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The effect of salinity on the leaf and shoot demography of two arctic forage species

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Summary

1 Two important graminoid forage species, *Puccinellia phryganodes* and *Carex subspathacea*, which are eaten by lesser snow geese, are widespread in arctic coastal salt marshes. Extensive grubbing of these plants by geese has led to increased soil salinity which may restrict their regrowth, particularly for the sedge which grows in less saline sites.

2 The effects of salinity on leaf and shoot birth and death rates and on mortality of plants of the two species were therefore examined when pot-grown plants of *Puccinellia* were exposed to different salinities under field conditions at La Pérouse Bay, Manitoba. A similar experiment on *Puccinellia* was also conducted in a growth chamber.

3 Leaf death rates increased with salinity and approached or exceeded leaf births at the highest salinities (40–80 g L⁻¹ dissolved salts containing sodium at a concentration between 568 mol m⁻³ and 1136 mol m⁻³). The salinities at which these changes were evident depended on the species and the growing conditions. When birth and death rates of leaves and plant deaths were compared, *Puccinellia phryganodes* was less salt-sensitive than *Carex subspathacea*.

4 As salinity increased, the decline in numbers of leaf births on axillary shoots and attached tillers of plants of *Puccinellia* and *Carex* was faster than the decline in leaf births on main shoots.

5 The growth responses of the two species to salinity are discussed in relation to the foraging activities of the geese and the long-term changes occurring in salt marshes on the coast of Hudson Bay.

Keywords: growth, halophytes, rhizomatous sedge, seawater, soil cultures, stoloniferous grass

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Introduction

Large populations of migratory wildfowl breed along the coasts of the eastern Canadian Arctic. Numbers of lesser snow geese, *Anser caerulescens caerulescens* (Linnaeus), for example, are more than two million in this region (Boyd *et al.* 1982). As goslings of this species grow in about seven weeks from c. 80 g at hatch to c. 1500 g at fledging, and the adults regain up to 40% of their body weight lost during incubation, demand for available forage is high. Within the coastal marshes of Hudson Bay, two graminoid species, a stoloniferous grass, *Puccinellia phryganodes* and a rhizomatous sedge, *Carex subspathacea* (Jefferies 1988a,b) are important forage plants for these birds.

Both species are widespread both in intertidal regions and beyond the upper limit of spring tides where exposed marine sediments result in saline or brackish conditions. Both species show continuous leaf and shoot production throughout much of the growing season and, as the geese rarely destroy basal or intercalary meristems when feeding, tissues lost by defoliation are replaced (Kotanen & Jefferies 1987; Bazely & Jefferies 1989). These two species occur as both mixed and monospecific swards. Field observations indicate that *Carex subspathacea* grows more frequently in areas which are less saline than those in which *Puccinellia phryganodes* is present (Chapman 1960; Kershaw 1976; Jefferies 1977; Jefferies *et al.* 1979a, Glooschenko 1980). The sedge is particularly abundant in intertidal marshes where fresh water from the Hudson Bay lowlands flows along shallow

drainage channels, whereas the grass grows on the intervening sediments between drainage channels.

In recent years lesser snow geese and Canada geese *Branta canadensis* (Linnaeus) have caused extensive damage to saltmarsh swards as a result of grubbing activities (digging in sediments for roots and rhizomes of saltmarsh plants) in early spring before the growth of above-ground vegetation (Kerbes *et al.* 1990; Iacobelli & Jefferies 1991; Srivastava 1993). The removal of vegetation by grubbing at many sites along the Hudson Bay coasts of Ontario, Manitoba and the Northwest Territories and the exposure of marine sediments result in increased evaporation from the soil surface and the development of hypersalinity in the upper layers of sediments (Iacobelli & Jefferies 1991; Srivastava & Jefferies 1995). As this grubbing is likely to continue, and as field observations suggest that *Carex subspathacea* may have a relatively low tolerance of high salinities, considerable changes in the relative abundance of the two species may be anticipated. The overall objective of this experimental study therefore was to determine the growth responses of these two species to increasing salinity in order to assess their salinity tolerances.

Most salt marsh plants show maximal growth under nonsaline conditions (Adam 1990; Ungar 1991). Frequently, growth has been measured as differences in the cumulative biomass of plants grown at a range of salinities (Stelzer & Lauchli 1977; Ashraf *et al.* 1986), although in some cases data from sequential harvests have been used to calculate incremental relative growth rates that provide information on overall patterns of growth during an experiment (e.g. Jensen 1985; Shennan *et al.* 1987). Measurements of cumulative biomass, however, give little information on growth patterns of plants in response to environmental variables, in contrast to demographic techniques which provide data on rates of leaf production and leaf loss during the time course of an experiment (Jefferies & Rudmik 1991). Munns & Termaat (1986) have suggested that an asymmetry between rates of leaf production and expansion and leaf death rates at high salinities results in plant mortality. Demographic methods were therefore used in this study to determine the effects of salinity on the growth of leaves and shoots of these two species and the asymmetry of leaf birth and death rates during the course of the experiment.

