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Initiation and maintenance of vegetation mosaics in an Arctic salt marsh

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Summary

1 Vegetation mosaics of grassland and exposed soil are often the outcome of intense herbivory and represent alternate stable states, although the vegetational and soil processes that both initiate and maintain the states in response to herbivory are poorly understood.
2 The vegetation mosaic resulting from grubbing by geese was examined on the intertidal flats at La Pérouse Bay, Manitoba. Soil properties of the alternate states were measured in conjunction with the ability of transplanted tillers of *Puccinellia phryganodes* to grow in exposed soil and intact swards. Simulated grubbed patches (2.5–40 cm diameter) were prepared at three sites and the soil properties and inward clonal growth of the grass in each patch were examined during two growing seasons.
3 Where an organic layer was still present on exposed areas, soil properties were similar to those in the rooting zone beneath intact swards, except that soils were hyper-rather than hyposaline. Older exposed mineral soils, where the organic layer had been eroded, were similarly hypersaline, but were also low in soil moisture and total nitrogen, and compacted with a low infiltration rate. Transplanted tillers survived in intact swards, but few survived in any hypersaline soils.
4 Changes in soil properties over two seasons depended on size of experimentally created patches. Again, high salinities developed in soils of the larger patches, and there was a loss of nitrogen and soil moisture and an increase in bulk density with increasing patch size. Although inward clonal growth of *P. phryganodes* took place from plot perimeters, this is likely to be curtailed by high salinities in plots over 20 cm diameter.
5 As in tropical Africa, intense herbivory can lead to an alternate stable state in this Arctic salt marsh. Small patches of exposed soil are characterized by deteriorating soil conditions and the inability of vegetation to re-establish. As patches coalesce with continued herbivory, an ecological sere (the intertidal salt marsh) is lost.

Key-words: alternate stable state, grubbing, hypersalinity, lesser snow goose, *Puccinellia phryganodes*

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Introduction

Herbivory can lead to a spatial mosaic of alternating patches of vegetation and exposed soil devoid of plants, which also differ in resource availability (Belsky 1986; Montana 1992; Wilson & Agnew 1992; Pickett & Cadenasso 1995; Bromley *et al.* 1997; Van de Koppel *et al.* 1997; Rietkerk *et al.* 2000; HilleRisLambers *et al.* 2001). Although the mechanisms that initiate these mosaics are debated (Boaler & Hodge 1962; Belsky 1986; Kellner & Bosch 1992; Bromley *et al.* 1997; Puigdefabregas *et al.* 1999), their presence in semi-arid ecosystems, where the mosaics have been studied intensively, is due to herbivory triggering the abiotic changes that occur in newly exposed soil. In particular, the infiltration rate of water through the surface layers of exposed soil is slower compared with that of vegetated soil (Graetz 1991; Wilson & Agnew 1992; Rietkerk & Van de Koppel 1997; Van de Koppel *et al.* 1997; HilleRisLambers *et al.* 2001). Rainfall, which infiltrates less easily on hardened soil surfaces (Glover *et al.* 1962; Box & Bruce 1996; Anderson & Hodgkinson 1997), is either trapped by adjacent

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vegetative patches, or drains from the system (Graetz 1991; HilleRisLambers *et al*. 2001).

Rapid loss of vegetative cover and reduced water supply combine to limit the ability of the surviving plants to cope with additional herbivory and increasing soil degradation (Charney *et al*. 1975). The changes in soil conditions are often irreversible (Sinclair & Fryxell 1985; Friedel 1991; Laycock 1991), leading to an alternative stable state characterized by loss of vegetation (Rietkerk & Van de Koppel 1997). Models of semi-arid grazing systems predict that, under the cumulative impact of intense herbivory, complete vegetative cover is replaced, initially by a spatial mosaic of vegetation and exposed soil, and then, provided propagule dispersal is low, entirely by exposed soil as the spatial scale of the alternative stable state increases (Klausmeier 1999; Rietkerk *et al*. 2000, 2002; HilleRisLambers *et al*. 2001).

Although a change in the infiltration rate is believed to be the primary factor controlling vegetation mosaics in semi-arid regions, changes in other soil variables may be expected to contribute (Graetz 1991; Anderson & Hodgkinson 1997). Little attention, however, has been given to the effects of nutrient availability and physical conditions on the ability of plants to re-colonize these soils. Similarly, processes that create, rather than maintain, mosaics are poorly understood. Van de Koppel & Rietkerk (2000) have stressed the need for further empirical investigations to test the predictions of theoretical studies.

At La Pérouse Bay, Manitoba, on the Hudson Bay coast, a breeding colony of lesser snow geese (*Chen caerulescens caerulescens*) has increased from 1300 pairs in 1968 to an estimated 44 500 pairs in 1997 (Rockwell, Abraham & Ross, unpublished aerial survey in 1997). Grubbing by the geese of intertidal vegetation leads to exposure of the underlying soil at spatial scales of less than 0.5 m, creating localized patches within salt-marsh swards early in each season after the ground has thawed, but before above-ground vegetative growth has commenced (Jefferies *et al*. 1979; Kerbes *et al*. 1990; Hik *et al*. 1992) and has led to the development of a mosaic consisting of intact swards and patches of exposed sediment, devoid of vegetation (Jefferies 1988a,b; Handa *et al*. 2002; Jefferies & Rockwell 2002). The exposed sediment becomes hypersaline and poor plant regeneration leads to an alternate stable state (Hik *et al*. 1992; Srivastava & Jefferies 1996; Handa *et al*. 2002). Over time, these localized patches coalesce into larger areas as a result of further grubbing, creating a larger-scale vegetational mosaic and, ultimately, exposed mudflats (Jefferies & Rockwell 2002).

Soil dynamics within a patch of exposed soil may be sensitive to its size and shape, as indicated by the ratio of circumference to area (Forbes *et al*. 2001). In relatively small patches, plants at the perimeter affect not only their immediate soil environment, but also the entire patch. Their facilitative interactions ameliorate adverse conditions for plant growth (Bertness & Hacker 1994; Holmgren *et al.* 1997; Brooker & Callaghan 1998), including increased oxygen diffusion (Armstrong 1979) and nutrient availability (Müller 1953; Callaway 1995). Plant canopies reduce evaporation from soils resulting in lower soil salinities (Iacobelli & Jefferies 1991; Bertness *et al.* 1992; Bertness & Hacker 1994; Srivastava & Jefferies 1996; Hacker & Gaines 1997). The reproductive strategy of plants surrounding a patch of exposed soil may also influence its re-colonization (Sousa 1984). For example, in Arctic and sub-Arctic environments clonal growth is widespread and the lateral spread of ramets, with either guerilla or phalanx growth strategies (*sensu* Lovett-Doust 1981), provides a search mechanism to exploit resources (Harper 1985; Hutchings & de Kroon 1994; Jónsdóttir *et al.* 1996). The guerilla strategy, characterized by a large distance between ramets, allows plants to exploit new patches rapidly, while the short distance between ramets and a dense front of rhizomes, roots and tillers, typical of phalanx growth, leads to a slower invasion of unexploited soil (Bertness & Ellison 1987). However, as patch size increases as a result of grubbing or similar disturbances, plants growing at the perimeter may have little influence on overall soil dynamics within a patch.

