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Aquatic macrophytes in saline lakes of the Canadian prairies

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Abstract

Vascular macrophyte species richness decreases with increasing salinity. Only three species of submerged plants (*Potamogeton pectinatus, Ruppia maritima, R. occidentalis*) tolerate hypersaline waters (> 50 g l^{-1}, total of ionic constituents). Eight emergent species occur in more saline habitats but only five (*Scirpus maritimus* var. *paludosus, Distichlis stricta, Puccinellia nuttalliana, Scirpus americanus, Triglochin maritima*) occur commonly over a range of saline lakes into the hypersaline category. Usually, species tolerant of high salinities are found over the entire saline spectrum and even extend into subsaline waters (< 3 g l^{-1}) and thrive there. A major increase in the number of species occurs below 5 g l^{-1}. As the water recedes plants such as *Salicornia rubra, Suaeda calceoliformes, Hordeum jubatum* and *Sonchus arvensis* invade.

Submerged angiosperm distribution is controlled by total ion concentration and substrate texture plays no apparent role. Although angiosperms normally grow in all kinds of substrates, they occupy coarse substrates in Wakaw lake because suitable fine substrates are densely colonized by charophytes. In this lake light limited growth occurs to a depth of 5% of surface light. Light was not limiting in Redberry Lake but angiosperm growth was limited to the upper 8 m (10% or more of surface light). Thermal stratification and depth (pressure) were probably limiting istead. In meromictic Waldsea Lake the depth of the chemocline (6 m, 5% surface light) delimits angiosperm growth.

Introduction

Early studies noted the presence of aquatic macrophytes in saline lakes of the northern central plains of North America. Huntsman (1922) found an abundance of *Potamogeton pectinatus* L. in the Quill Lakes, Saskatchewan (11–16.5 g l^{-1} TDS). Young (1924) stated that the only flowering plant of importance in the Devils Lake complex of North Dakota was *Ruppia maritima* L., but its role was very minor in Devils Lake in the 1960s (Armstrong *et al.*, 1966). Rawson & Moore (1944) listed only two flowering plant species, *P. pectinatus* and *R. occidentalis* S. Wats, in Saskatchewan lakes where salinities exceeded 20 g l^{-1} TDS.

On the Canadian prairies a halophytic flora is characteristic of saline lake margins which lack superficial water. Rawson & Moore (1944) found that with decreasing salinity in Saskatchewan a sequence of vegetation occurs which is characterized by the dominance of *Salicornia rubra* A. Nels, *Distichlis stricta* (Torr.) Rydb., *Suaeda erecta* (S. Wats.) A. Nels, *Atriplex hastata* L. and *Triglochin maritima* L. Dodd & Coupland (1966) found *S. rubra* on gleyed Regosol soils in wet depressed areas, *T. maritima, Puccinellia airoides* (= *P. nuttalliana* (Schult.) Hitchc.), *Distichlis stricta* (Torr.) Rydb. and *Hordeum jubatum* L. on saline meadow soil. *Sarcobatus vermiculatus* (Hook.) Torr., *Muhlenbergia richardsonis* (Trin.) Rydb. and *Agropyron* spp. occurred on dry saline chernozem soil (Dodd *et al.*, 1964). Tiku (1975) also included *Suaeda depressa* (Pursh) S. Wats. (now *S. calceoliformes* (Hook.) Moquin) and *Spergularia salina* J. & C. Presl. in the saline group.

In Alberta White & Hartland-Rowe (1968) noted that *Scirpus paludosus* grew in shallow slightly saline Wanek Lake. Daborn (1975) found *S. americanus* Pers. mixed with *S. paludosus* and some *Sparganium* and grasses in the shallows of Fleeinghorse Lake. Gallup (1978) observed the presence of *Ruppia maritima* in Lake Miquelon.

The distribution of macrophytic algae in saline lakes of Saskatchewan has been outlined and discussed by Hammer *et al.* (1983), Heseltine (1976) and Tones (1976). The charophytes are not common in Saskatchewan saline lakes. *Chara canescens* Desv. & Lois and *C. globularis* Thuill. form dense meadows on fine substrates at a depth of about 2 m in Wakaw Lake. *Chara buckelli* G. O. A. is abundant in some parts of mesosaline Waldsea Lake at depths of 3–6 m. Masses of filamentous attached and tychoplanktonic green algae (*Ctenocladus circinnatus* (Borzi), *Rhizoclonium hieroglyphicum* (Agardh) Kuetz, *Enteromorpha prolifica* (Fl. Dan.) J.G.Ag.) are present in mesosaline and hypersaline lakes and tolerate salinities in excess of 100 g l^{-1}.

We initiated studies to further elucidate the identification and distribution of vascular macrophytes that grow in and around saline lakes of Alberta and Saskatchewan. More detailed studies were conducted on three lakes to ascertain the environmental factors that determined the distribution of halophytes and their occupation of specific habitats.

The salinity classification used in this paper was proposed by Hammer (1978) and Hammer *et al.* (1983). Three major categories are used: hyposaline (3–20 g l^{-1}); mesosaline (20–50 g l^{-1}); hypersaline (>50 g l^{-1}). Subsaline includes the 0.5–3 g l^{-1} range whereas the lower salinities (0–500 g l^{-1}) encompass fresh waters. Salinity in athalassic saline lakes is defined as the total of ionic constitutents (Hutchinson, 1957) and is correlated with but not numerically equal to total filtrable residue (TFR) (formerly total dissolved solids (TDS)) and to conductivity (Hammer, 1978).

Description of study sites

Saline lakes whose basins were formed during the last glaciation are distributed throughout the prairies and aspen grove parklands of southern Alberta and Saskatchewan in endorheic drainage basins (Fig. 1). They encompass a broad spectrum of salinities that range from 3 to over 400 g l^{-1} and have been described in some detail in Hammer (1978) and Hammer & Haynes (1978). Low precipitation averaging 35 cm annually and high evaporation promotes the occurrence of these lakes. The water level varies up to one metre annually as snow-melt runoff adds water in the spring and evaporation lowers levels during the ice free period. Thus plants that are submerged in the spring may occur where surficial water is absent by midsummer or fall. The more saline lakes tend to be dominated by sodium sulphate but magnesium exceeds sodium in some lakes. The alkalinity (carbonate + bicarbonate) content is relatively higher in lakes in western Saskatchewan and Alberta. A few sodium chloride lakes also occur.

Chemical and physical data for representative lakes are presented in Table 1. They are all basic but the more western lakes tend to have relatively high pHs, i.e. pH >9. Summer temperatures in the littoral regions exceed 20 °C, but this zone is frozen to a depth about 1 m during the 5–6 month winter. Many saline lakes are turbid, but in Redberry Lake adequate light for photosynthesis occurs down to the bottom at 18 m.

Methods

Saline lakes in Alberta and Saskatchewan were examined during late June and early July when vascular plants were in flower. Seeds were collected subsequently to verify identifications. Observations were made on relative plant abundance and the depth of water at which plants grew. Specially noted was the presence or absence of surficial water where plants occurred. Water electrical conductance at 25 °C (Solu Bridge Model RB3-3341 Conductivity Meter), pH (Hellige Pocket Comparator) and temperature were measured. No physical or chemical measurements were made of the soils beyond the water margins.