Site description

La Perouse Bay, Manitoba (58°04'N, 94°03'W), is situated on the south-western coast of Hudson Bay. Much of the bay is surrounded by salt marshes that extend inland for up to 700 m. The vegetation of the marshes is dominated by the grass *Puccinellia phryganodes* and the sedge *Carex subspathacea*. The coastal regions of Manitoba derive much of their salt from buried marine clays deposited when the postglacial

Tyrell Sea covered the Hudson Bay lowlands (Price & Woo 1988a). The marine clays are capped by a veneer of highly humified organic matter (3–8 cm deep), in which the majority of plant roots are located. The marshes are dissected by shallow drainage channels and ponds, most of which dry out during the summer. Evaporative processes result in the deposition of salt in the upper layers of soil (Iacobelli & Jefferies 1991; Srivastava & Jefferies 1995). From the time of snow melt in early June until early August the upper levels of the intertidal flats are not inundated by tides, because the heights of spring tides close to summer solstice are relatively low. Tidal waters in the vicinity of La Perouse Bay are low in dissolved salts (DS) (c. 4 g L⁻¹ DS) and these waters flush salts from the top soil when they cover the intertidal flats in late summer (Jefferies *et al.* 1979a; Ewing & Kershaw 1986; Price & Woo 1988b; Price *et al.* 1988).

Study species

Puccinellia phryganodes (Trin.) Scribn. and Merr. and *Carex subspathacea* Wormskj, both of which have a circumpolar distribution (Porsild 1957; Hulten 1962; Porsild & Cody 1980), are generally restricted to coastal salt flats (Porsild 1957). At La Perouse Bay plants of both species are only about 2 cm tall, due, in part, to intensive summer grazing by the breeding colony of lesser snow geese.

Puccinellia phryganodes exhibits extensive stoloniferous growth. Although stolons can be extra-axillary (Polunin 1959; Dore & McNeil 1980), axillary shoots are most commonly observed at La Perouse Bay. Shoot production is iterative (Bazely & Jefferies 1989) and flowering infrequent. The grass is a sterile triploid in North America (Bowden 1961; Sadul 1987) and seed set has not been recorded (Dore & McNeil 1980).

The growth habit of *Carex subspathacea* at La Perouse Bay has been described by Kotanen & Jefferies (1987) as a cluster of tillers joined underground with the tillers emerging about 0.5 cm apart, and clusters joined by rhizomes c. 10 cm in length. As in *Puccinellia phryganodes*, flowering is infrequent and seeds have not been found at La Perouse Bay (Chou *et al.* 1992), but both flowering and seed set have been reported at other locations (Polunin 1959).

Methods

Demographic methods were used to study the growth responses of *Puccinellia phryganodes* and *Carex subspathacea* to salinity at La Perouse Bay.

In late June 1991, turves containing *Puccinellia phryganodes* and *Carex subspathacea* plants were collected from a small area (c. 1 m²) of sward in a salt marsh at La Perouse Bay. Care was taken to obtain plants from a small area, as previous studies have indicated considerable genetic variability and differ-

ences in growth patterns of plants, even within an area of 50 m × 50 m at La Pérouse Bay (Jefferies & Gottlieb 1983; Sadul 1987). Shoots of *Puccinellia* and *Carex* with roots but without axillary shoots or attached tillers, were removed from the turves ($n = 100$ for each species), and planted individually in pots (7 cm maximum diameter at top) containing a peat-silt-sand mixture obtained from sites where these species were growing. Potted plants of each species were randomly assigned to five salinity treatments (20 plants per species per treatment), and randomly positioned in a 1 m × 2 m area just inland from the salt marsh at the La Pérouse Bay Field Station. Plants were completely exposed to natural conditions, including rainfall.

Pots were watered daily with 10 mL of a saline solution. To minimize transplant shock, plants were watered only with nonsaline water for one week after transplanting. The salinity of the watering solution was then increased each day by 8 g of DS L⁻¹ until pots were watered with a solution of either 0, 8, 16, 24 or 40 g of DS L⁻¹ depending in the treatment to which they were assigned. The sodium concentrations in these respective solutions were approximately 0, 114 mol m⁻³, 228 mol m⁻³, 340 mol m⁻³ and 568 mol m⁻³. Saline solutions were made using 'Instant Ocean' aquarium salt (Aquarium Systems, Mentor, Ohio) dissolved in deionized water. The composition of aquarium salts was the same as the salt composition of oceanic sea water. The approximate ionic concentrations of the artificial seawater (32 g L⁻¹ dissolved solids) were as follows: chloride, 538 mol m⁻³; sodium, 454 mol m⁻³; magnesium, 55 mol m⁻³; sulphate, 25 mol m⁻³; calcium, 12 mol m⁻³ and potassium, 9 mol m⁻³. Salinity of the solutions (g L⁻¹ dissolved solids) was measured using a portable salinity meter (Yellow Springs Instrument Co., Ohio, model 33). Pots were flushed at least once a week by rain water, or by watering with fresh water to prevent excessive salt accumulation.