The first objective of this study was to examine the processes that maintain the vegetation mosaic in this intertidal marsh on the Arctic/sub–Arctic boundary. These included a comparison between exposed soils and vegetated soils of infiltration rates, physical and chemical characteristics and soil-nutrient availability. The second objective was to determine the survivorship of transplants of *Puccinellia phryganodes* (Trin.) Scribn. & Merr. in different components of the mosaic, particularly in exposed soil in which conditions may be inimical for establishment and growth. This asexual grass is the primary forage species of lesser snow geese on the intertidal flats at La Pérouse Bay. As increasing patch size may limit the overall impact of facilitative mechanisms in influencing plant re-establishment within a patch, our final objective was an experimental determination of the effect of newly created patches of different size within intertidal swards on soil dynamics and re-colonization of patches by *P. phryganodes*. Patches simulating grubbing were created at a variety of sizes, and changes in soil properties within each patch were determined during two growing seasons. Inwardly directed clonal growth of *P. phryganodes* was monitored during the second and third season after the establishment of patches, and these data, together with results of the final harvest in the third season are presented here.

Methods

SITE DESCRIPTION AND SELECTION

Experimental sites were selected on the intertidal flats at La Pérouse Bay (58°44′ N, 94°28′ W) in Wapusk National Park, located 32 km east of Churchill, Manitoba. The surface topography displays only minor relief that results from frost-heave and the presence of shallow ephemeral streams and ponds that are active during spring melt or during heavy rain. *Puccinellia phryganodes*, a stoloniferous grass, and *Carex subspathacea* Wormskj., a rhizomatous sedge, dominate the vegetated areas of the intertidal marsh. Low willows (*Salix* spp.) (< 1 m) define the upper limit of the intertidal salt marsh. Permafrost is continuous in the Churchill region (Rouse *et al.* 1997) and it is present approximately 25–30 cm below the surface of the sediment of the intertidal flats in mid-summer (Wilson 1993). The snow-free season usually extends from mid-June to late September, although snow can fall in any month of the year.

Sites selected were located along a soil ripening (ageing) gradient (cf. Pons & Zonneveld 1965) that was marked by a rise in elevation of approximately 50 cm over a distance of 1 km. The three selected sites, each about 100 m × 100 m and separated by at least 400 m, represented soils of increasing age and elevation along the 1-km gradient and patches with intact swards of *Puccinellia phryganodes* were still present in the low marsh, mid-marsh and high marsh sites selected. Elsewhere, the effects of grubbing had led to a complete loss of vegetation and the absence of well-defined mosaics.

STUDY OF ESTABLISHED VEGETATION MOSAICS

Soils beneath swards and exposed sediments at each of the three sites were collected and analysed in July 2001. Four soil types were recognized at each site and they were characterized in terms of their vegetative cover, namely: (a) below intact swards of *Puccinellia phryganodes*; (b) ephemeral black mats composed of cyanobacteria and diatoms growing on exposed soil surfaces devoid of vascular vegetation, but rich in organic matter; (c) ephemeral white mats that are dried-out black mats; and (d) exposed mineral soil devoid of plant cover. The last three types (b, c, d) represent exposed soil at different stages of degradation, marked by a progressive loss of the organic-rich surface layer following grubbing. The vernal black mats dry out in summer, crack and blister, turn white and are blown away, together with some of the attached organic-rich sediment. The black and white mats are collectively referred to as algal mats.

Soil characteristics examined were infiltration rate, moisture content, bulk density, salinity and the total nitrogen and organic contents of dried soil. Five replicate blocks of soil (10 cm × 10 cm × 5 cm) (except infiltration samples for which $n = 3$, see below) were collected at random from different patches of each of the four types at each of the three sites. Sampled patches were at least 20 m apart and individual patches were larger than 1 m^2. Upon return to the field laboratory, blocks were trimmed and soil samples (> 10 g) were taken from a newly exposed surface of each block for each soil variable examined. Soil moisture (g water g^{-1} soil dried at 50 °C for 1 week), bulk density (g dried soil cm^{-3}, based on a known volume of soil), total nitrogen content (% N on a mass basis of dried soil) and total organic content (g organic matter g^{-1} dried ground soil; Wiley Mill, mesh size 20) were measured in the top 3 cm of the profile after the vegetation layer (depth 0.5–1.0 cm) had been removed (the majority of *Puccinellia phryganodes* roots occur within 3 cm of the surface). Thus, soil samples were taken from the organic-rich layer, except in the case of the mineral soil where the organic layer was absent. Total nitrogen content of dried soil was determined using a LECO CHN Analyser (St Joseph, Missouri). Estimates of soil organic content were based on loss of weight on ignition at 500 °C of soil samples collected and dried in July 2000. Soil salinity was measured on soil water that had been extracted by centrifugation. Samples were frozen and later analysed for their sodium content using a Perkin-Elmer atomic absorption spectrophotometer (Model 3110, Rexdale, Ontario) in the flame-emission mode. All values of the sodium concentration in extracted water were converted to salinity using the regression equation: salinity (g dissolved solids L^{-1}) = 3.59 [Na$^+$] g L^{-1} +3.85 ($r^2 = 0.96$), where [Na$^+$] is the concentration of sodium ions in solution (Srivastava & Jefferies 1995a). Infiltration rate was measured using a Turf-Tec Infiltrometer (Forestry Supplies, Jackson, Mississippi). A 25 cm × 25 cm × 5 cm thick layer of each of the soil types was removed from the ground, placed on a wire mesh and saturated with water. Steady-state infiltration (Shainberg & Levy 1996) was measured as the amount of water (cm) that passed through the soil each minute, over 20 minutes.

Four chicken-wire exclosures (1 m × 1 m) were established in each soil type at each of the three sites (48 exclosures). Tillers of *Puccinellia phryganodes* (3 cm total length), which were taken from a sward at each site, were transplanted in mid-June 2001 into each of the four soil types at the three sites, including the original soil, and their survival and growth monitored during the growing season (June to August). In each case 20 tillers in a plug of soil were taken using a cork borer (2 cm diameter, 4 cm depth) and were transplanted into a selected soil within an exclosure at a minimum distance of 15 cm between transplants. The growth of tillers alive in late July was scored subjectively. Each transplant was given a score from 0 to 10 ('transplant vigour'), where 0 = all tillers dead and 10 = 100% alive. Scores for the 20 transplants within each exclosure were averaged and the average used in the statistical analyses ($n = 4$ for each soil type at each site).

