

Assisted revegetation trials in degraded salt-marshes

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Summary

1. At coastal sites adjacent to the Hudson Bay lowlands, intensive foraging by increasing numbers of lesser snow geese *Anser caerulescens caerulescens* has converted salt-marsh swards to hypersaline mudflats largely devoid of vegetation. Assisted revegetation trials were undertaken in order to determine the ability of plants to establish in degraded salt-marsh sediments.

2. Soil plugs of the former dominant graminoids, *Puccinellia phryganodes* and *Carex subspathacea*, were transplanted into plots of hypersaline bare soil. Some plots were treated with fertilizer and peat mulch to determine if ameliorations enhance plant growth.

3. Transplants of *P. phryganodes* established in degraded sediments, but those treated with fertilizer and peat showed significantly higher growth than those in bare soil after two growing seasons. The ratio of the mean basal area of plants in treated plots compared with bare plots was between 1.7 and 4.0:1 at different sites. Transplants of *C. subspathacea* did not establish readily in degraded sediments and no growth enhancement was observed with soil amendments.

4. Growth rate and mortality of plants both varied between sites and years, reflecting variation in the frequency of hot, dry weather from late June to early August of each year, and the salinity and water content of soils during that period. The potential for revegetation of mudflats is discussed in the context of the soil degradation processes. Fine-grain variation in soil conditions presents a major challenge for the restoration of plant assemblages in these coastal marshes.

5. The extent of soil degradation and of vegetation loss makes it unlikely that unassisted revegetation will occur at some sites, even in the absence of goose foraging, without erosion of consolidated sediments and the establishment of plant assemblages in fresh unconsolidated sediments.

Key-words: arctic, *Carex subspathacea*, lesser snow geese, *Puccinellia phryganodes*, recolonization, restoration.

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Introduction

Long-term chronic effects of agriculture, animal grazing and industrial activity have led to decreases in biodiversity, alterations to biogeochemical cycles, and land degradation on an international scale (Daily 1995; Chapin *et al.* 1997; Dobson, Bradshaw & Baker 1997; Vitousek *et al.* 1997). In the Arctic, land degradation (a decline in species diversity and primary production and an increase in soil erosion) is often a consequence of direct and indirect anthropogenic disturbances (Forbes 1997). Direct distur-

bances include those associated with the oil industry (Jorgenson & Joyce 1994; McKendrick 1997; Walker 1997), mining (Elliott, McKendrick & Helm 1987; Densmore 1994), pipeline construction (Kershaw & Kershaw 1987; Harper & Kershaw 1996), vehicle usage (Forbes 1993) and expansion of human settlements and military activity (Jorgenson 1997). Indirect disturbances include semi-domesticated animals that damage vegetation as a result of foraging (Klein 1967; Arnalds 1987; Jacobsen 1987; Vilchek 1997).

In systems damaged by grazing, restoration (*sensu* Bradshaw 1997a) is seldom as simple as lowering levels of herbivory, because degradation is frequently the consequence of secondary feedbacks in

the soil environment that cannot be easily reversed (Westoby 1980; Bazely & Jefferies 1996; Van de Koppel, Rietkerk & Weissing 1997). Because seed production is often irregular in arctic plant populations (Chambers 1997; Urbanska 1997a), most efforts to reverse degradation in northern regions have focused on re-establishing a closed canopy of vegetation with the use of non-native species or a mixture of native and non-native species, but without the goal of restoring former ecosystem function (Elliott, McKendrick & Helm 1987; McKendrick 1987; Younkin & Martens 1987, 1994; Magnússon 1997; McKendrick 1997; Forbes & Jefferies 1999). However, native plants are often superior at establishing in disturbed sites because populations are adapted to local environments (Chapin & Chapin 1980; Johnson 1987; McKendrick 1997; Urbanska 1997b). Their use is also more likely to prevent later successional changes that are unrepresentative of the area (Younkin & Martens 1987; Bradshaw 1989; Martens 1995; McKendrick 1997).

Land degradation has occurred in coastal marshes of the Hudson Bay lowlands, where foraging activities of staging and breeding lesser snow geese *Anser caerulescens caerulescens* L. (Jano, Jefferies & Rockwell 1998) have damaged vegetation and soil. In recent decades, the mid-continent population of snow geese has increased exponentially at a steady rate of about 7% per annum (Cooke, Rockwell & Lank 1995), probably as a result of the high-quality agricultural food subsidy that is available to the birds during winter and along migration routes (Abraham, Jefferies & Rockwell 1996). Grubbing by adults in the early spring (Jefferies 1988a,b; Kerbes, Kotanen & Jefferies 1990) and intense grazing by family groups in summer has led to loss of salt-marsh vegetation via a positive feedback mechanism that results in hypersaline soil (Iacobelli & Jefferies 1991; Srivastava & Jefferies 1995b, 1996). Former *Puccinellia-Carex* swards have been replaced by mudflats often devoid of vegetation. In some inland salt-marshes and at some sites in the upper levels of the intertidal marshes, transient populations of the annual halophytes *Salicornia borealis* (Wolff & Jefferies) and *Atriplex patula* var. *hastata* L. have colonized mudflats.

The objective of this study was to examine whether, in the absence of goose foraging, the two abundant native perennial salt-marsh graminoids, *Puccinellia phryganodes* (Trin.) Scribn. & Merr. and *Carex subspathacea* Wormskj., could re-establish in degraded salt-marsh soils as an initial step in the revegetation of these habitats. In particular, we assessed the potential for recolonization when (i) immigration into the soils was assisted by the transplanting of plugs of intact vegetation with soil from a non-degraded site, and (ii) the soil environment was ameliorated with fertilizer and/or peat mulch to assist establishment of transplants.

Materials and methods

SITE DESCRIPTION

Extensive coastal flats occur at La Pérouse Bay, Manitoba (58°44'N, 94°28'W). The topography of the land is flat with minor relief (< 2 m) resulting primarily from frost-heaving of unconsolidated sediments and ephemeral streams and ponds that develop following snow-melt or heavy precipitation events. The size of the lesser snow goose colony in the La Pérouse Bay area is estimated at 44500 breeding pairs (K.F. Abraham, R.F. Rockwell & K. Ross, unpublished aerial survey 1997). At present, 2500 ha of vegetation in tidal and fresh-water marshes in the vicinity of La Pérouse Bay have been adversely affected by geese (Jano, Jefferies & Rockwell 1998). In the few intact areas of intertidal salt-marsh that remain, the dominant graminoids are *P. phryganodes*, a stoloniferous grass, and *C. subspathacea*, a rhizomatous sedge (nomenclature follows Porsild & Cody 1980). At higher elevations in the supratidal salt-marsh (tidal cover ≤ 2 events every 3 years) or on frost-heave hummocks, two caespitose grasses, *Festuca rubra* L. and *Calamagrostis deschampsoides* Trin., and low-lying willow bushes of *Salix brachycarpa* Nutt. and *Salix myrtifolia* Anderss. replace the *Puccinellia-Carex* community (Jefferies, Jensen & Abraham 1979). The snow-free season usually extends from late June to late September.