The demography of leaves and shoots of plants was assessed on four dates, 13–14 days apart: 4 July, 17 July, 31 July and 13 August, 1991. Leaves were identified by a code of one to three small India Ink dots applied with a fine camel hair brush (Kotanen & Jefferies 1987). Existing leaves and shoots were identified, and new leaves and branch shoots marked. All leaves were examined on each occasion to determine whether they were alive, senescing, or dead. The leaf birth and death rates for each plant (leaves plant⁻¹ day⁻¹) were calculated as the number of leaf births or deaths which occurred between 4 July and 13 August, 1991 divided by the number of days (40) between these two dates. Leaf birth and death rates were calculated separately for main and axillary shoots of *Puccinellia* and for main and attached tillers of *Carex*. One *Carex* plant was destroyed by a gosling during the study, so the results of leaf demography for *Carex* were analysed by a general linear model approximation of

MANOVA and one-way ANOVA (type III sum of squares; SAS, 1988). Equal sample sizes existed for data of *Puccinellia*, so conventional MANOVA and one-way ANOVA analyses were performed. Some data had to be transformed to reduce heteroscedasticity (Bartlett's test, $P < 0.05$). Standard transformations, however, could not reduce the heteroscedasticity in the data of the leaf death rate of axillary shoots of *Puccinellia*. These data were analysed using the Kruskal-Wallis test (chi-squared approximation; Sokal & Rohlf 1981) and were excluded from the MANOVA analyses. All statistical analyses were performed using SAS software (SAS 1988).

Plants of *Puccinellia* grew well even at the highest salinities used in 1991 (40 g L⁻¹ DS) and their demographic responses to even higher salinity were therefore assessed in July 1992. Individual *Puccinellia* shoots were isolated from a 0.5 m × 0.5 m area of sward immediately adjacent to the site from which plants were removed in 1991 and planted in pots containing the same peat-sand-silt mixture. The pots were randomly assigned to five salinity treatments ($n = 31$ per treatment) and positioned outside, as described above.

As before, pots were watered daily with 10 mL of saline solution per pot. Plants were watered with nonsaline water for two days after transplanting, and then the salinity of the solutions was gradually increased during the next six days, as appropriate, until the plants were watered with solution of either 0, 20, 40, 60, or 80 g L⁻¹ DS.

The demography of leaves and shoots of plants of *Puccinellia* was assessed on three dates, 13 days apart: 12 July, 25 July and 7 August. The first demographic census, on 12 July, was immediately after the salinity of the most extreme treatment (80 g L⁻¹ DS) had reached the desired level.

At high salinities, there were no leaf births and almost all existing leaves died, causing low variances and non-normal distributions (Bartlett's and Shapiro-Wilks tests, respectively; SAS 1988). Data were therefore analysed by the use of the Kruskal-Wallis test (Sokal & Rohlf 1981), followed by the Steel-Dwass rank test for multiple comparisons (Miller 1966). The Steel-Dwass rank test was used because it is the most powerful simultaneous non-parametric test for unplanned multiple comparisons (Day & Quinn 1989), and controls for the experiment-wise error rate.

DEMOGRAPHIC METHODS USED TO EXAMINE THE GROWTH OF PLANTS OF *Puccinellia phryganodes* IN A GROWTH CHAMBER

In late August 1991, a 20 cm × 20 cm × 10 cm turf was removed from a *Puccinellia-Carex* sward in a salt marsh adjacent to the site from which plants were removed for the experiments described above. The turf was transported to the University of Toronto.

From the turf, 105 *Puccinellia* plants were isolated and planted individually in pots (6 cm maximum diameter at top, 5.5 cm tall) in a peaty soil mixture. Pots were randomly assigned one of seven salinity treatments: 0, 20, 30, 40, 50, 60 and 70 g L⁻¹ DS ($n = 15$ plants per treatment). Pots of the same treatment were suspended by a frame in a tray of solution of the appropriate salinity. The saline solution covered the bottom 1.5–2 cm of the pots.

The salinity of the solution appropriate for each pot was increased gradually by 10 g L⁻¹ DS, each week until the desired concentrations had been reached. The saline solutions were made and salinities measured as described above. The solution in each tray was changed two to three times a week, and the trays scrubbed weekly to remove any algae. All plants were grown in a growth chamber, at 15 °C, with a 12-h dark period and 12-h light period (photon-flux density $c. 300 \mu\text{mol m}^{-2} \text{s}^{-1}$). The temperature is similar to the average maximum daily temperature (15.5 °C) in summer at Churchill, Manitoba (Churchill Weather Office, Environment Canada). The light regime and the photon-flux density are poor approximations to summer conditions at La Pérouse Bay. Tray position within the growth chamber was randomized twice a week.

The demography of leaves and shoots was assessed on 9 weekly occasions from 18 October to 20 December, 1991, except that no measurements were made on 13 December. Demographic data were analysed for the last four weeks of the experiment, when all plants had had at least one week to adjust to the final salinities. All plants showed similar leaf birth and death rates in the first three weeks, before salt solutions were added to pots.

Data were non-normal and variances unequal for reasons described earlier. Kruskal–Wallis and Steel–Dwass rank tests were used to analyse the data.

