Vegetation–environment relations in a brackish marsh, Lulu Island, Richmond, B.C.

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A study of plant–environment relations was conducted on the foreshore marshes of Lulu Island in the Fraser River delta. Analysis of tidal records indicated that the marsh platform could be subdivided into three elevational zones: a low marsh dominated by *Scirpus americanus* and *S. maritimus*; a middle marsh dominated by *Carex lyngbyei*, *Triglochin maritimum*, and *S. maritimus*; and a high marsh community of *Agrostis exarata*, *Potentilla pacifica*, *Distichlis spicata*, and *Typha latifolia*. This is interpreted as a successional sequence. The low marsh experiences a maximum continuous submergence of 21–16 h, the middle marsh a maximum of 8 h, and the high marsh a maximum continuous exposure of >200 h. ANOVA results demonstrate the overwhelming importance of elevation (*Typha*, *Potentilla*, *Distichlis*) and elevation–salinity interactions (*Scirpus* spp., *Carex*, *Agrostis*) as controls on plant distribution. In addition substrate texture and moisture content are significantly associated with variations in species abundance. The Lulu Island marshes are floristically and ecologically similar to estuarine and deltaic marshes of Washington and Oregon. Variations in vegetation and successional pattern within this group are likely a function of fluvial regimes, which influence salinity and sediment characteristics.

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Une étude des relations plantes–environnement a été poursuivie dans les marais intertidaux de l'île Lulu dans le delta de la rivière Fraser. L'analyse des données de marées montre que la terrasse où se trouvent les marais peut être subdivisée en trois zones altitudinales: un marais inférieur dominé par *Scirpus americanus* et *S. maritimus*, un marais moyen dominé par *Carex lyngbyei, Triglochin maritimum* et *S. maritimus*, et un marais supérieur avec une communauté à *Agrostis exarata, Potentilla pacifica, Distichlis spicata* et *Typha latifolia*. Ces différences sont interprétées comme une séquence successionnelle. Le marais inférieur subit une submersion continue maximale de 21–16 h, le marais moyen, une submersion continue maximale de 8 h, et le marais supérieur, une exondation continue maximale de plus de 200 h. Les résultats de l'analyse de variance montrent l'importance majeure de l'altitude (*Typha, Potentilla, Distichlis*) et des interactions altitude–salinité (*Scirpus* ssp., *Carex, Agrostis*) pour le contrôle de la répartition des plantes. De plus, la texture et la teneur en eau du substrat sont significativement associées aux variations de l'abondance des espèces. Les marais de l'île Lulu sont floristiquement et écologiquement semblables aux marais estuairiens et deltaïques de l'Etat de Washington et de l'Orégon. Les variations dans la végétation et dans les patrons de succession à l'intérieur de ce groupe de marais dépendent probablement des régimes fluviaux, lesquels influencent les caractéristiques de la salinité et de la sédimentation.

[Traduit par le journal]

Introduction

The coastal marshes of western North America are not as extensive or as floristically diverse as their eastern counterparts (Chapman 1960). The tectonically active leading edge of the North American plate offers scope for coastal marsh development only in a few sheltered situations where fluvial action or longshore drift provide a large sediment supply. On the Pacific coast of Canada, marshes are restricted to the heads of protected inlets and the delta fronts of the major rivers. According to MacDonald and Barbour (1974), all of these marsh environments are "poorly known."

The most extensive of these marshes is the one that fringes the delta of the Fraser River. The impact of human settlement and changing land-use practices on the terrestrial and marine ecosystems of the Fraser estuary has become of major concern in the last decade (Dorcey 1976). Much of this concern focusses on alienation of marsh habitats, which are important feeding grounds for migratory waterfowl and some species of juvenile salmon (Dunford 1975). Botanical studies conducted on the Fraser marshes to date have, for the most part, been descriptive and fairly cursory (Gates 1967; Burgess 1970; Forbes 1972; McLaren 1972; Wade unpublished[1]; Taylor 1974). Recently, however, two studies have monitored the primary productivity of these marshes (Yamanaka 1975; Moody 1978), and the vegetation pattern of a small marsh area threatened by port expansion has been described in detail (Hillaby and Barrett 1976). The distribution patterns of plant species in the Fraser marshes are broadly known as a result of these studies, but the successional and environmental relations of the plant

[1]Wade, L. 1972. Sturgeon Banks: an ecological study. Richmond Nature Park, Richmond, B.C.