Three lakes (Wakaw, Redberry, Waldsea) were examined in detail during the May to October periods of 1973 and 1974. Light penetration was measured

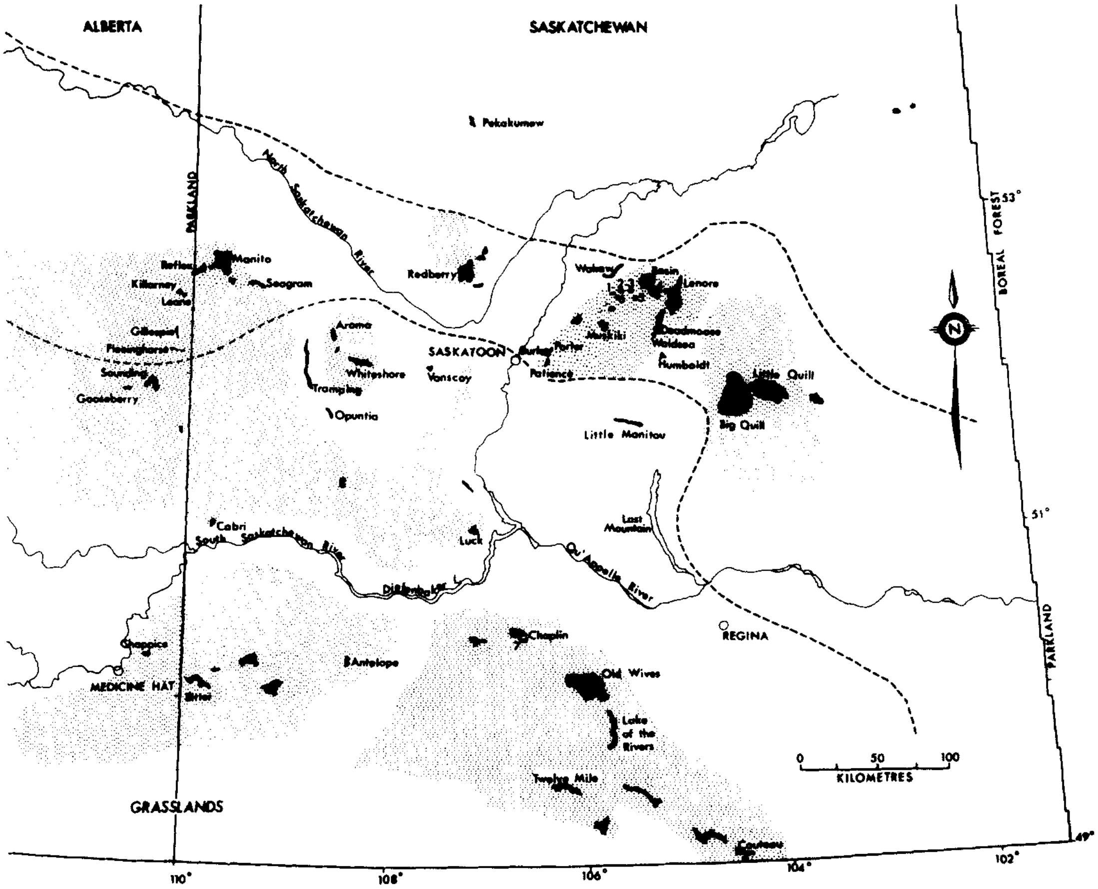

Fig. 1. A map of eastern Alberta and Saskatchewan showing the location of saline saline lakes (black), vegetation zones and endorheic drainage basins (stippled).

with a G. M. Model 15M02 submarine photometer (385–720 nm). Detailed water chemistry analyses (APHA, 1980) were made (total filtrable residue, conductance, pH, hardness, sodium absorption ratio, carbonate, bicarbonate, manganese, iron, sulphate, chloride, nitrate and ammonium nitrogen, phosphorus, potassium, sodium and magnesium). When plants were fruiting substrate samples were taken where the water depth was between 1 and 2 m. Plants were collected from three sites within each lake and several stands were sampled in each site. A corer operated by a diver was used to sample sediments in each stand to a depth of 25 cm, the maximum depth to which roots penetrated. Substrate analyses were performed by the Soil Testing Laboratory, University of Saskatchewan. This included texture dominance and measurements of nitrate nitrogen, phosphorus and potassium in bicarbonate extract. We performed multivariate analyses of the plant and substrate data using Bray Curtis ordination and principal components analysis.

Plant cover and biomass (including macrophytic algae) were determined from cores for stands in the littoral zone of six lakes (Basin, Big Quill, Deadmoose, Humboldt, Little Manitou, Waldsea) during June and August 1972 by Tones (1976).

Results

Distribution and environmental conditions

Table 2 lists the distribution of vascular macrophytes that are floating, submerged or emergent (for

Table 1. Canadian prairie saline lakes and their environmental characteristics.* Specific conductance (COND) is in mS cm^{-1} at 25 °C while total filtrable residue (TFR) is in g l^{-1}.

	COND	TFR	pH	Area (km^2)	Z_m (m)	Salt Dominance
LAKE						
ALBERTA						
Chappice	19.5–40	26. – 61	9.1	2	2	Na_2SO_4
Reflex West	50	50	9.1	6	4	$NaClSO_4$
Gooseberry	30 – 33	35 – 43	9.5	5	6	Na_2SO_4
Gough	–	16	8.9	?	1?	Na_2CO_3
Gillespie	8.5	8.2	9.4	6	1	$Na_2CO_3SO_4$
Miquelon	8.4	8.0	9.5	?	?	$Na_2CO_3SO_4$
Killarney	5.8– 6.4	4.2– 5	9.3	7	4	$Na_2CO_3SO_4$
Leane	7.5	4.9	9.5	3	3	Na_2SO_4
Fleeinghorse	3.8– 6.5	3.4– 4.4	9.1	3	2	Na_2SO_4
SASKATCHEWAN						
Whiteshore	80 – 89	103 – 308	8.6	23	2	Na_2SO_4
Muskiki	67	235	7.9	17	1	$NaMgSO_4$
Chaplin	120	222	9.0	93	2	Na_2SO_4
Little Manitou	73	96	8.8	13	5	$MgNaSO_4Cl$
Big Quill	35 – 45	45 – 53	8.7	307	3	$NaMgSO_4$
Burke	34	43	9.6	2.5	1	$NaMgSO_4Cl$
Seagram	29	38	9.5	3	1?	$NaSO_4Cl$
Middle	22	33	8.9	13	?	$NaMgSO_4$
Manito	24	28	9.3	79	21.5	$NaSO_4CO_3$
Deadmoose	21 – 28	22 – 27	8.9	10	48	$NaMgSO_4Cl$
Waldsea	21 – 25	23 – 25	8.5	4.6	14.3	$MgNaSO_4Cl$
Sayer	12.5	20	9.0	2	5	$MgNaSO_4$
Basin	13.5–16	19 – 22	9.1	41	14	$MgNaSO_4$
Redberry	15 – 16	15 – 19	8.7	54	18	$MgNaSO_4$
Old Wives	13	19	9.5	296	?	$MgSO_4CO_3$
Pekakumew	15	16	9.0	5.4	42	$MgNaSO_4$
Antelope	12	16	9.0	14	8.2	$NaMgSO_4$
Porter	6.8–24	6.5– 26	9.0	2	< 1	$NaMgSO_4Cl$
Arthur	6.5	6.1	8.6	2.5	4	$MgNaSO_4$
Little Quill	7.5	5.2	8.7	181	4.3	$MgNaSO_4$
Lenore	4.9	5.6	8.7	61	9.3	$MgNaSO_4$
Van Scoy	4	4.5	8.1	6.4	1	$MgNaSO_4$
Cabri	–	4.3	9.6	10	1	Na_2SO_4
L. of the Rivers	4.5	3.8	9.6	37	2	$MgSO_2CO_3$
Humboldt	3.5– 4.3	2.9– 4.7	8.9	17	8	$MgSO_4$
Wakaw	3.5– 4.1	3.2– 3.7	8.3	10	14	$MgNaSO_4$

* Alberta lakes morphometry data have been derived from Survey and Mapping Branch (Ottawa) maps while for other lakes the source is Hammer & Haynes (1978); Z_m is the maximum depth, chemical data is from Hammer (1978) except for Alberta and 1985 data; CO_3 includes bicarbonate.

at least part of the year) in some Canadian prairie and parkland saline lakes.

