

The biology of the annual *Salicornia europaea* agg. at the limits of its range in Hudson Bay

R. L. JEFFERIES, A. JENSEN AND D. BAZELY

Abstract

The biology of a marginal population of the annual *Salicornia europaea* agg. has been examined at La Perouse Bay, Manitoba, on the shores of Hudson Bay. Plants were confined to south-facing sites which became hypersaline in summer, but which were not covered by tides. The difference in temperature of surface sediments between south- and north-facing slopes was as much as 7°C. Although most seedlings emerged in June, germination continued throughout the summer, but plants that appeared late in the season failed to set seed. Mortality of both seedlings and adult plants was low. Seeds or seedlings from a south-facing slope were transplanted during a 2-year period within the same site, into another south-facing site, to a north-facing site, and to an intertidal site. Germination either failed to occur or else was poor at the latter two sites. In addition, seed production of mature plants was low compared with that for individuals transplanted within south-facing sites. Additions of nitrogen to north-facing slopes increased overall seed output per plant, but the ratio of unripened to ripened seeds remained the same as that in plants from untreated plots. The results are discussed in relation to the ecology of marginal populations.

Introduction

Populations close to the limit of a species' range are geographically peripheral and frequently ecologically marginal (Mayr 1963). Often the geographical boundary is ill-defined and fluctuates as a result of changes in the environment and the number of immigrants that reach favorable sites (Lewontin 1974).

Theories of range extension and evolution within a species, of necessity, are based on comparative studies of the biology of different populations (Mather 1953; Mayr 1963; Antonovics 1976). Not only do investigations of the biology of populations yield information on selection processes controlling a species' range, but ecologically marginal situations may adversely affect establishment, growth, and reproduction of plants, and thereby accentuate phenomena not otherwise detectable in central populations (Grant and Antonovics 1978).

The near absence of species with an annual growth habit from tundra communities in arctic North America is an example of the inability of a group of plants to extend their range northward. The short summers and the low temperatures apparently preclude the annual habit (Savile 1972). The southern shore of Hudson Bay represents a climatic transitional zone between subarctic and arctic conditions (Hare and Ritchie 1972). Within this narrow coastal zone a number of annual halophytic species, including *Salicornia europaea* agg., reach the northern limit of their geographical range in Canada

(Ritchie 1956; Scoggan 1957). The boundary provided an opportunity to conduct an experimental study of the dynamics of a peripheral population of *S. europaea* growing under marginal conditions.

Mortality and fecundity of plants have been investigated during three successive growing seasons to examine factors affecting the size of the population. Individuals have been transplanted within a site and to other sites devoid of *Salicornia*. The results have been compared with those of other populations of *Salicornia europaea* growing elsewhere, to establish whether life-cycle characteristics of peripheral and central populations are similar. Finally, the behaviour of this peripheral population has been examined in relation to the known responses of peripheral populations of other species.

Site description

The site selected for this study was the salt marsh at La Perouse Bay on the Hudson Bay coast, 30km east of Churchill. The vegetational development of the marsh has been described previously (Jefferies et al. 1979).

Salicornia europaea is absent from the open tidal flats at La Perouse Bay and from the lower reaches of the braided estuary of the Mast River. The species is restricted to low-lying areas in the upper marsh which frequently lie between frost-heave mounds on which *Salix brachycarpa* Nutt. grows. The low-lying sites are often cut by shallow creeks or pools (ca. 1-10m in width), in which slowly moving or standing water occurs up to a depth of approximately 50cm. The sites are above the high-water mark of spring tides. However, flooding of these low-lying areas occurs during spring when meltwater drains from the coastal hinterland, and because drainage is impeded, the sediments are saturated with water throughout the summer. Only during the occasional period of settled weather does the surface of the sediments dry out.

Salicornia europaea is restricted normally to either southfacing slopes or to small undulations on the surface of the sediments which are south facing. The former sites are on the north side of shallow drainage channels with an angle of slope not greater than 5°. The only other angiosperm present at these sites is the stoloniferous salt-marsh grass, *Puccinellia phryganodes* (Trin.) Scribn. and Merr. On gentle north-facing slopes, *Carex subspathacea* Wormsk., *Potentilla egedii* Wormsk., *Plantago maritima* L., and *Puccinellia phryganodes* occur, but *Salicornia europaea* is absent. Very occasionally a few depauperate plants may be found growing on the south side of small ponds, presumably because seeds are carried by water from the north slope.

The particular low-lying area selected for experimental studies was located in the upper reaches of the estuary of the Mast River. The area, which was approximately 30 X 30 m, was interrupted by mounds of *Salix brachycarpa*. *Salicornia europaea* was common on the north slopes (south facing) of small circular ponds (ca. 1-3 m in diameter) and drainage channels. Most of the latter were orientated along an east-west axis.

Methods

Measurement of temperature

To characterize the temperature regimes on north- and south-facing slopes, air and sediment temperatures were measured daily between May 23 and August 31, 1980, at the experimental site. A transect (18 m) was laid out along a north-south axis across a low-lying areathrough which a small drainage channel (3m in width) flowed in an east-west direction. Five sampling stations, spaced at intervals of 5 m were set up along the transect; three of these were on the south-facing slope and the other two were on the north-facing slope of the drainage channel. One of the stations on each slope was positioned at the bank (ca. 20 cm in height) of the shallow drainage channel. Temperatures of the surface sediments (0.5 cm in depth) were taken between 1300 and 1500 on each day at the sampling stations. A Yellow Springs multichannel tele-thermometer with appropriate soil thermistor probes was used to measure the temperatures. Five separate measurements of temperature were made at each station at the time of sampling, and in addition, the temperature of the water in the drainage channel was recorded. Air temperature at the site was measured 1 m above the ground. Additional information on the daily weather conditions was obtained from the Churchill Weather Office, Environment Canada.