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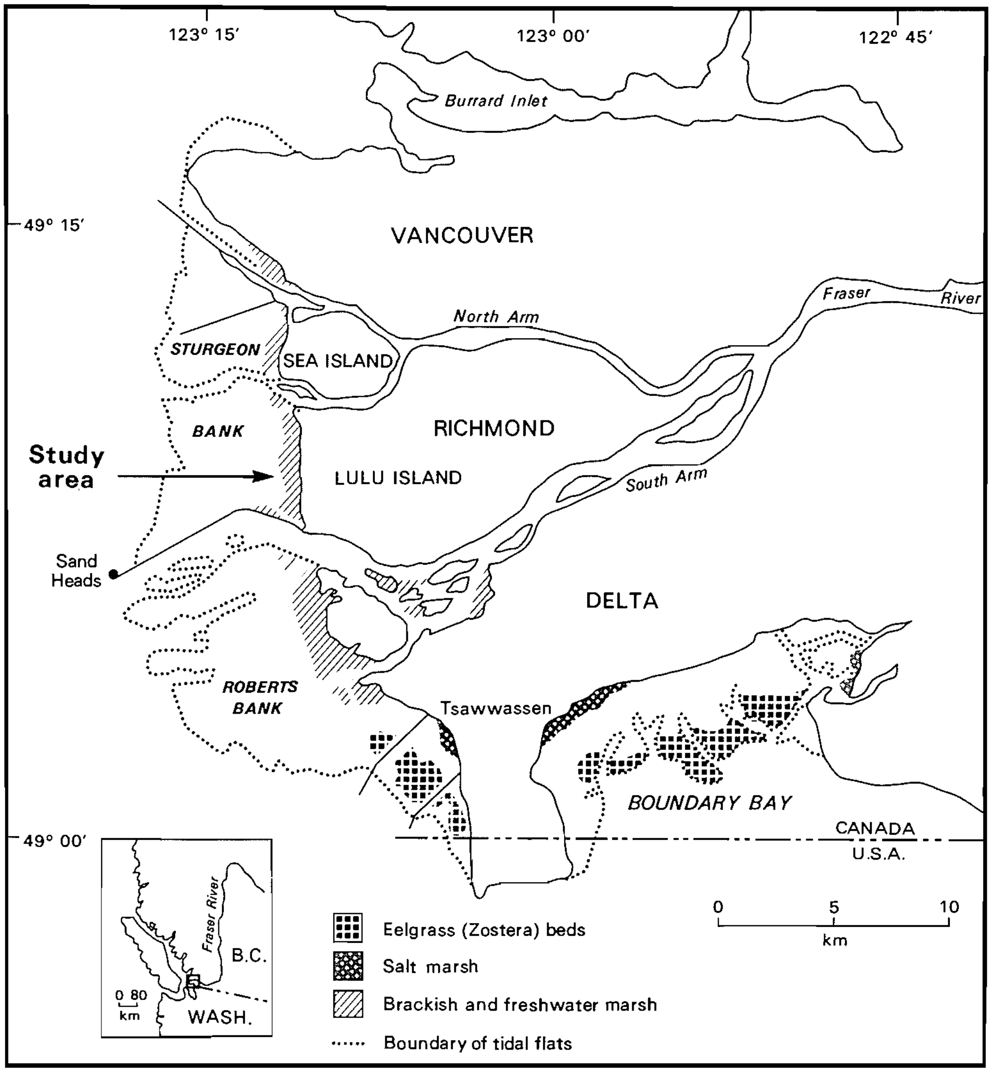

FIG. 1. Location of the study area.

communities have received attention only from Moody (1978). Kistritz (1978) identifies this problem as one of the major gaps in our current knowledge of the estuary of the lower Fraser.

The direct long-term observation of natural plant succession has not been undertaken in marsh habitats. All models of coastal marsh succession are based on the premise that the well-defined vertical zonation of plant species distributions is a spatial analogue of the successional process (e.g., Chapman 1938, 1939, 1941; Adams 1963; Beeftink 1977). Vertical zonation is regarded as a response to the varying duration of tidal submergence across the marsh platform and is influenced by interactions between tidal shear, sediment accretion, and substrate water content, and potential rates of photosynthesis by marsh phanerogams in turbid estuarine waters.