Submerged vascular macrophytes are limited to *Potamogeton pectinatus* and two species of *Ruppia* in saline lakes in excess of 5 g l^{-1} salinity. Figure 2 illustrates the distribution of the three submerged

Table 2. Vascular flora of some Alberta and Saskatchewan saline lakes in order of increasing salinity from Wakaw to Whiteshore.

LAKE	FLOATING, SUBMERGED										SHALLOW WATER EMERGENT															
	Lemna minor L.	Myriophyllum spicatum exalbescens Fern.	Potamogeton friesii Rupr.	Potamogeton pectinatus L.	Potamogeton richardsonii (Benn.) Rydb.	Potamogeton vaginatus Turcz.	Ruppia maritima L.	Ruppia occidentalis S. Wats.	Saggittaria cuneata Sheld.	Ultricularia vulgaris L.	Cicuta maculata angustifolia Hook.	Distichlis stricta (Torr.) Rydb.	Eleocharis palustris L.	Hippuris vulgaris L.	Lycopus americanus Muhl.	Mentha arvensis villosa (Benth.) S.R.S.	Puccinellia nuttaliana (Schult.) Hitchc.	Ranunculus cymbalaria Pursh.	Scirpus acutus Muhl.	Scirpus americanus Pers.	Scirpus maritimus paludosus Nels. (Kük.)	Scolochloa festucacea (Willd.) Link	Triglochin maritima L.	Triglochin palustris L.	Typha latifolia L.	Phragmites australis L.
Wakaw	+	+	+	+	+			+	+	+	+		+	+	+	+			+	+	+	+	+		+	
Fleeinghorse	not investigated												+				+		+	+	+				+	
Cabri	not investigated																+					+	+	+		
Humboldt		+		+		+		+											+	+						
Van Scoy	+		not investigated										+	+				+	+		+					
Porter							+					+			+		+		+	+	+		+			
Killarney				+				+					+							+						
Little Quill				+							+															
Lenore				+															+	+	+					
Arthur								+									+						+			
Antelope				+			+	+									+									
Pekakumew																			+				+			+
Old Wives				+				+									+			+	+					
Redberry				+				+				+					+						+			
Sayer																	+				+		+			
Basin				+				+				+					+			+	+					
Waldsea				+				+																		
Deadmoose				+				+									+									
Manito				+																						
Middle				+				+				+					+		+	+	+					
Seagram							+	+									+			+	+					
Gooseberry								+									+	+	+	+	+		+			
Burke							+										+	+		+			+			
Big Quill				+			+													+						
Chappice							+																			
Chaplin												+					+			+			+			
Muskiki												+					+						+			
Whiteshore																					+		+			

macrophytes in Alberta and Saskatchewan saline lakes. *Ruppia maritima* appears to grow in shallow water less than 0.5 m deep and near shore. *Ruppia occidentalis* grows in water down to 7 m deep in Waldsea and 8 m in Redberry Lake but is most abundant at depths from 1 to 4 m. *Potamogeton pectinatus* usually occurs in the same lakes and at the same depths as *R. occidentalis*. A few other submersed species are restricted to low hyposaline waters (< 5 g l^{-1}) such as those of Wakaw and Humboldt lakes (Table 2).

Macrophyte salinity tolerance is shown in Table 3.

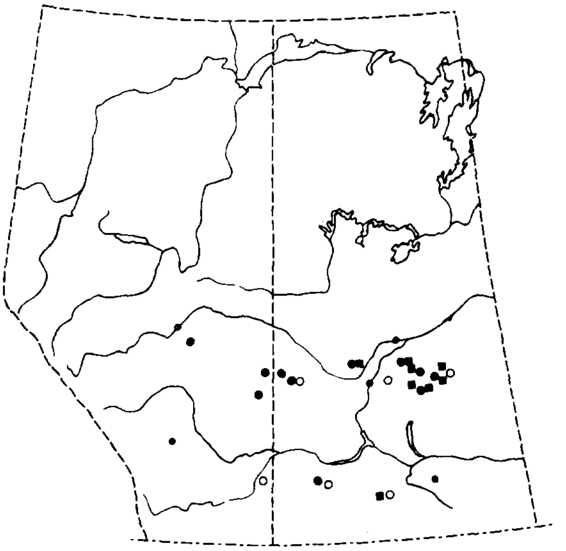

Fig. 2. The distribution of *Potamogeton pectinatus* (squares), *Ruppia maritima* (open circles) and *R. occidentalis* (closed circles) in Alberta and Saskatchewan saline lakes.

Table 3. The salinity tolerance range (g l^{-1} total filtrable residue) of some vascular plant species occupying Canadian prairie saline lakes.

Species Salinity	3 10 20 30 40 50 60 70
Scirpus maritimus	———————— to 308
Triglochin maritima	———————— to 308
Distichlis stricta	———————— to 235
Puccinellia nuttaliana	———————— to 235
Ruppia maritima	————————
Potamogeton pectinatus	——————
Ruppia occidentalis	——————
Scirpus americanus	——————
Ranunculus cymbalaria	—————
Scirpus acutus	————
Phragmites australis	—
Cicuta maculata	—
Hippuris vulgaris	—
Eleocharis palustris	—
Lemna minor	—
Lycopus americanus	—
Metha arvensis	—
Myriophyllum spicatum	—
Potamogeton friesii	—
Potamogeton richardsonii	—
Potamogeton vaginatus	—
Sagittaria cuneata	—
Scolochloa festucacea	—
Triglochin palustris	—
Typha latifolia	—
Ultricularia vulgaris	—

Ruppia maritima is the most tolerant, growing over a range of 16.2–61.4 g l^{-1} TFR in Antelope, Burke, Chappice and Seagram lakes. The more common *R. occidentalis* spans the range from subsaline to 53 g l^{-1} and is common in larger lakes (Table 2). The pH range of lake waters for *R. maritima* is 8.5–9.6 and for *R. occidentalis* it is 8.0–9.6. *Potamogeton pectinatus* is common in many lakes (Table 2) over a salinity range of subsaline to 53 g l^{-1} TFR. The pH range is also broad, i.e. 8.0–9.6.

