Vegetation–environment relationships of an inland boreal salt pan

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Vegetation composition and community structure of boreal inland salt pans near the shore of Dawson Bay, Lake Winnipegosis, Manitoba, were examined. Eight vegetation associations and eight species groups were described from the site. Most of the vegetation associations were dominated by a single graminoid or graminoid-like species. Species composition in the most saline areas was similar to that of prairie salt pans to the south, whereas the vegetation of less saline areas showed affinities to both prairie and boreal forest. Examination of vegetation–environment relationships indicated that soil salinity was the moost important factor determining vegetation pattern. Other soil factors such as nutient levels, bulk density, and percent organic matter were of secondary importance. Species richness increased with decreasing salinity, but trends in Shannon–Weaver diversity and evenness along the salinity gradient were more complex. Despite the salinity gradient being environmentally continuous, strong vegetational discontinuities were noted. It is suggested that these discontinuities arose through interspecific competitive interaction and displacement mediated by differences in the salt tolerance of species.

Key words: competition, discontinuity, gradient, halophyte, plant community, salinity.

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Les auteurs ont examiné la composition de la végétation et la structure de la communauté dans une cuvette salée boréale située près de la côte de Dawson Bay, au lac Winnipegosis, au Manitoba. Ils décrivent pour ce site huit associations végétales et huit regroupements de plantes. La plupart des associations végétales sont dominées par une seule espèce de graminées, ou graminoïde. La composition des espèces dans les parties les plus salées est semblable à celle des prairies de cuvettes salées du sud, alors que la végétation des parties moins salées montre des affinités à la fois avec la prairie et la forêt boréale. L'examen des relations entre la végétation et l'environnement indique que la salinité du sol est le facteur le plus important déterminant le patron de végétation. Les autres facteurs du sol tels que la teneur en nutriments, la densité en volume et le pourcentage de matière organique ne sont que d'importance secondaire. La richesse en espèce augmente avec la diminution de la salinité, mais les tendances de la diversité selon Shannon–Weaver et l'égalisation le long du gradient de salinité sont plus complexes. Bien que le gradient de salinité soit continu dans ce milieu, on observe de fortes discontinuités dans la végétation. Les auteurs suggèrent que les discontinuités proviennent de l'interaction compétitive interspécifique et de déplacements provenant de tolérances différentes chez les différentes espèces.

Mots clés : compétition, discontinuité, gradient, halophyte, communauté végétale, salinité.

[Traduit par la rédaction]

Introduction

Although the coastal salt marshes of North America have been intensively studied (Haines and Dunn 1985; Odum 1988), inland saline systems have received less attention. In saline environments, plants must adapt osmotically to high ion concentrations in the soil (Jefferies 1981; Yeo 1983). However, a major difference in environmental conditions between coastal and inland systems arises from the absence of tidal effects in the latter. Whereas species of coastal marshes must adapt to predictable tidal rhythms that impose strong environmental gradients (Haines and Dunn 1985), those of inland habitats are subject to highly variable soil-salinity concentrations and periods of desiccation (Ungar 1974*a*). This is particularly true in continental regions where annual precipitation is low, limited to particular seasons, and shows considerable variation from year to year (Borchert 1971). Inland halophytes are also subject to occasional submergence following spring runoff or heavy rains. The environment of an inland saline habitat is therefore somewhat less predictable than that of most coastal salt marshes, both seasonally and from year to year.

North American inland saline habitats are most commonly encountered in areas where potential evapotranspiration exceeds precipitation (McKell *et al.* 1986). In the United States, saline plant communities have been described from both prairie and desert regions (Ungar 1974*a*; Brotherson and Rushforth 1987 and references therein). In Canada, saline soils occur in the drier, southerly regions of the Prairie provinces (McKell *et al.* 1986). The only published surveys of associated plant communities are from southern Alberta (Keith 1958) and Saskatchewan (Dodd and Coupland 1966). Most of the North American studies are descriptive, with plant communities being delineated either by visual inspection or using a preexisting classification system. All have suggested that species are distributed along a salinity gradient reflecting their degree of salt tolerance, but few have included detailed quantitative soil analyses. Furthermore, multivariate statistical methods have rarely been used to objectively delineate vegetation types, describe trends, and examine vegetation–environment relationships.

Most inland saline habitats in Canada are internal drainage basins where evaporation forms surficial salt deposits. Seepage of saline groundwater into such depressions may also occur. Dryland farming practices may also increase soil salinity (McKell *et al.* 1986). The resulting salt pans or playas are common throughout the dry prairie regions. Salts are generally sodium and magnesium sulphates, though specific ionic composition varies widely Henry *et al.* 1987). Surficial salts may also occur naturally in areas where saline groundwater percolates to the surface. A number of studies have described the vegetation of artesian saltwater discharge sites in the United States (e.g., Chapman *et al.* 1985; Brotherson and Rushforth

1987). Saline springs also occur in Canada, but the vegetation of such sites has not been investigated in detail. Spring-fed saline flats are particularly well developed near the western shore of Lake Winnipegosis in west central Manitoba and along the Slave and Athabasca rivers in northeastern Alberta (Pearson 1963).

We investigated the vegetation of spring-fed, chloride-dominated boreal salt pans near Dawson Bay, Lake Winnipegosis, Manitoba. Our objectives were (*i*) to determine the nature of vegetation variation and zonation, and (*ii*) to examine the relationship between the vegetation and environmental factors. To address these objectives, we undertook an intensive sampling program involving the collection of both vegetation and environmental information and used multivariate statistical procedures to examine vegetation–environment relationships.

Study area

The Manitoba lowland, which includes lakes Winnipegosis and Manitoba (Fig. 1), is the drainage basin for Manitoba's western uplands and a major discharge area for formation waters from the western Canadian sedimentary basin. Saline groundwater seeps and springs from the Winnipegosis and Dawson Bay formations occur sporadically along the western shore of Lake Winnipegosis. Salts are probably derived from the mid-Devonian Prairie Evaporite formation that covers an extensive area beneath Alberta and Saskatchewan (Pearson 1963), although some may be derived from Silurian and Ordovician formations underlying the Winnipegosis formation (van Everdingen 1971). Many of the saline springs are associated with reefs, the folding and faulting of rock associated with these reefs having created favourable conditions for groundwater discharge. Chemical analyses of water from 24 saline springs in the Winnipegosis region indicated that sodium and chloride are the dominant ions (van Everdingen 1971). These are also the dominant ions of soils from the associated salt pans. By contrast, the saline soils of semiarid and subhumid regions of the Canadian prairie provinces and adjacent United States are generally sulphate dominated (McKell *et al.* 1986).

Many accessible saline flats in the Winnipegosis region show signs of disturbance, mainly from animal grazing and the haying of saline meadows. We chose for study a series of readily accessible, undisturbed saline flats located approximately 15 km south of Overflowing River, Manitoba (Fig. 2). The site is located between provincial Highway 10 and the shore of Dawson Bay, Lake Winnipegosis, at approximately 53°05′N and 101°07′W. Soil at the site is a heavy silt, with occasional intervening gravelly ridges. A clear zonation of vegetation is evident on the salt flats. The most saline areas are covered with extensive mats of blue-green algae but are otherwise unvegetated. Halophytic vascular plants occur in the somewhat less saline areas adjacent to the unvegetated flats, whereas wet-meadow, prairie, and boreal species are found in the least saline areas. White spruce forests occur on the gravelly ridges.