Measurement of salinity

Measurements of salinity of water in the sediments of north and south-facing slopes were made to determine whether conditions differed in the sediments of the two slopes. On one occasion in July 1979 and at intervals of 10 to 14 days between early June and mid-August 1980, duplicate samples of turfs (10 x 10 x 7.5 cm) were collected at random from two sampling stations, one on the north-facing and the other on the south-facing slope at the experimental site. Water was squeezed by hand from the saturated sediments, filtered through Whatman glass filter paper (grade C), and stored in polythene bottles in a freezer in the field. On return to Toronto, atomic absorption and flame spectrophotometric methods were used to measure concentrations of sodium, potassium, magnesium, and calcium in the samples. Amounts of chloride were determined by titrating the samples with silver nitrate.

*Density and fecundity of *Salicornia* plants in relation to aspect*

To establish that the distribution of *S. europaea* was strongly correlated with aspect, compass bearings were taken of the direction that slopes faced at 200 sites where *S. europaea* was growing. On one occasion individuals were found growing around the periphery of a small pool, the slopes of which faced in different directions and were devoid of other plants. The site provided an opportunity to record the density and seed production of the plants in relation to aspect. The pool was approximately 3 m long and 1.5 m wide, with its long axis orientated in a N-S direction. At the end of August 1980, a stake was placed in the centre of the pool and a set of strings was run from this post to the slopes at intervals of 15° through 360°; 0° faced towards magnetic north. All plants of *S. europaea* present on the slopes within each sector were collected and counted, dried at 80°C for 48 h. Numbers of ripened and unripened seeds and branches per individual were determined, since many seeds were produced on side branches. Where there were many plants in a sector (50), estimates of fecundity and degree of branching were based on a subsample of 50 plants taken at random. Ripened seeds were identified

subjectively on the basis of size and the brown colour of the seed coat. Small unripened seeds were greenish white in appearance. The area of slope within each sector was determined so that the density of *S. europaea* plants per unit area could be calculated.

Experimental studies

A series of experimental manipulations of populations of *S. europaea* was carried out between 1978 and 1980. These studies provided demographic data on survivorship of individuals and levels of fecundity. In early June 1980, 20 turfs (7 X 7 X 5 cm) from the south-facing slope within the experimental area were cut and returned to the site. These served as the control plots. Another set of 20 turfs was transplanted from the south-facing slope to another south-facing slope where *S. europaea* was absent. A similar series of 20 turfs from the same slope was transplanted in the opposite north-facing slope. The turfs were selected so that *S. europaea* was present at a range of densities in the different plots. The densities reflected the normal range of densities found at La Perouse Bay. On each turf a permanent quadrat (5 X 5 cm) was marked, and the initial density of *S. europaea* plants within the quadrat was recorded. Additional recordings of numbers of individuals in the quadrats were made every 10 to 14 days from June until late August. At that stage all surviving plants were harvested and dried at 80°C for 48 h. Numbers of ripened and unripened seeds and numbers of branches were recorded as described previously.

In 1979 a similar set of transplant experiments to those described above was set up in June, except that only 10 turfs were transplanted to another south-facing slope and 10 to a north-facing slope. Fecundity of the transplanted populations was measured in late August of that year following the procedures described earlier.

As indicated earlier, *S. europaea* was absent from the open tidal flats. To determine the ability of individuals to survive and set seed in such a habitat, 10 turfs of similar size to those above, in which young plants of *S. europaea* were present, were transplanted in a site on the open tidal flats in early June 1979 and another 10 in June 1980. Harvesting procedures in late August of both years were similar to those described above, except that plants in only five of the quadrats were harvested in 1980, as the remainder were used for long-term demographic studies. Numbers of individuals in plots during the growing season were recorded in 1980.

Because the restriction of *S. europaea* to south-facing slopes might have been an indirect result of temperature influencing microbial activity and therefore the rate of mineralization of nitrogen, a further transplant experiment was set up in mid-June 1980 in which turfs received additions of nitrogen. Nitrogen was added because a previous study had established that only this element amongst the major nutrients was limiting plant growth at the site (Cargill 1981). Sets of 20 turfs (7 X 7 X 5 cm) from south-facing slopes, in which *S. europaea* plants were present at a range of densities, were planted in sediment on both south- and north-facing slopes. Half of the turfs on each slope received additions of sodium nitrate, as crushed salts, once every 20 days from mid-June until late August 1980. The amounts of sodium nitrate applied were equivalent to 40.2 g m⁻² (Jefferies and Perkins 1977). The remainder of the plots received no nutrients and served as the controls. Numbers of plants in the permanent

quadrats (5 X 5 cm) on the turfs were recorded at intervals throughout the season. The plants were harvested in late August. Seed production, and the number of branches were determined, as described previously.

All of the experiments described above were based on the transplanting of seedlings or young plants within the marsh. Because the restriction of individuals to south-facing slopes might have involved selection at the seed or germination stages, the final set of experiments concerned the fate of seeds from plants which matured in permanent quadrats (5 x 5 cm) in 1979. In July 1979, sets of 12 turfs, in which plants of *S. europaea* were growing at different densities, were transplanted from a south-facing slope to each of the following sites: a south-facing slope devoid of *S. europaea* plants, a north-facing slope, and a site on the open tidal flats. The numbers of seedlings which emerged in 1980 and their subsequent survival were recorded. In late August 1980, all survivors were harvested and numbers of seeds and branches per plant determined.

In both 1978 and 1979 measurements were made of fecundity in populations of *S. europaea* from south-facing slopes within the experimental area. In the 1st year seed output in plants from six permanent quadrats (5 X 5 cm) was determined, while in the 2nd year the same measurements were made on plants in 21 quadrats of identical size. The positions of the quadrats were chosen to give a range of densities of *S. europaea*, and in both years plants were harvested in late August.

Statistical treatment of the data on seed production of the transplants involved an analysis of covariance. Results of the numbers of ripened seeds or unripened seeds produced by each individual in a plot were pooled, and the mean values of the two groups of seeds produced per plant for each plot were calculated. The statistical procedure involved three stages. Initially, a general linear regression model was applied to examine whether a significant relationship existed between the mean numbers of the two types of seed per individual and the covariate, density. The procedure involved testing whether the regression coefficients deviated from zero. In all cases the regression of the covariate (density) failed to account for all of the significant variation in seed output per plant in relation to treatment (i.e., direction of slope, addition of nutrients). In the second stage the heterogeneity of the regression slopes for the different treatments was tested. In some cases there were significant differences between the slopes, indicating it was not necessary to proceed with the third stage. However, to maintain uniformity all data were subject to the third stage in which the variation associated with density was removed and the general linear model applied to produce a type IV sum of squares. The statistical package used was the G.L.M. procedure (Blair 1979).