The relationship between plant species distribution and four of these physical factors (submergence, pore-water salinity, sediment texture, and substrate water content) is examined in this study.

Description of the study area

The total area covered by tidal marshes in the Fraser estuary is estimated by Yamanaka (1975) at 27 km^2 (see Fig. 1). Roughly 10% of this total area is found along the foreshore of Boundary Bay, to the south of the present Fraser distributaries. This has been an inactive section of the delta front for 6000 years (Blunden 1973) and supports true salt marsh (Kellerhalls and Murray 1969). The remainder of the marsh (apart from a small salt marsh enclave at Tsawwassen described by Hillaby and Barrett (1976)) forms a 1-km-wide fringe along the active delta front of Sturgeon and Roberts banks, and extends upriver, encompassing the islands of the South Arm. This study surveys the marshes of the Lulu Island foreshore on Sturgeon Bank, comprising some 20% of the total marsh area in the lower Fraser.

The Fraser tidal marshes have evolved as a result of the interplay between the maritime influences of the Strait of Georgia and the discharge and sediment load of the Fraser River. The Strait of Georgia experiences mixed tides, predominantly semidiurnal, with a pronounced daily inequality, and a mean range over the tidal platform of 2.6 m (Thomson unpublished[2]). Extreme lower low water takes place around midnight in winter and around noon near the summer solstice. The tidal flats are therefore exposed throughout much of the day during the growing season.

The Fraser River has a marked annual peak in discharge, with 80% of the annual flow occurring during the spring freshet from March to July. The mean annual flow of the river is 3500 m^3 s^{-1}, 80% of which is discharged through the South (or Main) Arm (Hoos and Packman 1974). Only slight entrainment of the river water occurs because of the moderate tidal range, and the surface waters of the Strait are consequently brackish for some distance from the delta front (Hoos and Packman 1974).

Methods

Topography and tidal submergence

Six transects were established in an E–W direction across the marsh surface, approximately 800 m apart (Fig. 2). A dumpy level was used to measure marsh surface elevation of survey stations at 50-m intervals from the sea dyke to the marsh edge. Each transect was tied to control bench marks in Richmond municipality. Recorded elevations were adjusted to local tide datum (300 cm below geodetic at Sand Heads). A total of 100 survey stations were established on the marsh for vegetation and soil sampling at a later date (stations on landfill close to the dyke were discarded).

The periods of tidal submergence and exposure were calculated for 10-cm intervals above local datum using the 1-h records for Vancouver in 1978. The results were then calibrated for Sturgeon Bank using the secondary tide gauge at Sand Heads. The duration of tidal flooding for each survey station can be interpolated from these data.

Vegetation survey

The vegetation survey was undertaken in May–June 1978. All plants growing in areas delineated by four random casts of a 0.25-m^2 quadrat frame around each survey station were clipped to ground level. Plants were shipped to the laboratory, dead tissue was discarded, and living material was separated by species and dried at 105°C for 24 h. The dry weight of each species at each site was then determined, and the specific composition of the vegetation was expressed as a percentage of total biomass at that station, following the recommendations of Smartt *et al.* (1974). Taxonomic nomenclature follows Hitchcock and Cronquist (1973).

