pérouse Bay

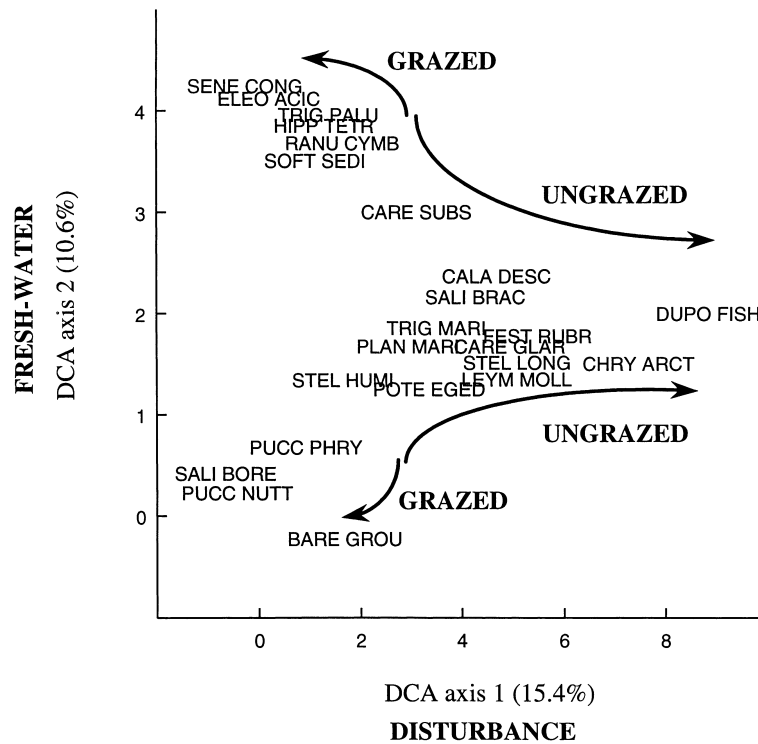|	Exclosure							
Species	1	2	3	4	5	6	7	8
Puccinellia phryganodes	×	×	×	×	×	×	×	×
Senecio congestus	×		×	×	×		×	
Ranunculus cymbalaria	×		×	×			×	
Hippuris tetraphylla			×	×	×			
Juncus albescens			×	×			×	
Carex subspathacea			×		×			
Ranunculus purshii			×				×	
Salicornia borealis		×						
Salix seedlings			×					
Stellaria humifusa			×					
Triglochin palustris			×					

Fig. 1 Species biplot of DCA axes 1 and 2 on the vegetation data of grazed and ungrazed plots over the 11-year period. Codes show the first four letters of the genus and the first four letters of the specific and/or sediment name as listed in Table 4. Arrows indicate the proposed direction of transition in the presence and absence of grazing. Variance explained by the axes is shown in brackets. Disturbance and the presence of fresh-water are interpretations of DCA gradients (see Results).

to 2 July but by 17 August 1997, mortality (death of all plants in a plug) ranged from 11% to 22%.

LONG-TERM VEGETATION RECORDS

A summary of the ordination model is shown in Fig. 1. Total variance accounted for by the first two axes of the DCA was 26%. The biplot vectors associated with each site (not shown) indicated that change in species assemblages occurred over time. Vector lengths varied from 1 to 5 gradient units in exclosed plots and 1 to 3 gradient units in open plots. Species groupings (Fig. 1) supported our current ecological understanding of vegetation dynamics in the system (see site description and references therein). We interpreted disturbance due to foraging (axis 1) and the presence of freshwater (axis 2) as environmental driving factors. On the first axis, species common in disturbed sites, such as *Salicornia borealis*, *Senecio congestus*, *Eleocharis acicularis* and early successional species, are clustered near the origin, and dicotyledenous species and later successional grasses at higher values. On the second axis, species of intertidal and supratidal sites have lower values than those that occur in estuarine (brackish) or riverine sites.

Records of all species that occurred at a frequency > 1% in plots are shown for all years and sites in Table 3. With the exception of three contrasts in the supratidal-willow grassland marsh, no comparisons in the rank order analyses were significantly correlated, indicating that differences in species composition and the rank order of species existed between treatments

and over time. Two significant correlations ($P < 0.05$) occurred between grazed and ungrazed plots in 1986 and between grazed plots in 1986 and 1992 at STW-1 and between grazed plots in 1992 and 1997 at STW-2. Results of the ANOVAs showed that species/sediment abundances varied significantly with time (d.f. 2.24; $P < 0.05$) in 20 of the 23 tests (i.e. except for *Triglochin palustris* ($P < 0.06$), *Ranunculus cymbalaria* and *Puccinellia nuttaliana*).

ANOVA results also indicated that the grazing treatment significantly affected abundance values in 18 of the 23 tests (d.f. 1.457; Table 4). Grazing resulted in significantly higher abundance of unconsolidated sediments (by slowing down the consolidation of sediments through plant colonization) and a larger area of bare, consolidated sediment (by accelerating the degradation of the established marsh) (Tables 3 and 4). Species that showed significantly higher abundances when grazed were predominantly those associated with the soft sediment estuarine site that were tolerant of moderate disturbance (Table 4). In contrast, species that showed higher abundances in ungrazed plots included later successional grasses, dicotyledenous plants and willow species (Table 4). *P. phryganodes* and *C. subspathacea* always varied significantly with treatment but the direction depended strongly on site (Table 4). At the soft-sediment estuarine site, as well as where the open marsh was being intensively foraged to the point of early (STG-1) or full (STG-2) destruction of vegetation (Table 3), both species were more abundant in ungrazed plots. In contrast, grazing favoured