Other data, such as numbers of branches per individual, were not subject to statistical treatment because of the large number of zero values.

Results

Environmental data

Maximum and minimum temperatures at Churchill Airport for the summers of 1979 and 1980 indicated that, unlike 1979, comparatively high temperatures prevailed in April and May of 1980, which resulted

in the early disappearance of snow cover. On most days between the end of April and early June 1980 minimum temperatures were between -2 and 5°C, whereas in 1979 temperatures fell to below -17°C on two occasions during the same period. The daily minimum temperature rose above 0°C at the end of June in both 1979 and 1980; it fell below the freezing point again in early September. In both years fine spells of weather lasting 1 or 2 days were punctured by wet weather as low pressure systems crossed the area. Temperatures exceeded 25°C on a number of occasions in July and August of both years. These two months were snow free, and in spite of the early thaw in 1980, snow falls during April and May of both years were similar in amount. *Salicornia europaea* germinated at the end of May in 1980 and on two occasions in June the plants were covered with a thin layer of snow which did not persist more than 24 h.

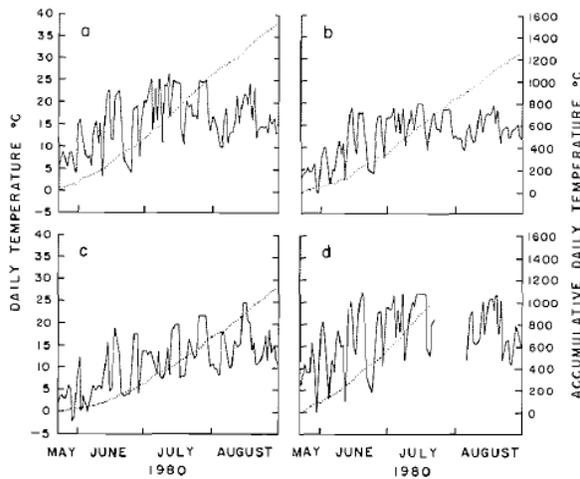


FIG. 1. Daily measurements (solid lines) and accumulative totals (dotted lines) of air, water, and sediment temperatures (degrees Celsius) at the experimental site at La Pérouse Bay. Temperatures were measured between 1300 and 1500 each day. (a) Temperature of sediments on a south-facing slope (site 1). (b) Temperatures of sediments on a north-facing slope (site 6). (c) Air temperature. (d) Temperature of water in a shallow pond which dried out in late July and early August.

Air, water, and sediment temperatures at La Perouse Bay during the summer of 1980 are shown in Fig. 1. Lower temperatures were recorded in the upper layers of sediment on a north-facing slope compared with those for a south-facing slope, particularly early in the season. For example, from May 23 to June 11, when *S. europaea* first germinated, the mean recorded temperature (5.88°C) at site 6 (north-facing slope) was only 63% of the similar value at site 1 (south-facing slope). In July and August the corresponding percentage was 85%. Sediment temperatures were significantly higher than air temperatures, particularly in the early part of the season. In late May and the first part of June when air

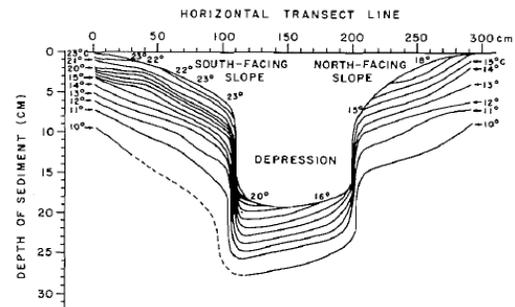


FIG. 2. Temperature profiles in sediments along a 3 m north-south horizontal transect line which traversed a small pond at La Pérouse Bay. Measurements were made at 1200 Central Standard Time, July 18, 1979.

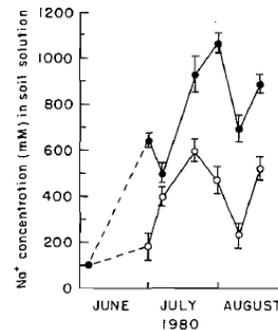


FIG. 3. Concentration of sodium (millimolar \pm SE) in the interstitial water of the upper layers of sediment at the experimental site in La Pérouse Bay. (●), south-facing slope; (○), north-facing slope.

temperatures were close to 0°C, the temperatures of sediments on the south-facing slope were frequently 5°C or more above ambient temperatures. However, the temperatures of the pond water and the air showed the biggest difference. On a number of days in May and June, the temperature of the water was 10°C warmer than the air temperature; later in the season the pond dried out. A temperature profile of sediments beneath a small depression at 1200 Central Standard Time on July 18, 1979, depicts the characteristic differences in temperature of surface sediments from north- and south-facing slopes (Fig. 2). As the depression was dry there was an asymmetry in the temperature profiles of the sediments below the depression; higher temperatures prevailed in surface sediments on the north side of the depression.

TABLE 1. Concentrations of chloride, potassium, calcium, and magnesium ions (millimolar) in the interstitial water of the surface sediments from south and north-facing slopes at La Pérouse Bay, Manitoba (\pm SE, $n = 3$)

	Chloride	Potassium	Calcium	Magnesium
1979				
July 15				
South facing	872.0 \pm 108.0			
North facing	378.0 \pm 59.0			
1980				
June 4				
South facing		4.0 \pm 0.4	10.7 \pm 3.5	21.3 \pm 3.4
North facing		*	*	*
July 1				
South facing		16.2 \pm 0.2	47.3 \pm 3.0	88.0 \pm 6.7
North facing		6.7 \pm 1.5	32.2 \pm 13.2	41.3 \pm 14.8
July 6				
South facing		20.4 \pm 2.5	26.5 \pm 5.7	45.5 \pm 7.6
North facing		10.8 \pm 1.7	41.5 \pm 4.7	58.5 \pm 8.0
July 20				
South facing		23.0 \pm 2.0	94.3 \pm 15.4	192.6 \pm 36.0
North facing		12.8 \pm 0.1	48.0 \pm 4.5	88.5 \pm 7.2
August 1				
South facing		22.5 \pm 0.8	97.7 \pm 5.2	217.3 \pm 11.3
North facing		13.3 \pm 0.2	56.7 \pm 5.0	113.7 \pm 7.2
August 17				
South facing		21.9 \pm 1.1	77.3 \pm 2.3	145.0 \pm 4.0
North facing		13.6 \pm 0.4	41.0 \pm 4.2	73.7 \pm 9.6

*Not determined.