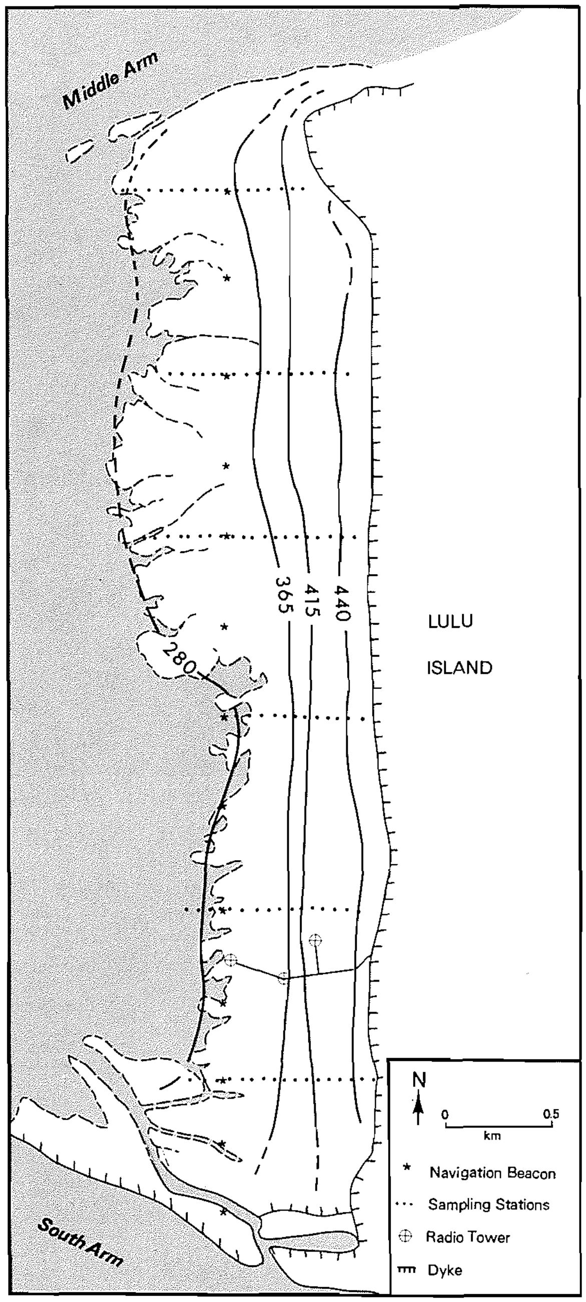

FIG. 2. Generalized topography of the Lulu Island foreshore marsh. The positions of sampling–survey stations are shown, and the location of the tidal thresholds in the marsh is given. All elevations are given as centimetres above Sand Heads tide datum.

Soil survey

A single surface (< 10 cm depth) soil sample of ~ 250 g was

[2]Thomson, R. E. 1976. The oceanographic setting of the Fraser River delta front. Institute of Ocean Sciences, Sidney, B.C.

taken at each survey station at low tide for textural and moisture content determination. Moisture losses were calculated as percent dry soil weight after drying at 105°C for 24 h. The ovendried samples were ground and the particle-size distribution in a 100-g sample was determined after the method of Bouyoucos (1951). No sieving was necessary as all fractions were < 2 mm. Interstitial water was allowed to collect in a single hole at each site, and the salinity of the water was determined at the date of vegetation collection using a portable Y-S-I model 33 salinometer.

Data analysis

The role of the various physical factors in controlling plant species distribution was assessed using an analysis of variance (ANOVA) procedure. The factors to be examined are non-independent, and in a field survey the number of cases falling in the cells of the cross-classification are unlikely to be equal. A nonorthogonal hierarchical ANOVA design was therefore employed for data analysis. The "treatment" cells were constructed by assigning high and low values to salinity, sand content, and water content in substrate. The division between high and low categories was taken as the median value for all three variables. Elevation was subdivided into three categories based on tidal thresholds.

Results

Topography and tides

The seaward edge of the marsh corresponds with an elevation of circa 280 cm above tide datum, and there is a rise in elevation of less than 200 cm across the marsh platform to the base of the sea dyke (Fig. 2). The duration of maximum submersion, maximum exposure, and the ratio of submergence to emergence across this elevational gradient are depicted in Fig. 3.

The marsh platform may be subdivided into four zones based on tidal thresholds. The leading edge of the marsh lies close to 280 cm above local datum, just above Mean Higher Low Water. At this elevation there is a rapid increase in maximum exposure period, from 9 h below this level to 17–18 h immediately above. The maximum continuous submersion period at this elevation is 21 h, and the marsh is submerged some 60% of the time.