STUDY SPECIES

Puccinellia phryganodes establishes exclusively by clonal propagation; it is sterile (Bowden 1961). Seed set by *C. subspathacea* is a rare event at La Pérouse Bay because of heavy grazing of inflorescences (Chou, Vardy & Jefferies 1992). Both species can also establish from single leaves and other plant fragments generated by goose grazing (Chou, Vardy & Jefferies 1992).

EXPERIMENTAL DESIGN

Sites were selected where intact and degraded patches were present in close proximity. For each species, three sites were chosen where irregularly shaped patches of remnant swards existed, most of which were about 20 m² or less in area. The graminoid that was to be transplanted was the dominant plant species of the remnant sward. Transplant sites for *P. phryganodes* on the east shore of La Pérouse Bay were separated by 75–100 m. Sites for *C. subspathacea* were in a supratidal marsh 3 km inland from the coast, each separated by 25–50 m. Care was taken to choose patches at roughly equal elevation and on level ground to control for differences in snow-melt and water drainage.

Four replicated pairs of 1 × 1-m chicken wire enclosures were erected at each site approximately 15–20 m apart. Each pair consisted of an enclosure on a degraded vegetation patch proximal (< 5 m) to one on an intact sward. Degraded patches were chosen where an undisturbed cyanobacteria–diatom crust occurred. Cyanobacteria typically colonize bare sediments (Bazely & Jefferies 1989a) in early spring and form a continuous algal crust (1–2 mm) on the surface. As summer progresses, however, the crust blisters, dries out and cracks, and is blown away.

Transplants were cored from a single intact patch of the appropriate species (5 × 5 m) adjacent to the three experimental sites, in order to minimize genotypic variation (Jefferies & Gottlieb 1983). Each cored soil plug was 22 mm in diameter × 40 mm in depth and typically consisted of three to five tillers of *P. phryganodes* or *C. subspathacea*. The rooting zone for these graminoids was in the top 50 mm of the soil. Each 1 × 1-m enclosure was planted with 42 plugs (7 columns × 6 rows), that were 7 cm apart. The 22 plugs close to the perimeter of each enclosure acted as a buffer zone. The remaining 20 plugs in the inner 5 × 4 matrix were designated as experimental plants and scored for rates of growth and senescence. Plugs of *P. phryganodes* and *C. subspathacea* were planted on 17–21 June 1996 and 25–28 June 1996, respectively.

Five treatments were applied in total to each replicated pair of enclosures. Plugs were transplanted into enclosures with intact swards to ensure that the transplanting itself did not cause plant death. Each enclosure in a degraded area was subdivided into four plots and each plot was randomly assigned one of the following treatments: (i) bare sediment (no amelioration); (ii) addition of nitrogen and phosphorus fertilizer; (iii) addition of peat mulch; and (iv) a combination of nitrogen and phosphorus fertilizer and peat mulch additions. Fertilizer was sprinkled evenly across the plots as inorganic salts at the time of transplanting (10.5 g of N m⁻² as NH₄Cl and 4.45 g of P m⁻² as NaH₂PO₄·2H₂O) (Jefferies & Perkins 1977; Cargill & Jefferies 1984). The peat mulch consisted of fully decomposed surface organic material from beneath *Salix* bushes that grew on frost-heave hummocks in the supratidal marsh. All living moss, large roots and rhizomes were removed from the mulch and a 5-mm layer was applied uniformly by hand on a treatment plot. Edge effects in adjacent subplots were absent. Individual tillers of these plants were only about 2.5 cm in length and leaf lengths were between 0.5 and 0.75 cm.

MONITORING OF ABOVE-GROUND BIOMASS

Plants were monitored for growth, senescence and death during the growing seasons of 1996 and 1997,

except that plants in the intact swards were scored only in 1996. Plants were scored as 'dead' when there was no visible greenery in the shoot system, and as 'senescing' when shoots were predominantly yellow in appearance with only between one and three shoots entirely green. Both species showed a combination of 'guerrilla' and 'phalanx' growth strategies (*sensu* Lovett Doust 1981). In order to monitor both growth patterns, the basal area of plant cover was measured based on a system of concentric circles that extended outwards at increments of 11 mm from each plug centre. For each plug, the mean radial extension (to the nearest 11 mm) and percentage cover (within the mean radial extension circle) were estimated visually. Basal area of plant growth (A) was calculated by using the formula $A = (\% \text{ cover}) \pi r^2$, where r = the radius of the mean radial extension circle. This non-destructive technique was used to measure growth of living plants in all treatments in enclosures in degraded areas on sampling dates in 1996 and 1997. On three dates in 1997, turves (12 × 4 cm) were collected from the buffer zone of treatment plots, including the intact swards in three of the four enclosures (selected at random) at each site, to measure above-ground biomass. These turves were clipped and washed to remove dirt and dead biomass, dried at 50 °C for 1 week and weighed on an analytical balance to the nearest milligram.

MONITORING OF ENVIRONMENTAL VARIABLES

Measurements of plot elevation were made with a quick-set level. Soil characteristics that were recorded included profile descriptions and measurements of particle size, bulk density, sodium content, gravimetric water content, redox potential, total carbon and nitrogen, relative surface evaporation and surface temperature. In June 1996, plots (40 × 60 cm) of each of the bare, mulched and intact vegetation treatments were established adjacent to nine of the twelve paired enclosures (three per site chosen at random). Soil samples were collected by cutting 5 × 5 × 5-cm blocks within each plot. In 1997, in addition to soil samples taken from outside enclosures, samples of similar size were taken from inside three of the four treatment enclosures (chosen at random) at each site. These samples were collected from the outer edges of the buffer zone, in order to avoid destruction of transplanted plants in the inner matrix.

With the exception of measurements of particle size, surface temperature and evaporation, which were made only in the intertidal marsh, all measurements were made at both marshes. Methods followed Srivastava & Jefferies (1995a) for the determination of sodium and gravimetric water content, redox potential and surface evaporation, and

Wilson & Jefferies (1996) for the determination of total carbon, nitrogen and bulk density (the latter calculated for soil depths at 0–2 cm and 2–4 cm). Proportions of sand, silt and clay were determined using the hydrometric method (Sheldrick & Wang 1993). Surface temperature was measured with the use of a fine thermistor wire inserted in soil to a depth of 0.5 cm and attached to a precalibrated voltmeter.

Elevation of all enclosures, relative to a Department of National Defence benchmark (set to an arbitrary zero), was determined using a quick-set level and surveying staff.

STATISTICAL METHODS

Estimates of the above-ground growth, senescence and plant death of plants from plugs were analysed using the S-PLUS statistical software (version 3.3; Math Soft Inc. 1995). All analyses were based on a split-plot factorial design (Kirk 1982) with site crossed with treatment and enclosure nested within site. A plot mean was calculated based on values recorded for plugs within a plot ($n \leq 20$). Data of plant death and senescence were analysed by the use of a general linear model (McCullagh & Nelder 1983). The models were generated with a binomial 'family' specification and subsequently tested for significance with a chi-square test that used a likelihood ratio argument (Venables & Ripley 1997). For these analyses, the percentage deviance explained by significant factors in the model is reported ($D_{\text{d.f. of factor, total d.f.}} = \text{deviance of the factor/total residual deviance} \times 100$). Estimates of above-ground growth of plants from plugs were analysed with a mixed-model ANOVA in which treatment was defined as a fixed factor, while site and enclosure were defined as random factors.