A consequence of the higher temperatures of the surface sediments on south-facing slopes was the development of hypersaline conditions (i.e., $\text{Na}^+ > 0.5 \text{ M}$) in both 1979 and 1980 (Fig. 3, Table 1). On the north-facing slope the sodium concentration exceeded 0.5 M on only one occasion in mid-July 1980. The site was not inundated by tidal water and after the spring thaws, river water did not flood the site. In 1980, there was a 10-fold increase in salinity of the water in the upper layers of sediment from the south-facing slopes between early June and late July. At the latter date the salinity of the interstitial water exceeded 1 M with respect to sodium (ca. 64‰ salinity). Corresponding increases in the concentrations of other ions occurred as well. The salinity of sediments from the north-facing slope only increased fivefold during the same period. During the summer of 1980 as a result of precipitation large changes in salinity occurred between sampling dates, particularly in July and August.

Distribution of Salicornia europaea

The distribution of clumps of *S. europaea* plants in relation to aspect is shown in Table 2. Although compass bearings made by us of the direction of slope indicated that 98% of the clumps occurred at sites which faced between 120 and 270° N, the aspect of the majority of these sites was southerly (i.e., 150 to 239° N). Similar results were obtained for the distribution of *S. europaea* around the slopes of the small pond (Fig. 4).

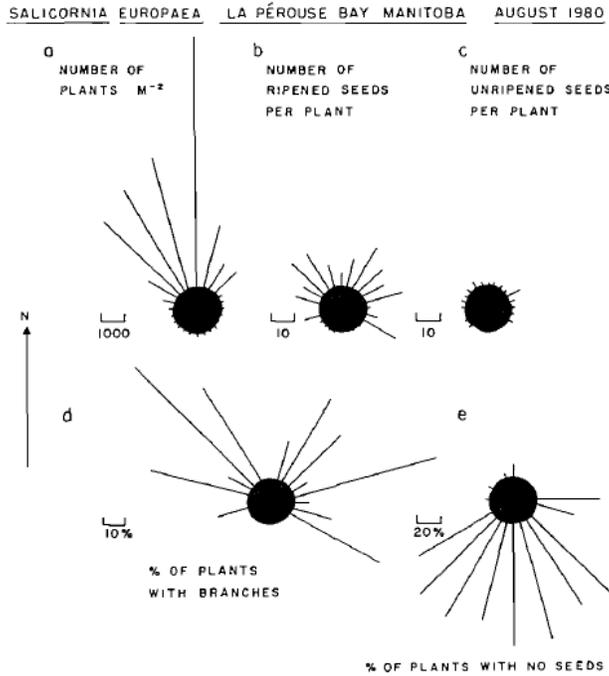


FIG. 4. Density and fecundity in relation to aspect of plants of *Salicornia europaea* agg., growing on the banks of a shallow circular pond at La Pérouse Bay, Manitoba. (a) Number of plants per square metre. (b) Number of ripened seeds per plant. (c) Number of unripened seeds per plant. (d) Percentage of plants with branches. (e) Percentage of plants with no seeds.

TABLE 2. Percentage distribution of clumps of plants of *S. europaea* at 200 sites in relation to aspect at La Pérouse Bay, Manitoba, based on compass bearings; 0, 90, 180, 270° refer to sites facing due north, east, south, and west respectively

Degrees	0-29	30-59	60-89	90-119	120-149	150-179	180-209	210-239	240-269	270-299	300-329	330-360
Percentage	0	0	2	0	16	26	26	20	10	0	0	0

On the south-facing slope at the northern end of the pond, the density of plants exceeded 10 000 mP2 in August 1980, corresponding densities on the north-facing slope at the other end of the pond were less than 100 individuals - m⁻¹. Densities exceeding 1000 plants m⁻² were confined to sectors which were located at the northern edge of the pond. Density-dependent effects were evident in the sector facing directly south. No branches were produced by individuals and the number of mature seeds per plant was less than that for plants growing in less dense stands in adjacent sectors. However, on the slope which was north facing at the south end of the pond depauperate plants failed to produce branches or

seeds. Mean levels of seed production in plants growing on slopes which were predominantly north facing ranged from 0 to 0.4 ripened seeds per plant. No unripened seeds were produced. In contrast, plants from slopes facing south showed a mean seed production of between 5.4 and 17.76 ripened seeds and 0.1 and 2.1 unripened seeds per individual. The lowest value reflected the effects of density on seed production in the sector facing due south. In conclusion therefore, aside from the density-dependent effects, progression from south-facing to north-facing slopes around the edge of the pond is associated with a fall in density and a decrease in the number of branches and seeds per plant, both of which drop to zero in the plants from north-facing slopes.

Fluctuations in population density

Curves of the number of individuals in the permanent quadrats for the different experiments in 1980 are shown in Fig. 5. Although the results are for plants of *S. europaea* which grew under very different conditions the graphs show two common features. Firstly, although individual plants were not marked, twice-weekly observations of the plots indicated that there was little mortality of plants in all quadrats until late in the season, irrespective of where the plants were growing. The low amount of mortality that occurred in some transplanted populations took place in late July and August. Secondly, the curves show an increase in the number of plants as seeds continued to germinate in the plots for much of the season. In all treatments seedlings were present in some plots at the time of harvest in late August.