Within the marsh the major tidal threshold occurs immediately below Mean Lower High Water (MLHW = 380 cm), at 365 cm above tide datum. Maximum continuous submergence declines from 16 to 8 h at this elevation, and exposure times increase to a maximum of 63 h. This tidal threshold has a physical counterpart on the marsh platform. There is a well-marked erosional step, 30–50 cm in height at this level on the marsh surface. This minor scarp marks a geomorphic boundary between a zone of compacted, fine-grained sediments, which are cut by a dense network of narrow, deep anastomosing ditches above the scarp, and a zone of semistabilized muds and sandy silts with diffuse drainage patterns and many tidal pans, below. Two further tidal thresholds in the upper marsh are associated with rapid increases in maximum emergence periods. The first occurs at 415 cm and corresponds with the transition between "submergence" and "emergence" marsh according to Chapman's (1960) definition. This datum is some 10 cm below Mean Higher High Water (MHHW) on the Lulu Island foreshore. A further rapid increase in exposure periods occurs at 440 cm. Above this level the marsh surface is virtually extratidal throughout the year, the platform remaining emergent for weeks or months at a time. Only small remnants of marsh at this elevation exist along the base of the sea dyke; most of this high marsh was reclaimed at the turn of the century. In the discussion that follows the zone below 365 cm will be referred to as low marsh, that between 365 and 415 cm as middle marsh, and that above 415 cm as high marsh. Marsh remnants above 440 cm are grouped with the high marsh.

Salinity

The mean interstitial salinity recorded for all stations in May–June 1978 was 10.1 ± 0.3 g L^{-1}, with a range of 3.5–15.5 g L^{-1}. Salinity levels are lowest in the upper marsh (generally below 8 g L^{-1}), partly as a result of the influx of freshwater from pumping stations in the dykes.

Sediment texture

The marsh substrate consists primarily of silt-sized fractions, with a variable admixture of fine sand and clay. The mean grain size decreases with marsh surface elevation, reflecting the lower tidal energy environment of the upper marsh platform (Fig. 4). The proportion of fine sand varies from over 40% along the northwestern marsh littoral (and close to the dyke culverts) to less than 10% in the middle marsh. The sources of these coarser sediments are the Middle Arm of the Fraser River, a series of sand swells on the unvegetated tidal flats, and erosion of the reclaimed lands east of the dyke.

Soil water content

Surprisingly, the soil water content is highest in the high and middle marsh at low tide. Low marsh sediments generally contain less than 70% water, whereas in the upper marsh values are over 100% of soil dry weight. This results from two factors. The higher proportion of fine sand in the low marsh substrate results in fairly rapid drainage of these soils during ebb tide. In the upper marsh the soil moisture content may be locally increased during low tides by discharge of water from the dyke pumphouses.

Vegetation zonation

Chapman (1977) has observed that marsh successions on the Pacific Coast of North America "appear to be very simple." This may be partially the result of widespread alienation of mature marsh by draining and dyking, but is also likely due to the depauperate flora of these marshes. Only 19 species of vascular plants were