Statistical analyses of soil variables and transplants were based on fixed-effects ANOVAS (Zar 1999). Two-factor (site and soil type), fully crossed ANOVAS were used to examine differences between soil variables or transplant vigour at all sites. In most overall ANOVA models, interaction terms were significant and hence soil variables were examined independently at each site. All statistics were calculated using JMP 4.0 SAS Institute 2000).

EXPERIMENTAL MANIPULATION OF PATCH SIZE

Thirty-five experimental plots (1 m × 1 m), fenced with chicken wire and separated from each other by at least

5 m, were established in the few remaining areas of intact swards at each of the three sites in June 2000. Circular patches of exposed sediment with diameters 2.5, 5, 10, 20 and 40 cm, were prepared in each plot by removing litter, above-ground vegetation and surface rhizomes and roots to a depth of 1.0–1.5 cm by hand, thus simulating grubbing. Each experimental plot contained all patch sizes, and smaller patch sizes were replicated (2.5 cm patch replicated six times, 5 cm patch replicated three times) within a plot to ensure that adequate amounts of soil were available for sampling. A vegetated area of sufficient size to serve as a control was left undisturbed in each plot. Patches were weeded in the first season (2000) to ensure complete removal of remaining vegetation.

Soil characteristics were determined when plots were established and then twice during the growing seasons of 2000 (three plots per site) and 2001 (four plots) in mid-July and late July. Soil moisture, bulk density and total soil nitrogen content were measured in the upper 3 cm of the sediment profile, after removal of vegetation as described above. Soil salinity was measured when the experiment was initiated and then in mid-July and early August 2000, but only in mid-July in 2001. All salinity measurements, except those of the last samples collected in 2000, were determined using the procedure of Iacobelli & Jefferies (1991). Water from a soil core (depth 3 cm) taken from each of the designated patches was extracted manually by squeezing the soil. It was filtered and diluted with deionized water. Salinity (g solutes L^{-1}) was measured using a portable salinity meter (Yellow Springs Instrument Co., Ohio, USA) and the value corrected for the dilution factor. At the last sampling in 2000, the soil was dry and water was extracted by centrifugation and analysed for its sodium concentration as above (Srivastava & Jefferies 1995b).

Clonal growth of *Puccinellia phryganodes* from the patch perimeter into exposed sediment was measured approximately 1 and 2 years after establishment of patches (mid-July 2001 and 2002). Growth was estimated as percentage cover and grass biomass was measured in each patch in 12 plots at each of the three sites. No other plant species invaded the exposed patches. A clear polyethylene sheet with concentric rings spaced at intervals of 1 cm was laid on top of exposed sediment of patches with diameters of 10, 20 and 40 cm. Percentage cover was estimated subjectively between adjacent concentric rings located within each of the four quadrants of a plot, beginning with the outermost ring and moving to the centre of a patch until the cover estimate fell below 5% (i.e. four estimates of cover per ring, note average values may be below 5%). In the case of patches that were 2.5 and 5.0 cm in diameter, a single patch of each was selected at random within a plot. Plant cover of the entire smaller patch was estimated subjectively, while the larger patch was divided into four quadrants and cover estimated for each. Above-ground biomass of *P. phryganodes* within each patch for each of the 12 plots was determined at each site in mid-July 2002. Biomass was measured by quadrant for all plots, except for the smallest plot (2.5 cm), where biomass in the entire plot was pooled. The biomass was clipped from the surface of the patch, washed and dried at 50 °C for 1 week before being weighed.

Statistical analyses of soil variables, cover estimates and biomass measurements were carried out using general linear models treating sampling date and site as nominal variables and patch size as a continuous variable (Zar 1999). In most overall models, two- or three-way interaction terms were significant, and thus the effect of patch size was examined independently for each site and each date. All statistics were calculated with JMP 4.0 (SAS Institute 2000).

Results

THE ESTABLISHED VEGETATION MOSAIC

There were substantial differences in the properties of the soil types of the vegetation mosaic at the sites in the low, mid- and high marsh (Table 1). Results from the high marsh site are presented in Fig. 1. Data from the first year are available from JRM (jmclaren@interchange.ubc.ca) or are in McLaren (2003). Exposed mineral soil in comparison with soil beneath intact swards of *P. phryganodes* had a lower infiltration rate (Fig. 1a), lower soil moisture (Fig. 1b), higher bulk density (Fig. 1c), higher salinity (Fig. 1d) and a lower total N content (Fig. 1e). Values under algal mates were similar to those under intact vegetation, except for salinity, which showed intermediate values. Patterns of salinity, soil moisture and bulk density did not differ between sites. Results of infiltration rate indicated significant site and soil type effects ($P < 0.05$ and $P < 0.001$ respectively) and a significant interaction between site and soil type ($P < 0.01$). Across all sites, the infiltration rate was lowest for exposed mineral soil (BM) and highest in the intact swards.

The soil qualities of the mineral soil also had a large impact on transplant survival. At all sites transplant vigour was much lower in exposed mineral soil than that in intact swards (Fig. 1f), with very few tillers surviving. At the high marsh site the vigour of transplants planted on algal mats was not significantly different from those on bare soil, but at the other two sites, values were intermediate and significantly different from the two extremes.

Of particular interest in relation to survival of transplants were the seasonal trends in soil salinity. Water from the mineral soil (EM) at all sites was already hypersaline by mid-June 2001, which was soon after spring melt. In contrast, hyposaline conditions prevailed in all other soil types at the three sites at that time and values were not significantly different between these soils in the low and high marsh (Fig. 2). By 20 July the soil water had become hypersaline in all soil types, except that below intact swards. The salinity of some soils with algal mats approached values twice that of seawater (*c.* 65 g L^{-1} of solutes) and the salinity of the water in the mineral soil increased still further.