Within the experimental site seedlings of *S. europaea* first appeared on south-facing slopes at the end of May. The majority of germination occurred between the end of May and mid-July, a relatively long period of time. As mentioned above, small numbers of seedlings continued to appear throughout the growing season; those that appeared from mid-August onwards failed to grow beyond the cotyledon stage. Young seedlings lacked the characteristic succulent appearance of *S. europaea*, and the cotyledons were small and linear-ovate. However, as the plants aged they became succulent. All four sets of experiments set up in 1980, including the control transplants, showed a rise in the mean number of individuals per quadrat from early June to mid-July; thereafter there was little change in the mean population size. Those plants which died late in the season were individuals that did not develop beyond the cotyledon stage; they remained at that stage of development for much of the growing season before turning brown.

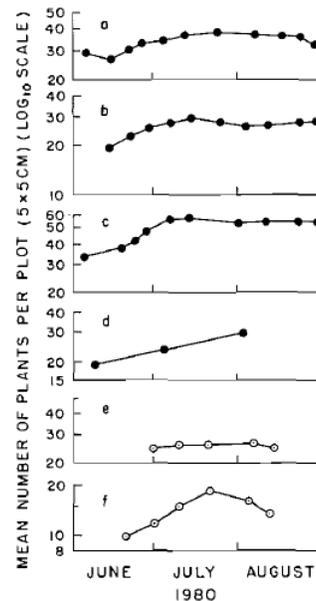


FIG. 5. Mean number of plants of *Salicornia europaea* agg. in 5×5 cm turfs in 1980 at La Pérouse Bay. (a) Turfs transplanted within the same south-facing slope. (b) Turfs transplanted into another south-facing slope devoid of *S. europaea*. (c) Turfs transplanted into a north-facing slope. (d) Turfs transplanted in the open-tidal flats. (e) Turfs transplanted into a south-facing slope devoid of *S. europaea* in July 1979. (f) Turfs transplanted to a north-facing slope in July 1979 (note differences in vertical scales).

The fate of progeny of plants transplanted in 1979 was somewhat different (Fig. 5). No seedlings appeared on the open tidal flat in 1980, nevertheless the dead plants of the parents were standing in the plots in June of that year. Although the overall densities of plants transplanted to the north-facing slope within the experimental site were similar to those from the south-facing slope, the mean density of seedlings which appeared in 1980 on the north-facing slope was lower than the corresponding figure for the control population. In addition, germination was slow on the north-facing slope and the highest mean density occurred as late as July 20. However, this was followed by some mortality of individuals, so that at the time of harvest in August the mean density had fallen by one-third. The corresponding density on south-facing slopes at harvest was double that for the north-facing slope.

TABLE 3. Density at harvest, branching habit, and fecundity of populations of *S. europaea* present on south-facing slopes at La Pérouse Bay, 1978 to 1980

Year	Sample size	Density range per 5 × 5 cm	Ripened seeds per plant (\bar{X} and range)	Unripened seeds per plant (\bar{X} and range)	Plants with no seeds (%)	Plants with branches (%)
1978	100	*	0.6 (0–3.1)	0.9 (0–3.2)	57.0	0
1979	529	1–138	4.3 (0–12.2)	1.2 (0–2.9)	10.0	0.6
1980	775	6–129	7.9 (0–21.6)	0.8 (0–4.6)	3.6	10.4

NOTE: The overall mean and the range of means for individual plots of the number of seeds per plant are given.
*Not determined.

Fecundity

Seed production of plants of *S. europaea* from south-facing slopes was markedly affected by year-to-year variations in weather (Table 3). From 1978 to 1980 weather conditions improved each year, which resulted not only in a greater number of seeds per plant but also the proportion of ripened seeds increased. The number of ripened seeds as a percentage of the total seeds produced was 40,78, and 90% in 1978, 1979, and 1980 respectively. This rise in seed production per plant was associated with a fall from 57 to 3.6% of the percentage of plants which failed to produce seeds, and an increase in the number of individuals bearing branches. In 1978 the spring thaw did not occur until June and cold wet weather prevailed for much of the growing season. When the plants were harvested at the end of the season many were less than 1 cm high. As mentioned previously, an early thaw occurred in 1980 and there was a comparatively long growing season.

Fecundities of populations from south- and northfacing slopes and open tidal flats in 1979 and 1980 are shown in Table 4. All plants were transplanted into the different sites as seedlings. In both years the production of ripened seeds per plant was between two- and three-fold greater in plants from south-facing slopes compared with plants from the north-facing slopes. In addition, the transplanting of individuals onto northfacing slopes led to an increase in the proportion of plants which failed to produce seeds and a fall in the ratio of ripened to unripened seeds per plant. In 1980 individuals transplanted to the open tidal flat were as fecund as those from the south-facing slope. However, in 1979 when a large percentage of the plants (47%) failed to produce seeds, the production of ripened seeds per plant was only half of that of individuals from south-facing slopes. Statistical analysis of the fecundity data for 1980 indicated that there was a significant difference in the mean number of ripened seeds (but not unripened seeds) produced per plant in the different sites (Table 7, a)

TABLE 4. Density at harvest and fecundity of transplanted populations of *S. europaea* on south- and north-facing slopes and on open tidal flats at La Pérouse Bay, Manitoba, in 1979 and 1980

Treatment	Sample size	Density range per 5 × 5 cm	Ripened seeds per plant (\bar{X} and range)	Unripened seeds per plant (\bar{X} and range)	Plants with no seeds (%)	Plants with branches (%)
1979						
South-facing slope (controls)	1573	21–479	1.8 (0.6–8.1)	1.9 (0.1–2.2)	30.4	0
North-facing slope	1912	21–345	0.7 (0.3–1.8)	0.3 (0–0.9)	56.6	0
Tidal flat	1318	21–482	0.9 (0–2.5)	0.7 (0.3–1.25)	47.0	0
1980						
South-facing slope (controls)	775	6–129	7.9 (0–21.6)	0.8 (0–4.6)	3.6	10.4
South-facing slope	563	2–72	5.3 (1.9–12.3)	1.1 (0–4.6)	13.4	11.2
North-facing slope	1119	4–162	2.7 (0–6.7)	1.3 (0.3–2.6)	27.6	2.9
Tidal flat	141	15–36	5.8 (2.9–8.0)	1.4 (0.2–2.9)	6.5	39.2

NOTE: The overall mean and the range of means for individual plots of the number of seeds per plant are given.