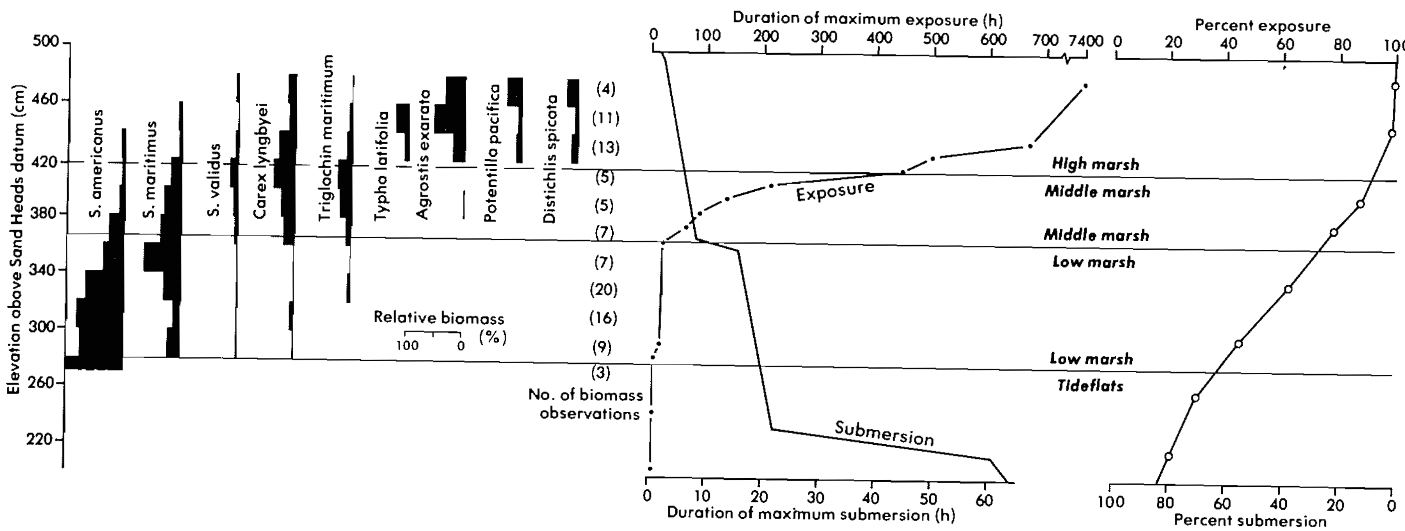

FIG. 3. Distribution of species abundances (measured as relative aboveground biomass) as a function of elevation and tidal variables.

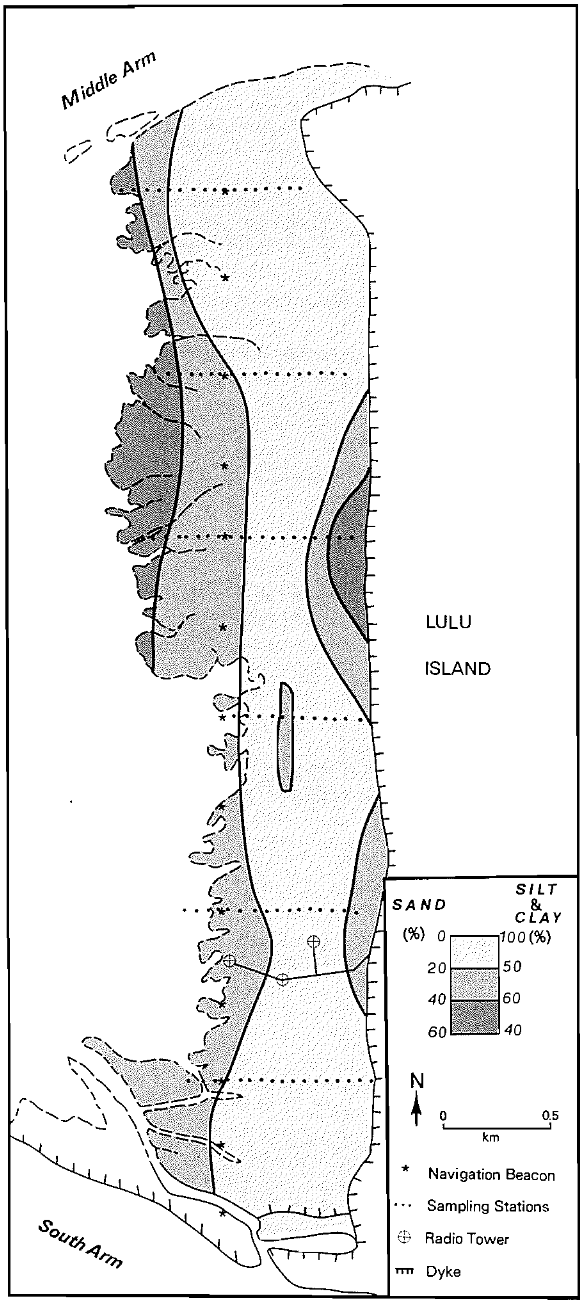

FIG. 4. Substrate texture in the Lulu Island foreshore marsh.

encountered in the field survey, and three of these, *Scirpus americanus*, *S. maritimus*, and *Carex lyngbyei*, account for almost 75% of the total plant biomass. *Scirpus validus*, *Triglochin maritimum*, *Typha latifolia*, *Agrostis exarata*, *Potentilla pacifica*, and *Distichlis spicata* account for more than 20% and the remainder is produced by *Puccinellia pumila*, *Glaux maritima*, *Lathyrus palustris*, *Sonchus arvensis*, *Ranunculus cymbalaria*, *Atriplex patula*, *Spergularia canadensis*, *Sagittaria latifolia*, *Deschampsia caespitosa*, and *Eleocharis acicularis*.