Emergent vegetation grows in the spring in the shallows of lake margins less than a meter deep. As lake levels fall they may become stranded above the water line. Their distribution among lakes is given in Table 2. The most widespread emergents associated with saline lakes are species of *Scirpus*. Their distribution is illustrated in Fig. 3. *Scirpus maritimus* L. var. *paludosus* Nels (Kük.) (*S. maritimus* subsequently) is most widely distributed with respect to salinity from 3.2 g l^{-1} TFR (Wakaw) to 308 g l^{-1} in Whiteshore Lake. *Scirpus americanus* (var. *langispicatus* Britt.) occurs as frequently as *S. maritimus* but has a narrower salinity range, i.e. subsaline to 53 g l^{-1} (Big Quill Lake). Both plants form dense swards usually in fairly distinct bands but sometimes they grow in mixed stands. *Scirpus americanus*

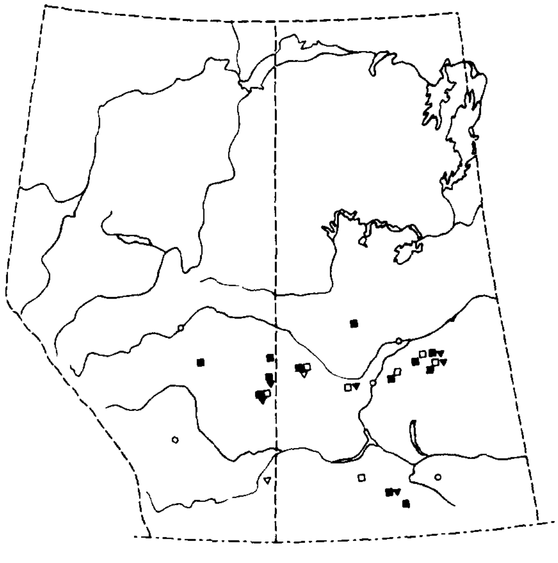

Fig. 3. The distribution of *Scirpus americanus* (closed square), *S. nevadensis* (open triangles), *S. maritimus* (open squares) and *S. acutus* (closed triangles) in and/or around Alberta and Saskatchewan saline lakes.

grows more frequently in shallow water. *Scirpus acutus* Muhl. tends to occur in hyposaline waters but was noted in shallow waters of Middle and Gooseberry lakes (33 to 43 g l^{-1}). *Scirpus nevadensis* Wats. was noted near only two lakes, Seagram and Chappice, and in both cases the stands were away from the water's edge in relatively dry environments.

Triglochin maritima occurs in water and immediately adjacent to open water of most lakes between 3.2 and 308 g l^{-1} (Table 2, Fig. 4). It was most abundant in and beside the most saline lakes where it was relatively short (10 cm). It grew very tall (1 m) but less abundantly in hyposaline lakes such as Wakaw Lake. *Triglochin palustris* L. was only found by Cabri Lake (4.3 g l^{-1}).

Ranunculus cymbalaria Pursh was collected from the wet shores of Vanscoy, Burke and Gooseberry lakes. The salinity variation of these lakes ranged from 4.5 to 43 g l^{-1}. *Typha latifolia* was only present in two hyposaline lakes (Table 2). *Phragmites australis* L. only occurred in and near Pekakumew Lake (16.3 g l^{-1}). *Eleocharis palustris* L. is an inhabitant of the shallows and shores of lakes of lower salinity (Table 2) and has a salinity range up to about 5 g l^{-1}.

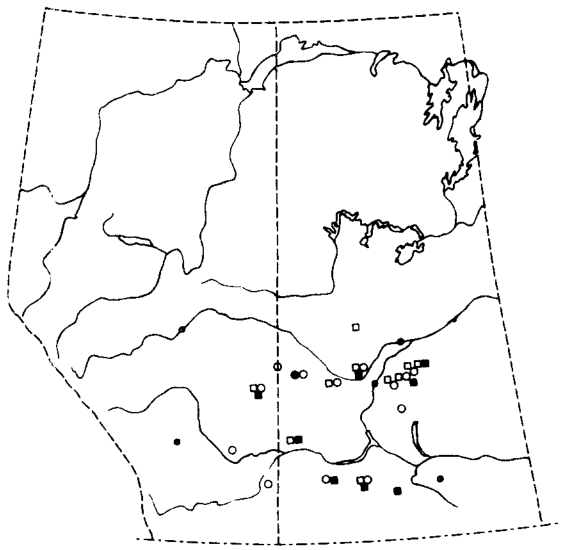

Fig. 4. The distribution of *Puccinellia nuttalliana* (closed squares), *Salicornia rubra* (circles) and *Triglochin maritima* (open squares) in and/or around Alberta and Saskatchewan saline lakes.

The most common grasses were *Distichlis stricta* and *Puccinellia nuttalliana*. They were associated with a salinity range of 6 to 235 g l^{-1}. The distribution of the latter is shown in Fig. 4. *Juncus balticus* Willd. occurs frequently in the vicinity of saline lakes. The soil salinity is probably lower in its habitats that were usually about 0.5 m above the lake level. Burke, Killarney and Gooseberry lakes have fairly extensive stands adjacent to them.

A considerable number of species invade the lake shores as the water recedes. *Salicornia rubra* is of common occurrence in the saline soils adjacent to mesosaline and hypersaline lakes (Fig. 4, Antelope, Basin, Redberry, Deadmoose, Sayer, Middle, Burke, Seagram, Gooseberry, Reflex (Salt), Chappice, Little Manitou, Chaplin, Whiteshore, Muskiki) throughout the area. Although rarely found where surficial water occurs, it was present in shallow water of Redberry Lake. *Suaeda calceoliformes* occupies similar but drier habitats but is not as frequent or abundant. *Glaux maritima* L. was collected from the shores of Van Scoy and Deadmoose lakes but is probably more common. *Chenopodium rubrum* L. grows in similar locales (Wakaw, Deadmoose, Chaplin, Whiteshore). An *Agropyron* species grew in the water and on the shore of Lake Lenore (5 g l^{-1} TFR) but it occurs more frequently on the drier soils adjacent to saline lakes. *Hordeum jubatum* and *Sonchus arvensis* L. are frequent inhabitants of saline soils around prairie lakes.

No vascular macrophytes were found in the water of any lake where salinities exceeded 75 g l^{-1} (Bitter, Chaplin, Coteau, Little Manitou) except for Muskiki and Whiteshore lakes. Typically, plants are absent from a lake bed where salt is deposited.

Factors influencing plant distribution

Three lakes were more extensively studied with respect to factors affecting plant distribution. Redberry and Waldsea Lakes are about 5 and 7 times as saline as Wakaw Lake (3.5 g l^{-1}). Dominant ion concentrations are proportionally higher in more saline lakes. Other ions are similar in concentrations. Water was between pH 8 and 9. Electrical conductivity increased seasonally in each lake but only increased vertically in the euphotic zone prior to June as an effect of mixing with low salinity snowmelt water. Temperature in the upper 3 metres of the euphotic zone increased to about 20 °C by early July. The 1% light level (of surface intensity) reached 6–7 m in Wakaw and Waldsea lakes but 16–18 m in Redberry Lake. In meromictic Waldsea Lake the euphotic zone was delimited by a chemocline beginning between 6 and 7 m. Since environmental conditions are similar in the water medium of the 1–2 m depth zone in any one lake, differences in species presence may be attributable to variations in the nature of the substrate.

Most vascular plants in Wakaw Lake were found at depths of less than 3 m and were scattered and sparse. The maximum depth (6 m) of angiosperms was at about 5% of surface light levels. This was also the case in Waldsea Lake where the 5% level coincided with the upper part of the chemocline at 6 m. In Redberry Lake maximum depth for angiosperm growth was 8 m which coincided with 10% surface light and the position of the thermocline. *Ruppia occidentalis* and *Potamogeton pectinatus* were distributed at all light levels while other species were only in shallow waters.

Ruppia occidentalis and *P. pectinatus* begin growth by the middle of May when the water temperature reaches about 10 °C. Seeds were observed sprouting at 8 °C. Flowering of both species began when the water temperature reached 15 °C about late June. Both species produced fruit by the middle July when the water reached 20 °C. Plants continued to flower and fruit into August. Fruits were released towards the end of August. Plants began to senesce and turn brown by September even though water temperatures remained at 10–15 °C. Nevertheless,

Table 4. Macrophyte occurrence and substrate analyses of 25 stands in three sites in each of three Saskatchewan saline lakes, 1975. Ions (NO_3^--N, P, K) are in mg l^{-1}; conductivity (Cond) is in mS cm^{-1} at 25 °C.