Environmental data were analysed with the MINITAB statistical software (version 10.2; Minitab Inc. 1994) based on a mixed model two-factor ANOVA (Kirk 1982) for treatment (fixed) crossed by site (random). 'Enclosure' was not treated as a factor in the environmental analyses because edaphic samples were not as spatially concentrated as the above-ground growth measurements that were taken from within an enclosure. For the analysis of soil redox data in 1997 at both intertidal and supratidal marshes, the midpoint of the recorded range was used. Redox data from the intertidal marsh in 1996 were not amenable to ANOVA techniques because of unequal variances and non-parametric distributions. Although Kruskal–Wallis tests also assume equal variances (Underwood 1997), they were used as a non-parametric alternative to examine redox data. All experiments were originally established with a balanced design, but because of difficulty in extracting soil water from samples as well as sodium contamination there was some loss of replicates. In such

cases, a general linear model, in which equal importance was assigned to each treatment mean, was used (Neter, Wasserman & Kutner 1990).

Homogeneity of variance for all analysis of variance tests was verified ($P > 0.05$) based on Bartlett's test statistic for normal data (Zar 1984) and Levene's test statistic for data with slight deviations from normality (Minitab Inc. 1994). Slight deviations from normality were tolerated as analysis of variance techniques have been considered to be robust to such deviations (Underwood 1997). Some transformations were necessary to correct for heteroscedasticity. Data of gravimetric soil water content in the intertidal marsh in 1996, and sodium contents of soil solutions in 1996 and 1997 from both intertidal and supratidal marshes, were transformed by taking the natural logarithm. Data of above-ground biomass from the intertidal marsh and basal area of plants for the supratidal marsh were transformed by taking the square-root of values. Unplanned pair-wise comparisons for testing differences among means were based on Tukey's contrasts (controlling for experiment-wise error) with appropriate modifications for the design in question (Kirk 1982).

Results

GROWTH OF TRANSPLANTS OF *PUCCINELLIA PHRYGANODES*

All plants of *P. phryganodes* that were transplanted into enclosed intact patches of vegetation survived the first growing season (Fig. 1). Some plants died that were transplanted into enclosed degraded soils by 29 July 1996, and further deaths were recorded on all sampling dates in 1997. On all dates in 1997, plant death varied significantly with site ($D_{2,47} = 18.2\text{--}18.7\%$; $P \leq 0.05$) and enclosure ($D_{9,47} = 52.4\text{--}54.6\%$; $P \leq 0.05$) but not with treatment. The highest incidence of plant death was recorded at site 1, followed by sites 3 and 2, respectively (Fig. 1a). Peak plant senescence varied significantly with treatment on 9 July 1996 ($D_{3,47} = 34.3\%$; $P < 0.01$) and with site on 20 July 1996 ($D_{2,47} = 25.7\%$; $P < 0.05$) but with none of the factors in 1997.

Basal area of plants (Fig. 2) varied significantly with treatment ($F_{3,6} = 33.3, 14.0, 3.13, 19.0, 18.8, 17.6$; $P < 0.01$), site ($F_{2,6} = 31.1, 19.3, 16.5, 16.3, 22.4, 12.6$; $P < 0.01$) and enclosure ($F_{8,26} = 9.7, 21.1, 17.9, 20.2, 18.1, 17.6$; $P < 0.001$) on 29 July 1996 and on all five dates, respectively, in 1997. On all sampling dates, plants with no amelioration had a significantly lower basal area than plants that received amelioration treatments (Tukey, $P < 0.05$). Plants that were given the fertilizer or mulch (the growth of the plants was not significantly different from one another) had significantly lower values of

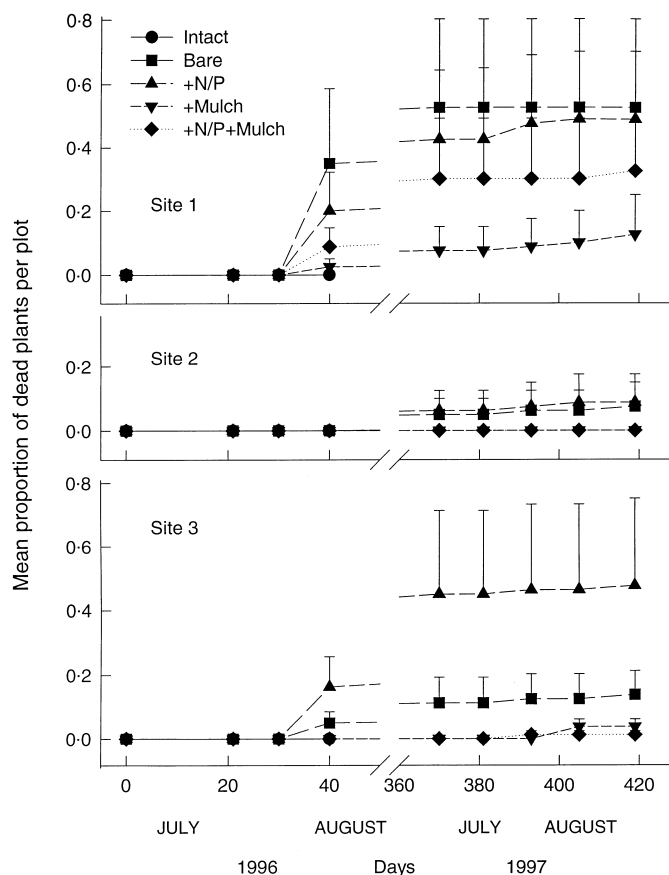


Fig. 1. Death of plants of *Puccinellia phryganodes* shown by treatment and site (1–3) in the intertidal marsh of La Pérouse Bay, Manitoba. Planting was completed on 20 June 1996 and plugs were scored on 11, 20 and 29 July 1996 and on 25 June, 6, 17, 29 July and 12 August 1997. Each point shows the mean value per plot (error bars show 1 SEM; $n = 4$ plots per treatment, per site) of dead plants as a proportion of total plants transplanted as plugs into plots. The intact vegetation treatment was monitored in 1996 only.

growth than plants that received the combined treatment of fertilizer and mulch (Tukey, $P < 0.05$ to $P < 0.001$). On all sampling dates, plants from site 1 had significantly lower basal areas than comparable values for plants at site 2 (Tukey, $P < 0.001$ to $P < 0.01$). Plants from site 3 had significantly lower basal areas than plants in site 2 (Tukey, $P < 0.01$ on all dates).