Results

LEAF AND SHOOT DEMOGRAPHY OF PLANTS OF *Puccinellia phryganodes* AND *Carex subspathacea* GROWN IN POTS UNDER FIELD CONDITIONS IN 1991

Overall, there was a highly significant effect of salinity on the leaf demography of *Carex* (MANOVA, Wilk's λ , $P < 0.0001$; Fig. 1a). Specifically, there was a significant effect of salinity on main tiller leaf birth rate (MTLB), attached tiller leaf birth and death rates (ATLB and ATLD), and total (main plus attached tiller) leaf birth and death rates (TLB and TLD; ANOVA, $P < 0.05$). Main tiller leaf death rate (MTLD) was not affected by salinity (ANOVA, $P \geq 0.05$). Leaf birth rates on both main and axillary shoots decreased markedly as salinity increased from 0 to 40 g L⁻¹ DS (Tukey's test on ATLB, MTLB and TLB data, $P < 0.05$; results for TLB shown in Fig. 1a). In

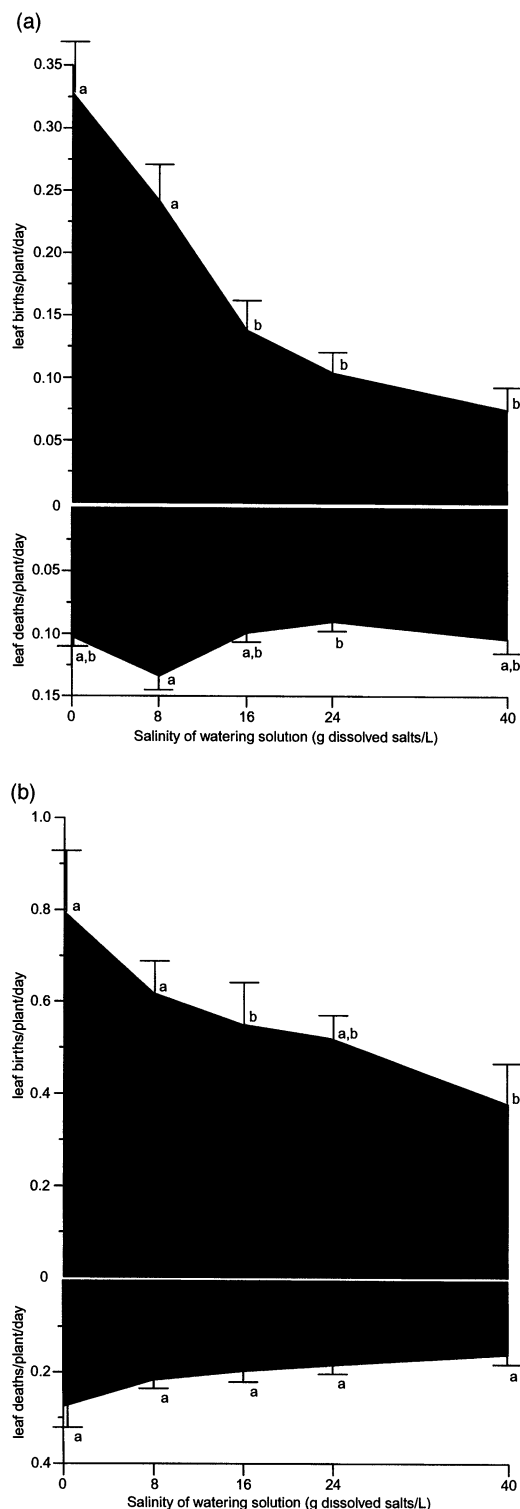


Fig. 1 Mean leaf birth and death rates of plants of (a) *Carex subspathacea* and (b) *Puccinellia phryganodes* grown at different salinities in pots at La Pérouse Bay in 1991. Leaf births and deaths occurred either on main shoots (solid areas) or on axillary shoots and attached tillers (hatched areas). Total leaf birth or leaf death rates of plants in treatments with the same letter are not significantly different from each other (Tukey's test, $P \geq 0.05$). Note that for *Puccinellia* the mean ASLB and TLB are higher at 16 than at 24 g L⁻¹ dissolved salts when plotted in the linear form in this Figure, but when transformed for statistical analysis by the use of square roots or logarithms the reverse is true. This is a consequence of the underlying distribution of the data. Error bars are ± 1 SE. $n = 19$ –20 plants.

general, leaf birth and death rates both tended to decrease as salinity increased. In highly saline treatments, the number of leaf deaths was limited by the supply of living leaves. Plants in such saline treatments were characterized by a substantial number of dead plants and by living plants with only a few live leaves (Table 1).

The ratio of *ATLB* to *MTLB* was 1.20, 1.05, 0.51, 0.30 and 0.36 for plants watered with 0, 8, 16, 24 and 40 g L⁻¹ DS, respectively: plants appeared to allocate resources preferentially to main tillers rather than attached tillers, when exposed to high salinities.