Table 3 Percentage frequencies (± SEM) of species (> 1%) in grazed and ungrazed plots at different sites in 1986, 1992 and 1997 in coastal marshes at La Pérouse Bay, Manitoba

	Grazed			Ungrazed		
	1986	1992	1997	1986	1992	1997
Soft sediment estuarine (SSE-1)						
Carex subspathacea	19.3 ± 4.7	9.1 ± 2.6	4.8 ± 0.8	8.3 ± 2.2	33.5 ± 4.5	44.9 ± 1.9
Puccinellia phryganodes	8.4 ± 2.3	7.7 ± 1.9	10.9 ± 1.9	24.1 ± 2.7	19.8 ± 2.4	9.6 ± 2.5
Hippurus tetraphylla	20.2 ± 2.5	41.4 ± 2.4	24.9 ± 2.2	23.5 ± 2.7	31.0 ± 3.5	18.4 ± 1.5
Eleocharis acicularis	1.8 ± 0.3	13.9 ± 3.1	23.6 ± 4.4	12.6 ± 1.7	3.1 ± 0.9	< 1
Triglochin palustris	9.4 ± 1.0	15.7 ± 2.5	11.9 ± 1.6	4.2 ± 4.2	3.7 ± 0.7	5.8 ± 0.8
Ranunculus cymbalaria	7.3 ± 1.3	6.7 ± 0.9	10.6 ± 2.3	10.0 ± 2.0	7.8 ± 1.5	13.3 ± 0.9
Senecio congestus	0	0	7.5 ± 1.3	0	< 1	1.2 ± 0.4
Dupontia fisheri	0	0	3.1 ± 0.7	0	0	2.4 ± 0.7
Ranunculus purshii	0	0	1.8 ± 1.1	0	< 1	2.1 ± 1.1
Bare	33.5 ± 5.3	5.0 ± 1.4	0	20.7 ± 4.9	0	0
Supratidal graminoid swards (STG-1)						
Puccinellia phryganodes	50.6 ± 6.2	61.7 ± 1.2	51.9 ± 11	41.4 ± 1.9	19.1 ± 6.8	3.7 ± 2.5
Salicornia borealis	31.5 ± 11.7	26.5 ± 0.6	13.0 ± 1.9	45.7 ± 7.4	1.2 ± 1.2	0
Stellaria humifusa	9.9 ± 5.0	0	0	6.8 ± 6.8	25.9 ± 6.2	2.5 ± 0.0
Carex subspathacea	3.7 ± 1.2	0	0	< 1	6.8 ± 0.6	17.3 ± 6.2
Plantago maritima	1.9 ± 1.9	0	< 1	< 1	30.3 ± 1.9	54.3 ± 2.5
Potentilla egedii	< 1	0	0	0	9.9 ± 0.0	9.9 ± 4.9
Puccinellia nuttaliana	0	0	0	0	4.3 ± 3.1	< 1
Festuca rubra	0	0	0	0	< 1	8.6 ± 0.0
Ranunculus cymbalaria	0	0	0	0	1.2 ± 1.2	< 1
Bare	1.8 ± 0.6	11.7 ± 0.6	34.6 ± 9.9	3.7 ± 3.7	< 1	0
Supratidal graminoid swards (STG-2)						
Puccinellia phryganodes	56.5 ± 3.2	0	0	35.6 ± 3.8	87.8 ± 4.5	79.3 ± 2.5
Carex subspathacea	31.8 ± 3.0	0	0	47.9 ± 3.1	0	0
Potentilla egedii	8.1 ± 1.8	0	0	8.2 ± 1.9	0	< 1
Plantago maritima	< 1	0	0	3.8 ± 0.7	0	1.2 ± 0.5
Salicornia borealis	0	0	0	0	1.6 ± 0.7	5.2 ± 1.7
Puccinellia nuttaliana	0	0	0	0	0	6.5 ± 2.2
Bare	2.9 ± 1.0	100	100	3.8 ± 1.2	10.8 ± 4.6	< 1
Fresh-water/brackish graminoid swards (FWG-1)						
Carex subspathacea	42.0 ± 7.4	61.1 ± 9.3	95.1 ± 3.7	34.6 ± 9.9	31.5 ± 1.9	29.0 ± 6.8
Festuca rubra	15.4 ± 0.7	0	0	11.7 ± 1.9	1.2 ± 1.2	21.0 ± 6.2
Calamagrostis deschampsioides	10.5 ± 5.6	0	0	< 1	0	0
Triglochin maritima	7.4 ± 1.2	0	0	12.3 ± 0.0	19.8 ± 3.7	11.7 ± 1.9
Plantago maritima	0	0	0	20.4 ± 6.8	21.6 ± 0.6	14.2 ± 5.6
Potentilla egedii	20.4 ± 3.1	0	< 1	21.0 ± 4.9	24.1 ± 1.9	17.9 ± 3.1
Puccinellia phryganodes	0	1.8 ± 0.6	3.1 ± 1.9	0	1.9 ± 1.9	< 1
Parnassia palustris	0	0	0	0	0	4.3 ± 3.1
Salix brachycarpa	0	0	0	0	0	1.2 ± 1.2
Bare	4.3 ± 3.1	37.0 ± 9.9	0	0	0	0
Fresh-water/brackish graminoid swards (FWG-2)						
Carex subspathacea	35.2 ± 5.8	16.8 ± 5.3	6.6 ± 3.2	32.8 ± 3.5	6.9 ± 2.0	0
Puccinellia phryganodes	47.3 ± 8.0	3.9 ± 1.5	2.9 ± 1.2	10.7 ± 1.8	18.2 ± 4.1	0
Plantago maritima	2.4 ± 0.8	< 1	0	24.0 ± 3.8	9.1 ± 2.3	7.7 ± 3.6
Potentilla egedii	< 1	< 1	0	21.9 ± 1.7	24.9 ± 5.9	24.2 ± 2.5
Ranunculus cymbalaria	3.6 ± 1.2	< 1	< 1	1.1 ± 0.3	1.2 ± 0.4	0
Calamagrostis deschampsoides	< 1	0	0	2.2 ± 1.4	1.2 ± 0.7	6.2 ± 2.7
Triglochin palustris	< 1	< 1	1.7 ± 1.2	0	< 1	0
Puccinellia nuttaliana	0	0	0	1.6 ± 0.5	1.6 ± 0.6	0
Stellaria humifusa	0	0	0	1.5 ± 0.3	< 1	< 1
Chrysanthemum arcticum	0	0	0	< 1	1.2 ± 0.6	5.2 ± 0.9
Festuca rubra	0	0	0	< 1	4.4 ± 2.5	55.8 ± 5.9
Bare	9.9 ± 1.9	78.2 ± 6.8	85.5 ± 4.5	1.7 ± 0.4	30.6 ± 9.0	0
Supratidal willow-grassland (STW-1)						
Festuca rubra	46.5 ± 1.6	30.4 ± 2.6	22.1 ± 3.3	32.7 ± 1.7	55.6 ± 1.8	40.6 ± 2.8
Carex subspathacea	29.8 ± 1.4	46.1 ± 2.8	49.6 ± 3.7	42.3 ± 2.6	30.6 ± 2.7	14.3 ± 2.8
Calamagrostis deschampsioides	15.8 ± 1.1	8.2 ± 1.6	1.9 ± 0.8	13.7 ± 1.7	3.9 ± 0.8	4.2 ± 1.2
Carex glareosa	0	0	0	0	< 1	31.7 ± 2.5