Lake	Site	Stand	Species	Texture	NO_3^--N	P	K	pH	Cond
Wakaw	A	1	S. cuneata, P. pectinatus, P. richardsonii, P. friesii	gravel	2	11	60	7.7	2.58
		2	bare	gravel	2	7	35	7.8	2.48
		3	P. pectinatus	gravel	2	7	40	7.5	2.89
	B	4	R. occidentalis, M. spicatum	gravel	0	10	185	7.3	4.62
		5	bare	gravel	1	4	45	7.6	3.33
		6	Chara spp.	gravel	2	8	80	7.7	4.44
	C	7	R. occidentalis	gravel	1	7	40	8.1	2.56
		8	bare	gravel	2	5	30	7.7	2.43
Redberry	D	9	P. pectinatus	silty clay	0	12	450	8.6	27.1
		10	R. occidentalis	silty clay	0	13	450	9.0	26.3
		11	bare	silty clay	0	7	450	9.0	23.2
	E	12	P. pectinatus	loamy sand	1	6	415	8.7	21.4
		13	R. occidentalis	loamy sand	0	3	165	9.0	14.7
		14	bare	loamy sand	0	2	130	9.2	13.9
	F	15	P. pectinatus	loamy sand	1	5	375	9.2	15.2
		16	R. occidentalis	loamy sand	2	6	325	8.9	19.4
		17	bare	sand	0	2	145	8.8	11.6
Waldsea	G	18	P. pectinatus	sandy clay	0	3	450	8.4	19.4
		19	R. occidentalis	sandy clay	1	6	450	8.2	23.2
		20	P. pectinatus	sand	0	4	180	8.2	18.3
		21	R. occidentalis	sand	0	2	140	7.8	16.8
		22	bare	sand	1	3	110	8.0	15.0
		23	P. pectinatus	clay loam	0	6	450	8.1	20.6
		24	R. occidentalis	sandy loam	0	5	315	8.4	18.1
		25	bare	sandy loam	2	4	303	8.0	15.5

green shoots were collected from under the ice in winter.

Table 4 includes data on the occurrence of macrophytes in 25 stands in three sampling sites each for Wakaw, Waldsea and Redberry lakes. *Ruppia occidentalis* occurred alone in 7 sites, and *P. pectinatus* occurred alone in 7 sites. These monospecific stands occurred in all three lakes. *Ruppia occidentalis* was associated with *Myriophyllum spicatum* in one site in Wakaw Lake whereas *P. pectinatus* occurred with several other species at another site in this lake. Sites with no plants present (bare substrate) occurred in each lake.

Table 4 also includes data from substrate analyses. The Wakaw sites tended to be coarser (gravel) than the sites in the other lakes where clay or sand dominated the sediments. All species, however, were found growing in coarse sediments, and in Wakaw Lake *Potamogeton friesii, P. richardsonii, Sagittaria cuneata* and *M. spicatum* appeared to occupy only coarse sediments. Nitrate, total P concentrations and saturation per cent overlapped within and among lakes. Major ions, pH, sodium absorption ratio and conductivity tended to be different for each lake although overlap occurred between Redberry and Waldsea lakes.

Ordinations provided only two meaningful axes with respect to species and environmental factors. Bray Curtis ordinations are illustrated in Figs. 5, 6, 7 and 8. The first ordination (Fig. 5) separates the Wakaw Lake stands from those of Redberry and Waldsea lakes which are intermingled. The horizontal axis appears to relate to substrate conductivity decreasing from left to right. Ordinations of stands in the three lakes are characterized for substrate conductivity in Fig. 6. When Redberry and Waldsea Lake stands are ordinated together (Fig. 7) the horizontal axis corresponds to substrate texture with coarser substrates on the right and finer ones towards the left and higher sulphate characterizing those stands in the upper part of the ordination. Figure 8 shows the ordination of stands with respect to substrate texture. Usually, the second axis could not be related to any environmental factors. *Potamogeton pectinatus* and *R. occidentalis* are distributed over the complete range of substrate conductivity ($2-28$ mS cm^{-1}) while other species are restricted to lower substrate conductivities. These species also occupy the complete range of soil texture from silty clay to gravel. Sites with an absence of plants could be found all along the environmental gradients. Principal components analysis of stands corroborated the Bray Curtis ordination and did not provide any further information.

Standing crop

Table 5 summarizes data on plant cover and biomass dry weight (including algae) in littoral sites of six lakes.

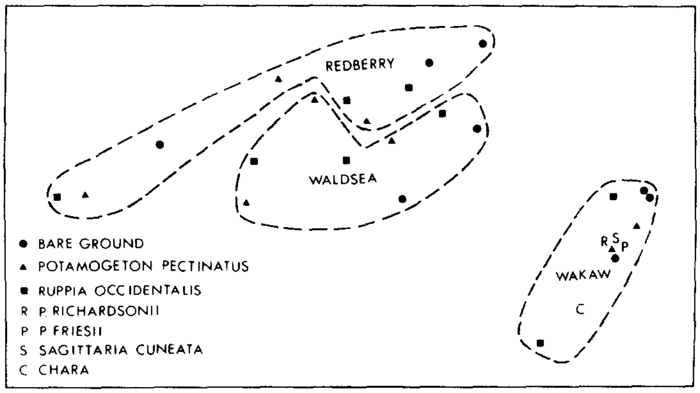

Fig. 5. Bray Curtis ordination of stands from Wakaw, Redberry and Waldsea lakes. The absence or presence of plant species is indicated.

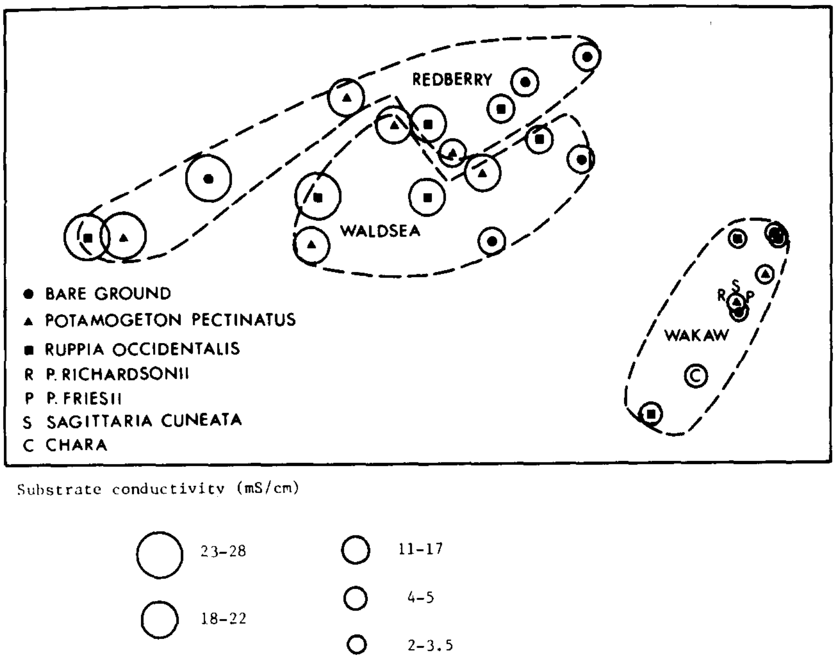

Fig. 6. Bray Curtis ordination of stands from Wakaw, Redberry and Waldsea lakes with decreasing conductivity towards the right. The size of circles correspond to substrate conductivity.