The study area lies within the boreal forest of the Manitoba lowlands (Rowe 1972) and the subhumid midboreal (MBs) ecoclimatic region (Ecoregions Working Group 1989). It is characterized by flat relief and poor drainage, with black spruce and larch developing on mesisolic soils. Upland areas consisting of calcareous glacial till or alluvial deposits are dominated by white spruce and trembling aspen. Extensive freshwater marshlands dominated by *Phragmites communis* occur along the western shore of Dawson Bay. Climate is subhumid continental, with mean annual precipitation at The Pas, Manitoba (about 100 km north of the study area), of 50 cm, of which 33 cm falls as rain. Mean annual air temperature is −0.3°C, with monthly means ranging from −22.7 (January) to 18.0°C (July). The Pas receives an average of 2167.5 h of bright sunshine per year (Campbell–Stokes recorder), 59% of which is received between May and September. These data are means for the years 1951–1980 (Environment Canada 1982).

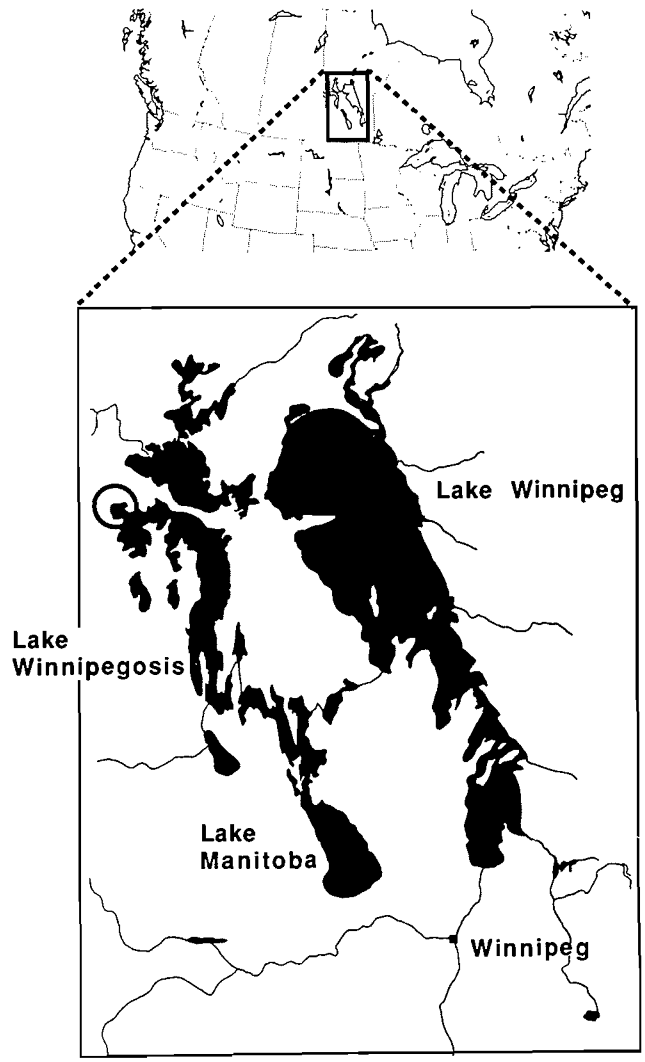

FIG. 1. Map of the Manitoba lowlands of central North America. The study area is located near the northwestern shore of Dawson Bay, Lake Winnipegosis (circled).

Materials and methods

Field sampling

Three sites within the study area were surveyed. The first was a salt flat, adjacent to the lake and approximately 800 m long by 400 m wide. The second was a smaller salt flat (approx. 200 m long by 100 m wide) separated from the first site by a gravelly ridge. The third was a saline meadow, 220 m long by 50 m wide, located north of the two salt flats. The second and third sites were not adjacent to the lake. An inventory of all plant species occurring in and around the sites was undertaken in June 1987 and August 1988. A total of 79 species were identified, voucher specimens of which have been deposited in the University of Manitoba herbarium (WIN). Species nomenclature follows Looman and Best (1987).

Five base lines for the sampling transects (three at the first site, and one each at the other two) were located parallel to vegetation fronts at each site. Each baseline was divided into 10-m segments, and a transect starting position randomly located within each segment. All transects were perpendicular to their base line and extended into the vegetation to the nearest height of land (usually a gravel ridge). There were 54 transects ranging in length from 20 to 110 m. Vege-

FIG. 2. Oblique aerial view from the northwest of one of the salt flats studied. Dawson Bay, Lake Winnipegosis, is in the background.

tation was sampled along all transects in August 1987 using 0.5 × 0.5 m quadrats located at 2-m intervals. Quadrat size and shape were based on considerations of vegetation physiognomy and the objectives of the study (Kenkel *et al.* 1989). In each quadrat, percent cover of each species was estimated in 5% increments. A total of 1176 quadrats were enumerated.

In June 1987 elevations above sea level were measured at 2-m intervals along each transect using a surveyor's level and metric rod. Because the study area sloped gently toward the lake, elevations were expressed relative to the height above the nearest unvegetated mudflat. They are referred to as relative elevations.

Soil collection and analysis

A soil core, 10 cm deep and 6 cm in diameter, was taken in every second quadrat (usually one, but occasionally two, for a total of 693) between August 10 and 21, 1987. Each was air dried in the field and later transported to the laboratory and stored at 4°C. In the fall of 1987, the soils were ground and sieved to remove gravel. Bulk soil density was determined for 480 of the cores.

Soil pH and conductivity ($\mathrm{ms \cdot cm^{-1}}$) were measured immediately after mixing 10 g of soil and 50 g of distilled water in a 125-mL Ehrlenmeyer flask and mechanically shaking for 1 h. Conductivity values were converted to millgrams salt per millilitre of solution using the 0.64 conversion factor for chloride salts (Bower and Wilcox 1965). Organic matter was determined by ashing 10 g of soil at 430°C for 18 h, and expressed as a percentage of initial dry mass.

Nutrient contents for 149 of the soil cores were also determined. Sodium bicarbonate extractable nitrate-nitrogen, available phosphorus (sodium bicarbonate extractable), and available potassium (ammonium acetate exchangeable) were determined at the Manitoba Soil Testing Laboratory. In addition, carbonate content was assessed by placing a drop (<1.0 mL) of 0.05% HCl solution on 5 g of soil. Reaction was recorded on a four-point ordinal scale from low to very high.

Total salts and nutrient values were originally measured on a per unit mass basis. However, since bulk soil density varied within the study area, values were converted to per unit volume measures to better reflect soil conditions in the rooting zone (Mehlich 1973; Gosselink *et al.* 1984).