Above-ground biomass in the second growing season (Table 1a) did not vary significantly by site or enclosure, but showed significant differences in response to treatment on 21 June 1997 ($F_{4,7} = 10.2$; $P < 0.01$), 19 July 1997 ($F_{4,8} = 14.7$; $P < 0.001$) and 10 August 1997 ($F_{4,8} = 22.0$; $P < 0.001$). On these dates, plants from intact swards showed significantly higher biomass than those from other treatments (Tukey, $P < 0.01$). In addition, on 19 July 1997 plants that received no amelioration had significantly lower biomass than those that were given fertilizer, mulch or the combined treatment (Tukey, $P < 0.01$).

ENVIRONMENTAL MEASUREMENTS AT THE INTERTIDAL MARSH

Soils in degraded sites lacked an organic layer, and had significantly higher bulk densities, clay content, surface temperatures and evaporation rates than soils in sites where swards were intact (Table 2a). Although elevation did not differ significantly by treatment, on average (mean \pm SEM; $n = 12$ per treatment) intact swards (16.5 ± 1.5 cm) were 3 cm higher than degraded soils (13.1 ± 0.8 cm). Sand and silt content, total carbon, total nitrogen and the soil water content of degraded sediments did not vary significantly with treatment, but did vary significantly with site (Table 2b). Soils from inside enclosures at site 1 had significantly higher sand content, lower silt content and lower soil moisture than corresponding values for soils at sites 2 and 3. Soils from site 2 had significantly greater total carbon and greater total carbon and nitrogen than soils from sites 1 and 3, respectively.

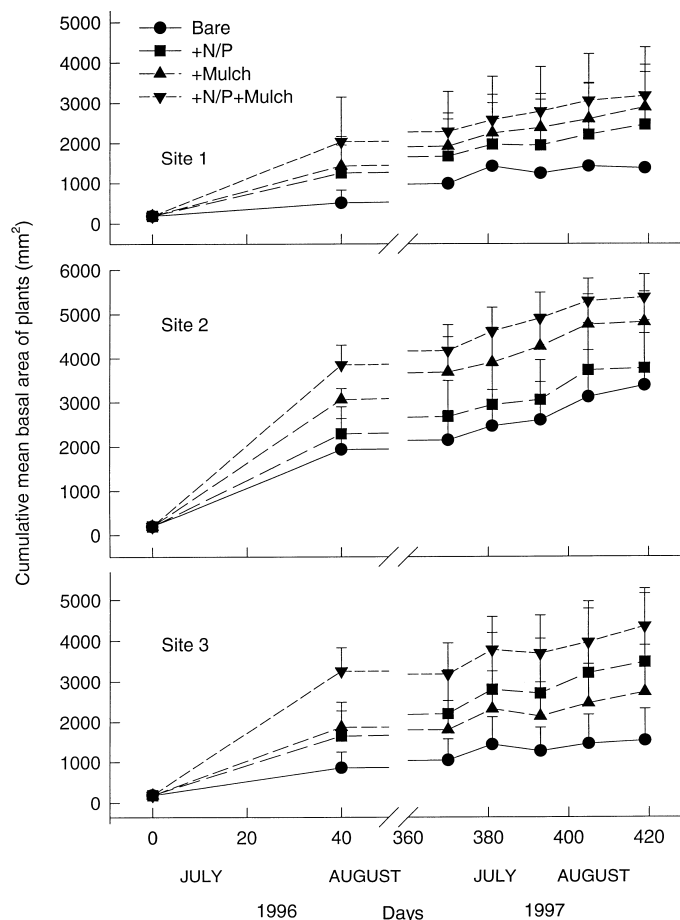


Fig. 2. Mean cumulative basal area of plants of *Puccinellia phryganodes* shown by treatment and site (1–3) in the intertidal marsh at La Pérouse Bay, Manitoba. Planting was completed on 20 June 1996 and plants were scored on 29 July 1996 and 25 June, 6, 17, 29 July and 12 August 1997. The plotted points show the mean value per plot (error bars show 1 SEM when $n = 4$ per treatment, per site), except where all plants in a plot died. On sampling dates $n = 4$ plots, except for the bare treatment at site 1 in 1997 where $n = 2$ because of mortality of all plants in two plots.

Soil salinity (Fig. 3) varied significantly with treatment on all sampling dates in 1996 and 1997 ($F_{2,4} = 136.6$, $F_{2,4} = 95.3$, $F_{2,4} = 13.3$, $F_{4,8} = 10.4$, $F_{2,4} = 30.4$,

$F_{6,12} = 40.7$, $F_{6,12} = 4.10$; $P < 0.0001$ to $P < 0.05$) and varied significantly with site on 29 July 1996 ($F_{2,18} = 6.16$; $P < 0.01$) and 19 July 1997 ($F_{2,42} =$

Table 1. Mean above-ground biomass for each treatment (expressed as $\text{g m}^{-2} \pm \text{SEM}$), data pooled over all three sites due to plant death, $n \leq 9$, at (a) the intertidal marsh dominated by *Puccinellia phryganodes*, and (b) the inland supratidal marsh dominated by *Carex subspathacea*, at La Pérouse Bay, Manitoba

(a) Treatment	21 June 1997	19 July 1997	10 August 1997
Intact vegetation	136.8 \pm 19.0	141.6 \pm 24.1	141.6 \pm 19.2
Bare soil	29.4 \pm 15.9	77.4 \pm 44.1	98.8 \pm 56.4
+ N/P	47.1 \pm 26.5	108.3 \pm 47.1	122.3 \pm 58.5
+ Mulch	44.5 \pm 16.5	91.6 \pm 30.9	77.7 \pm 25.5
+ N/P + mulch	84.5 \pm 34.1	134.9 \pm 49.0	178.2 \pm 67.4
(b) Treatment	27 June 1997	24 July 1997	15 August 1997
Intact vegetation	83.40 \pm 21.2	120.60 \pm 16.2	137.90 \pm 27.0
Bare	0.54 \pm 0.17	0.72 \pm 0.31	3.24 \pm 1.33
+ N/P	2.72 \pm 1.28	29.4 \pm 12.0	4.38 \pm 1.85
+ Mulch	2.27 \pm 0.89	34.7 \pm 11.0	3.97 \pm 1.86
+ N/P + mulch	0.98 \pm 0.31	25.5 \pm 8.23	3.49 \pm 1.22

Table 2. Mean values for soil environmental variables that differed significantly by (a) treatment or (b) site at the intertidal marsh on the east shore of La Pèrouse Bay, Manitoba (\pm SEM; $n=9$, unless otherwise indicated), dominated by *Puccinellia phryganodes*