Table 1 Interaction terms of two-factor fixed effects ANOVAs examining the effect of soil type and site on soil properties of an intertidal salt marsh at La Pérouse Bay, Manitoba, in 2001, except for organic content, which was measured only in 2000. Due to the positive interaction terms, soil properties were examined independently for each site, and the *F*-ratio for the effect of soil type within each site is presented. Degrees of freedom are consistent across sites. Levels of significance are *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

	Soil type × Site		Within site			
Soil Variable	d.f.	*F*-ratio	d.f.	Low marsh *F*-ratio	Mid-marsh *F*-ratio	High marsh *F*-ratio
Infiltration	6,24	4.74**	3,8	51.93**	33.99***	26.22***
Soil moisture	6,48	2.75*	3,16	4.15*	3.49*	7.20**
Bulk density	6,48	2.34*	3,16	6.05**	7.49**	13.59***
Salinity	6,48	8.33***	3,16	157.45***	219.67***	26.64***
Total soil N	6,48	1.53	3,16	14.85***	4.54*	6.59**
Organic content	6,48	21.74***	3,16	1.69	89.32***	25.32***
Transplant vigour	6,36	4.62**	3,12	20.10***	50.8 ***	300.24***

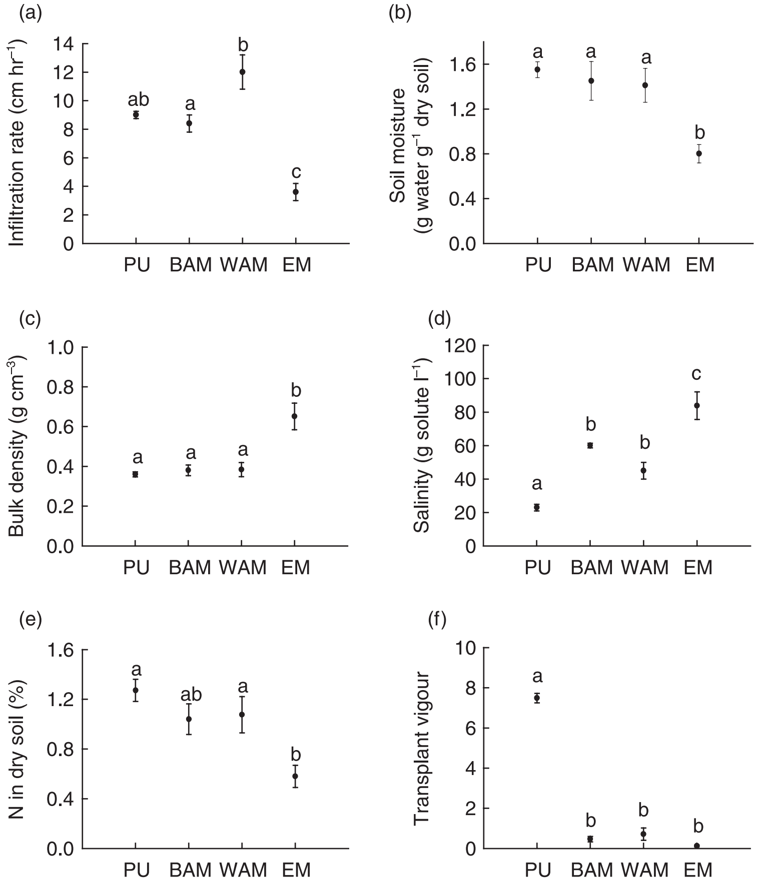

Fig. 1 Properties (mean ± SEM) of four soil types based on vegetative cover (PU = *Puccinellia phryganodes*; BAM = black mat of algae; WAM = white mat of algae; EM = exposed mineral soil) in the high intertidal marsh at La Pérouse Bay, Manitoba in 2001. Different letters indicate significant differences between means (Tukey's comparison of all means, $P < 0.05$). Soil properties measured include: (a) rate of water infiltration; (b) soil moisture; (c) bulk density; (d) salinity; (e) total nitrogen; and (f) transplant vigour. Vigour scores range between 0 and 10, where 0 = all tillers dead, and 10 = 100% alive.

Results of the total nitrogen content of the soils indicated that there was a significant effect of site and soil type, but no interaction between site and soil type (Table 1). Across all sites, total nitrogen content of dry soil was lower in exposed mineral soil than in soil beneath swards of *P. phryganodes*. In general, total nitrogen of soils with algal mats was not significantly different from values for soils beneath intact swards on the different sampling dates.

Values of the soil organic content indicated an interaction between site and soil type (Table 1). Organic matter in soils beneath intact swards increased from 22.5% to almost 30% of soil dry weight from low to high marsh sites, respectively. In contrast, organic matter as a percentage of the dry weight of exposed mineral soils fell from 21% in the low marsh to 15% or less in the mid- and high marsh sites (Fig. 3). The organic content of the

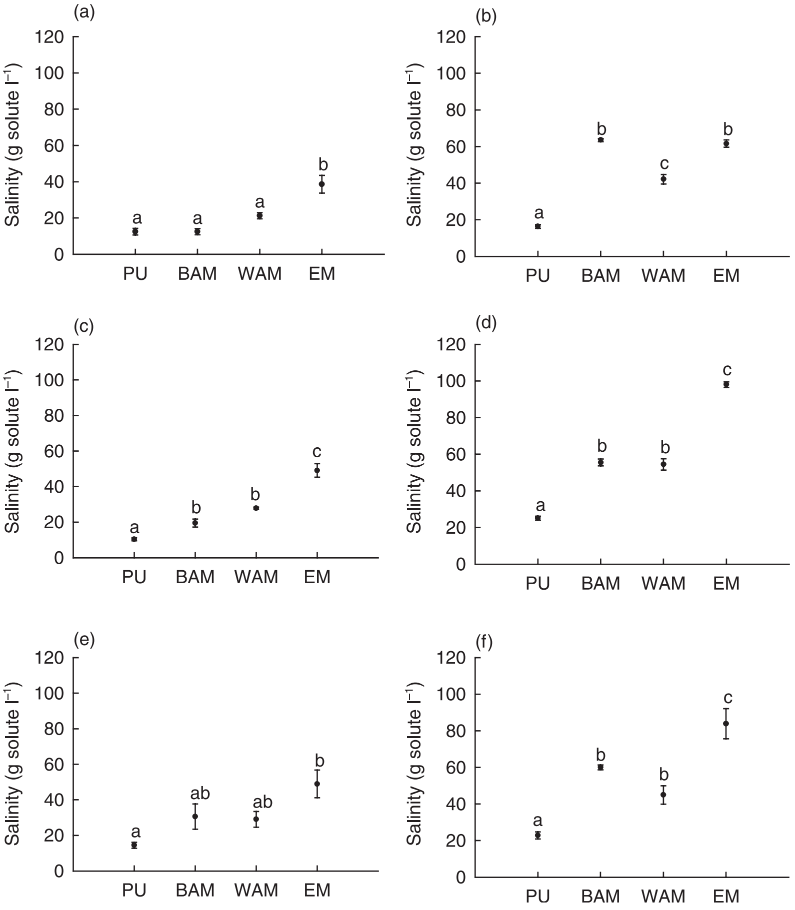

Fig. 2 Salinity (mean g l^{-1} of solutes ± SEM, $n = 5$) of soil water in the four soil types indicated in Figure 1 in the low (a, b), mid- (c, d) and high (e, f) intertidal marsh at La Pérouse Bay, Manitoba. (a), (c) and (e) refer to samples collected on 13 June and (b), (d) and (f) to those collected on 20 July 2001. Different letters on the graphs indicate significant differences in salinity between soil types (Tukey's comparison of means: $P < 0.05$).

soil types in the low marsh did not differ, and values for soils with algal mats in the mid- and high marsh were not significantly different from the organic content of soil beneath intact swards.