Table 3 *Continued*

	Grazed			Ungrazed		
	1986	1992	1997	1986	1992	1997
Potentilla egedii	1.8 ± 0.4	6.5 ± 1.0	8.8 ± 1.1	3.8 ± 0.6	1.9 ± 0.4	0.9 ± 0.4
Salix brachycarpa	1.1 ± 0.3	0.7 ± 0.2	8.7 ± 0.9	1.9 ± 0.5	5.8 ± 1.4	3.0 ± 0.5
Puccinellia phryganodes	0	2.9 ± 0.7	4.4 ± 1.8	0	0	0
Parnassia palustris	1.5 ± 0.2	0	< 1	2.3 ± 0.5	< 1	0
Stellaria humifusa	0	< 1	2.3 ± 0.9	0	0	< 1
Stellaria longipes	1.3 ± 0.3	< 1	0	1.6 ± 0.3	< 1	< 1
Ranunculus cymbalaria	0	< 1	1.5 ± 0.6	0	0	0
Bare	0	2.1 ± 0.7	0	0	0	3.1 ± 1.3
Supratidal willow-grassland (STW-2)						
Festuca rubra	66.6 ± 1.8	74.5 ± 1.8	60.7 ± 2.1	57.7 ± 1.1	61.8 ± 2.0	56.6 ± 4.5
Calamagrostis deschampsioides	12.4 ± 1.3	2.2 ± 0.6	1.6 ± 0.4	16.7 ± 1.1	8.4 ± 3.5	4.0 ± 1.0
Leymus mollis	7.8 ± 1.4	13.7 ± 1.1	18.9 ± 2.2	6.2 ± 0.6	17.7 ± 1.1	13.6 ± 3.1
Stellaria longipes	5.8 ± 0.7	3.3 ± 0.7	6.3 ± 0.7	10.4 ± 1.0	7.4 ± 1.1	17.6 ± 2.9
Carex subspathacea	2.1 ± 0.8	0	< 1	2.0 ± 0.5	0	0
Chrysanthemum arcticum	< 1	1.2 ± 0.4	3.6 ± 0.8	2.4 ± 0.4	< 1	< 1
Parnassia palustris	1.7 ± 0.5	1.1 ± 0.4	2.6 ± 0.7	1.9 ± 0.6	< 1	< 1
Potentilla egedii	2.8 ± 0.6	2.4 ± 0.6	2.3 ± 0.7	2.1 ± 0.4	< 1	< 1
Salix brachycarpa	< 1	1.2 ± 0.5	2.6 ± 0.7	< 1	2.8 ± 1.1	4.6 ± 1.8
Bare	< 1	0	< 1	< 1	0	1.6 ± 0.6
Fresh/brackish willow-grassland assemblage (FWW-1)						
Calamagrostis deschampsioides	61.2 ± 1.1	8.0 ± 1.1	1.5 ± 0.8	43.4 ± 2.6	17.5 ± 3.5	2.5 ± 0.7
Carex subspathacea	16.5 ± 1.3	78.2 ± 1.8	87.2 ± 2.1	34.7 ± 2.3	19.8 ± 1.9	< 1
Dupontia fisheri	9.3 ± 1.4	1.2 ± 0.4	3.6 ± 0.8	6.9 ± 1.0	5.2 ± 1.1	73.9 ± 2.8
Festuca rubra	6.4 ± 1.1	5.7 ± 1.2	0	10.0 ± 1.4	45.2 ± 3.6	2.9 ± 1.0
Puccinellia phryganodes	0	< 1	4.4 ± 0.9	0	0	0
Chrysanthemum arcticum	1.3 ± 0.3	0	0	< 1	2.8 ± 1.0	6.5 ± 1.0
Salix brachycarpa	< 1	< 1	< 1	< 1	3.6 ± 1.1	4.9 ± 0.8
Potentilla egedii	1.7 ± 0.5	< 1	< 1	1.9 ± 0.5	3.3 ± 0.6	1.6 ± 0.6
Ranunculus cymbalaria	< 1	< 1	< 1	< 1	0	1.2 ± 0.6
Parnassia palustris	1.4 ± 0.4	0	< 1	< 1	< 1	< 1
Triglochin palustris	0	1.8 ± 0.5	1.6 ± 0.5	0	< 1	0
Stellaria humifusa	1.1 ± 0.4	0	< 1	< 1	0	< 1
Stellaria longipes	0	0	0	0	< 1	2.5 ± 0.9
Potentilla palustris	0	0	0	0	< 1	2.1 ± 0.5
Bare	0	3.1 ± 0.8	0	0	0	0