(a) Factor	Bare soil	Vegetated soil	Significance level	Tukey contrast	
Depth of organic layer (cm)	Organic layer absent	0.40 \pm 0.20	–	–	
Bulk density (g cm ⁻³)					
0–2 cm depth	0.60 \pm 0.03	0.46 \pm 0.03	$F_{1,14} = 10.6$ $P < 0.01$	$P < 0.05$ Bare > Veg.	
2–4 cm depth	0.56 \pm 0.04	0.44 \pm 0.04	$F_{1,14} = 6.1$ $P < 0.05$	$P < 0.05$ Bare > Veg.	
Clay content (%)	12.8 \pm 0.6	9.6 \pm 1.0	$F_{1,14} = 7.2$ $P < 0.05$	$P < 0.05$ Bare > Veg.	
Evaporated water (%)					
June 20 1997 ($n=9$)	15.6 \pm 1.3	10.2 \pm 1.3	$F_{2,4} = 5.0$ $P = 0.08$	NS	
July 19 1997 ($n=27$)	30.4 \pm 0.8	13.8 \pm 3.5	$F_{2,4} = 24.43$ $P < 0.01$	$P < 0.05$ Bare > Veg.	
Temperature (°C)					
19 July 1997 ($n=9$)	20.1 \pm 0.4	16.1 \pm 0.6	$F_{2,4} = 41.8$ $P < 0.01$	$P < 0.05$ Bare > Veg.	
17 August 1997 ($n=30$)	18.8 \pm 0.1	16.5 \pm 0.2	$F_{2,4} = 10.6$ $P < 0.05$	$P < 0.05$ Bare > Veg.	
(b) Factor	Site 1	Site 2	Site 3	Significance level	Tukey contrast
Sand content (%) ($n=6$)	43.2 \pm 1.4	33.1 \pm 1.6	37.8 \pm 2.0	$F_{2,12} = 8.3$ $P < 0.01$	$P < 0.05$ S1 > S2 = S3
Silt content (%) ($n=6$)	45.6 \pm 1.5	54.9 \pm 1.9	52.3 \pm 1.8	$F_{2,12} = 7.0$ $P < 0.01$	$P < 0.05$ S1 < S2 = S3
Total soil carbon (% dry weight of soil)	11.5 \pm 0.3	12.2 \pm 0.3	10.8 \pm 0.3	$F_{2,18} = 6.9$ $P < 0.01$	$P < 0.05$ S2 > S1 = S3
Total soil nitrogen (% dry weight of soil)	0.58 \pm 0.03	0.65 \pm 0.04	0.52 \pm 0.04	$F_{2,18} = 5.4$ $P < 0.05$	$P < 0.01$ S2 > S3
Soil water content measured inside exclosures (g of water g ⁻¹ dry weight) ($n=12$)	0.43 \pm 0.02	0.84 \pm 0.02	0.80 \pm 0.04	$F_{2,24} = 60.8$ $P < 0.0001$	$P < 0.001$ S1 < S2 = S3

4.84; $P < 0.05$). On all dates, soils from intact swards were significantly less saline than those from bare and mulched plots adjacent to exclosures (Tukey, $P < 0.05$). Soils from intact swards were also significantly less saline than those from treatment plots inside exclosures on 21 June 1997 (Tukey, $P < 0.05$), but not on 19 July 1997 or 10 August 1997.

Soil water content and soil redox potential did not vary significantly with treatment or site. Mean water content generally varied between 0.48 and 0.78 g of water g⁻¹ dry weight of soil except on 11 July 1996, when mean values calculated for some bare and mulch-treated plots exceeded 1.0 g of water g⁻¹ dry weight of soil. Median redox potential values in both years typically ranged from 250 to 270 mV in degraded and intact sites. At these E_h values, aerobic decomposition of organic matter and nitrification can still occur (Metting 1993).

GROWTH OF TRANSPLANTS OF *CAREX* *SUBSPATHACEA*

Plants of *C. subspathacea* that were transplanted into exclosed intact swards of this species survived the first growing season (Fig. 4). Some plants that were transplanted into exclosed degraded soils had died by 28 July 1996, and on all subsequent sampling dates in 1997 further deaths were recorded. On all dates, mortality varied significantly with exclosure ($D_{9,47} = 91.6\text{--}93.0\%$; $P < 0.0001$ to $P < 0.000001$) but not with site or treatment. By the second growing season, more than 75% of plants from transplanted plugs had died in 28 of the 48 plots in degraded soils; these plots were located in eight of the 12 exclosures. Peak plant senescence values were observed generally on 10 and 18 July 1996. Plant senescence varied significantly with exclosure on 10 July 1996 ($D_{9,47} = 79.7$; $P < 0.0001$), 18 July 1996

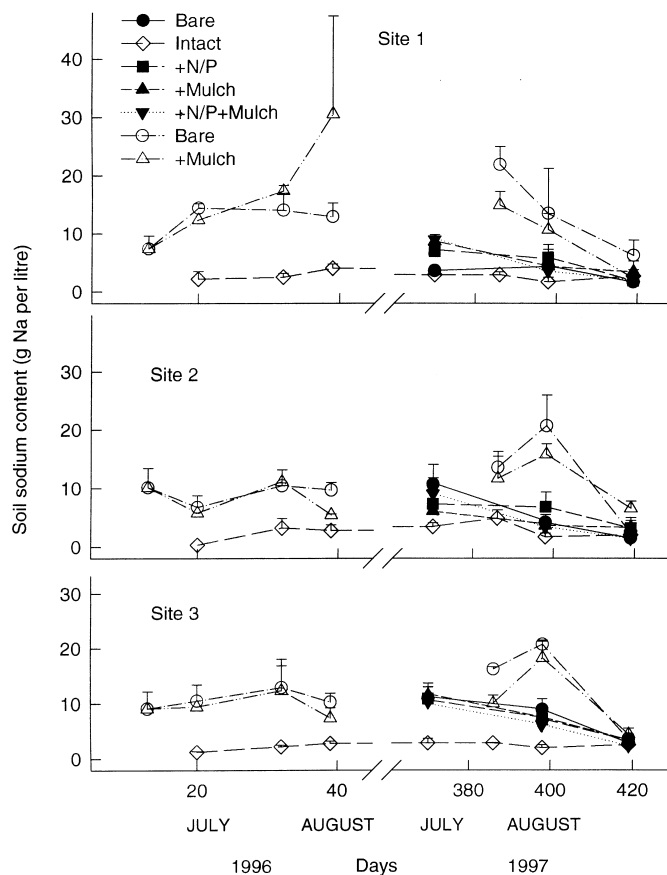


Fig. 3. Sodium content of soil solution in 1996 and 1997 shown by treatment and site (1–3) at the intertidal marsh, La Pèrouse Bay, Manitoba. Day 0 is 20 June 1996. Open symbols show soils sampled from excluded edaphic plots or intact vegetation plots, while closed symbols show the soils sampled from treatment plots inside revegetating exclosures (error bars show 1 SEM; $n = 3$ per treatment per site, except where $n = 2$ because of insufficient extracted soil solution).

($D_{9,47} = 57.7$; $P < 0.001$) and 28 July 1996 ($D_{9,47} = 80.9$; $P < 0.01$), but no significant differences were detected in 1997.

Basal area of plants (Fig. 5) did not vary significantly with treatment on any dates, but varied significantly with site ($F_{2,6} = 70.9, 6.15, 7.96, 9.99, 8.52, 13.8$; $P < 0.05$ to $P < 0.001$) and exclosure ($F_{6,18} = 27.6, F_{2,8} = 51.1, 91.7, 59.0, 64.2, 69.8$; $P < 0.001$) on 28 July 1996 and on all sampling dates in 1997, respectively. Site 1 had plants with significantly greater basal area than those in sites 2 (Tukey, $P < 0.01$ on all dates) and 3 (significant on 28 July 1996 and 26 June 1997 only; Tukey, $P < 0.01$). On all dates, site 3 had plants with significantly greater basal area values than those in site 2 (Tukey, $P < 0.01$ to $P < 0.05$).