EFFECT OF EXPERIMENTAL MANIPULATION OF PATCH SIZE ON SOIL PROPERTIES

Soil deterioration in experimentally grubbed patches at most sites increased as patch size increased, as indicated by decreases in soil moisture (Fig. 4a–c), increases in bulk density (Fig. 4d–f) and salinity (Fig. 4g–i) and decreases in total soil nitrogen (Table 2) with increasing patch size. These changes took place during the 2 years of the experiment and values only from the last sampling date in 2001 are shown in Fig. 4. Data from the first year are available from JRM or are in McLaren (2003).

The effects of sampling date, site and patch size on soil moisture were significant, unlike the interaction terms (Table 3) and soil moisture generally decreased with patch size (Fig. 4). On the first sampling date in 2001 (13 July) there was no significant relationship between decreasing soil moisture and increasing patch size, except in the mid-marsh ($F_{1,13} = 6.24$, $P = 0.022$). On the final sampling date (25 July 2001) soil moisture decreased with increasing patch size in the low marsh ($F_{1,13} = 4.47$, $P = 0.049$) and the mid-marsh ($F_{1,13} = 5.26$, $P = 0.034$), but not in the high marsh. The water content of these soils in the high marsh was higher than corresponding values for the other two sites (Fig. 4). The results of bulk density were similar to those of soil moisture (Fig. 4, Table 3). On the final sampling date in 2001, an increase in patch size led to an increase in bulk density in the low marsh ($F_{1,18} = 10.83$, $P = 0.004$) and the mid-marsh ($F_{1,18} = 5.81$, $P = 0.027$), but not the high marsh plots that showed no trend in bulk density as patch size increased.

Salinity increased with patch size and this effect became more significant with time (Fig. 4g,h,i, Table 2). On the final sampling date (25 July 2001), the effect of patch size on salinity was significant for all three sites (low marsh plots, $F_{1,18} = 13.63$, $P = 0.002$; mid-marsh plots, $F_{1,18} = 17.99$, $P = 0.001$; high marsh plots, $F_{1,18} = 20.01$, $P = 0.001$). At all three sites hyposaline conditions prevailed at small patch sizes, whereas soil salinity reached or exceeded that of seawater at the largest patch size (40 cm). By the time of the final harvest, the relationship between increasing patch size and salinity was logarithmic. (Fig. 4). Soil nitrogen decreased with an increase in patch size (Table 2) after 2 years but there was no significant interaction between sampling date and patch size.

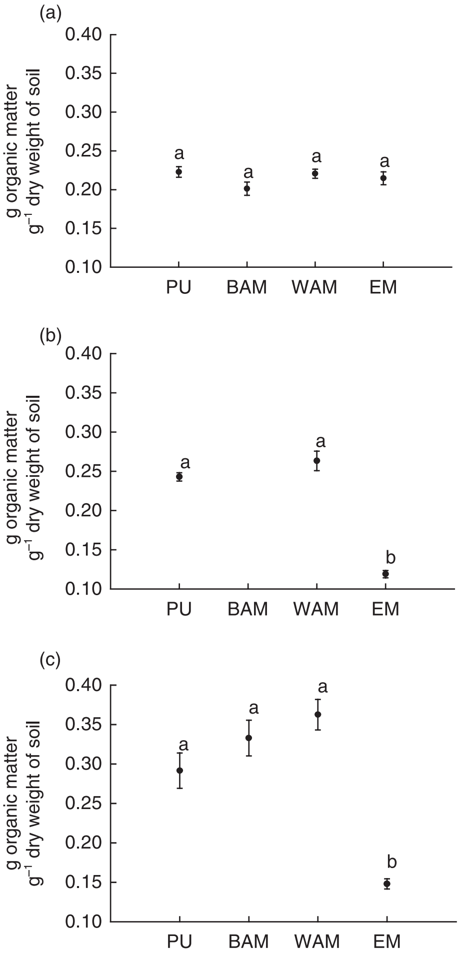

Fig. 3 Soil organic content (g organic matter g^{-1} dry soil, mean ± SEM, $n = 5$) in the four soil types indicated in Fig. 1 in the low (a), mid- (b) and high (c) intertidal marsh at La Pérouse Bay in July 2000. Different letters above the means indicate significant differences between soil types (Tukey's comparison of means: $P < 0.05$). Note y-axis does not begin at zero. BAM is missing for the mid-marsh because of a sampling error: the soil was not sampled from the site.

As aspect had no effect on plant cover or biomass in plots of different sizes ($P > 0.05$), results for the different quadrants were pooled and expressed either as percentage cover per plot or per ring depending on plot size, or as biomass m^{-2}. As the pattern of results of plant cover in 2001 was very similar to that in 2002, only results from the later date are shown. Cover data for the first year are in McLaren (2003). At the final harvest in July 2002, the proportion of patches covered by the inward growth of *Puccinellia phryganodes* from the perimeter declined as patch size increased (Fig. 5a,b,c, Table 4), although the total re-vegetated area increased in a curvilinear manner with increasing patch size. This led to a significant positive relationship between the area of plant cover and patch size after the data for all three sites were log-transformed (low marsh, $F_{1,58} = 57.89$, $P = 0.001$; mid-marsh, $F_{1,58} = 216.77$, $P = 0.001$; high marsh, $F_{1.58} = 68.54$, $P = 0.001$). When the area of plant cover (cm^2) was standardized for patch size based on its circumference (cm), the incremental increase in the ratio of cover to length of the circumference declined with increasing patch size, particularly at the larger patch sizes (Fig. 5d, e,f). When expressed as a double logarithmic plot this relationship increased linearly with patch size, indicating little constraint on incremental increase in cover in relation to patch size. Lateral growth of stolons of *Puccinellia* from the periphery of plots towards the centre extended in a linear manner from less than 1.25 cm in the smallest plot to about 10 cm in the largest (Table 4).