Data analysis

The data were entered as a matrix of 1176 quadrats by 37 species and eight environmental variables (species with a frequency of less than 0.1% were removed). All analyses were performed using the SAS statistical system (SAS Institute Inc. 1985) and programs written by the authors.

Cluster analysis was used to classify the 1176 quadrats into vegetation associations and the 37 species into species groups. In both cases a chord-distance matrix was used as the input dissimilarity matrix in sum of squares agglomerative cluster analysis (Orlóci 1967), and the results presented as dendrograms.

For each vegetation association, means and variances were calculated for the following soil variables: pH, percentage organic matter, available potassium, total nitrate-nitrogen, available phosphate, bulk density, and total salts. Mean elevation above the unvegetated salt pan (in metres), total number of annuals and perennials, and mean number of species per quadrat were also computed for each association. It should be noted, however, that per quadrat measures of species diversity are only meaningful at the spatial scale of the chosen quadrat size (Kenkel *et al.* 1989). This can lead to erroneous interpretations when comparisons are made between communities (Juhász-Nagy and Podani 1983). One alternative is to use jacknife or bootstrap techniques to obtain estimates of community species richness, but these have recently been shown to give biased results (Palmer 1990). We used the following approach. A computer program was written to take a random sample of size $n = 25$ from the population of quadrats from a given vegetation association. From this sample, three vegetation parameters were computed: Shannon–Weaver diversity and evenness (Pielou 1977), and species richness. The procedure was repeated 1000 times, and the mean and variance computed for each parameter. This was done for each vegetation association.

Concentration analysis (Feoli and Orlóci 1979) was used to examine relationships within and between vegetation associations and species groups. The method begins by ordering (or blocking) the data matrix by species group and vegetation association. The number of occurrences of species within a given group in each of the vegetation associations is then computed. The resulting $r \times c$ contingency table (where r = no. of species groups, and c = no. of vegetation associations) is subjected to correspondence analysis (Hill 1974) after adjusting for differences in block size. The result is a simultaneous ordination of vegetation associations and species groups through a partitioning of the total contingency χ^2.

Vegetation–environment relationships were examined using a two-step procedure. First, a vegetation ordination of the 136 quadrats for which all seven soil variables were measured was obtained using nonmetric multidimensional scaling (NMDS), specifying a two-dimensional solution. Since the data structure was highly nonlinear, the input distance measure was Euclidean chord distance modified using flexible shortest path adjustment (Kenkel and Orlóci 1986; Bradfield and Kenkel 1987). This reduced the dimensionality of the species space to a mangeable level. Next, the extent to which trends in the reduced vegetation (ordination) space reflect environmental variability was examined. Canonical correlation analysis (Gittins 1985) was used, with the two-dimensional NMDS configuration representing one variable set and the eight environmental variables (seven soil variables plus relative elevation) the other. The two canonical eigenvectors were then superimposed on the ordination configuration, and structure correlations calculated to determine which environmental variables best accounted for variability in vegetation composition (Kenkel and Burchill 1990). Analysis of variance (ANOVA) was used to determine if there were significant differences in soil salinity among plant associations, and the salinity variation within each association was presented using box plots (Emerson and Strenio 1983).

Results

Vegetation associations

Cluster analysis (Fig. 3) delineates eight associations, seven of which are named for the dominant (highest mean percent cover) species in the group; the eighth association (Salt Pan) includes quadrats occurring at the periphery of the unvegetated salt flats. Soil and other environmental factors are summarized in Table 1, and vegetation characteristics in Table 2. In both tables the associations are ordered from highest (Salt Pan) to lowest (Rosa) salinity.

The Hordeum association, containing approximately 30% of the quadrats, is the most common vegetation association. Its large size, together with its distinctive flora, resulted in it being the last to fuse with other groups in the dendrogram. This association is found at intermediate relative elevations and at intermediate soil salinities. The Salt Pan association, which forms a second outlying group, is characterized by very low plant cover and the presence of salt-tolerant annuals. Quadrats in this association have the highest salinity and occur at the lowest relative elevations. The Puccinellia, Triglochin, and Spartina associations form a third major group in the dendrogram. These associations are found at low relative elevations (though higher than the salt pan), and have intermediate to high soil salinities. A fourth group consists of the Agropyron, Calamagrostis, and Rosa associations. These occur at the highest relative elevations and have the lowest soil salinities.

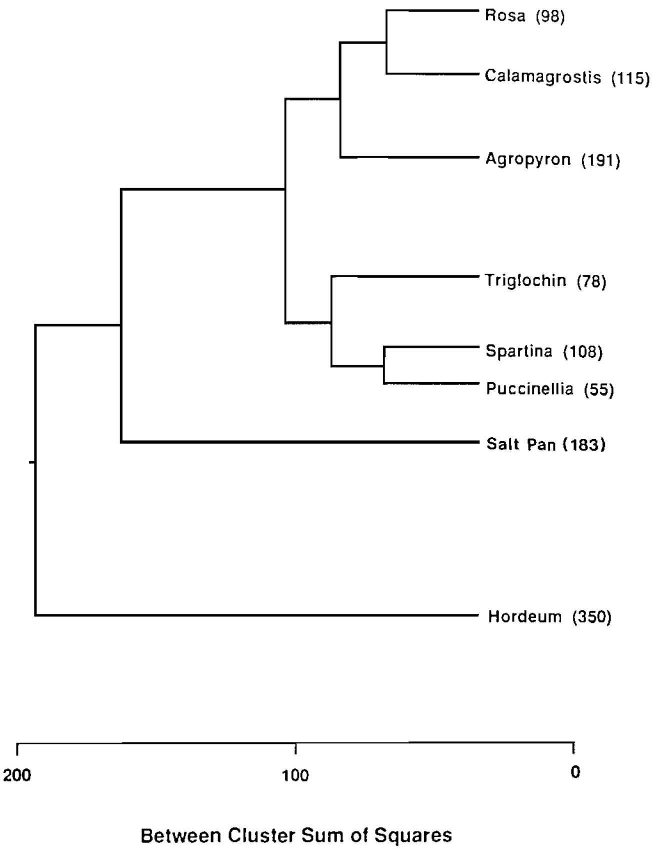

FIG. 3. Sum of squares agglomerative cluster analysis of the 1176 quadrats, showing the eight vegetation associations. Lower level bifurcations are not shown. Values in parentheses are the number of quadrats in each association.