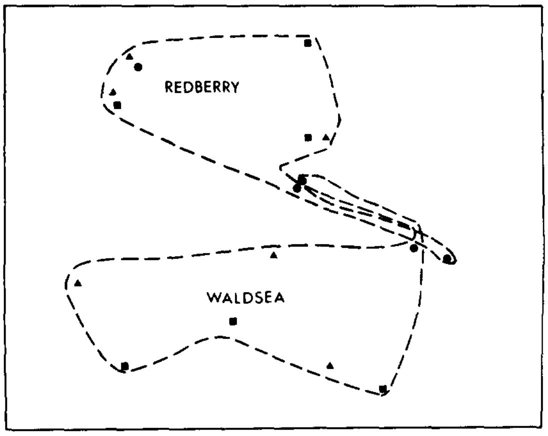

Fig. 7. Bray Curtis ordination of stands from Redberry and Waldsea lakes. The horizontal axis represents increasing coarser texture to the right while the vertical axis represents increasing substrate sulphate.

Table 5. Mean plant cover indices (complete coverage equals 10) at littoral sampling sites of six Saskatchewan saline lakes and mean plant biomass (g dry weight m^{-2}) at the same sites in June and August 1972 (from Tones 1976). The range of water conductivity (mS cm^{-1} at 25 °C) is also shown.

Lake	Conductivity	Index (0–10)	June	August
Humboldt	3.2– 4.0	7	45	365
Basin	13.5–16.5	3	1	9
Waldsea (site 1)	7.5–18.1	8	367	264
Waldsea (site 2)	7.5–17.0	3	19	20
Deadmoose (site 1)	9.4–26.7	10	574	2265
Deadmoose (site 2)	15.3–22.0	2	51	199
Big Quill	19.5–37.0	3	0	123
Little Manitou	57.3–67.0	4	193 (July)	837

Discussion

This study demonstrates that the number of plant species decreases with increasing salinity. Table 3 shows the 'salinity' tolerance for each aquatic or amphibious species in saline lakes on the Canadian prairies and parklands. Unless species were found in water or in saturated soils at the water's edge they were not included in the table. In the hypersaline range (>50 g l^{-1}) a total of eight aquatic species

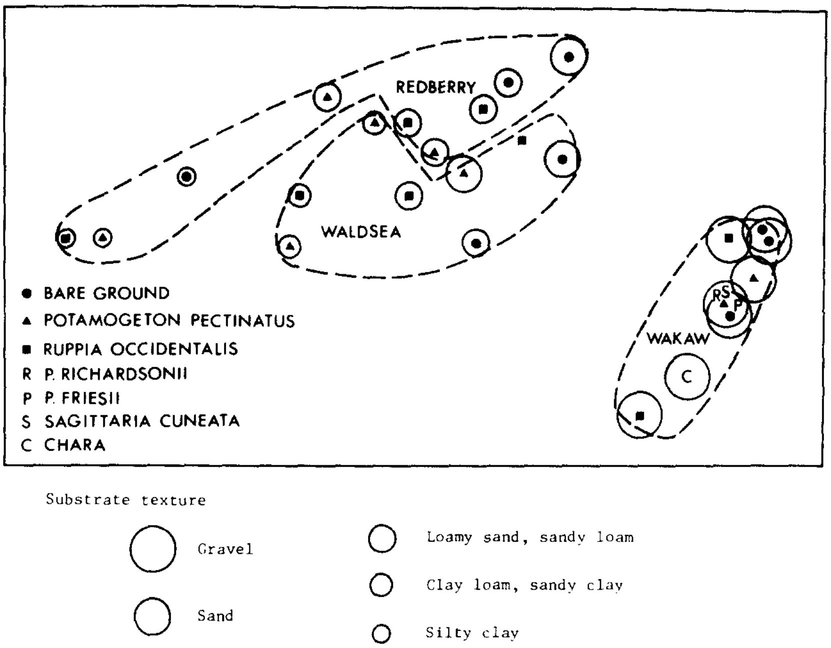

Fig. 8. Bray Curtis ordination of stands in Redberry, Waldsea and Wakaw lakes with increasing size of substrate particles to the right. The relative size of particles is represented in the key.

were present. Only *Ruppia maritima* (Chappice Lake), *R. occidentalis* and *Potamogeton pectinatus* (Big Quill Lake) persist as submerged plants whereas the emergents *Scirpus maritimus, Distichlis stricta, Puccinellia nuttalliana* and *Triglochin maritima* grow in water and on the lake shores of Muskiki and/or Whiteshore lakes. The ability of *S. maritimus* and *T. maritima* to tolerate the extremely saline conditions in Whiteshore Lake (up to 308 g l^{-1}) is indeed remarkable. In spite of this these species do not normally occur in water in other saline lakes above a salinity of about 75 g l^{-1}. The most saline site where *S. americanus* occurred was in Big Quill Lake. Millar (1976) included only *R. maritima* in his hypersaline category (>45 mS cm^{-1}).

In the mesosaline range (20–50 g l^{-1}) *P. pectinatus, R. maritima* and *R. occidentalis* are the only common submerged plants while the emergents *S. paludosus, S. americanus, T. maritima, D. stricta* and *P. nuttalliana* are characteristic plants which live in or near the water. A few other species (*Ranunculus cymbalaria, Scirpus acutus*) also occur in these lakes or their margins but their occurrence tends to be sporadic. Stewart & Kantrud (1972) considered *R. cymbalaria* as a secondary emergent inhabiting a conductance range of 1–15 mS cm^{-1} in North Dakota ponds. Although *Scirpus acutus* occurred in mesosaline Middle and Gooseberry lakes, it is normally an inhabitant of subsaline and hyposaline lakes. The mesosaline category embraces ten species in Saskatchewan saline lakes but only seven species can be considered as consistent inhabitants (Table 2).

In the hyposaline range (3–20 g l^{-1}) species numbers only increase significantly in waters below 4–5 g l^{-1}. If a species occurs at 3 g l^{-1} salinity (Table 3), it likely also occurs in subsaline (0.5–3 g l^{-1}) waters and may occur in fresh water (<0.5 g l^{-1}). All of the species that inhabit mesosaline and hypersaline lakes and their margins are also associated with hyposaline lakes particularly in the upper half of the range. Twenty-one species (Table 2) were present in marginally saline lakes but even here all species did not occur in each lake. Seven submerged species were present in Wakaw Lake but an additional twelve floating and emergent species occurred in the associated marshes. Other lakes in this salinity range (Fleeinghorse, Humboldt, Van Scoy) are habitats for fewer species although they were not examined as thoroughly as Wakaw Lake.

In the Chilcotin region of British Columbia, Reynolds & Reynolds (1975) found *Ruppia maritima* but only in highly alkaline waters up to 3 mS cm^{-1}. St. John & Courtney (1924) found the species in Epsom Lake, Washington, in a solution of almost pure magnesium sulphate. Metcalf (1931) found *R. maritima rostrata* over a salinity range of 0.457 to 77.4 g l^{-1} in North Dakota lakes, but *R. occidentalis* occurred in less alkaline (= saline) lakes. Stewart & Kantrud (1972) considered *R. maritima* and *R. occidentalis* as primary species in North Dakota ponds over conductivity ranges of 5–100 mS cm^{-1} and up to 5 mS cm^{-1} respectively. Wetzel (1964) investigated *R. maritima* in Borax Lake (24–60 g l^{-1}), California. Ungar (1967) reported *R. maritima* present over a range of 1.02–2.25% salt in Kansas water bodies. In Australia *Ruppia maritima* only occurs up to 3 g l^{-1} salt (Brock & Lane, 1983) but it appears to be a different form than is found on the North American plains.