By contrast, the range of salinities used in this experiment did not have an overall effect on the leaf demography of *Puccinellia* (MANOVA, Wilk's λ , $P \geq 0.05$; Fig. 1b). When demographic parameters were examined individually, *ASLB* and *TLB* but not *MSLB*, *MSLD* or *TLD* were significantly reduced over the range of salinities used (ANOVA, $P < 0.05$; results of Tukey's test on *TLB* data shown in Fig. 1b). As the data for axillary shoot leaf deaths were non-parametric they were analysed separately, but the axillary shoot leaf death rate was unaffected by salinity (*ASLD*; Kruskal-Wallis test, Chi-squared statistic, $P \geq 0.05$). The ratio of axillary shoot leaf births to main shoot leaf births decreased with increasing salinity (3.71, 3.30, 3.00, 2.35 and 1.99 for plants watered with 0, 8, 16, 24 and 40 g L⁻¹ DS, respectively). This allocation response to salinity is similar to that of *Carex*.

Plants of both *Puccinellia* and *Carex* showed a decrease in total leaf births when watered with solutions of increasing salinity. It is not valid to compare leaf birth rates of these two species directly, since they differ in the type of ramet production and in leaf size and structure. However, the percentage decrease of *TLB* at the highest salinity relative to that of the

Table 1 Percentage mortality of plants of *Puccinellia phryganodes* and *Carex subspathacea* grown at different salinities, either in pots at La Pérouse Bay, or in pots in a growth chamber. Salinities (g L⁻¹ dissolved salts) not represented in a given experiment are indicated by—

Salinity	<i>Puccinellia</i>			
	<i>Carex</i> 1991 field	1991 field	1992 field	1991 growth chamber
0	0	0	0	0
8	5	5	—	—
16	25	0	—	—
20	—	—	16	7
24	25	0	—	—
30	—	—	—	7
40	68	0	71	0
50	—	—	—	7
60	—	—	77	40
70	—	—	—	67
80	—	—	97	—

control treatment (0 g L⁻¹ DS) is greater in *Carex* than in *Puccinellia* (Fig. 1). By the end of the experiment, nearly 70% of all the *Carex* plants grown at 40 g L⁻¹ DS had died (Table 1), while all the *Puccinellia* plants were healthy at this treatment (no plants of either species died at 0 g L⁻¹ DS).

LEAF AND SHOOT DEMOGRAPHY OF PLANTS OF *Puccinellia phryganodes* GROWN IN POTS UNDER FIELD CONDITIONS IN 1992

Only those *Puccinellia* plants which were watered with nonsaline solution produced axillary shoots in this second experiment (Fig. 2), so only values of *TLB* and *TLD* were analysed. Both *TLB* and *TLD* were significantly affected by salinity (Kruskal-Wallis test, Chi-squared statistic, $P < 0.0001$). Substantial decreases in *TLB* occurred between 0 and 20, and between 20 and 40 g L⁻¹ DS, but *TLB* in salinity treatments of, or greater than, 40 g L⁻¹ DS or more were uniformly low (Steel-Dwass rank test, $P < 0.05$; Fig. 2). The effects of the salinities on *TLD* were more complex, but generally *TLD* increased as salinity increased (Steel-Dwass rank test, details of results in Fig. 2). By the end of the experiment, most plants had died in salinity treatments of greater than or equal to 40 g L⁻¹ DS (Table 1), as a result of low leaf birth rates and high leaf death rates.

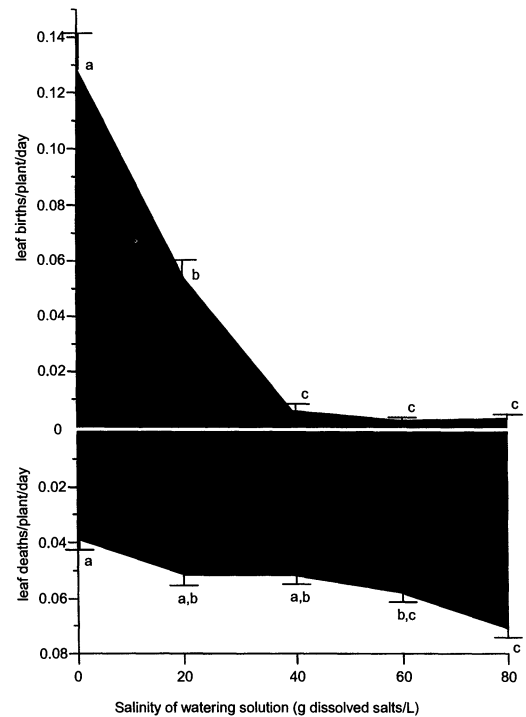


Fig. 2 Mean leaf birth and death rates of plants of *Puccinellia phryganodes* grown at different salinities in pots at La Pérouse Bay in 1992. Total leaf birth and deaths occurred either on main shoots (solid areas) or on axillary shoots (hatched areas). Leaf birth or death rates of plants in treatments with the same letter are not significantly different from each other (Steel-Dwass rank test, $P \geq 0.05$). Error bars are ± 1 SE. $n = 15$ plants.