An interesting feature of the salt flats is the zonation of vegetation along a gradient from the unvegetated salt pan to the gravel ridges, which corresponds to an increase in relative elevation and a concomitant decrease in soil salinity. Along this gradient, sharp vegetation discontinuities or edges occur at which species composition changes dramatically over short distances. However, analysis of trends in soil variables and relative elevation indicate that these vegetation ecotones are not the result of discontinuities in environmental factors. One consequence of vegetation discontinuities is that associations show little overlap in species composition (Fig. 4). No single species dominates the Salt Pan association. *Triglochin maritima* and *Puccinellia nuttalliana* have the highest mean cover but occur infrequently. Species of highest frequency are the small, salt-tolerant annuals *Salicornia rubra* and *Spergularia marina*. Other small species such as *Glaux maritima* and *Suaeda depressa* also occur. Five of the remaining associations (Puccinellia, Triglochin, Spartina, Agropyron, and Calamagrostis) are dominated by a single graminoid (or graminoid-like) species; cooccurring species have much lower cover. The grasses *Hordeum jubatum* and *Distichlis stricta* are codominant in the Hordeum association, and again other species have low cover. No one species dominates the Rosa association,

TABLE 1. Soil and environmental factors (mean ± 1 SD) for the eight vegetation associations

	Salt Pan	Puccinellia	Triglochin	Hordeum	Spartina	Agropyron	Calamagrostis	Rosa
Total salts ($mg{\cdot}mL^{-1}$)	20.1±6.0 (54)	16.4±4.9 (46)	14.8±6.1 (33)	10.2±3.6 (150)	7.9±3.7 (40)	7.1±3.2 (92)	4.7±2.3 (39)	3.9±3.1 (26)
Relative elevation (m)	0.05±0.04 (183)	0.15±0.05 (55)	0.14±0.07 (78)	0.19±0.15 (350)	0.18±0.11 (108)	0.32±0.21 (191)	0.27±0.15 (115)	0.45±0.23 (98)
pH	8.8±0.2 (92)	8.3±0.2 (48)	8.1±0.5 (47)	7.8±0.4 (213)	8.1±0.4 (52)	7.9±0.39 (118)	7.9±0.3 (57)	7.5±0.3 (59)
Potassium (ppm)	255±108 (19)	332±94 (24)	357±249 (47)	470±158 (41)	272±88 (9)	319±158 (21)	453±185 (17)	504±167 (14)
Nitrogen (ppm)	1.7±1.4 (19)	7.10±4.8 (24)	0.6±0.3 (47)	5.0±5.3 (41)	3.6±2.3 (9)	6.5±5.08 (21)	3.9±3.0 (17)	9.7±14.5 (14)
Phosphorus (ppm)	11.8±13.7 (19)	19.0±8.8 (24)	17.2±13.3 (47)	37.8±14.4 (41)	27.2±11.0 (9)	33.5±14.7 (21)	47.5±14.0 (17)	53.4±13.0 (14)
Bulk density ($g{\cdot}mL^{-1}$)	1.36±0.24 (54)	0.83±0.26 (46)	0.69±0.30 (33)	0.49±0.19 (150)	0.70±0.33 (40)	0.59±0.28 (92)	0.47±0.29 (39)	0.39±0.19 (26)
Organic matter (%)	5.9±2.8 (93)	11.3±4.7 (50)	17.0±16.1 (47)	22.4±15.9 (212)	14.3±11.0 (53)	20.7±11.7 (121)	19.8±9.9 (57)	27.9±12.4 (60)
Carbonates	Very high	High	High	Medium	Medium	Low	Low	Low
Observed drainage	Poor	Poor	Poor	Poor	Moderate	Good	Moderate	Very good

NOTE: Sample size is given in parentheses.

TABLE 2. Vegetation characteristics (mean ± 1 SD) for the eight vegetation associations

	Salt Pan	Puccinellia	Triglochin	Hordeum	Spartina	Agropyron	Calamagrostis	Rosa
Number of quadrats	183	55	78	350	108	191	115	98
Mean species number*	2.3±1.1	3.3±0.8	4.0±1.3	3.7±1.0	4.8±1.2	5.4±1.6	4.8±2.0	8.3±2.4
Shannon–Weaver†	1.88±0.22	1.02±1.05	1.56±0.09	1.37±0.10	1.74±0.08	2.21±0.11	1.89±0.11	2.62±0.05
Evenness†	0.84±0.06	0.49±0.02	0.59±0.03	0.56±0.04	0.67±0.04	0.71±0.03	0.63±0.03	0.82±0.02
Species richness†	9.48±1.73	7.93±0.26	13.84±0.88	11.83±1.63	13.98±3.30	23.39±2.37	20.20±1.61	24.59±1.42
Mean total cover*	15.9±20.9	120.1±13.9	112.2±22.0	116.5±14.2	134.3±22.0	137.2±24.5	142.7±31.2	158.2±37.9
Annuals	5	4	6	5	4	5	2	1
Perennials	9	4	9	15	19	29	22	27

*Per quadrat.
†Mean of 1000 random samples of 25 quadrats (see text).

and it is the only one in which shrubs (*Rosa acicularis* and *Symphoricarpos alba*) commonly occur. Other species with high cover include *Sonchus arvensis, Helianthus maximilianii*, and *Solidago canadensis*.

The mean number of species per quadrat, and mean total cover, increase with decreasing soil salinity (Table 2). There is also an increase in the proportion of annuals at higher salinities. Species richness increases with decreasing soil salinity, with the trend appearing to be linear ($r^2 = 0.713$, $P < 0.001$, Fig. 5): a random sample of 25 quadrats from the least saline associations (Calamagrostis, Agropyron, and Rosa) yields on average from 20 to 25 species, whereas a sample of the same size from the most saline associations (Salt Pan and Puccinellia) yields only 8 or 9. Shannon–Weaver diversity and evenness values generally increase with decreasing salinity. The exception is the Salt Pan association, which has the greatest evenness and relatively high Shannon–Weaver diversity.

Species groups

Cluster analysis of the 37 species delineates eight groups (Fig. 6). The first dendrogram subdivision separates species of saline habitats (Salt Pan, Hordeum, Spartina, and Triglochin species groups) from those characteristic of nonsaline or slightly saline soils. The Salt Pan group contains the grass *P. nuttalliana* and three annuals that are known to be highly salt tolerant. The Triglochin group includes two small salt-tolerant species (*G. maritima* and *Atriplex patula*) and the short-lived perennial *Plantago maritima*. These species are also characteristic of saline habitats. The Hordeum species group includes *H. jubatum* and *D. stricta*, which occur at intermediate salinities. The former is a short-lived, densely tufted species, whereas the latter has extensive creeping rhizomes. Associated with these grasses is the composite *Grindelia squarrosa*. The final species group in the first subdivision of the dendrogram consists of two species, the grass *Spartina gracilis* and the composite *Aster pauciflorus*. Both are characteristic of moderately saline soils in the Prairie provinces.

The other half of the first subdivision of the dendrogram contains 23 species in four groups. *Agropyron trachycaulum* occurs in a group with the composites *Aster pansus* and *Ambrosia psilostachya*. All three tolerate low salinities. *Calamagrostis inexpansa* occurs in a large group of nine species that includes another grass (*Hierochloe odorata*) and five composites; most are salt intolerant. The final two groups (Rosa and Symphoricarpos) include species characteristic of the nonsaline sites adjacent to the gravel ridges.