them when marshes were still relatively intact (FWG-1 and 2, STW-1, FWW-1).

In grazed graminoid-dominated plots in the supratidal and brackish island marshes, foraging led to a loss of species richness over time (1986–97) at all four sites (Table 3: from six to three species at STG-1, six to zero species at STG-2, six to four species at FWG-1 and eight to four species at FWG-2; τ < 0.500 for all contrasts). Several species that disappeared were dicotyledenous plants, including *Potentilla egedii* (STG-2, FWG-1, FWG-2), *Plantago maritima* (STG-1, STG-2, FWG-2) and *Stellaria humifusa* (STG-1, STG-2). At sites STG-1, STG-2 and FWG-2, there was a decrease in vegetation in grazed plots (respectively 35%, 100% and 86% of positions beneath wire intersections). Disappearance of *Carex subspathacea* and *Puccinellia phryganodes* at the supratidal site STG-2 and their declines in frequency to less than 15% in the brackish marsh island site FWG-2 indicated that heavy grazing and grubbing caused a shift towards bare sediments at these sites. At the supratidal site STG-1, the frequency of *P. phryganodes* remained constant from 1986 to 1997,

although *C. subspathacea* disappeared. At site FWG-1, foraging (< intensity than at the supratidal marsh, personal observation) led to a substantial increase in the frequency of *C. subspathacea* and the appearance of *P. phryganodes* (3% frequency). These species replaced *F. rubra* and *C. deschampsioides*, which had frequencies of 15% and 11%, respectively, in 1986, but had both disappeared by 1997 (Table 3).

Changes were also evident in species composition of ungrazed plots of the supratidal and brackish island marshes from 1986 to 1997 (τ-values were 0.428–0.679). At supratidal site STG-1, frequencies of *P. phryganodes* and *Salicornia borealis* decreased by 37% and 46%, while frequencies of *C. subspathacea* and *F. rubra* increased by 16% and 9%, respectively (Table 3). In contrast, at supratidal site STG-2, where goose grubbing of vegetation inside the exclosure in the early 1990s resulted in increased salinity (cf. Srivastava & Jefferies 1996), frequencies of *P. phryganodes* and *S. borealis* increased by 44% and 5%, respectively, while the frequency of *C. subspathacea* decreased by 48%. At both ungrazed island sites FWG-1 and FWG-2, the presence of

Table 4 Overview of the 38 vascular plants and two sediment states recorded from 1986 to 1997 in grazed and ungrazed vegetation plots in coastal marshes of La Pérouse Bay. Significance levels (***$P < 0.0001$, **$P < 0.001$, *$P < 0.05$) refer to ANOVA results where grazing had an effect on the abundance of species/sediments that occurred at a frequency > 5% in any treatment or year

Sediments (> 5% that showed higher abundances in grazed plots than ungrazed plots)
***Bare ground (consolidated sediment)
Soft sediment (unconsolidated sediment)

Species (> 5% that showed higher abundances in grazed plots than ungrazed plots)
†***Carex subspathacea
**Eleocharis acicularis
*Hippuris tetraphylla
†***Puccinellia phryganodes
***Senecio congestus
***Triglochin palustris

Species (> 5% that showed higher abundances in ungrazed than grazed plots)
***Carex glareosa
†***Carex subspathacea
***Chrysanthemum arcticum
***Dupontia fisheri
***Festuca rubra
***Plantago maritima
***Potentilla egedii
***Puccinellia nuttalliana
†***Puccinellia phryganodes
**Salix brachycarpa
***Stellaria longipes
***Triglochin maritima

Species (> 5% that showed no significant difference ($P > 0.05$) in response to grazing)
Calamagrostis deschampsioides
Leymus mollis
Stellaria humifusa
Ranunculus cymbalaria
Salicornia borealis

Rare species (< 5%)
Cardamine pratensis
Calamagrostis stricta
Cochlearia officinalis
Euphrasia arctica
Galium palustre
Hippuris vulgaris
Juncus bufonius
Lomatogonium rotatum
Myriophyllum exalbescens
Parnassia palustris
Potentilla palustris
Potamogeton filiformis
Primula stricta
Ranunculus aquatilis
Ranunculus purshii
Rhinanthus borealis
Rumex occidentalis

† *P. phryganodes* and *C. subspathacea* are listed in both categories given that their abundance pattern is contingent on the sediment state of the site (see Results).