The vegetation pattern of the marsh was mapped from survey data and interpretation of aerial imagery. The pattern consists of a series of well-defined meridional zones (Fig. 5); species distribution is clearly controlled by the elevation of the marsh platform and the associated tidal regime. Although species ranges are fairly clearly delimited by the tidal thresholds (Fig. 3) there are variations in the dominance of species within each zone which can be attributed to other physical factors.

Table 1 presents a synopsis of the ANOVA results and delineates the two-way interactions and main effects influencing species distribution. Variations in species abundance are primarily due to interactions between elevation and salinity, or elevation and sediment texture operating singly or in concert, without significant interaction. The mean percentage biomass values, ordered by elevational categories and substrate conditions are presented in Table 2.

Variations in the abundance of *Scirpus americanus*, the dominant plant species in the marsh, can be attributed to an interaction between elevation and salinity in the middle and high marsh, and the physical properties of the substrate in the low marsh. *Scirpus americanus* forms dense monotypic stands along the marsh littoral on well-drained, silty–sand substrates of relatively low moisture content. The seaward expansion of this pioneer species is greatest in the northern part of the marsh where a series of megaripples approach the shore from the southwest and provide a supply of sand-sized material (Medley and Luternauer 1976). These sand swells have created a low tidal energy environment in their lee along the southern marsh littoral (Medley and Luternauer 1976). Expansion of *S. americanus* onto the resultant mud flat has taken place primarily along tidal creek margins and in other well-drained microhabitats. The expanding clones of *S. americanus* act as sediment traps and surface aggradation occurs in the form of broad hummocks, which gradually coalesce to form a fairly flat marsh surface with a microrelief of 30–50 cm. Interhummock areas close to the marsh front, and patches of senescent *S. americanus* in the centre of expanding clones may be scoured to form small tidal ponds, which are gradually infilled with mud, and invaded by *S. maritimus*. The annular clones of this species are a common feature of the outer margin of the low marsh. In the upper reaches of the low marsh, *S. maritimus* forms closed, but sparse stands on substrates of moderately high salinity and high water content. Better drained microhabitats in this part of the marsh are occupied by *S. americanus*. In the middle and upper marsh this species is restricted to areas of well-drained, coarser textured sediments of moderate