In 1979 some of the transplants were not harvested at a south-facing site, a north-facing site, and an intertidal site. The following year survivorship and fecundity of the progeny were recorded (Table 5). No seedlings appeared in plots on the open tidal flat, although the remains of plants from the previous year were present at the site. Significant differences in production of both ripened and unripened seeds occurred between plants on north- and south-facing slopes (Table 7, b). Production of ripened seeds per plant was 8.8-fold greater in plants from the south-facing slope; 60% of plants on the opposite slope failed to set seeds.

TABLE 5. Density at harvest, branching habit and fecundity of progeny in 1980 of plants of *S. europaea* which were transplanted to south- and north-facing slopes in July 1979

Treatment	Sample size	Density range per 5 × 5 cm	Ripened seeds per plant (\bar{X} and range)	Unripened seeds per plant (\bar{X} and range)	Plants with no seeds (%)	Plants with branches (%)
South-facing slope	342	3–84	6.3 (1.8–14.8)	0.6 (0–2.0)	4.5	6.7
North-facing slope	157	3–41	0.7 (0–2.3)	0.3 (0–0.8)	60.0	0

NOTE: The overall mean and the range of means of the number of seeds per plant for individual plots are given.

Where additions of sodium nitrate were made to plots the production of seeds increased dramatically, particularly in plants from the north-facing slopes (Table 6). Significant differences in the mean number of ripened and unripened seeds per plant were recorded between nutrient-treated and untreated plots and between plots on south- and north-facing slopes (Table 7, c). The ratio of ripened to unripened seeds was the same in plants from treated and untreated plots at the north-facing site, indicating that additions of nitrogen led to an increase in the numbers of seeds produced, but not to a shift in the ratio in favour of ripened seeds. The mean number of unripened seeds as a percentage of the corresponding number of ripened seeds produced by a plant south-facing site was 12.8 and 7.4% respectively for treated and untreated plots. Corresponding percentages for the north-facing slope were 55.7 and 58.8%

respectively. The rise in seed output in plants from treated plots was correlated with a fall in the number of plants that failed to set seeds and an increase in the degree of branching of plants.

TABLE 6. Density at harvest, branching habit, and fecundity in populations of *S. europaea* grown in unfertilised and fertilised plots on south- and north-facing slopes at La Pérouse Bay, Manitoba, in 1980

Treatment	Sample size	Density range per 5 × 5 cm	Ripened seeds per plant (\bar{X} and range)	Unripened seeds per plant (\bar{X} and range)	Plants with no seeds (%)	Plants with branches (%)
South-facing slope						
Controls	319	8–92	5.9 (1.2–10.8)	0.4 (0.2–1.9)	9.7	10.8
Nitrate-treated	258	7–54	10.5 (5.5–31.3)	1.3 (0.3–2.8)	7.4	47.9
North-facing slope						
Controls	249	10–42	0.7 (0–4.3)	1.5 (0–3.9)	29.1	13.3
Nitrate-treated	288	6–71	9.3 (4.3–14.9)	5.2 (1.4–9.6)	6.4	61.7

NOTE: The overall mean and the range of means for individual plots of the number of seeds per plant are given.

TABLE 7. Analysis of covariance of mean production of ripened and unripened seeds per plant per plot (5 × 5 cm) in relation to density of plants, location of plot, and addition of sodium nitrate where applicable

Source	df	Type I SS	Type IV SS	F value	PR F
(a) Seedlings transplanted in 1980 within a south-facing site, to another south-facing site, to a north-facing site, and to an open-tidal flat					
Dependent variable (ripened seeds)					
Slope	3	282.5	239.1	8.10	0.0002
Density	1	11.0	(11.0)	1.12	0.2950
Error	57	560.9			
Corrected total	61	854.4			
Dependent variable (unripened seeds)					
Slope	3	2.2	1.9	0.37	0.7763
Density	1	4.0	(4.0)	2.39	0.1273
Error	57	95.9			
Corrected total	61	102.1			
(b) Seedlings transplanted in 1979 to a south-facing slope and a north-facing slope, and seed output of the progeny measured in 1980					
Dependent variable (ripened seeds)					
Slope	1	18.0	15.9	5.48	0.0297
Density	1	7.1	(7.1)	2.46	0.1327
Error	20	58.2			
Corrected total	22	83.3			
Dependent variable (unripened seeds)					
Slope	1	2.0	2.0	7.93	0.0107
Density	1	0.1	(0.1)	0.44	0.5144
Error	20	5.0			
Corrected total	22	7.1			
(c) Seedlings transplanted to a south-facing site and a north-facing site in 1980 (half of the plots at each site received additions of sodium nitrate)					
Dependent variable (ripened seeds)					
Slope	1	101.3	123.8	5.4	0.0278
Nutrients	1	463.5	430.1	18.6	0.0001
Density	1	47.4	(47.4)	2.1	0.1614
Error	34	786.4			
Corrected total	37	1398.6			
Dependent variable (unripened seeds)					
Slope	1	71.3	65.1	20.8	0.0001
Nutrients	1	43.4	42.4	13.6	0.0008
Density	1	0.2	(0.2)	0.1	0.8085
Error	34	106.0			
Corrected total	37	220.9			

Discussion

Salicornia europaea is widespread at coastal and inland saline sites in the Northern Hemisphere (Hulten 1968). In Europe, populations occur as far north as the Lofoten Islands (69°N) on the northwest coast of Norway and at 66°N along the Gulf of Kandalaksha (Hulten 1971), whereas La Perouse Bay, Manitoba, is only at 54°N. However, all of these sites experience a mean July temperature of approximately 10°C (Hulten 1971; Fremlin 1974). The position of the 10°C isotherm for July may be used as a climatic indicator to predict the northern limit of this species in coastal regions. This isotherm has been used by Kijppen (1931) to define the boundary between sub-Arctic and Arctic climatic zones. Populations of the annual appear unable to persist north of this boundary, and as such, the species cannot be considered member of the Arctic flora.