C. subspathacea decreased, while that of *F. rubra* increased (Table 3). With the exception of supratidal site STG-2, frequencies of dicotyledenous plants in ungrazed plots increased or were unchanged and seedlings of *Salix brachycarpa* established in the island exclosure FWG-1 at a low frequency.

In grazed plots at willow-grassland sites (supratidal marsh sites STW-1, STW-2 and island site FWW-1), between 1982 and 1992, decreased frequencies of *F. rubra* and *C. deschampsioides* were recorded (Table 3). At sites STW-1 and FWW-1, there was a corresponding increase

in the frequency of *C. subspathacea* (Table 3) and at site STW-2 an increase in *L. mollis* (11%). Frequencies of *S. brachycarpa* increased at both supratidal marsh sites (2% and 8%, respectively). As well, *P. phryganodes* established at low frequencies in grazed plots at sites STW-1 and FWW-1.

Decreases in the presence of *C. deschampsioides* occurred in ungrazed willow-grassland plots at sites STW-1, STW-2 and FWW-1 and *C. subspathacea* at sites STW-1 and FWW-1, but *Carex glareosa*, *L. mollis* (8% at site STW-2) and *Dupontia fisheri* increased in

frequency. *S. brachycarpa* also increased over the 11 years but frequency values were still less than 5%. Some dicotyledenous species, such as *Stellaria longipes* (STW-2) and *Chrysanthemum arcticum* (FWW-1), showed increases above frequencies of 5%.

The weakest correlation coefficients ($\tau < 0.300$) for comparisons of species present in plots in the presence and absence of grazing from 1986 to 1997, were observed at the soft-sediment estuarine site (SSE-1) (Table 3). Here, grazing resulted in strong differences in the species assemblage. The decrease overtime in *C. subspathacea* and the increase in vegetative cover, particularly *E. acicularis* in grazed plots, was reversed in ungrazed plots (Table 3). *Ranunculus cymbalaria* was present at frequencies between 7% and 13% in both grazed and ungrazed plots and *S. congestus* and *D. fisheri* (< 5%) were among the invaders.

ANOVA results confirmed what was evident from our *a priori* selection of sites: species/sediment abundances varied significantly with site (d.f. 7,457; $P < 0.0001$) in all 23 tests. Interactions (treatment × site, treatment × time, site × time, treatment × site × time) were also significant ($P < 0.05$) in over 80% of the tests, partially reflecting selection of sites across a gradient of marsh types and successional stages (Tables 1 and 3). Direction of change (increased or decreased abundance in response to grazing) is closely linked to successional state of the site (as for *P. phryganodes* and *C. subspathacea* above), while differences in rates of change and species abundance between sites may also be likely due to differences in foraging intensity and edaphic conditions.

Discussion

Models involving multiple-state dynamics have been widely used to study the effects of foraging on vegetation (Holling 1973; Noy-Meir 1975; May 1977; Westoby *et al.* 1989). Alternative vegetation states within a system can result from asymmetry in feedback processes between consumers and the physical environment (Peterson 1984; DeAngelis & Waterhouse 1987). Examples include positive feedbacks between reduced plant standing crop and herbivores that result in deteriorating soil conditions and multiple states (Charney *et al.* 1975; Belnap 1995; Rietkerk & Van de Koppel 1997). The importance of scale in testing for origins of alternative states and the necessity to distinguish between mechanisms of origin and those of maintenance has been emphasized by Hobbs & Norton (1996) and Petraitis & Latham (1999). We have attempted to synthesize our understanding of these mechanisms in a state and transition model for the system (Fig. 2).

VEGETATION CHANGE IN THE ABSENCE OF HERBIVORY

In the absence of intense foraging pressure from geese, vegetation dynamics at La Pérouse Bay are driven largely by geomorphological change and autogenic

succession (Fig. 2). The complete shift between salt- and fresh-water plant assemblages occurs on a time scale of 10^2–10^3 years (Scott 1994) and thus within this time frame the assemblages can be treated as examples of quasi-stable states, where positive and negative feedbacks are broadly balanced. Results from exclosed, ungrazed plots (Tables 3, 4) and from earlier studies when swards were less heavily grazed (Jefferies *et al.* 1979; Bazely & Jefferies 1986; Hik *et al.* 1992) indicate that where frost-heave occurs and sediments are well drained in the upper intertidal and supratidal marshes, the graminoid, halophytic plant assemblage (Sites STG-1 and STG-2) is replaced by a willow-grassland community (Sites STW-1 and STW-2). Both an elevational rise associated with isostatic uplift and development of an organic layer are necessary for this change (Jefferies *et al.* 1979; Bazely & Jefferies 1986).

Another vegetation shift occurs when sediments are less well drained and surface water is present for at least some months of the year (Fig. 2). Under such conditions, intertidal marshes are replaced by fresh-water sedge meadows (Kershaw 1976; Jefferies *et al.* 1979; Kerbes *et al.* 1990; Kotanen & Jefferies 1997). Isostatic uplift and the seaward presence of beach ridges (a consequence of uplift) result in a low elevational gradient and impeded drainage in these meadows, where permafrost is about 50 cm below the surface. The timing of the change to fresh-water conditions is not easily predictable, but the closure of low-lying areas to tidal incursions is also likely to occur at intervals of between 10^2 and 10^3 years.