Plants of *Puccinellia* in this experiment came from the same sward and were planted and watered in a similar manner to those in 1991, yet the demography of leaves and shoots of plants grown at salinities between 0 and 40 g L⁻¹ DS was different between the two years. Besides the differences in axillary shoot production mentioned above, the *ASLB* of plants watered with nonsaline solution in 1992 was an order of magnitude lower than even those plants watered with 40 g L⁻¹ DS in 1991. There was a marked decrease in *MSLB* and an increase in *TLD* between salinities of 0 and 40 g L⁻¹ DS in 1992, but not in 1991. Plant deaths increased substantially over this salinity range in 1992 in contrast to the results for 1991 (Table 1). These differences in leaf and shoot demography of *Puccinellia* and in the survival of plants in 1991 and 1992 are similar to differences in the demography of plants of *Puccinellia* transplanted directly into the salt marsh at La Pérouse Bay in 1991 and 1992 (Srivastava 1993).

DEMOGRAPHY OF PLANTS OF *Puccinellia phryganodes* GROWN IN POTS IN A GROWTH CHAMBER

Leaf birth and death rates during the last four weeks of the experiment were analysed. At the start of this period, all plants had received the appropriate saline solution for at least one week. At low salinities plants had been watered with the appropriate solution for up to 4 weeks. Leaf number at the beginning of the last four weeks of the experiment was significantly higher in plants receiving the treatments containing 20 g L⁻¹ DS (mean = 15 leaves) than in plants from the more saline cultures (mean = 9 leaves), because of this adjustment time (Tukey's tests after ANOVA, $P < 0.05$; no other comparisons significant). In such situations it has been suggested that leaf births and deaths should be expressed as a percentage of the initial leaf number (Jefferies & Rudmik 1991). Results were very similar, however, whether relative or absolute values of leaf birth and death were used; for simplicity only absolute values are presented.

Salinity had a highly significant effect on *MSLB*, *ASLB*, *MSLD*, *ASLD*, and hence *TLB* and *TLD* in plants of *Puccinellia* (Kruskal–Wallis test, χ^2 statistic, $P < 0.0001$). Both *MSLB*, *ASLB* and their sum (*TLB*) decreased dramatically in plants grown at 30 g L⁻¹ DS compared with corresponding values for plants grown in the control nonsaline solution. The values of *MSLB*, *ASLB* and *TLB* were uniformly low at salinity treatments of 40 g L⁻¹ DS or higher (Steel–Dwass rank test, $P < 0.05$, results for *TLB* shown in Fig. 3). As the salinity increased from 0 to 40 g L⁻¹ DS, leaf births on axillary shoots were reduced before main shoot leaf births (the ratio of *ASLB* to *MSLB* was 2.82, 3.12, 1.59 and 1.65 for 0, 20, 30 and 40 g L⁻¹ DS, respectively).

At both low and high salinities (≤ 20 and ≥ 60 g L⁻¹

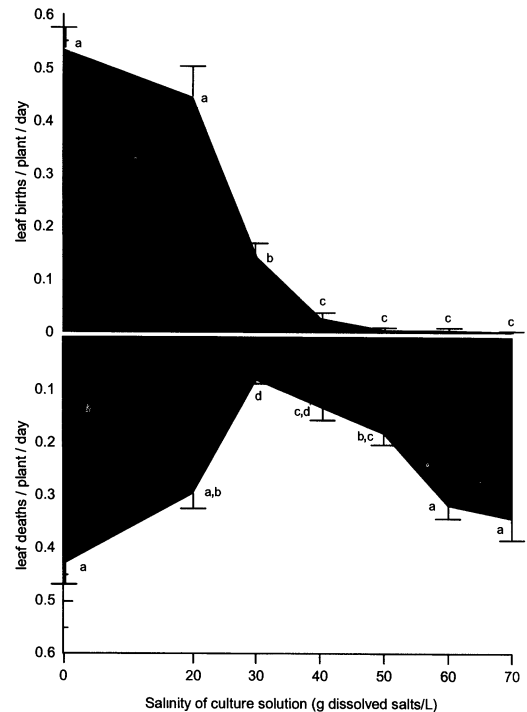


Fig. 3 Mean leaf birth and death rates of *Puccinellia phryganodes* plants grown at different salinities in pots in a growth chamber in 1991. Total leaf birth and deaths occurred either on main shoots (solid areas) or on axillary shoots (hatched areas). Leaf birth or death rates of plants in treatments with the same letter were not significantly different from each other (Steel–Dwass rank test, $P \geq 0.05$). Error bars represent ± 1 SE. $n = 31$ plants.

DS) both the *ASLD* and the *TLD* of plants was high, while at intermediate salinities (30 and 40 g L⁻¹ DS) the *ASLD* and the *TLD* of plants were significantly lower (Steel–Dwass rank test, $P < 0.05$; results for *TLD* shown in Fig. 3). The *MSLD* of plants was also significantly lower at 30 g L⁻¹ DS than at low and high salinities (≤ 20 and ≥ 60 g L⁻¹ DS; Steel–Dwass rank test, $P < 0.05$).