Within the Churchill area plants are confined to one type of habitat, namely south-facing slopes in low-lying areas of restricted drainage beyond the limit of spring tides. The gently shelving Hudson Bay coastline is emerging at the rate of 1 m per century (Hunter 1970), and the saline sediments of the low-lying areas adjacent to the shore are saturated with water for most of the summer. A number of halophytes, including *Triglochin maritima*, *Plantago maritima*, and *Salicornia europaea*, grow within these areas. As a result of evapotranspiration, very large changes in salinity occurred during the summer at the experimental site, particularly on south-facing slopes (Fig. 3). Recently, Glooschenko (1980) has recorded a similar phenomenon in the upper levels of marshes in the vicinity of James Bay. The inversion of the salinity gradient, such that sites beyond the direct influence of the tides are more saline than intertidal areas, appears to be characteristic of this emergent coastline. The salinity of inshore waters around arctic coasts is often low in summer (Jefferies 1977).

Beyond the Churchill area *S. europaea* is scarce along much of the southern shore of Hudson Bay, except in the vicinity of James Bay. The population therefore appears to be isolated geographically, in spite of the fact that over 85% of the coastline of Ontario is salt marsh (Glooschenko and Martini 1978). *Salicornia europaea* consists of highly inbred populations, as the breeding system is strongly cleistogamous (Ball and Tutin 1959; Dalby 1962). Seeds are shed in the immediate vicinity of the parent plant in late August or early September, and an indumentum of mucilaginous hairs anchors seeds to the sediment (Petch and Swan 1968). Seeds could be seen clearly on the surface of the sediment adjacent to the parent plants in early September.

A number of factors have reduced fecundity in the population at La Perouse Bay. Most seeds germinated in late May or early June but some seeds germinated throughout the summer; seedlings appearing in August failed to develop beyond the cotyledon stage. The occurrence of this extended period of germination suggests that the germination requirements are only just being met in this environment. Although field observations by the authors indicate that in northwest Europe germination in *S. europaea* populations may occur over 2 months or more, particularly when winters are mild, no germination appears to occur after early summer. Year to year variation in weather patterns may have a catastrophic effect on germination and the subsequent size of the population. For example, the summer of 1978 was wet and cold; on July 10th plants of *S. europaea* were only at the cotyledon stage, and at harvest just prior to freeze-up mean fecundity was less than one ripened seed per plant (Table 3). In

addition to some plants failing to produce seeds, seeds did not ripen in a number of individuals (Table 3). A high ratio of unripened to ripened seeds in plants reflected a response to adverse environmental conditions (e.g., short growing season, lack of nitrogen, and low temperature). Ball and Brown (1970) also have reported the presence of unripened seeds in plants of *S. europaea* in Wales in late autumn. In this geographically nonperipheral population, unripened seeds were produced on side branches which developed late in the season. Flowers in *S. europaea* are borne in cymes consisting of one to three flowers. Often the small unripened greenish-yellow seeds are produced by the two lateral flowers, whereas the median flower frequently produces a brown ripened seed. However, under suitable growing conditions the lateral flowers are also capable of producing a brown ripened seed. Hence, the ratio of ripened to unripened seed is not fixed, as is indicated, for example, by the different values of the ratio for plants on south- and north-facing slopes.

Although populations of *S. europaea* in England (Jefferies et al. 1981; A. J. Davy, H. Smith, and R. L. Jefferies, unpublished data) and Denmark (A. Jensen and R. L. Jefferies, unpublished data) consist of non-overlapping generations, a geographically nonperipheral population at an inland site in Ohio (Ungar et al. 1979) possesses a seed bank. Preliminary studies indicate that a seed bank is also present in sediments at La Perouse Bay, although it is not known whether the seeds are viable. In an environment where there is considerable unpredictability, provided seeds retain their viability, the presence of a seed bank offers a selective advantage when a shortfall in seed output occurs.

Mortality of seedlings and adult plants was very low in this marginal population. In a number of plots on both north- and south-facing sites all plants survived. In contrast, high mortality has been reported in geographically nonperipheral populations, particularly at the seedling stage. Loss of individuals as a result of drying out of sediments was an important cause of mortality in a population in Ohio (Ungar et al. 1979). Mechanical damage from wave action led to reduction in the size of populations at coastal sites in northwest Europe (Wiehe 1935; Ball and Brown 1970; A. J. Davy, H. Smith, and R. L. Jefferies, unpublished data; A. Jensen and R. L. Jefferies unpublished).

The absence of germination, or else late germination coupled with poor growing conditions, may account for the inability of *S. europaea* to establish on open-tidal flats and north-facing slopes. Both of the latter sites were exposed to cold onshore winds blowing off the ice in Hudson Bay. On some days the ground of the north-facing slope was frozen, unlike the ground of the south-facing slope. On the open-tidal flats exposure to wind and the presence of ice and meltwater produced very unfavorable conditions early in the season. On the few occasions the temperature of the open-tidal sediments was measured in May and early June was 4 to 6°C lower than that of the south-facing slope. Low temperatures may also have retarded mineralization of organic nitrogen, since both ammonification and nitrification are temperature-dependent processes. Significant increases in seed output occurred when nitrogen was applied to plots on north-facing slopes. Mean production of ripened seeds per plant was 9.26 and 10.45 respectively on nitrogen-treated north- and south-facing slopes (Table 6), values not significantly different from one another.

We know of only one similar experimental study to that described above. The distribution of the stemless thistle (*Cirsium acaulon* (L.) Scop.) at the northern edge of its range appears to be strongly

influenced by climatic conditions (Pigott 1968). At the limit of its range the species is found predominantly on south to southwest facing slopes of hills in the Derbyshire and Yorkshire Wolds in England. Studies involving cultivation and transplanting showed that the plant is dependent on high summer temperatures for the production of ripe fruit. Further north and west and on north-facing slopes a combination of lower maximum temperatures and higher rainfall prevents the maturation of the fruits. High rainfall encourages infection of the capitulum by *Botrytis cinerea* Pers. which causes the seeds to rot. The most northerly populations of this perennial plant rely almost exclusively upon clonal growth and only rarely regenerate by seed, unlike *S. europaea*.