The species names *Ruppia maritima* and *R. occidentalis* appear to have been used interchangeably at times for the same plant in the northern Great Plains region of North America. Muenscher (1944) states that *R. occidentalis* 'appears to be a form of' *R. maritima*. Rydberg (1932), Fernald (1970) and Scoggan (1978) separate the species so that *R. occidentalis* adequately describes the plant commonly found in saline prairie lakes. Distinguishing features are 'leaves in fan-like groups, to about 2 dm long, their sheaths to about 7 cm long'. It also tends to have long coiled peduncles which coil towards the distal end in contrast to *R. maritima* var. *maritima* which coils at the base. The description of *R. maritima* given by Jacobs & Brock (1982) is much narrower than that of Scoggan (1978) who describes 8 varieties. Only *R. maritima* var. *rostrata* Agardh has been found in Saskatchewan with specimens lodged in the Fraser Herbarium, University of Saskatchwan. A similar plant inhabits shallow waters of some saline lakes. Its sheaths are less than 2 cm long and leaves are relatively short but the peduncles which do not coil may be up to 20 cm long compared to a plant about 10 cm tall. In this treatment, the tall coiled 'variety' is referred to as *R. occidentalis* while the short 'variety' is called *R. maritima*.

The taxonomic problem of *Ruppia* variation in North American prairie-parkland lakes may be an environmental one. *Ruppia maritima* as described above invariably grows in shallow water of more saline Canadian lakes. This in itself results in shorter plants and obviates the necessity of long peduncles. *Ruppia occidentalis* grows in deeper water where its growth form is advantageous to its survival. In shallow locales and in more highly saline waters plants often fail to flower and this poses taxonomic problems. The habitat may impose vegetative variations that taxonomists interpret as genetic variations.

Potamogeton pectinatus does not flower, apparently, in Big Quill Lake, Saskatchewan, (>45 g l^{-1} TFR) but is able to grow there vegetatively. Below this salinity it produces flowers and fruits normally. It was present from fresh water to 36 g l^{-1} salinity in North Dakota lakes (Metcalf, 1931) and its range in ponds there was from fresh water to 45 mS cm^{-1} conductivity (Stewart & Kantrud, 1972). In northern Kansas water bodies the species occurred over a 0.32 to 0.40% salinity range (Ungar, 1967). It was only present in conductivities up to 3 mS cm^{-1} in highly alkaline lakes of the Interior Plateau of British Columbia (Reynolds & Reynolds, 1975). It is also tolerant of only low salinities (up to 6 g l^{-1}) in Australia (Brock & Lane, 1983). Comelles (1981) found this species in Spanish hypo- and mesosaline waters. It was present in Russian lakes in the southern Urals over a range of 6 to 19 g l^{-1} salinity (Orabkova *et al.*, 1978) and in Qinghai Hu, China, at 12 g l^{-1} (Academia Sinica, 1979). It occurred in Rocher Pan, South Africa (Coetzer, 1981) and in hyposaline Egyptian lakes where it made up more than 90% of the submerged vegetation of Lake Mariut (Aleem & Samaan, 1969).

Other submergents were restricted to waters below 5 g l^{-1} in Humboldt, Wakaw and Van Scoy lakes. *Myriophyllum spicatum, Utricularia vulgaris, Potamogeton richardsonii* and *Sagittaria cuneata* occurred in North Dakota ponds below 5 mS cm^{-1} (Stewart & Kantrud, 1972). *Potamogeton vaginatus* occurred over a range of 2–15 mS cm^{-1}, and *Hippuris vulgaris* was not found in saline water. *Polygonum* species have been reported growing in saline waters in British Columbia (Reynolds & Reynolds, 1975), North Dakota (Stewart & Kantrud, 1972) and in Australia but are not present in saline waters of the Canadian prairies and parklands. Steward & Kantrud list a great many more species of plants in North Dakota ponds than we have listed for Canadian saline lakes. This is probably an effect of greater fluctuation of water levels and salinity in ponds and associated marshes.

The most prominent emergent species of saline lakes of the Canadian prairies and parklands is *Scirpus maritimus* var. *paludosus*. There are few saline lakes where it is not found. Millar (1976) found it to be successful over the range of 2–45 mS cm^{-1} conductivity in Canadian prairie wetlands. Ungar (1967) found it over the conductivity range of 7–27.2 mS cm^{-1} in northern Kansas water bodies while Ungar (1974) gives a salinity range of 0.7 to 4.6% for this species. Lieffers & Shay (1982a) found that it grew in water conductivities of 0.8 to 58 mS cm^{-1} in 24 sites in prairies and parklands of Alberta, Saskatchewan and Manitoba. It dominated the deep marshes (2–45 mS cm^{-1}) of North Dakota ponds (Stewart & Kantrud, 1972). *Scirpus maritimus* has been reported from the Oldesloe salt waters (Germany) (Koppe, 1925), from Spain (Alonzo & Comelles, 1981) and from Rocher Pan, South Africa (Coetzer, 1981) but this may not be the same variety as occurs on the North American plains.

Ungar (1967) noted that *S. americanus* occurred in northern Kansas over a conductivity range of 2.4–11.2 mS cm^{-1}. In North Dakota ponds it dominated the shallow marsh system where the conductivity range was 1 to 45 mS cm^{-1} (Stewart & Kantrud, 1972). This is similar to the range in which it was found in our study.

Puccinellia nuttalliana developed normally over the 15–45 mS cm^{-1} range in Saskatchewan wetlands (Millar, 1976) and dominated the shallow marsh emergents of North Dakota ponds over the same range (Stewart & Kantrud, 1972). It occurred over a 1.2–20 mS cm^{-1} range in the sulphate soils of South Dakota (Ungar, 1970). Other species, presumably ecological equivalents, occur in the saline soda lakes in Austria (Hofler & Fetzmann, 1959) and Hungary (Komaromy, 1980).

Triglochin maritima is a common species around Alberta and Saskatchewan saline lakes and occurs in the water or just beyond the water margin. In North Dakota ponds it is a common secondary species in wet meadows over the range 2–45 mS cm^{-1} (Stewart & Kantrud, 1972) but is unimportant on South Dakota sulphate soils (Ungar, 1970). This species is a prominent member of marsh vegetation elsewhere: Oldesloe, Germany (Koppe, 1925); Burgenland lakes, Austria (Stundl, 1939). Equivalent ecological species occur in Australia (Brock & Lane, 1983).

Scirpus acutus was present in fresh to 15 mS cm^{-1} water (but *S. validus* only occurred under 2 mS cm^{-1}) in North Dakota (Stewart & Kantrud, 1972), a similar range to that found by Millar (1976) in Canadian prairie wetlands. Our range was similar but it also occurred in small quantities in Middle and Gooseberry lakes with conductivities of 22 and 33 mS cm^{-1} respectively. Reynolds & Reynolds (1975) found *S. validus* associated with conductivities of 1.5–12 mS cm^{-1} in waters of the Chilcotin region of British Columbia. This species has a much lower range on the Canadian prairies and it may, therefore, have been *S. acutus* in British Columbia.