As salinity was increased from 0 to 70 g L⁻¹ DS, the absolute difference between total leaf births and deaths decreased markedly (Tukey's test after ANOVA, $P < 0.05$) (Fig. 4). This net change in live leaves was not significantly different between plants grown at 0, 20 and 30 g L⁻¹ DS (Tukey's test, $P \geq 0.05$). Between 0 and 30 g L⁻¹ DS, the *TLB* exceeds the *TLD* and live leaves accumulate, while at salinities greater than 30 g L⁻¹ DS, the *TLD* exceeds the *TLB* and live leaves are depleted. High rates of leaf depletion account for deaths of 40% and 67% of all plants, respectively, at salinities of 60 and 70 g L⁻¹ DS, compared with a mortality of only 0–7% of plants in the less saline treatments (Table 1).

Asymmetry between leaf birth and death rates can be expressed in relative, as well as absolute terms. The ratios of *TLB/TLD* values were significantly higher in plants grown at 0–30 g L⁻¹ DS when compared with ratios for plants grown at 40–70 g L⁻¹ DS; other comparisons were not significant (Steel–Dwass rank test

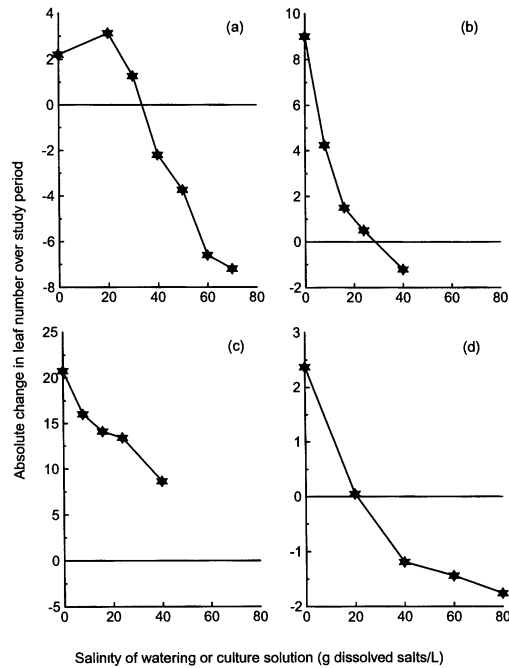


Fig. 4 Changes in leaf numbers of (a,c,d) *Puccinellia phryganodes* and (b) *Carex subspathacea* plants grown at different salinities, calculated as the difference between total leaf births and total leaf deaths. Positive values indicate a net accumulation of leaves, negative values indicate a net depletion of leaves over the duration of the experiment. Plants were grown in pots in a growth chamber (a), or in pots at La Pérouse Bay either in 1991 (b,c) or in 1992 (d). The experiments lasted for 28, 40, 40, and 26 days for a, b, c and d, respectively. Note that the vertical axes are on different scales.

after Kruskal–Wallis test, $P < 0.05$). Plants grown at intermediate salinities of 30 and 40 g L⁻¹ DS tend to have small absolute differences between the *TLB* and *TLD*, since both the *TLB* and the *TLD* are low at these salinities. However, values of the ratio of *TLB/TLD* decreased sharply from 1.88–0.26 in plants grown at 30 and 40 g L⁻¹ DS, respectively.

Discussion

Carex subspathacea appears to be more salt-sensitive than *Puccinellia phryganodes*, at least over the range of salinities examined (Figs 1 and 4). This is consistent with the observed distribution of these two species at La Pérouse Bay and elsewhere. *Puccinellia* is abundant on salt-marsh soils which are often hypersaline in mid-summer, while *Carex* is frequent in salt-marshes, where soil salinity is reduced by brackish and freshwater stream flow (Srivastava 1993). Although differences in the distributions of *Puccinellia phryganodes* and *Carex subspathacea* have been attributed to salinity (Jefferies 1977; Glooschenko 1980), the relative salt tolerances of the two species have not been examined experimentally until this study.

Total leaf births in *Puccinellia* were unaffected by moderate increases in salinity and they were only reduced when the salinity was high. Most halophytes

exhibit a similar response to salinity, although in a few species growth is stimulated at very low salinities (Jennings 1976; Flowers *et al.* 1977; Ungar 1991). The salinity at which leaf births were markedly reduced depended on the growing conditions of each experiment.

When *Puccinellia* plants were grown either at La Pérouse Bay or in a growth chamber, increasing salinity affected leaf birth rates differently from leaf death rates (Figs 1–3). At low salinities (0 and 20 g L⁻¹ DS) both leaf birth and death rates were high. At salinities similar to that of oceanic sea water (32 g L⁻¹ DS) both birth and death rates of leaves tended to decline to a low value, whereas at 40–70 g L⁻¹ DS, leaf death rates greatly exceeded leaf birth rates. At high salinities an increasing asymmetry between rates of leaf births and deaths is evident. Similar demographic studies of plants of *Triglochin maritima* also indicated that increased salinity resulted in reduced leaf birth and death rates (Jefferies & Rudmik 1991).