Above-ground biomass (Table 1b) varied significantly with exclosure on 27 June, 24 July and 15 August 1997 ($F_{4,8} = 5.78, 7.28, 11.02$, respectively; $P < 0.05$ to $P < 0.01$). On all dates, values measured in intact swards were significantly higher than those measured in treatments on degraded soils (Tukey, $P < 0.001$).

ENVIRONMENTAL MEASUREMENTS AT THE INLAND MARSH

Soils at the inland marsh were organic in the top 3 cm of the soil profile. Although bulk density did not vary significantly by treatment or site, mean bulk density was slightly lower in soils beneath intact swards than those from degraded soils. Mean bulk densities of soils in exclosures beneath intact swards and degraded soils, respectively (\pm SEM, $n = 6$ per treatment), were 0.80 ± 0.07 and 0.72 ± 0.10 at a depth of 0–2 cm, and 1.11 ± 0.28 and 0.72 ± 0.08 at a depth of 2–4 cm. Total carbon, total nitrogen and soil moisture content recorded on all dates in 1996 varied significantly with treatment, but not with site (Table 3a). In all cases, values were significantly greater in soils from intact swards than in soils from degraded sites (Table 3a).

Soil sodium content (Fig. 6) varied significantly by treatment on all dates in both years ($F_{2,4} = 689.4, F_{2,4} = 183.9, F_{2,4} = 480.8, F_{4,8} = 14.2, F_{2,4} = 101.8, F_{6,12} = 11.9$ and $F_{6,12} = 20.9$; $P < 0.0001$ to $P < 0.001$). On all dates, sodium content in soils with

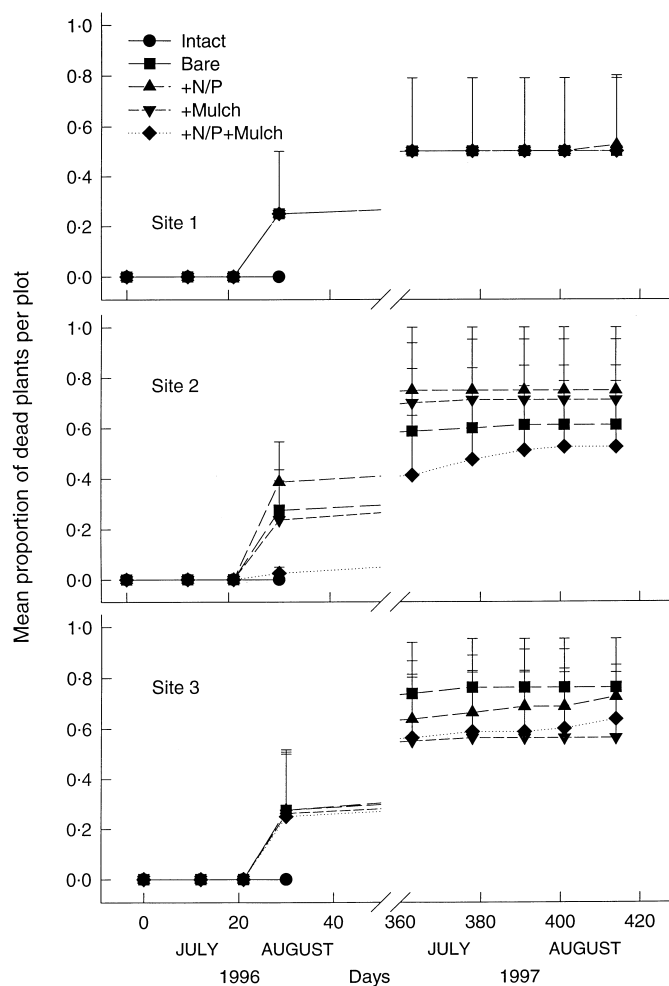


Fig. 4. Death of plants of *Carex subspathacea* shown by treatment and site (1–3) at the inland supratidal marsh at La Pérouse Bay, Manitoba. Planting was completed on 28 June 1996 and plugs were scored on 10, 19, 28 July 1996 and on 26 June, 10, 23 July and 2, 15 August 1997. Each point shows the mean value per plot in relation to treatment and site of dead plants as a proportion of total plants transplanted as plugs into plots (error bars show 1 SEM; $n=4$ plots per treatment, per site). The intact vegetation treatment was monitored in 1996 only.

intact vegetation was significantly less than that measured in other treatments, both inside and outside exclosures (Tukey, $P < 0.001$ to $P < 0.01$). Sodium content varied significantly by site on 27 June 1997 only (Fig. 6; $F_{2,45} = 3.48$; $P < 0.05$). Sites 1 and 2 showed higher salinity values than those at site 3 (Tukey, $P < 0.001$ and $P < 0.01$ for respective contrasts). Most other treatment contrasts were insignificant.

Redox potential ranges were -160 to 260 mV in 1996 and 30 to 320 mV in 1997. Redox potential did not vary significantly by treatment or site, with the exception of values measured on 10 July 1996 (by treatment, $F_{2,4} = 11.2$; $P < 0.05$) and 24 July 1997 (by site, at a depth of $0-2$ cm, $F_{2,9} = 6.24$; $P < 0.05$; and at a depth of $2-4$ cm, $F_{2,9} = 23.2$; $P < 0.001$). Other significant differences among sites were observed in measurements of soil moisture (1997 only) and elevation of plots (Table 3b). Although

differences were not strong, site 3 was at a higher elevation and generally wetter than the other two sites (Table 3b; I.T. Handa, personal observation).

Discussion

All plants of *P. phryganodes* and *C. subspathacea* survived when transplanted into intact swards; in contrast, only some plants of both species established in degraded sediments (Figs 1 and 4). Establishment was greater with plugs of *P. phryganodes* than with those of *C. subspathacea*, as observed by Srivastava & Jefferies (1996) when both graminoids were transplanted from high biomass swards into low biomass swards. The difference is due, in part, to the higher salt tolerance of *P. phryganodes* than that of *C. subspathacea* (Srivastava & Jefferies 1995b). Seasonal shoot production is greater in *Puccinellia* plants than in *Carex* plants (Kotani & Jef-