Relationship between vegetation associations and species groups

The two-dimensional scattergram representation of the concentration analysis results (Fig. 7) displays the characteristic horseshoe shape of correspondence analysis, which strongly suggests that a single environmental gradient underlies vegetational variation (Kenkel and Orlóci 1986; Wartenberg *et al.*

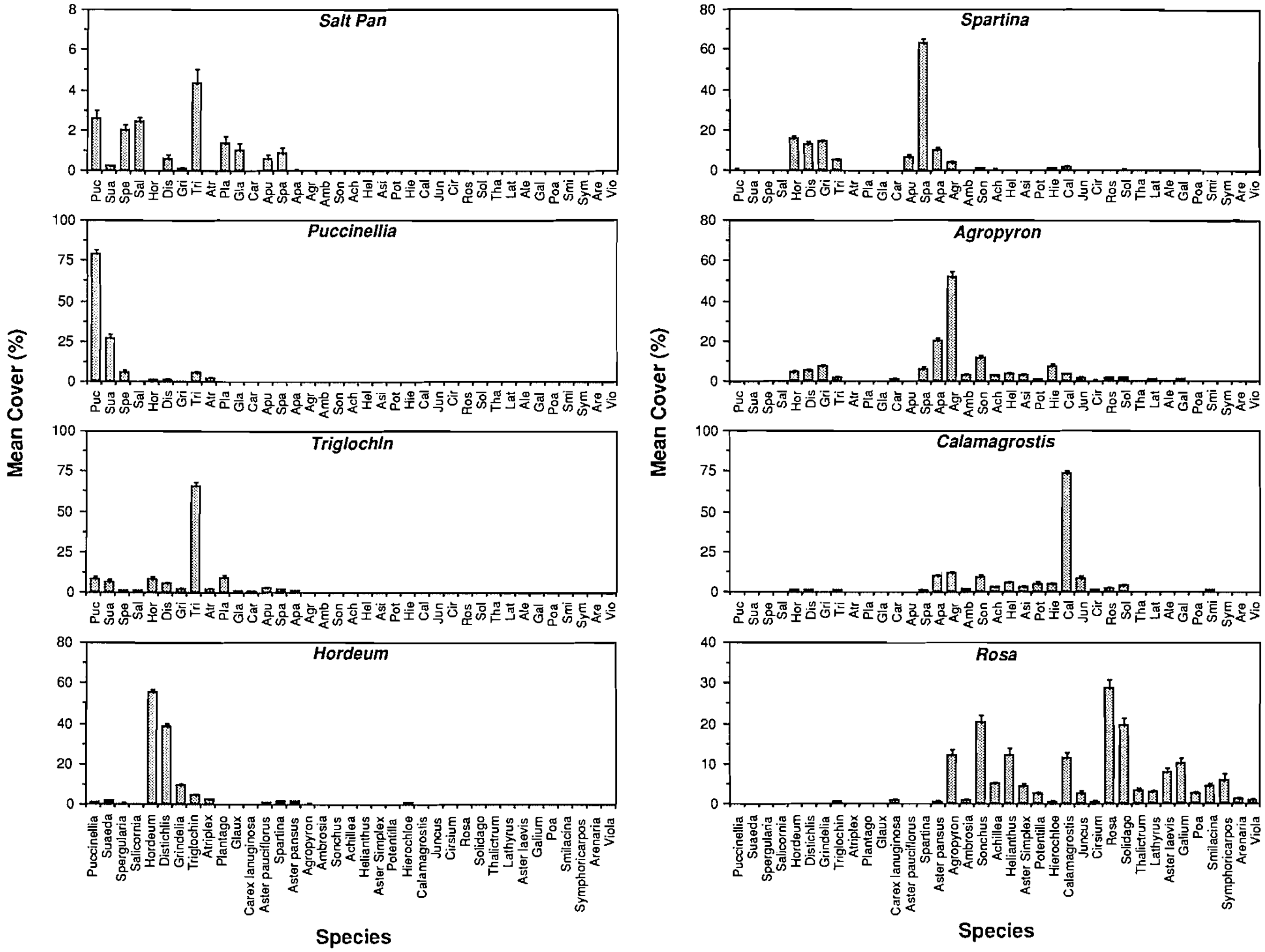

FIG. 4. Mean percent cover (± 1 SE) of species in each of the eight vegetation associations.

1987). The first axis appears to represent a salinity gradient, with salinity increasing from left to right. In general there is a close one-to-one correspondence between the vegetation associations and species groups, indicating the discontinuous nature of vegetation variation.

Vegetation-environment relationships

In the two-dimensional NMDS ordination of 136 quadrats (Fig. 8), the vegetation associations to which quadrats were assigned (see Fig. 3) are presented to aid interpretation. The two canonical correlation analysis axes are also displayed. Note that these axes, although linearly uncorrelated, are not orthogonal (Gittins 1985; Kenkel and Burchill 1990). Both canonical correlations are significant: axis I, $R^2 = 0.674$, $P < 0.001$; axis II, $R^2 = 0.275$, $P < 0.001$. However, the redundancy values for canonical axes I and II (which indicate the proportion of vegetational variation accounted for by the environmental variables) were 56.5 and 4.4%, respectively, indicating that the majority of trended vegetation–environment variation occurs along the first axis. Structure correlations for the eight environmental factors are presented in Table 3. The variable "total salts" shows the highest structure correlation with the first axis, indicating a strong trend of decreasing salinity from left to right. Soil pH shows a similar trend, reflecting the higher carbonate levels of more saline soils. Salinity and relative elevation are inversely correlated. Soil nutrients, organic content, and bulk density all show low correlations with the first and second axes. Structure correlations on the second axis are gen-

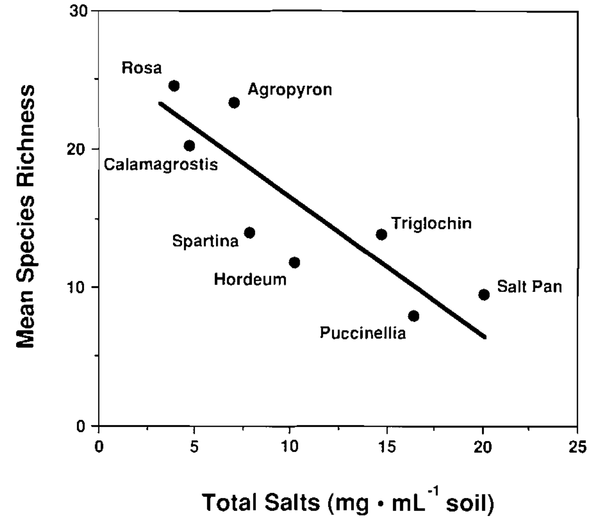

FIG. 5. The relationship between mean species richness and mean soil salinity for the eight vegetation associations. The fitted line was obtained using principal components analysis.