In all experiments, fewer leaves accumulated as salinity was increased (Fig. 4). Although the accumulation of live leaves of *Puccinellia* plants grown in growth chambers decreased linearly as salinity increased from 20 g L⁻¹ DS (Fig. 4a), the relative accumulation (*TLB/TLD*) was similar from 0 to 30 g L⁻¹ DS, decreased by almost an order of magnitude between 30 and 40 g L⁻¹ DS and was very low (< 0.05) at salinities from 40 to 70 g L⁻¹ DS. These results suggest that over a wide range of salinities (0–30 g L⁻¹ DS), plants of *Puccinellia* maintain existing leaves by reducing both total leaf births and total leaf deaths equally. At salinities greater than 30 g L⁻¹ DS, a threshold of salinity tolerance has been exceeded and leaf deaths increase and the population of leaves is depleted. It is possible that leaf depletion is only a short-term response to salinity. In *Triglochin maritima*, plants were initially depleted of many leaves for 2 months after the salinity was increased, but by 10 months after salinization, plants had similar rates of leaf accumulation (measured either in absolute or relative terms) as the nonsaline controls (Jefferies & Rudmik 1991). High rates of mortality of plants of *Puccinellia* at the high salinities of 60 and 70 g L⁻¹ DS in this experiment, however, indicate that leaf depletion was not reversible. In less saline treatments, plants had 2–4 weeks to adjust to the final salinity and as leaf birth and death rates were an order of magnitude faster in *Puccinellia* than in *Triglochin maritima*, this period of adjustment to new conditions should have been adequate.

In the experiment of 1992 plants of *Puccinellia* did not accumulate leaves except in the treatment of 0 g L⁻¹ DS (Fig. 4d). Total leaf deaths exceeded leaf births at salinities greater than 20 g L⁻¹ DS resulting in depletion of leaves. By contrast, leaves were accumulating between 0 and 40 g L⁻¹ DS in the experiment conducted in 1991 at La Pérouse Bay (Fig. 4c). Differences in the accumulation and depletion of

leaves on plants of *Puccinellia* in 1991 and 1992 are attributed to weather differences between these years. The summer of 1991 was both warmer and wetter than the summer of 1992, based on data supplied by the Churchill Weather Office (Environment Canada). On almost every day between early May and early September, mean air temperature was higher in 1991 than in the unusually cold year of 1992, and this difference exceeded 5 °C on most days. The total rainfall in July was unusually high (168 mm) in 1991, but only 20 mm in 1992. The adverse (cold, dry) weather in 1992 appeared to have compounded the adverse effects of salinity stress. Although it was not formally tested in this study, weather and salinity interact: the reduction in total leaf births in 1992 compared to that of 1991 was greater at high salinities than at low salinities. Similar interactions between salinity and adverse weather conditions have been reported earlier (Gale 1975).

In all experiments as salinity increased, growth of axillary shoots or attached tillers declined before the growth of main shoots or main tillers. Axillary shoots and attached tillers may serve nonessential functions, such as horizontal expansion of a clone (Lovett-Doust 1981; Schmid & Harper 1985), avoidance of grazing (Bazely & Jefferies 1989; Srivastava 1993), and acting as vegetative propagules for dispersal (Chou *et al.* 1992) and colonization (Jefferies 1988a). In the control treatment (0 g L⁻¹ DS) of the field experiment conducted in 1991, up to 33 axillary shoots were produced on one *Puccinellia* plant, many of which developed roots and became detached from the mother plant. Under increasing salinity, rooting and survival of individual axillary shoots are reduced compared with the survival and growth of the main shoots of plants (Ungar 1978, 1991). By contrast, resource demands for plant maintenance are increased under increasing salinity because of the 'costs' of salinity tolerance (Popp & Albert 1980; Yeo 1983; Rozema *et al.* 1985), which include proline synthesis for osmoregulation in *Puccinellia* species (Stewart & Lee 1974). According to life history theory, investment in axillary shoots and attached tillers under adverse conditions should therefore be selected against and resources preferentially allocated to maintaining the main shoot. Indeed, allocation of resources to sexual reproduction is reduced in many halophytes growing under saline conditions (Jefferies 1972; Jefferies *et al.* 1979b; Ungar 1987; Jefferies & Rudmik 1991). In *Triglochin maritima*, for example, increased salinity caused the conversion of shoot systems with many large leaves into shoot systems with a few small leaves; only the former shoots bore inflorescences (Jefferies & Rudmik 1991).

Despite the prevalence of vegetative reproduction in salt-marsh plants, effects of salinity on the allocation of resources to vegetative reproduction have been largely ignored. These results suggest that if environmental conditions result in increased salinity within

these arctic coastal salt-marshes, both vegetative growth and reproduction may be reduced. Over the long-term, the combined effects of reduced vegetative growth and reproduction may result in reduced abundance of *Puccinellia* and *Carex* particularly as sexual reproduction is a rare event or absent in these species. Since *Carex* is less salt-tolerant than *Puccinellia* the relative abundance of *Carex* to *Puccinellia* is also predicted to decrease as the salinity of the salt marsh increases.

Reduced availability of these preferred forage species of lesser snow geese could lead to a decrease in the number or fitness of birds. Indeed, it has been suggested that previous loss of salt-marsh vegetation has resulted in a reduction in juvenile size and survivorship, clutch size, brood size, and the body size of adult females (Cooch *et al.* 1989, 1991; Francis *et al.* 1992; Williams *et al.* 1993).

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