Vegetation patterns in riverine sites (FWG-1, FWG-2, FWW-1) did not correspond to either of the quasi-stable states described above, but represented an intermediate state with affinities to both sedge meadows and willow-grassland. The centre of islands often showed plant assemblages similar to supratidal sites (Table 3, Fig. 1). However, the hydrological regime enabled moss carpets to establish, especially adjacent to banks, in which *Dupontia fisheri*, *Primula stricta* and *Saxifraga hirculus* often occur.

VEGETATION CHANGE IN THE PRESENCE OF HERBIVORY

At low to moderate grazing intensity, foraging activities of geese reset the successional clock (Bazely & Jefferies 1986; Jefferies 1988a,b), but do not trigger a change in the trajectory of vegetation development. Two decades ago, moderate summer grazing on intertidal salt-marshes led to rapid re-growth of grazed swards, so that above-ground net primary production exceeded that of ungrazed plots (Cargill & Jefferies 1984). Geese maintained above-ground biomass of swards of *P. phryganodes* and *C. subspathacea* between 30 and 50 g m^{-2} throughout the season. When swards in the extreme upper intertidal marsh were enclosed and the fence was removed after 2 years, geese failed to forage on the ungrazed biomass, no longer characteristic of the
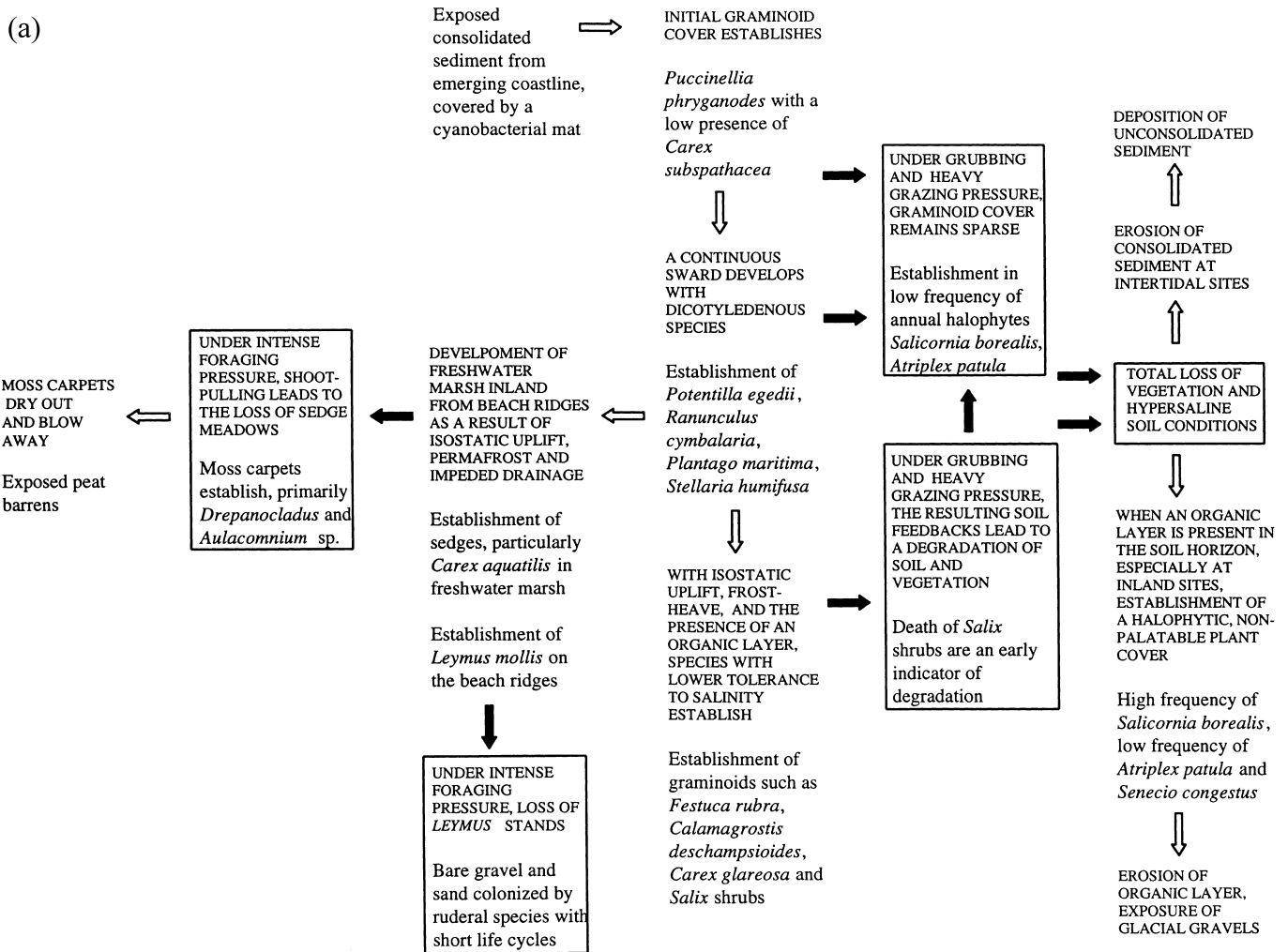
(a)

Exposed consolidated sediment from emerging coastline, covered by a cyanobacterial mat ⟹ INITIAL GRAMINOID COVER ESTABLISHES

Puccinellia phryganodes with a low presence of *Carex subspathacea*

⇩

A CONTINUOUS SWARD DEVELOPS WITH DICOTYLEDENOUS SPECIES

Establishment of *Potentilla egedii*, *Ranunculus cymbalaria*, *Plantago maritima*, *Stellaria humifusa*

⇩

WITH ISOSTATIC UPLIFT, FROST-HEAVE, AND THE PRESENCE OF AN ORGANIC LAYER, SPECIES WITH LOWER TOLERANCE TO SALINITY ESTABLISH

Establishment of graminoids such as *Festuca rubra*, *Calamagrostis deschampsioides*, *Carex glareosa* and *Salix* shrubs

MOSS CARPETS DRY OUT AND BLOW AWAY

Exposed peat barrens

⟸ UNDER INTENSE FORAGING PRESSURE, SHOOT-PULLING LEADS TO THE LOSS OF SEDGE MEADOWS

Moss carpets establish, primarily *Drepanocladus* and *Aulacomnium* sp.