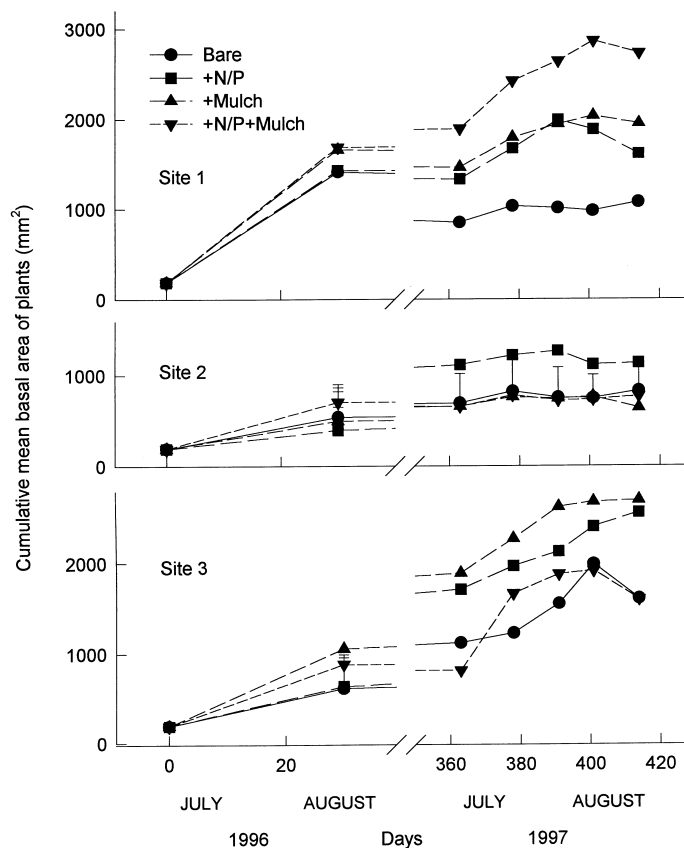


Fig. 5. Mean cumulative basal area of plants of *Carex subspathacea* during the growing seasons of 1996 and 1997 at the inland supratidal marsh at La Pérouse Bay, Manitoba. Plugs were planted by 28 June 1996 (mean planting date) and plants were scored in 1996 on 29 July and in 1997 on 25 June, 6, 17, 29 July and 12 August. The plotted points show the mean value per plot (error bars show 1 SEM; $n=4$ plots per treatment per site for sites 1–3), except where mortality of all plants in plots occurred.

fries 1987; Bazely & Jefferies 1989b), which may also facilitate quicker establishment by the stoloniferous grass than the rhizomatous sedge.

High spatial and temporal variability in successful establishment of plants has been reported in other arctic studies (Holt 1987; Kershaw & Kershaw 1987; Harper & Kershaw 1996; Jorgenson 1997; Strandberg 1997). Results from this study indicate that the establishment (Figs 1 and 4) and basal area of growth (Figs 2 and 5) of both species were affected significantly by the location of exclosures, and to a lesser extent by the location of the site (*c.* 2500 m²) in the respective marshes in which the four exclosure pairs were nested. This effect of location on establishment and growth reflected the fine-grained spatial variation of the edaphic environment within degraded areas, which was invisible to the eye when selecting sites for exclosures. Although some edaphic measurements differed between sites on some dates, such as sand and silt content, salinity, total carbon, nitrogen and water content (Tables 2b and 3b, Figs 3 and 6), many measurements showed greater within-site variance than between-site variance.

Much of the edaphic variance may be associated with temporal and spatial components of the degradation processes. Degradation of the marsh occurs in patches (Srivastava & Jefferies 1995a). Measurements that compared soils from intact and degraded swards, separated by a distance of less than 5 m, indicated significant differences in soil salinities at both marshes (Figs 3 and 6). Differences were also recorded in bulk densities, temperatures and evaporation rates of soils in the intertidal marsh (Table 2a), and in total carbon, nitrogen and moisture (in 1997) in soils at the inland marsh (Table 3a). Soils that have been bare for a long time will probably be more degraded than soils that have recently lost vegetative cover, based on the above characteristics. Hence, revegetation potential of a patch may depend strongly on the time since cover was lost.

The revegetation potential of a degraded patch is also dependent on weather conditions. Plants of *P. phryganodes* transplanted in spring 1997 showed much lower establishment and growth rates than those initiated in 1996 (Handa 1998). A comparison of weather conditions in the 2 years indicated that

Table 3. Mean values for soil environmental variables that differed significantly by (a) treatment or (b) site at the supratidal, inland marsh at La Pérouse Bay, Manitoba (\pm SEM; $n=9$, unless otherwise indicated), dominated by *Carex subspathacea*

(a) Factor	Bare soil	Vegetated soil	Significance level	Tukey contrast	
Total soil carbon (% dry weight of soil)	22.9 \pm 2.4	32.6 \pm 2.4	$F_{2,4}=27.0$ $P < 0.01$	$P < 0.01$ Veg. > Bare	
Total soil nitrogen (% dry weight of soil)	1.7 \pm 0.2	2.5 \pm 0.2	$F_{2,4}=56.8$ $P < 0.01$	$P < 0.001$ Veg. > Bare	
Soil water content (g of water g ⁻¹ dry weight)					
10 July 1996	1.36 \pm 0.13	2.30 \pm 0.14	$F_{2,4}=48.3$ $P < 0.01$	$P < 0.01$ Veg. > Bare	
19 July 1996	1.35 \pm 0.15	1.97 \pm 0.15	$F_{2,4}=52.1$ $P < 0.001$	$P < 0.01$ Veg. > Bare	
28 July 1996	1.89 \pm 0.13	1.73 \pm 0.27	NS	NS	
(b) Factor	Site 1	Site 2	Site 3	Significance level	Tukey contrast
Elevation ($n=8$)	94.4 \pm 2.0	98.2 \pm 1.6	100.6 \pm 15.0	$F_{2,18}=3.6$ $P < 0.05$	$P < 0.05$ S3 > S1 = S2
Soil water content (g of water g ⁻¹ dry weight)					
10 July 1997	1.15 \pm 0.16	1.50 \pm 0.10	1.72 \pm 0.16	$F_{2,18}=4.4$ $P < 0.05$	NS
24 July 1997	1.23 \pm 0.06	1.69 \pm 0.18	1.68 \pm 0.11	$F_{2,40}=4.0$ $P < 0.05$	NS
15 August 1997	1.62 \pm 0.09	1.32 \pm 0.06	1.62 \pm 0.08	$F_{2,40}=5.1$ $P < 0.05$	NS

in 1997 there was lower precipitation, higher temperatures, lower relative humidity and higher wind speeds (Handa 1998). All these factors contributed to increasing evaporative loss from soils and thus probably decreased the growth potential of plants transplanted at that time. The conditions observed in 1997 may be indicative of changes that are predicted to occur in the Arctic in response to global climate change (Kane *et al.* 1992; Maxwell 1992). Such changes could make revegetation increasingly difficult.

Despite differences in growth observed among sites (Fig. 2), plants of *P. phryganodes* that received fertilizer and/or mulch grew significantly more than plants in bare plots. After two growing seasons, the ratio of the mean basal area of plants from treated plots compared with bare plots varied between 1.7:1 and 4:1, depending on the site. Nutrient supply often limits plant growth in arctic sites (Jonasson 1992; Chapin *et al.* 1995). At La Pérouse Bay, the availability of nitrogen has been shown to limit net above-ground primary production of *Puccinellia-Carex* swards (Cargill & Jefferies 1984). Furthermore, in degraded swards, the levels of total nitrogen, exchangeable nitrogen and net mineralization rates were reduced (Wilson & Jefferies 1996). The results of the trials with *P. phryganodes* were consistent with the results of other arctic and alpine studies that have shown that fertilizer enhanced recovery (McKendrick & Mitchell 1978; Chapin &

Chapin 1980; McKendrick 1987; Chambers 1997; Magnússon 1997; McKendrick 1997).