The above investigation of the effects of microclimate involved a study of the responses of individuals which were transplanted from a south-facing to a north-facing slope of a valley, a distance of several hundred metres. The movement of individuals of *S. europaea* just a few metres across open flat terrain was sufficient to result in poor germination and a fall in seed output of the experimental plants. The near absence of this annual from north-facing sites indicates that populations of the annual are unable to establish in such sites. These microhabitats represent a microcosm of conditions further north. In these more northerly sites a combination of low soil temperatures, particularly earlier in the season, a decrease in the number of days when the air temperature is above 0°C and a lack of available nutrients, such as nitrogen, probably act to restrict the successful establishment of populations of this annual.

Acknowledgements

We thank S. Cargill and P. Cargill for their excellent field assistance and Dr. T. J. Carleton for advice and help on the statistical treatment of the data. Dr. F. Cooke and students at Queen's University Tundra Biology Station and Mr. W. Erikson of the Churchill Northern Studies Centre generously provided logistic support. Mr. R. MacLeod of Environment Canada kindly allowed us access to climatic data at the Churchill Weather Office. We also wish to thank the reviewers for their useful comments. The authors gratefully acknowledge grants from the Natural Sciences and Engineering Research Council of Canada and the Danish Natural Science Research Council.

REFERENCES

- ANTONOVICJS. , 1976. The limits to natural selection. *Ann. Mo. Bot. Gard.* 63: 224-247. BALL,P . W., and K. G. BROWN1. 970. A biosystematic and ecological study of *Snlicornia* in the Dee estuary. *Watsonia*, 8: 27-40.
- BALLP, . W., and T. G. TUTIN1. 959. Notes on annual species of *Salicornia*. *Watsonia*, 4: 193-205.
- BLAIR, W. H. 1979. S.A.S. user's guide. S.A.S. Institute, Raleigh, NC.
- CARGILLS,. M. 1981. The effects of grazing by lesser snow geese on the vegetation of an arctic salt marsh. M.Sc. thesis, University of Toronto, Toronto.
- DALBYD, . H. 1962. Chromosome number, morphology and breeding behaviour in British *Snlicorniae*. *Watsonia*, 5: 150-161.
- FREMLING, . 1974. The national atlas of Canada. 4th ed. Macmillan, Toronto.
- GLOOSCHENKWO., 1980. Coastal salt marshes in Canada. In *Proceedings of the Workshop on Canadian Wetlands*. Edited by C. D. A. Rubec and F. C. Pollet. *Environ. Can. Land Directorate, Ecological Land Class. Ser. No. 12.* pp. 39-47.
- GLOOSCHENKWO., A,, andl. P. MARTINI1.9 78. Hudson Bay lowlands baseline study-coastal zone 1978. *Proceedings of the Symposium on Technical, Environmental Socioeconomic and Regulatory Aspects of Coastal Zone Management*. American Society of Chemical Engineers, San Francisco, CA. pp. 663-679.
- GRANT,M . C., and J. ANTONOVICS1.9 78. Biology of ecologically marginal populations of *Anthoxantlzum odoratum* l. Phenetics and dynamics. *Evolution (Lawrence, Kans.)*, 32: 822-838.
- HARE, F. K., and J. C. RITCHIE. 1972. The boreal bioclimates. *Geogr. Rev.* 62: 333-365.
- HULTEN,E. 1968. *Flora of Alaska and neighbouring territories*. Stanford University Press, Stanford.
- 1971. *Atlas of the distribution of vascular plants in northwestern Europe*. Generalstabens Litografiika Anstalt Fiirlag, Stockholm.
- HUNTER, G. T. 1970. Postglacial uplift at Fort Albany, James Bay. *Can. J. Earth Sci.* 7: 547-548.
- JEFFERIES R. L., 1977. The vegetation of salt marshes at some coastal sites in arctic North America. *J. Ecol.* 65: 661-672.
- JEFFERIES, R. L., A. J. DAVY,a nd T. RUDMIK.1 981. Population biology of the salt-marsh annual *Snlicorrlin europaea* agg. *J. Ecol.* 69: 1-15.
- JEFFERIES, R. L., A. JENSENa, nd K. F. ABRAHAM1.9 79. Vegetational development and the effect of geese on vegetation at La Pirouse Bay, Manitoba. *Can. J. Bot.* 57: 1439-1450.

- JEFFERIES, R. L., and N. PERKINS. 1977. The effects on the vegetation of the additions of inorganic nutrients to saltmarsh soils at Stiffkey, Norfolk. *J. Ecol.* 65: 867-882.
- KOPPEN, W. 1931. *Grundriss der Klimakunde*. Walter de Gruyter, Berlin.
- LEWONTIN, R. C. 1974. *The genetic basis of evolutionary change*. Columbia University Press, New York.
- MATHER, K. 1953. The genetical structure of populations. *Symp. Soc. Exp. Biol.* 7: 66-95.
- MAYRE, . 1963. *Animal species and evolution*. Belknap Press, Cambridge, MA.
- PETCH, C. P., and E. L. SWANN. 1968. *Flora of Norfolk*. Jarrold, Norwich.
- PIGOTT, C. D. 1968. Biological flora of the British Isles: *Cirsium acnulon* (L.) Scop. *J. Ecol.* 56: 597-612.
- RITCHIE, J. C. 1956. The native plants of Churchill, Manitoba. *Can. J. Bot.* 34: 269-320.
- SAVILE, D. B. O. 1972. Arctic adaptations in plants. *Can. Dep. Agric. Monogr. No. 6*.
- SCOGGAN, H. J. 1957. The native flora of Churchill, Manitoba with notes on the history, geology and climate of the area. National Museum of Canada, Ottawa.
- UNGAR, I. A., D. K. BENNER and D. C. MCGRAW. 1979. The distribution and growth of *Salicornia europaea* on an inland salt pan. *Ecology*, 60: 329-336.
- WIEHE, P. O. 1935. A quantitative study of the influence of tide upon populations of *Salicornia*. *J. Ecol.* 23: 323-333.