Typha latifolia occurs in only a few marginally saline lakes (Wakaw, Van Scoy) but is common in fresh and subsaline waters of western Canada. Stewart & Kantrud (1972) considered it a secondary species in North Dakota ponds over a range up to 5 mS cm^{-1}. They noted the presence of *T. angustifolia* over a 1–15 mS cm^{-1} range but this species does not occur in Canadian saline lakes. Decksbach (1924) found *T. latifolia* in weakly saline lakes north of the Sea of Aral in Russia. It also occurs in Egypt (Aleem & Samaan, 1969), but other *Typha* species replace it elsewhere in Africa and Asia (Hammer, 1986).

Juncus balticus was a primary dominant species of North Dakota wet meadows with a conductivity range up to 45 mS cm^{-1} (Stewart & Kantrud, 1972). In British Columbia it was found in the 1.5–12 mS cm^{-1} range but was stranded beyond the water margin by midsummer (Reynolds & Reynolds, 1975). We never observed it growing in water even though lake levels were generally high in 1985.

Millar (1976) found *Eleocharis palustris* over the fresh water to 15 mS cm^{-1} range, and it was dominant in shallow water over the same range in North Dakota ponds (Stewart & Kantrud, 1972). Lieffers & Shay (1982a) found the species present outside the *Scirpus maritimus* zone in western Canada sites. It grows mixed with other species in the Wakaw Lake marsh.

As the water level recedes, *Salicornia rubra, Suaeda calceoliformes, Chenopodium rubrum, Hordeum jubatum, Sonchus arvenis* and *Glaux maritima* invade the exposed shores. Millar (1976) noted that *S. rubra* and *S. calceoliformes* developed normally in the 15–45 mS cm^{-1} category in Canadian wetlands whereas *C. rubrum* and *H. jubatum* were only found in up to 15 mS cm^{-1} waters. Ungar (1967) reported a soil conductivity of 8–110.4 mS cm^{-1} for *S. calceoliformes* in northern Kansas. *Salicornia rubra* occurred over a range of 2.3–8.0% salt in sulphate soils of South Dakota (Ungar, 1970). It was a primary dominant in the 5–45 mS cm^{-1} range in the shallow marsh of North Dakota ponds, but *S. calceoliformes* was a secondary dominant over the same range (Stewart & Kantrud, 1972).

Stewart & Kantrud (1972) considered *Scirpus nevadensis* a common shallow marsh emergent in the 15–45 mS cm^{-1} conductivity range in North Dakota potholes. It was never found in Canadian saline lakes in our study and occurred in frequently well above lake water levels.

The only major factor apparently affecting aquatic vascular vegetation and its distribution in Saskatchewan saline lakes appears to be specific conductance of the substrate or, in effect, the total concentration of ions in the substrate. This conclusion was drawn from Bray Curtis ordinations of stands with respect to environmental factors in Redberry, Wakaw and Waldsea lakes. The initial ordination separates lakes into stands from Wakaw Lake and a combination of stands from the two other lakes (Fig. 5). The substrate conductivity of Wakaw Lake in markedly different from that of the other two lakes and this coincides with the difference in vegetation (Figs. 5, 6). *Potamogeton pectinatus* and *Ruppia occidentalis* have a very broad tolerance to conductivity, but the other submerged species can only tolerate low conductivities. It is noted that the substrate conductivities of Redberry Lake were relatively higher than conductivities of the water mass whereas in Waldsea Lake the reverse is the case (Table 4). Thus substrate conductivity cannot be taken as equivalent to water conductivity. Stewart & Kantrud (1972) also concluded that total concentration of ions was the determining factor for vegetation in North Dakota ponds. Halophytes grow well in subsaline waters but do not compete successfully with glycophytes at low salinities and may thus be excluded from such habitats (Ungar, 1974). Lack of competition permits their success at higher salinities. This is probably true for *Ruppia* species, *Potamogeton pectinatus, Scirpus americanus, S. maritimus, Salicornia rubra* and *Triglochin maritima* that tend to be dominant in more saline habitats in prairie and parkland lakes.

When Redberry and Waldsea lake stands are ordinated together, differences in texture characterized the horizontal axis with coarser soils towards the right (Fig. 7). A similar separation is achieved in Fig. 8. Although this separated stands within lakes, the same changes in texture were found within each lake, and *Ruppia occidentalis* and *Potamogeton pectinatus* were found in all textures in each lake (Fig. 7). In Wakaw Lake all vascular species inhabited coarse substrates (Fig. 8). *Chara* species grew densely on fine substrates excluding other species. High sulphate characterized stands towards the top of the ordination (Fig. 7) and were more characteristic of Redberry Lake than Wakaw lake. Again, there was no effect on the distribution of the two macrophytes present. Apparently these aquatic species have a broad tolerance to salinity, specific ions such as sulphate, and substrate texture. No other substrate feature appeared to relate to plant distribution.

Ungar (1970) noted that the South Dakota flora on sulphate soils was similar to that in Nebraska on chloride dominant soils. This supports our results which show no ion effects. In terrestrial soils Dodd *et al.* (1964) found no relationship between plant distribution and soil ion concentration. They were able, however, to relate plant occurrence to general soil types. Dodd & Coupland (1966) related osmotic pressure of plant sap to salinity of the soil and its osmotic pressure. The highest osmotic pressure was associted with the most saline dry soils on which *Salicornia rubra* was very successful. Other species, e.g. *S. maritimus, E. palustris*, occurred on soils with successively lower osmotic pressures. Lieffers & Shay (1982a) found that *S. maritimus* was limited in distribution by the degree of salinity of the substrate during germination and seedling establishment.

This was most successful below a conductivity 20 mS cm^{-1}. Fluctuating water levels result in fluctuating substrate conductivities and different zones of establishment of this plant in different years.

pH does not seem to affect the distribution of the more salt tolerant species but there are far fewer vascular plant species present in low hyposaline waters with high pH (Fleeinghorse, Lake of the Rivers, Killarney).

A most surprising result was that extensive areas of the substrate were not occupied by plants and were not apparently different than stands that were overgrown. It does not seem likely that propagules were unavailable. Plants that have overwintering rhizomes or bulbs undoubtedly have an advantage. Seeds are also extensively produced and waterfowl utilization should result in good dissemination.

Plants did not grow below 10% of surface light in Redberry Lake so light was not limiting. Both *Ruppia occidentalis* and *Potamogeton pectinatus* did not grow below the thermocline but water temperature is probably not limiting because initial growth begins at low temperatures. It is more likely that water pressure delimits the depth at which plants grow in this lake. Plants such as these grow well in a broad spectrum of light intensities, but other species (*Sagittaria cuneata, Myriophyllum spicatum, P. richardsonii, P. friesii, Utricularia vulgaris*) are high light species and thus are found only in shallow waters. Emergents are characteristically high light species. The meromictic nature of Waldsea Lake probably precludes macrophytic growth below 7 m where the environment is anoxic and light limited (bacterial plate absorbs all light).

There are considerable differences in plant cover between lakes and within lakes (Table 5). There is no apparent relationship to salinity differences. In fact the greatest differences are within lakes where the salinities are essentially the same. Usually low plant cover is associated with low plant biomass. Considerable differences are also apparent between June and August biomass results and these are not always consistent. It should be noted that the high biomass results for Little Manitou Lake are attributable to the alga *Rhizoclonium*. The amount of biomass is not related directly to salinity in the littoral sites of these six lakes.

Lieffers & Shay (1982b) determined seasonal growth patterns of *S. maritimus* in some Saskatchewan lakes. The maximal standing crop of 625 g m^{-2} was achieved by early August but yearly fluctuations in salinity and water level markedly affected the standing crop. High salinity associated with low water levels had a negative effect on productivity.

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