In contrast, above-ground biomass of *P. phryganodes* expressed as m^{-2} decreased in a curvilinear manner with increasing patch size, indicating that growth in the smaller patches was denser than that in the larger patches (Fig. 6a,b,c). The overall general linear model of biomass contained a significant effect of site and the covariate, patch size, but no significant interaction term. There was a significant negative relationship between biomass and patch size after the biomass data were log-transformed at all three sites (low marsh, $F_{1,58} = 9.85$, $P = 0.003$; mid-marsh, $F_{1,58} = 38.76$, $P = 0.001$; high marsh, $F_{1,58} = 39.32$, $P = 0.001$).

Discussion

Differences were detected between the soil types of the established mosaic in infiltration rate, soil moisture, bulk density, salinity, organic content and total nitrogen

Table 2 General linear model used to analyse the effect of sampling date, site and patch size on salinity and soil N as a percentage of dry weight of soil in low, mid- and high marsh sites of an intertidal salt-marsh at La Pérouse Bay, Manitoba. Salinity and soil N content measured in 2000 and 2001 and from 2000 to 2003, respectively. The effect of plot nested within site is blocked. Levels of significance are *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

		Salinity (‰)		Soil N (%)	
Source	d.f.	SS	*F*-ratio	SS	*F*-ratio
Sampling	2	24.471	130.76***	0.1242	6.42**
Site	2	0.619	3.31	0.412	21.28***
Sampling × Site	4	0.162	0.43	0.075	1.93
Patch Size	1	3.726	39.82***	0.044	4.52*
Sampling × Patch size	2	0.717	3.83*	0.008	0.39
Site × Patch size	2	0.029	0.16	0.040	2.05
Sampling × Site × Patch size	4	0.442	1.18	0.078	2.01
Block	27	1.57	0.62	0.270	1.16

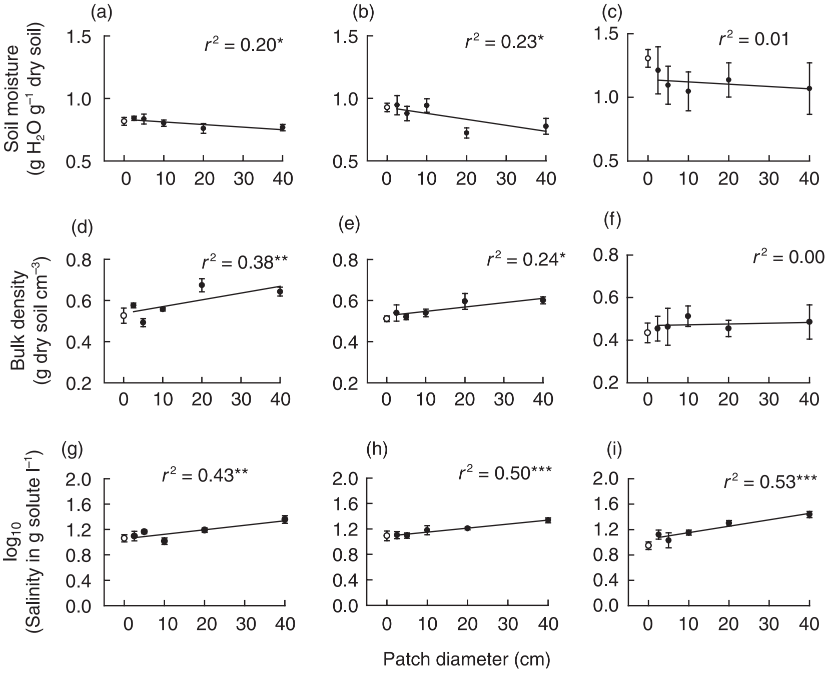

Fig. 4 Properties of soil on 27 July 2001 (soil moisture (a–c); bulk density (d–f) and salinity (g–i)) from different patch sizes that simulated goose grubbing for the low (a, d, g), mid- (b, e, h) and high (c, f, i) intertidal marsh at La Pérouse Bay, Manitoba. Open and closed circles are mean values (± SEM), respectively, for soil below intact swards and grubbed patches of different size. Regression lines are calculated based only on grubbed patches as the sward represents an alternate state. The r^2 values with a significance level are indicated on each graph (levels of significance are $*P < 0.05$, $**P < 0.01$, $***P < 0.001$). Note ordinate axes do not start at zero.

Table 3 General linear model used to analyse the effect of sampling date, site and patch size on soil moisture and bulk density in low, mid- and high marsh sites of an intertidal salt-marsh at La Pérouse Bay, Manitoba in 2000 and 2001. The effect of plot nested within site is blocked. Levels of significance are $*P < 0.05$, $**P < 0.01$, $***P < 0.001$

		Soil moisture		Bulk density	
Source	d.f.	SS	*F*-ratio	SS	*F*-ratio
Sampling	3	1.659	10.75***	0.493	11.88***
Site	2	5.608	54.52**	0.759	27.44*
Sampling × Site	6	0.583	1.89	0.288	3.48
Patch size	1	0.297	5.78*	0.127	9.15*
Sampling × Patch size	3	0.001	0.01	0.132	3.18
Site × Patch size	2	0.093	0.91	0.022	0.79
Sampling × Site × Patch size	6	0.339	1.10	0.078	0.94
Block	3	0.302	1.96	0.163	3.92**

(Figs 1–3). Transplanted tillers of *Puccinellia phryganodes* differed in their survival and growth (vigour) when placed in the different soil types (Fig. 1). The pattern of results for both soil properties and transplants was generally similar at all three sites within the intertidal marsh at La Pérouse Bay.

Soil below swards of *Puccinellia phryganodes* had a higher infiltration rate than exposed mineral soil devoid of an algal crust, consistent with results from mosaics in the tropics. The maintenance of vegetation mosaics in semi-arid regions of the tropics is almost always attributed to differences in infiltration in the various soils of the mosaic (Belsky 1986; Wilson & Agnew 1992; Aguiar & Sala 1999; Seghieri & Galle 1999; HilleRisLambers *et al.* 2001), an outcome that also is predicted from theoretical studies (Rietkerk & Van de Koppel 1997; Van de Koppel *et al.* 1997; Klausmeier 1999).