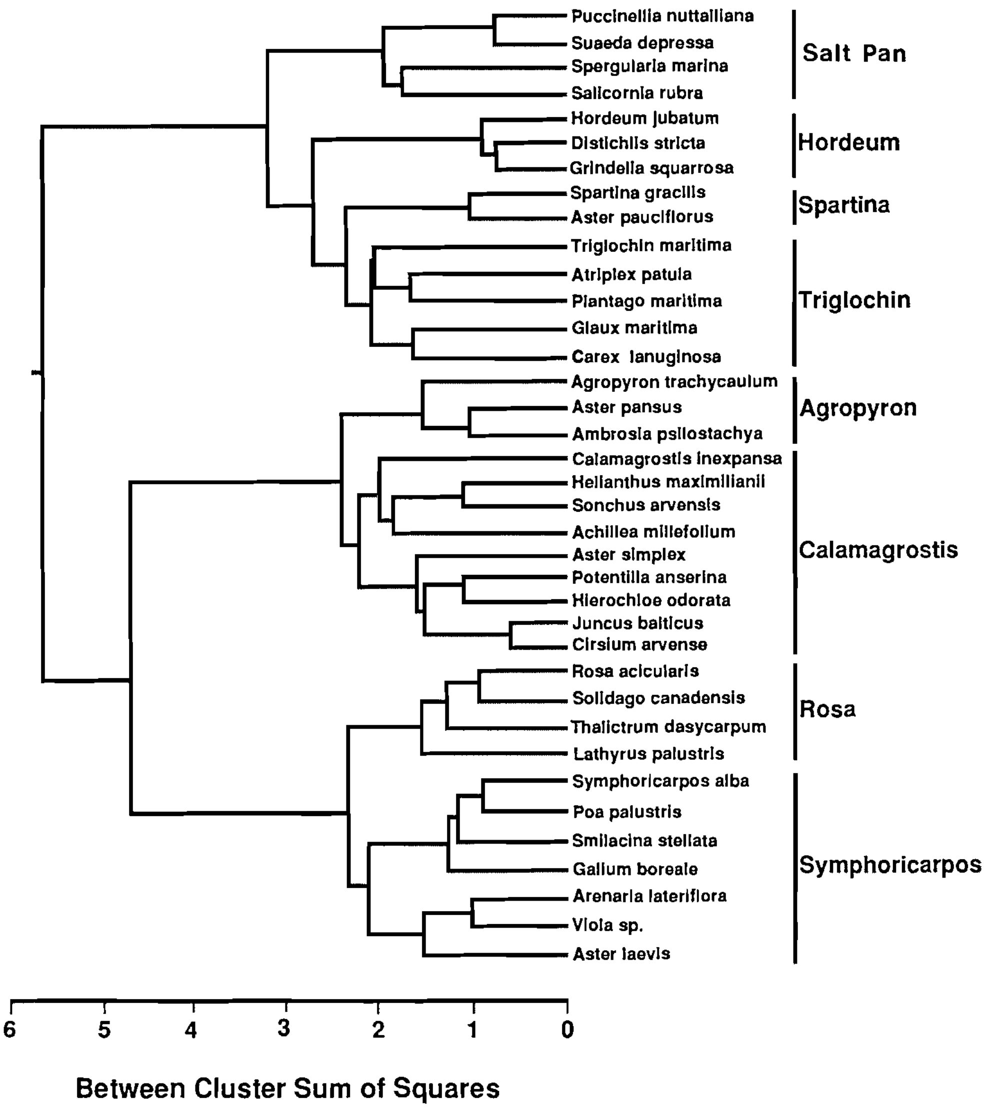

FIG. 6. Sum of squares agglomerative cluster analysis of the 37 species, showing the eight species groups.

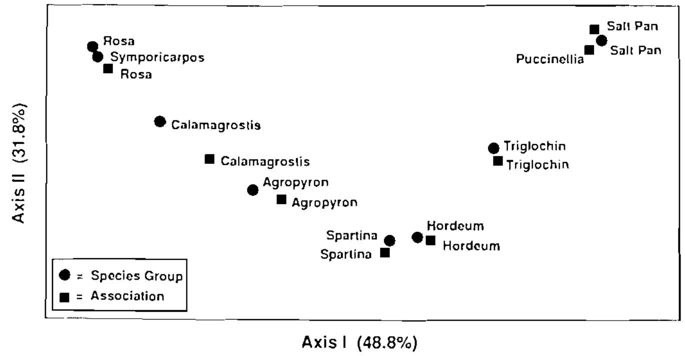

FIG. 7. Two-dimensional concentration analysis ordination of the eight vegetation associations and eight species groups. Salinity increases from left to right.

erally weak, with total salts and bulk soil density showing the strongest trends. ANOVA results indicated a significant difference ($F = 65.06$, $p < 0.001$) in the salinity levels among the eight vegetation associations (Fig. 9).

We further examined the relationship between vegetation and salinity by plotting mean percent cover of the nine most frequently occurring species against salinity (Fig. 10). All species show a general bell-shaped response to the salinity gradient. The response of *S. rubra* is truncated at the high-salinity end, indicating that it is most common where salinity is highest. *Puccinellia nuttalliana* also occurs in highly saline areas, and *T. maritima* is found at both intermediate to high salinities. *Hordeum jubatum* and *D. stricta* both have highest cover at intermediate salinities. *Spartina gracilis* was most commonly found at low to intermediate salinities but occasionally occurred in highly saline areas. *Agropyron trachycaulum, C. inexpansa*, and *R. acicularis* all have distributions that are truncated at the low-salinity end of the gradient. Of the three, *Agropyron* appears to be the most salt tolerant.

Discussion

Plant communities of inland saline sites

The halophytic species composition of the boreal Winnipegosis salt flats is remarkably similar to that of prairie salt

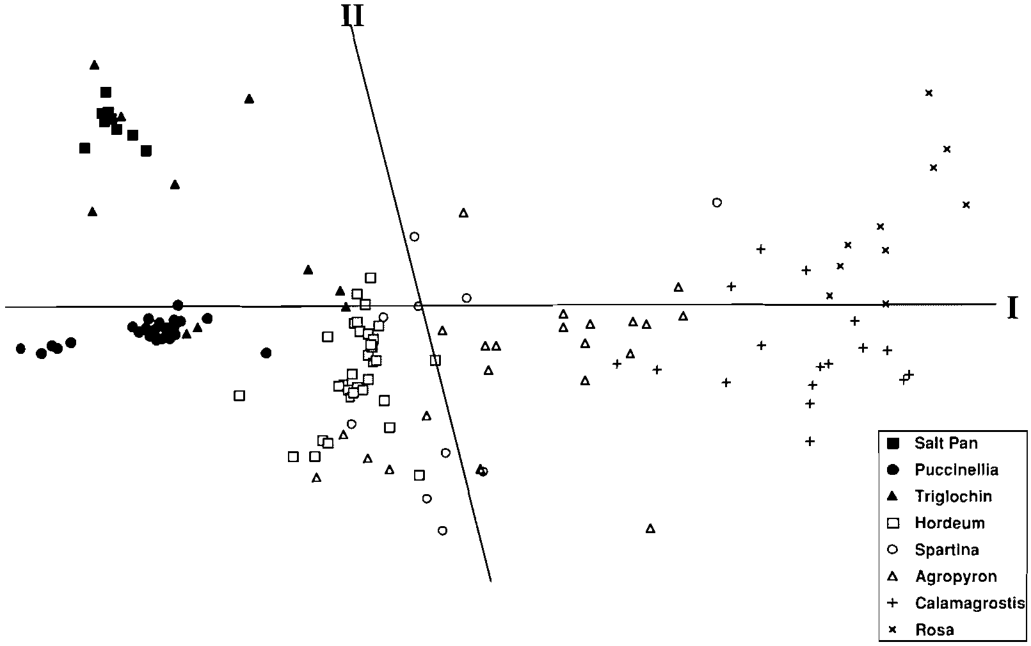

FIG. 8. Two-dimensional nonmetric multidimensional scaling ordination of 136 quadrats, with axes I and II of canonical correlation analysis superimposed. Vegetation association affinities for quadrats are also indicated. The angle between axes I and II is 103.7°.