Results also indicated that peat mulch was more effective at enhancing growth of *P. phryganodes* than fertilizer alone (Fig. 2). Several authors have stressed the importance of organic soil and the manipulation of the microclimate to ensure adequate soil moisture for plant growth in revegetation trials (Cargill & Chapin 1987; Ferchau 1988; Chambers 1989; McKendrick 1997). The organic layer can provide a continual release of nutrients to colonizers in the growing season (Cargill & Chapin 1987), and peat mulch increases the water retention capacity of soils (Bradshaw 1997b), particularly under hypersaline conditions (Ungar 1996). The mulch also decreases the surface albedo and provides insulation, thereby raising surface temperatures (Rosenberg, Blad & Varma 1983; Oke 1995). Experiments in 1997 that manipulated the water and temperature regimes of soil surrounding transplanted plugs of *P. phryganodes* indicated that the growth of *P. phryganodes* was significantly enhanced by the addition of water, but was not affected by differences in thermal regimes (Handa 1998). In addition, the levels of inorganic nitrogen (0.1 g of N m⁻²) in the mulch were low relative to those in the fertilizer treatment (Handa 1998). These results all suggest that the effect of mulching created a more favourable soil moisture regime.

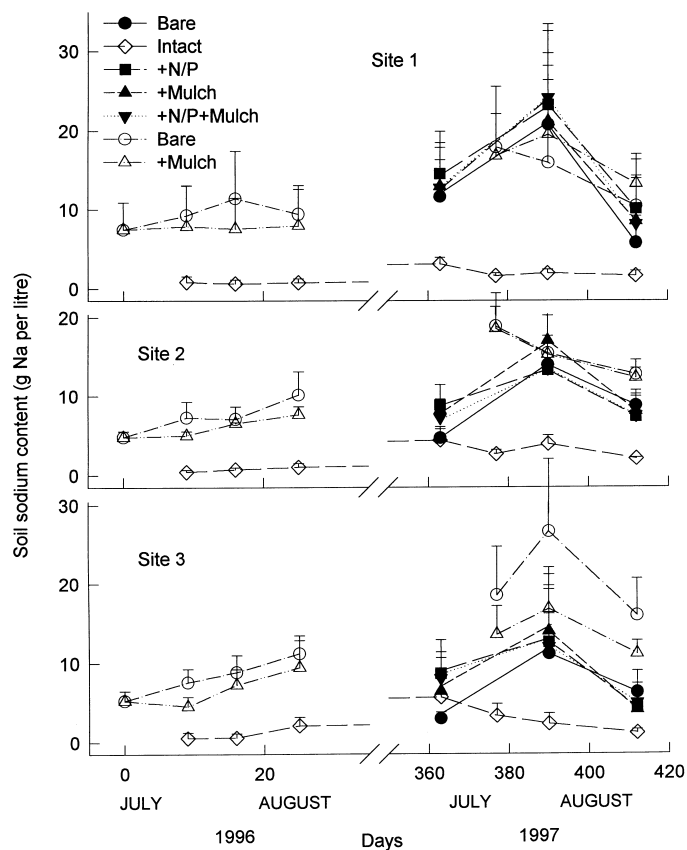


Fig. 6. Sodium content of the soil solution in 1996 and 1997 shown by treatment and site (1–3) in the inland supratidal marsh at La Pérouse Bay, Manitoba. Open symbols show soils sampled from exclosed edaphic plots or intact vegetation plots, while closed symbols show soils sampled from treatment plots inside revegetating enclosures (error bars show 1 SEM; $n = 4$ per treatment per site on 27 June 1997, $n = 3$ per treatment per site on all other dates, except $n = 2$ at site 2 on 24 July 1997 for the bare soil and combined fertilizer and mulch treatments).

Unassisted revegetation of consolidated bare intertidal sediment in degraded areas, even in the absence of goose foraging, appears increasingly a rare event. Hypersalinity and the absence of moisture in summer create hostile conditions for plant establishment either by clonal propagation or from seed. Field observations indicate that erosion followed by the accumulation of unconsolidated sediment provides suitable conditions for revegetation, but these changes in geomorphology may take a decade or more before plant establishment is possible.

Unlike *P. phryganodes*, the growth of *C. subspathacea* was not significantly affected by the soil treatments (Fig. 5). Although organic soils are saturated with water in spring and early summer, the surface layer (< 2 cm) dries out rapidly in summer and, in addition, the slight changes in land elevation (1 m drop every 3 km) impede drainage in the inland marsh and lead to anaerobic conditions just below the surface of the soil, particularly in spring when soils are wet. Soil anoxia may have been a stress in some enclosures that had a seemingly favourable

water regime. While *C. subspathacea* can grow in soils with negative redox potentials, *P. phryganodes* rarely establishes under such conditions; hence, it would not be a suitable species to revegetate the sediments of the inland marsh.

Transplants in other small-scale experiments have shown promise in revegetating disturbed areas with native species (Forbes 1993; Urbanska 1997a, > b; Shirazi *et al.* 1998). Transplants allow control of the density and spatial organization of plants and may help prevent problems such as densities of seeded graminoids out-competing other species (Densmore 1992; Chambers 1997; McKendrick 1997). Results from this study indicate that plugs of these graminoid plants need to be spaced at distances of the order of 10 cm in order to facilitate sward development within 2 years at favourable sites. In the summers of 1998 and 1999, dicotyledonous plants such as *Potentilla egedii*, *Ranunculus cymbalaria* and *Stellaria humifusa* were observed inside enclosures of mats of *Puccinellia* in the intertidal marsh (R.L. Jefferies, personal observation), emphasizing the need for long-term observations of experimental plots.

Urbanska (1997b) has argued that the creation of small diverse patches can act as 'safety islands'. Continuous patches of *P. phryganodes* trap seed and vegetative fragments from the strand-line, from snow-melt and from the seed rain, and thus facilitate the establishment of other species. The strand-line is considered an important seed source for salt-marsh plants (Ranwell 1972; Packham & Willis 1997) and has been shown to influence the seed bank at a site 30 km from La Pérouse Bay (Staniforth, Griller & Lajzerowicz 1998).

The inclusion of native soil in transplant plugs offers the advantage of transferring seed and facilitating seedling emergence. Recent studies at La Pérouse Bay have shown that the seed bank sampled from soils beneath intact vegetation has a higher diversity than that in degraded sediments approximately 10 m away (E. Chang, unpublished data). In addition, soil cores help maintain the native thermal regime (Shirazi *et al.* 1998) and may promote nutrient cycling by restoring the microbial and mycorrhizal communities (Haselwandter 1997). Although the removal and transplanting of soil plugs has limited application because of labour costs in large-scale revegetation projects, especially where there is the added constraint of excluding geese in order for revegetation to occur, pilot autoecological studies on the establishment ecology of native species are a necessary prelude to the restoration of damaged plant communities (Chambers 1997).

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