⟸ DEVELPMENT OF FRESHWATER MARSH INLAND FROM BEACH RIDGES AS A RESULT OF ISOSTATIC UPLIFT, PERMAFROST AND IMPEDED DRAINAGE

Establishment of sedges, particularly *Carex aquatilis* in freshwater marsh

Establishment of *Leymus mollis* on the beach ridges

UNDER INTENSE FORAGING PRESSURE, LOSS OF *LEYMUS* STANDS

Bare gravel and sand colonized by ruderal species with short life cycles

UNDER GRUBBING AND HEAVY GRAZING PRESSURE, GRAMINOID COVER REMAINS SPARSE

Establishment in low frequency of annual halophytes *Salicornia borealis*, *Atriplex patula*

UNDER GRUBBING AND HEAVY GRAZING PRESSURE, THE RESULTING SOIL FEEDBACKS LEAD TO A DEGRADATION OF SOIL AND VEGETATION

Death of *Salix* shrubs are an early indicator of degradation

DEPOSITION OF UNCONSOLIDATED SEDIMENT

⇧

EROSION OF CONSOLIDATED SEDIMENT AT INTERTIDAL SITES

⇧

TOTAL LOSS OF VEGETATION AND HYPERSALINE SOIL CONDITIONS

⇩

WHEN AN ORGANIC LAYER IS PRESENT IN THE SOIL HORIZON, ESPECIALLY AT INLAND SITES, ESTABLISHMENT OF A HALOPHYTIC, NON-PALATABLE PLANT COVER

High frequency of *Salicornia borealis*, low frequency of *Atriplex patula* and *Senecio congestus*

⇩

EROSION OF ORGANIC LAYER, EXPOSURE OF GLACIAL GRAVELS

Fig. 2 State and transition model for vegetatio∏n change at La Pérouse Bay, Manitoba in (a) coastal and (b) estuarine marshes. Upper case text denotes the transition and lower case text denotes the vegetation and/or geomorphological state. Black arrows and boxes indicate states and transitions triggered directly by high numbers of foraging geese. White arrows indicate vegetational or geomorphological processes that are independent of geese, although some may have been triggered by their foraging activities.

grazing lawn (cf. McNaughton 1984) with a short turf and preponderance of young leaves (Bazely & Jefferies 1986). This 'escape' from foraging, the build-up of plant litter and the increase in abundance of *F. rubra* represents a microcosm of long-term vegetational change as a consequence of isostatic uplift. The numbers of geese at that time could only delay the change associated with uplift, they could not halt it (Bazely & Jefferies 1986; Hik *et al.* 1992).

Since then, numbers of lesser snow geese have continued to increase, and since 1998 Ross' geese (*Chen rossi*) and Canada geese (*Branta canadensis*) together are as abundant or more abundant than snow geese on intertidal flats. The increased foraging pressure has led to reductions in vegetative cover (Table 4; Jano *et al.* 1998), increased soil evaporation, hypersalinity and the death of salt-marsh swards (Srivastava & Jefferies 1995, 1996). In swards that are only in a partial state of degradation, the landscape shows a spatial mosaic of different patch sizes in which alternate vegetation states can be recognized on a spatial scale of 10^0–10^1 m^2.

As the preferred forage species of the geese (i.e. *P. phryganodes* and *C. subspathacea*; Gadallah & Jefferies 1995) decreased further in abundance, birds sought other forage species. These included *F. rubra* and *C. deschampsioides* from willow-grassland assemblages, *L. mollis* that colonizes the beach ridges, *Carex aquatilis* from the sedge meadows, and *H. tetraphylla* and *Potamageton filiformis* in estuarine sites. In willow-grassland sites, the grazing of *Festuca-Calamagrostis* swards has led to 'retrogressive succession' (*sensu* Bakker 1985), that is, an enhanced establishment of the early successional *Puccinellia* and *Carex* plants that in turn may be lost if foraging pressure increases (Table 3). This result differs from the observations made when the goose population was appreciably lower, and the shift of *Puccinellia-Carex* swards to *Festuca-Calamagrostis* swards was argued to be asymmetric (Hik *et al.* 1992). In the last few years, we have observed another example of retrogressive succession at the site. Bare, consolidated sediments, that have resulted from the degradation of the marsh, undergo erosion (wind, ice and water)

(b)

Soft unconsolidated sediment

⇓

SEDIMENT CONSOLIDATION

Establishment of *Hippurus tetraphylla* and *Myriophyllum exalbescens*

⇓

INITIAL GRAMINOID COVER ESTABLISHES

Establishment of *Carex subspathacea* with a low presence of ruderal species (e.g. *Triglochin palustris* and *Eleocharis acicularis*)

⇓

A CONTINUOUS SWARD DEVELOPS WITH DICOTYLEDENOUS SPECIES

Establishment of *Potentilla egedii*, *Ranunculus cymbalaria*, *Plantago maritima*, *Stellaria humifusa*