TABLE 3. Structure correlations for eight environmental factors on canonical correlation axes I and II of Fig. 8

	Canonical correlation axis	
	I	II
Total salts	−0.813	0.415
pH	−0.756	−0.101
Relative elevation	0.643	−0.026
Bulk density	−0.488	0.456
Potassium	−0.440	0.328
Phosphorus	0.220	−0.132
Nitrogen	−0.170	−0.180
Percent organic matter	0.145	0.301

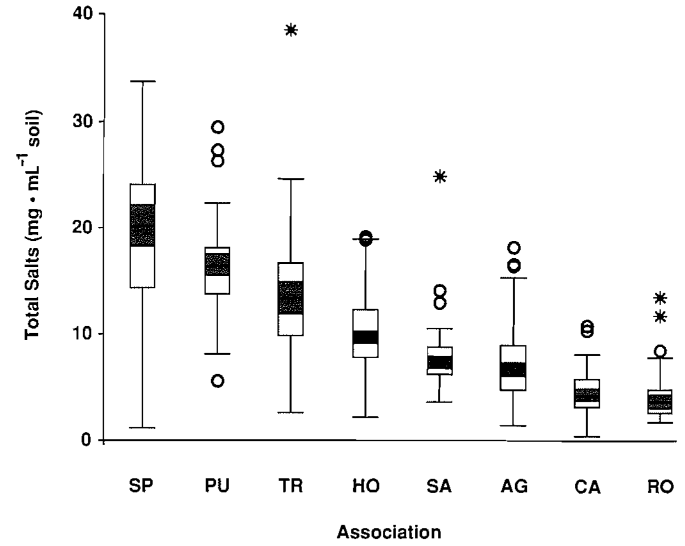

FIG. 9. Box plots summarizing salinity variation among associations. Shaded areas represent the 95% confidence interval of the means. Boxes represent the interquartile range; the horizontal line within each box is the median. Whiskers extend from the box to the nearest point within ±1.5 × interquartile range. O, outliers less than ±3.0 × interquartile range; *, outliers greater than ±3.0 × interquartile range. Associations: SP, Salt Pan; PU, Puccinellia; TR, Triglochin; HO, Hordeum; SA, Spartina; AG, Agropyron; CA, Calamagrostis; RO, Rosa.

pans in Saskatchewan, Colorado, and the Dakotas (Ungar 1974*b*) and to boreal salt flats in northeastern Alberta (Lieffers 1984). Similarities between the vegetation of prairie and boreal salt pans suggest that soil salinity may largely override climatic and other environmental factors in determining species composition and that species able to tolerate saline conditions are widely distributed. Nonetheless, differences in structure and composition of halophytic vegetation do occur along north–south and east–west gradients in North America (Ungar 1974*b*). Species restricted to or more common in southern areas include *Sporobolus airodes*, *Sporobolus texanus*, and salt-tolerant shrubs such as *Tamarix pentandra* and *Sarcobatus vermiculatus*. *Salicornia rubra* is restricted to northern areas; in parts of Oklahoma, Kansas, and Nebraska salt pans are dominated instead by *Sesuvium verrucosum* or *S. depressa*. Other species that are more common in northern and western saline habitats include *G. maritima*, *P. nuttalliana*, *S. gracilis*, *T. maritima*, *A. psilostachya*, *G. squarrosa*, *A. pauciflorus*, and *S. marina*. The presence of *P. maritima* in our study area is particularly interesting, as it has a very restricted distribution inland (Harms *et al.* 1986). *Plantago maritima*, *T. maritima*, and *Salicornia europaea* agg. (which includes *S. rubra*) are the only species in our study area that also occur in the nearest coastal salt marshes, approximately 700 km northeast on Hudson Bay near Churchill (Jefferies *et al.* 1983).

Zonation patterns found in our study are similar to those observed along salinity gradients in other inland North American salt flats (Ungar 1974*a*, 1974*b*). The most saline areas are generally dominated by succulent annual species (e.g.,

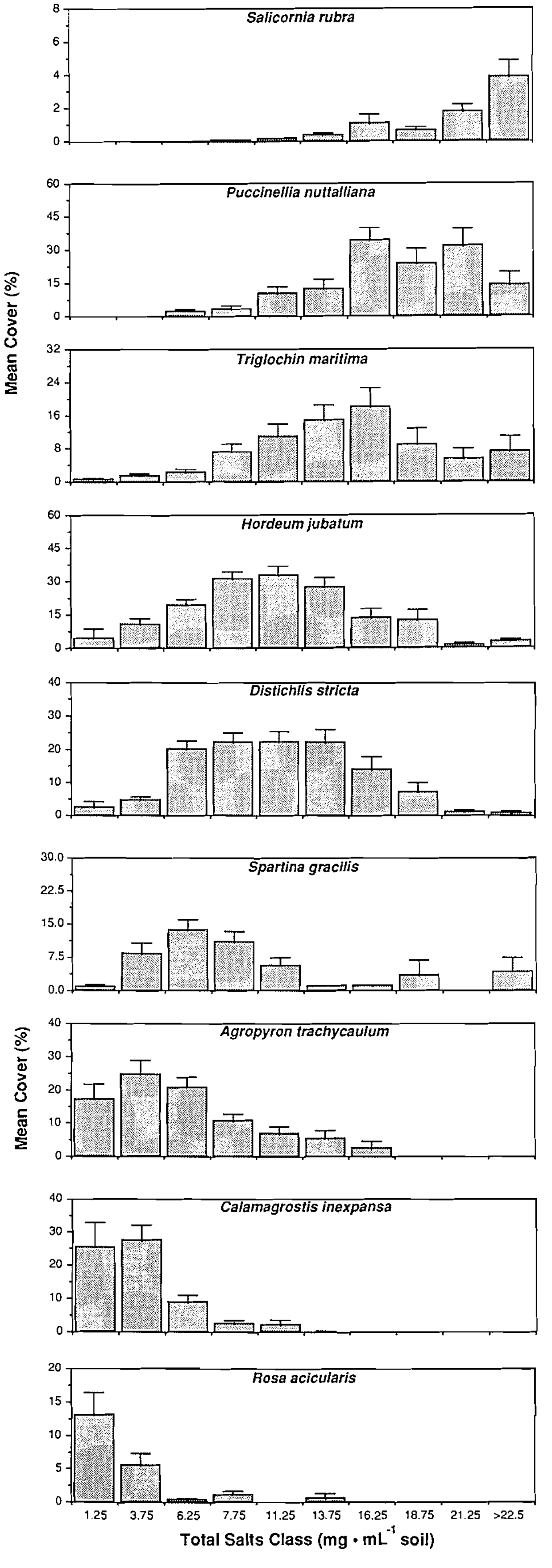

FIG. 10. Mean percent cover (± 1 SE) vs. soil salinity class for the nine most frequently occurring species.