In addition to a low infiltration rate, low soil moisture can cause reduced plant growth and compacted soils result in low nutrient uptake (Masle & Passioura 1987; Arvidsson 1999). Finally, most halophytes, including *P. phryganodes*, are adversely affected by high soil salinities (Adam 1990; Srivastava & Jefferies 1995a) and low availability of nitrogen is a frequent constraint on plant growth (Epstein 1972). The impact of all of these characteristics on survival and growth of *P. phryganodes* contributes to the maintenance of the vegetation mosaic and the inability of this grass to establish readily from

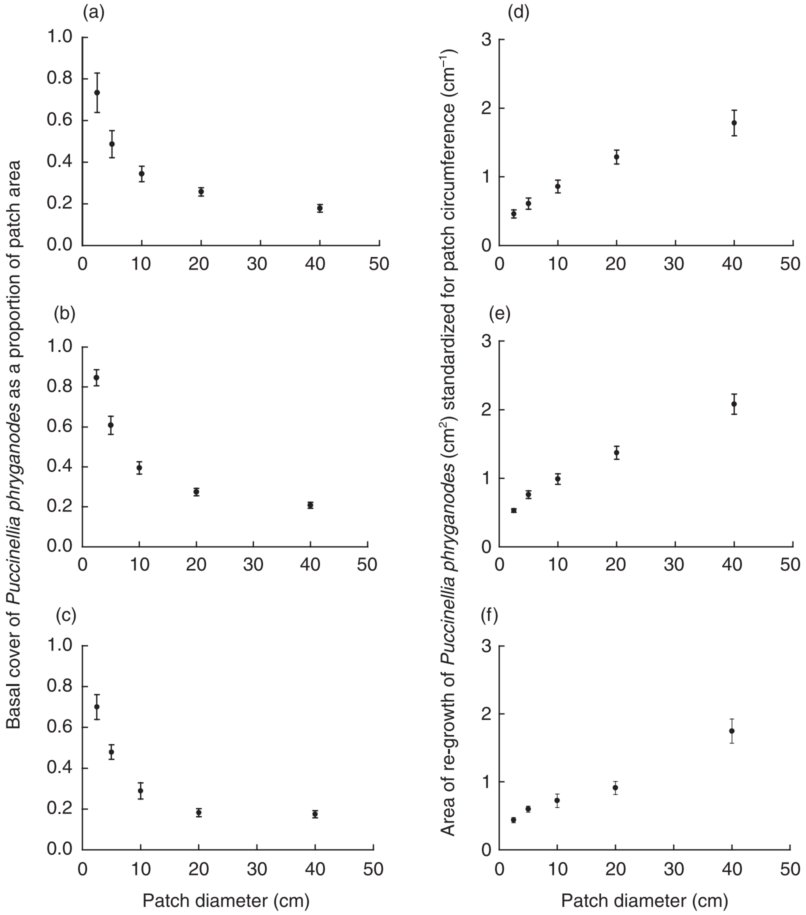

Fig. 5 Proportion (mean ± SEM, $n = 12$ for each patch size at each site) of the area of patches of different size covered by *Puccinellia phryganodes* (basal cover) in July 2002 in the low (a), mid- (b) and high (c) intertidal marsh at La Pérouse Bay, Manitoba. (d), (e) and (f): area (cm^2) of regrowth of *Puccinellia* standardized for patch circumference in the low, mid- and high marsh, respectively, in July 2002 (mean ± SEM, $n = 12$).

Table 4 Average (± standard error) percentage cover of *Puccinellia* regrowth in 2002 for each 1-cm concentric ring within the disturbed patches, with ring no. 1 being the outermost ring for each patch. The cover within each ring in a patch in each plot was averaged across the four quadrants and the average cover presented is these values averaged across plots for each patch size ($n = 12$) at each of the three sites Average percentage cover of 0 indicates that the average is < 0.01, but > 0.

	Low marsh			Mid-marsh			High marsh		
Ring	10 cm	20 cm	40 cm	10 cm	20 cm	40 cm	10 cm	20 cm	40 cm
1	58.1 (5.2)	66.0 (4.2)	65.0 (4.0)	70.2 (2.6)	73.3 (2.9)	78.8 (1.8)	53.3 (5.0)	51.9 (4.3)	63.7 (5.1)
2	34.8 (4.7)	45.6 (3.9)	53.1 (5.1)	38.9 (5.6)	49.6 (4.1)	65.2 (3.3)	26.8 (4.8)	33.4 (4.1)	51.3 (4.8)
3	15.3 (2.9)	24.0 (2.6)	36.9 (4.3)	14.7 (3.0)	22.4 (3.3)	41.8 (4.1)	10.0 (3.7)	14.3 (2.6)	36.1 (4.1)
4	4.6 (1.6)	10.3 (1.8)	21.9 (3.8)	3.4 (0.9)	9.7 (2.1)	22.6 (4.0)	3.0 (1.7)	4.8 (1.2)	22.9 (3.8)
5		3.8 (0.8)	12.3 (3.2)	0.5 (0.3)	3.0 (0.6)	11.0 (2.6)	1.0 (1.0)	1.4 (0.5)	12.0 (2.3)
6		0.8 (0.5)	5.4 (1.6)		1.0 (0.4)	5.7 (1.6)		0.2 (0.1)	5.8 (1.4)
7		0.2 (0.1)	2.3 (0.8)			2.4 (0.8)		0.0 (0.0)	1.8 (0.6)
8			0.7 (0.4)			1.0 (0.4)		0.0 (0.0)	0.6 (0.3)
9			0.3 (0.2)			0.6 (0.3)			0.1 (0.1)
10			0.1 (0.1)			0.4 (0.2)			0.1 (0.0)
11						0.2 (0.1)			

leaf and shoot fragments in areas where the soil has become exposed (Chou *et al.* 1992). Impact of faecal pellets to exposed sediment is minimal (< 1 m^{-2} in spring and < 2 m^{-2} in summer per week), especially as those deposited in spring consist largely of soil and dry-out and are wind-blown across the exposed surfaces.

Of particular interest is the development of microbiotic crusts in which mites are abundant (Milakovic 1999). In the intertidal areas they develop after melt has occurred on exposed sediment rich in organic matter. Hence, they can be used as an ecological indicator of recently exposed soils where the organic veneer beneath the

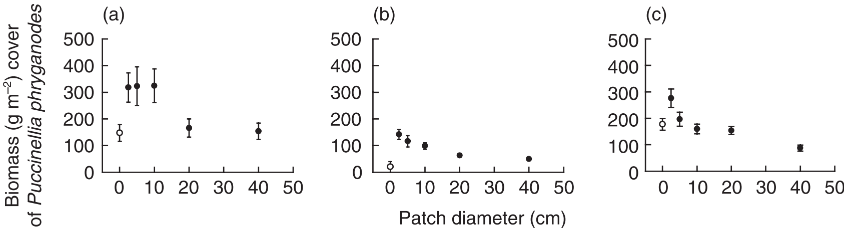

Fig. 6 Above-ground biomass (g m^{-2} ± SEM, n = 12) of growth of *Puccinellia phryganodes* in patches of different size in the low (a), mid- (b) and high (c) intertidal marsh in July 2002. Open circles are biomass values in intact swards of *Puccinellia*, closed circles refer to the biomass in grubbed patches of sediment.