⇓

WITH ISOSTATIC UPLIFT, FROST-HEAVE, AND THE PRESENCE OF AN ORGANIC LAYER, SPECIES WITH LOWER TOLERANCE TO WATERLOGGING AND SALINITY ESTABLISH

Establishment of graminoids such as *Puccinellia phryganodes*, *Festuca rubra*, *Calamagrostis deschampsioides* and *Salix* shrubs

UNDER GRUBBING AND HEAVY GRAZING PRESSURE, GRAMINOID COVER REMAINS SPARSE WITH A HIGH PRESENCE OF RUDERAL SPECIES

UNDER GRUBBING AND HEAVY GRAZING PRESSURE, THE RESULTING SOIL FEEDBACKS LEAD TO A DEGRADATION OF SOIL AND VEGETATION

Death of *Salix* shrubs are an early indicator of degradation

DEPOSITION OF UNCONSOLIDATED SEDIMENT

⇑

EROSION OF CONSOLIDATED SEDIMENT AT INTERTIDAL SITES

⇑

TOTAL LOSS OF VEGETATION AND HYPERSALINE SOIL CONDITIONS

Fig. 2 *Continued*

creating unconsolidated sediment that is deposited in estuarine channels. In these unconsolidated sediments, a *Hippuris*-dominated community (e.g. Site SSE-1) can establish and the plant succession process is re-initiated (Fig. 2).

RECOVERY OF DEGRADED SITES

In intertidal sites, some natural re-vegetation occurred in sediments within 5 years in all eight exclosures (Table 2), but there was significant spatial and temporal variability in establishment success. Large differences were observed between exclosures and colonies, and the highest re-vegetation rates occurred in moist soils, near drainage channels. Microsite differences associated with fine-grain geomorphological variation in surface sediment properties, effectively determine whether re-vegetation is possible (Handa & Jefferies 2000).

Death of transplanted *Festuca-Calamagrostis* plants in degraded sites demonstrates that the willow-grassland assemblage cannot develop directly on bare sediments in the upper intertidal marsh, but will develop on an intermediate template of *Puccinellia-Carex* cover as soil organic matter builds up (Tables 3 and 4; Hik *et al.* 1992). *Puccinellia* can re-establish from vegetative units (cf. Chou *et al.* 1992) produced by goose grazing. However, as partially denuded swards loose remaining vegetation, the availability of vegetative fragments of *Puccinellia* becomes increasingly limited. Likewise, recruitment of other salt-marsh species is limited by availability of propagules (Chang *et al.* 2001). In 1985 Bazely & Jefferies (1986) showed that in an exclosed foremarsh plot, 12 new species were recruited over a period of 5 years. However, in 1997, in intertidal plots where intact swards of *Puccinellia* have re-established, recruitment of other species has been slow (Table 2; Handa & Jefferies 2000). This observation appears to be a consequence of a depleted seedbank and poor entrapment of seed where vegetation has been lost as a result of grubbing (Chang *et al.* 2001). The only species to establish readily in unassisted or assisted trials was

Ranunculus cymbalaria (Table 2; Jefferies, unpublished data), which is one of the few species that is still well represented in the seedbank (Chang *et al.* 2001). Hence, limitations in propagule dispersal may extend the length of the initial recruitment phase, in spite of the presence of a vegetative mat of *P. phryganodes*.

In the supratidal marsh, no re-vegetation by the former graminoids appears possible where the surface layer has been lost and underlying sediments are poorly drained. For example, close to the inland (but saline) exclosure devoid of vegetation since 1984, establishment of *C. subspathacea* was poor, even with soil amelioration (Handa & Jefferies 2000). Waterlogging in spring, the presence of anoxic conditions below the immediate surface, followed by drying out of the soil in summer, and the development of hypersalinity, produce conditions inimical to most plants. Where some organic soil remains, cyanobacterial mats and halophytic annuals, *Salicornia borealis* and *Atriplex patula*, may establish (personal observation). However, the plant cover is ephemeral and does not remain. Every season, the algal mats dry out, crack, blister and are blown away, and the necromass of annuals is washed away. Absence of vegetation ultimately leads to erosion and exposure of marine sediments or glacial gravels (Fig. 2).

Longer term successional change in this system is highly dependent on geomorphological abiotic processes, such as isostatic uplift, frost heave, the presence of permafrost and surface hydrology, that limit the type of plant assemblages that are possible. Establishment may also be dependent on episodic events, such as a succession of fine summers, the absence of winter storms and fast spring run-offs. Increased goose foraging has led to vegetation loss and the development of alternate stable states. Spatial and temporal scales that characterize these degraded sites are approximately 100 m^2–$62\ 500 \text{ m}^2$ and the sites appear to persist from 10 to at least 50 years. In addition, degraded areas may coalesce into larger units over time (Jano *et al*. 1998). The limitation on recovery is re-enforced by the absence of a soil seedbank of former species (Chang *et al.* 2001) and the irregular and episodic production of seed in most arctic species (Urbanska 1997).

Overall, the degraded sites show irreversible or near irreversible changes in soil properties and propagule loss. The change in soil properties is associated with loss of the surface organic veneer, hypersalinity, water logging, anoxia and erosion (Srivastava & Jefferies 1996; Kotanen & Jefferies 1997; Handa & Jefferies 2000). Pedological change linked to surface hydrology and geomorphology severely limit re-vegetation processes and maintain alternate states.

Acknowledgements

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