S. rubra, S. depressa, S. marina), although we occasionally found *P. nuttalliana* and a dwarf form of *T. maritima* on the salt pans. Both *Puccinellia* and *Triglochin* were most abundant along salt-pan edges; this has also been noted in other northern and western North American saline regions (Ungar 1974*b*). At our sites, the next vegetation zone consisted of a mixture of *H. jubatum* and *D. stricta*. While *Hordeum–Distichlis* codominance has been noted previously (e.g., Keith 1958; Dodd and Coupland 1966), in most areas they form distinct vegetation zones (Ungar 1974*a*). In Saskatchewan, *D. stricta* was also found associated with *P. nuttalliana* and *Agropyron smithii* (Dodd and Coupland 1966). In drier areas in the south *Distichlis* is often found at the edge of salt pans (e.g., Ungar 1968).

Previous studies reveal that species composition shows greater intersite variation at the low-salinity end of the gradient than at the high end (Ungar 1974*b*). This suggests that whereas at high salinities the flora is determined primarily by soil osmotic potential, at lower salinities climatic and floristic influences operating at larger spatial scales are more important. In our study, the species composition at lower soil salinities indicates floristic affinities with both prairie and boreal forest. *Spartina gracilis* has previously been described from meadows adjacent to salt pans in northern areas (e.g., Dodd and Coupland 1966). *Agropyron trachycaulum*, a wet meadow species known to be somewhat salt tolerant (Looman 1982), has not been previously recorded from saline areas (although *A. smithii* has been, Ungar 1974*b*). The two associations found at the lowest salinities (Calamagrostis and Rosa) are characterized by a mixture of grasses and forbs of boreal and prairie affinity.

Trends in species richness and diversity along the salinity gradient

Our observation of a monotonic decrease in species richness with increasing salinity has been noted previously (Ungar 1974*a*). Since few plant species have developed the adaptations necessary to survive in saline environments, it is not surprising that species richness is low at higher salinities. The high osmotic potential of soils on the salt pan presumably prevents any species from permanently establishing there. For coastal marshes, Odum (1988) hypothesized a similar decrease in vascular plant species richness with increased salinity, which he attributed to greater osmotic stress in more saline habitats.

We also demonstrated a general increase in diversity and evenness with decreasing salinity. The exception to this trend was the Salt Pan association, which had a diversity similar to the Spartina and Calamagrostis associations and the highest evenness value. A possible explanation for this discrepancy is forthcoming when one considers the mean percent cover of the Salt Pan association (16 vs. 112–158% for the others). There is likely little interspecific competition for available resources when plant cover is this low. When competition is unimportant, no one species dominates, and high diversity and evenness result (see also Strong *et al.* 1984, who used a similar argument to explain the high diversity and evenness of phytophagous insect communities). Six of the other associations have similar evenness values, indicating that higher diversities at lower salinities are mainly attributable to increased species richness. The high evenness value of the Rosa association is explained by noting that the other three low-salinity associations (Spartina, Agropyron, and Calamagrostis) are each dominated by a single stoloniferous graminoid. Species with this growth form tend to exclude other species, resulting in a low evenness. In the Rosa association, the absence of a strongly clonal species and greater stratification (owing to the presence of shrubs) explain its high diversity and evenness.

Spatial and temporal dynamics of inland saline habitats

A number of authors have proposed successional sequences for plant communities on saline soils in western North America (see Ungar 1972). Early schemes generally proceeded in a linear sequence from higher to lower salinity over time, under the assumption that the observed zonation along a salinity gradient reflected a successional sequence. Other studies recognized that retrogressive change was also possible (e.g., Keith 1958). Ungar (1972) developed a model of dynamic change in which the vegetation tracks changes in environmental conditions over time. For example, a series of wet years leads to a decrease in soil salinity and a shift toward less salt-tolerant communities. Conversely, species composition reverts to that characteristic of higher salinities in dry years. We noted that in a very dry season (1988) *S. rubra* germinated successfully but died well before setting seed (see also Ungar 1970), whereas during a wet season (1990) cover of this species was high. Furthermore, in 1990, seedlings of *H. jubatum, P. nuttalliana*, and *Typha* spp. were found on the normally unvegetated salt pans. We suggest that species are sorted out along a salinity gradient according to their physiological limits of salt tolerance. This implies that it is the maximum soil salinity reached, rather than mean salinity, that ultimately determines species distributions. Borders of vegetation zones may fluctuate slightly from year to year but are expected to remain at approximately the same location in the long term. Evidence for this comes from an oblique aerial photograph of our study area taken in 1927 that indicates that the general pattern of vegetation – salt pan borders has changed little over 60 years.

Vegetation zonation in inland saline habitats

Inland saline pans are characterized by plant associations dominated by a single (or occasionally two) species.These are ordered along the salinity gradient reflecting different degrees of physiological salt tolerance. Many workers have noted the occurrence of vegetation discontinuities or ecotones along this gradient, even though there appear to be no discontinuities in environmental factors (Ungar 1974*a*). By contrast, vegetation boundaries in coastal salt marshes often correspond to tidally imposed environmental edges, though interspecific competition may play a secondary role (Bertness and Ellison 1987; Odum 1988). In our study area, vegetation discontinuities were apparent across the entire salinity gradient, though they were most pronounced at higher salinities (see also Flowers 1934; Ungar 1974*a*; Skougard and Brotherson 1979).

If environmental edges do not underly vegetation discontinuities in inland saline systems, it seems likely that biotic processes are involved in boundary development. Indeed, recent simulation models of plant communities have suggested that competitive displacement may result in the development of vegetation discontinuities along continuous environmental gradients (Czárán 1989; Smith and Huston 1989). In Smith and Huston's model of species interaction along a moisture gradient it was assumed that all species have highest growth rate at the same optimal soil moisture level, and that growth rates decrease monotonically from this optimum. However, Austin and Smith (1989) argue that species responses along an environmental gradient are unimodal rather than monotonic and that each species has a unique position along the gradient where its growth is optimal. This is unlikely to be true of a salinity gradient, however, since even the most salt-tolerant halophytes show optimal growth at low salinities; there are apparently few if any obligate halophytes (Barbour 1970; Flowers *et al.* 1977). We assume that salt-tolerant species are excluded from areas of low salinity through competitive exclusion by less salt-tolerant but faster growing glycophytes. With competition, the degree of species overlap decreases and vegetation discontinuities develop (see also Mueller-Dumbois and Ellenberg 1974; Walter and Breckle 1985).

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