soil surface remains after loss of vegetation. Values for moisture content, nitrogen and organic contents, bulk density and infiltration rate in these soils were not significantly different from those of soil beneath intact swards, yet most transplants of *Puccinellia phryganodes* died when planted in soils with algal mats, probably due to the hypersaline conditions that prevailed in these patches by mid-July (Fig. 1) (Srivastava & Jefferies 1995a,b). In contrast, soils were hyposaline beneath intact swards at this stage of the season (Fig. 1). Over time the surface layers of these recently exposed soils become eroded and the residual seed bank, which does not include propagules of the asexual *P. phryganodes* or *Carex subspathacea* (which flowers very irregularly), is destroyed (Chang *et al.* 2001). Irrespective of the soil salinity, it is very difficult for leaf fragments of *P. phryganodes* or *C. subspathacea* to establish beneath or within these hardened crusts. In calcareous dune slacks hardened microbial mats similarly reduce shoot and leaf survival of vascular plants (Grootjans *et al.* 1997). The mats at La Pérouse Bay are unstable and transitory, and only mineral soil remains after a few years, when it comes to represent an alternative stable state (Hik *et al.* 1992; Handa *et al.* 2002).

Numerous residual leaf and shoot fragments of *Puccinellia phryganodes* and *Carex subspathacea* result from goose foraging (they are messy grazers) and their subsequent movement by water, wind and by the geese themselves aids their dispersal. However, although there is the potential for high dispersal rates, the adverse soil conditions of exposed soils and the continual presence of foraging geese in the snow-free season, means that successful establishment from leaf fragments is a rare event (Handa & Jefferies 2000; Handa *et al.* 2002). Most mature tillers died when transplanted in soil plugs into exposed mineral sediments (Fig. 1). In re-vegetation trials conducted in the same area, amendments of peat and inorganic nutrients to exposed soils were necessary to achieve high rates of survival of tillers (Handa & Jefferies 2000). Hence, intertidal swards undergo increasing fragmentation at spatial scales of 1 m^2 as a result of the cumulative effects of grubbing. The patches coalesce into larger units over time, marked by increasingly adverse soil conditions and the inability of vegetative units of these graminoid species to re-establish in these degraded soils.

This is similar to degraded soils in semi-arid areas in Africa, where re-establishment of vegetation is not easily accomplished (Walker *et al.* 1981; Le Houérou 1989). Hence, the sequence of change in these Arctic intertidal marshes where dispersal and establishment of propagules are limited, can be linked to the model described earlier (Klausmeier 1999; Rietkerk *et al.* 2000, 2002; HilleRisLambers *et al.* 2001), in which intact swards are replaced by a vegetation mosaic that, in turn, is lost as exposed sediments develop. At La Pérouse Bay, water erosion of hypersaline consolidated sediment and the accumulation of unconsolidated soft sediment are necessary before extensive re-vegetation can occur naturally (Handa *et al.* 2002). Enclosed patches of consolidated sediments (1 m^2 and 16 m^2) have remained unvegetated for 20 years (R. L. Jefferies, unpublished data).

The experimental removal of above-ground vegetation in order to produce different patch sizes of exposed soil led to soil deterioration within 1 year. Changes in soil properties were dependent on patch size; conditions became less favourable for plant growth with increasing patch size. Soil moisture and total soil nitrogen decreased with increasing patch size, while bulk density and soil salinity increased (Fig. 4, Tables 2, 3). The effect of patch size on the decline in soil moisture and the increase in bulk density was pronounced by mid-July in 2001, 1 year after patch creation. Previous studies had shown that soil moisture was lower under naturally grubbed soils than beneath swards of *Puccinellia phryganodes* (Wilson & Jefferies 1996), but in this earlier study patch sizes of exposed soil were greater than 16 m^2. The presence of a sward reduces evaporative water loss from soils (Iacobelli & Jefferies 1991; Srivastava & Jefferies 1995b), and effects of surrounding vegetation are likely to be highest in the smallest patches. Soil salinity increased with increasing patch size (Fig. 4). Although experimental removal of vegetation has been shown to lead to higher soil salinities, both at La Pérouse Bay (Iacobelli & Jefferies 1991) and in New England salt marshes (Bertness 1991; Bertness *et al.* 1992: Bertness & Hacker 1994; Callaway 1994), the changes detected in this investigation are at a smaller spatial scale than these earlier studies. The low plant canopy and the surface roughness of the vegetation adjacent to small patches (< 20 cm in diameter) reduce the evaporative demand on exposed soils. Plants at the boundary of a patch have a positive effect on all the soil variables examined. However, where the patch is large (> 40 cm in diameter), soil evaporation rates increase after removal of vegetation and this draws inorganic salts from the underlying marine sediments to the surface layers of soil (Srivastava & Jefferies 1995b).

As patches become larger there is a decreased ability of plants growing at the perimeter of patches to facilitate re-colonization by alleviating adverse soil conditions inimical for establishment and growth. The area of soil exposed directly to solar radiation increases with patch size, which results in higher temperatures in the surface layers of larger patches and as a consequence higher rates of oxidation of organic matter and the volatilization of carbon and nitrogen from soil (Schlesinger *et al*. 1990). The magnitude of change of these different soil parameters is strongly dependent on both the spatial scale and the seasonal temporal patterns of evaporative demand. Even at relatively small spatial scales (< 40 cm) considerable change can be expected in soil properties once the vegetation is removed.

The re-colonization of patches indicated that the growth form of plants of *Puccinellia phryganodes* growing inwards from the periphery to the centre was patch-size dependent (Figs 5 and 6, Table 4). In the smaller patches biomass was higher per unit area compared with larger patches (Fig. 6); although the spatial extent of inward growth increased from less than 1.25 cm to 10 cm as patch size increased (Table 4), biomass per unit area of plant cover decreased. While determination of clonal growth form (guerilla vs. phalanx growth *sensu* Lovett-Doust 1981) requires examination of individual plants, rather than, as here, populations of plants, the pattern of slow, dense (high biomass) regrowth in small patches and fast, sparse (low biomass) regrowth in large patches is consistent with a transition from a phalanx to a guerilla growth form as patch size increases and soil conditions worsen. The extent to which stolons can exploit larger patches before soil conditions become too hypersaline for plant growth is clearly patch-size dependent and involves the interaction of both biotic and abiotic variables. Extended stolons present in the larger patches, that have not fully established as independent plants, require the transfer of at least some resources from the parent plant. Clearly, there is a spatial limit over which this can occur, even under favourable conditions. Above patch sizes of diameter 20 cm, high salinities are likely to restrict the re-vegetation of exposed soil. It requires a theoretical study now that empirical data are available to parameterize a model, whose predictions of the rate of clonal growth with respect to patch size and salinity can be tested experimentally in relation to goose foraging and patch dynamics.

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