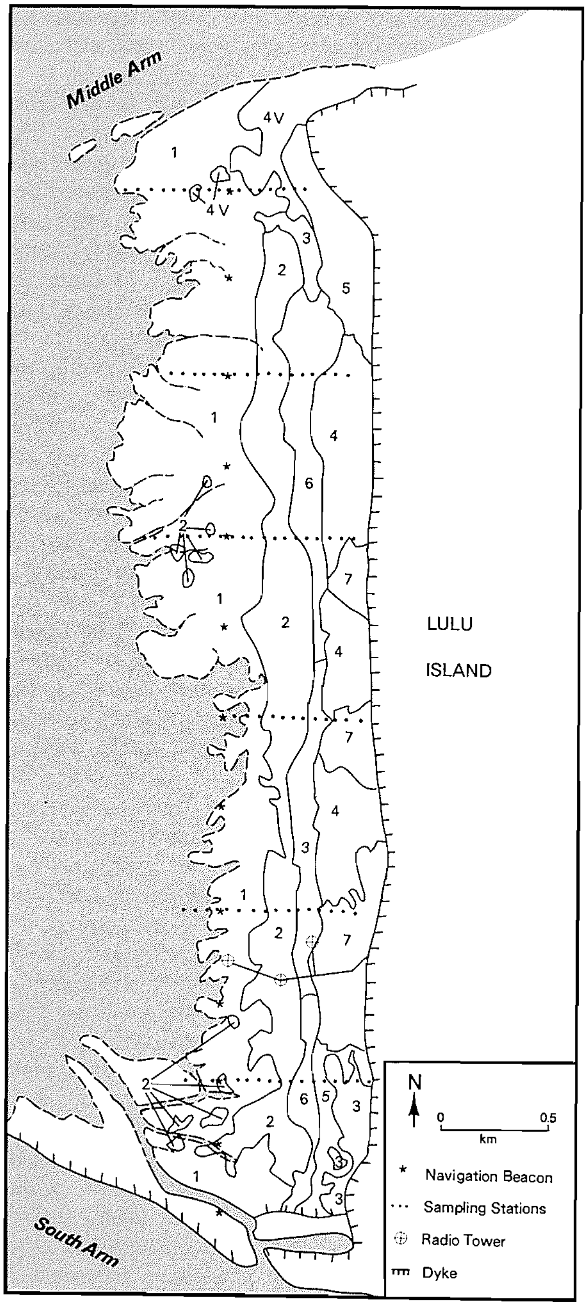

FIG. 5. Vegetation map of the Lulu Island foreshore marsh. Map based on field survey and interpretation of 1 : 12 000 imagery. Dominants are as follows: 1, *Scirpus americanus*; 2, *Scirpus maritimus*; 3, *Carex lyngbyei*; 4, *Potentilla pacifica – Distichlis spicata* (V, with significant admixture of *Scirpus validus*); 5, *Typha latifolia*; 6, *Triglochin maritimum*; 7, *Agrostis exarata*.

TABLE 1. Synopsis of ANOVA results: *F* ratios and significance levels

Species	Main effects				Interactions					
	Elevation (A)	Salinity (B)	Sediment texture (C)	Water content (D)	AB	AC	AD	BC	BD	CD
Scirpus americanus	54.4***	0.0	7.9**	4.0*	3.1*	0.3	0.1	0.5	2.4	0.0
Scirpus maritimus	7.0**	3.9*	0.0	5.4*	3.7*	0.2	0.0	0.9	4.3*	0.7
Scirpus validus	9.7***	5.3*	0.1	3.5	4.8*	2.1	2.1	0.1	0.3	0.3
Carex lyngbyei	10.3***	0.0	9.6**	0.1	8.3***	0.2	0.5	0.1	0.3	0.4
Triglochin maritimum	5.4**	1.3	7.1**	11.8***	0.6	0.5	13.6***	0.0	0.0	1.0
Typha latifolia	6.3**	1.8	0.9	0.0	2.9	1.5	0.9	0.0	0.0	0.0
Agrostis exarata	36.2***	4.6*	1.8	0.9	4.2*	0.1	2.0	0.0	0.0	0.0
Potentilla pacifica	13.0***	3.0	1.9	0.6	1.9	0.3	0.7	0.0	0.0	0.0
Distichlis spicata	7.8***	1.6	1.5	0.0	0.6	0.4	0.3	0.0	0.0	0.0

NOTE: Variance ratio significant at $P \leq 0.05$(*), ≤ 0.01(**), ≤ 0.001(***).

TABLE 2. Mean (±SEM) percentage biomass of plant species by substrate categories for each elevational zone in the Lulu Island marsh. Significant interactions or single factors are in italic type

	Elevational zone	Salinity		Sand content		Moisture content	
		Low	High	Low	High	Low	High
Scirpus americanus	Low	*68.0±7.3*	*63.8±6.2*	*45.4±9.9*	*72.9±4.9*	*71.2±5.0*	*40.2±5.8*
	Middle	*2.5±2.0*	*11.0±8.7*	*2.4±1.5*	*28.4±0*	*2.2±0*	*5.7±3.6*
	High	*0.8±0.6*	*10.5±6.1*	*4.4±2.3*	*0*	*13.0±0*	*3.2±0.6*
S. maritimus	Low	*21.1±6.4*	*30.6±6.0*	29.4±9.9	26.2±5.0	*23.1±4.6*	*40.6±11.9*
	Middle	*10.5±14.8*	*65.7±16.7*	23.5±12.3	71.0±0	*4.5±0*	*31.9±13.3*
	High	*3.0±1.8*	*6.2±2.8*	3.2±1.1	6.7±6.1	*0*	*4.1±1.5*
S. validus	Low	*1.8±1.1*	*0.1±0.1*	2.5±1.4	0.1±0.1	0.1±0.1	3.0±1.7
	Middle	*19.5±8.0*	*0*	14.6±8.3	0	0	14.6±8.3
	High	*3.9±2.3*	*0.4±0.4*	0.7±0.6	11.4±7.5	0	3.0±1.8
Carex lyngbyei	Low	*7.6±4.1*	*2.9±2.2*	*16.4±7.0*	*0.2±0.2*	3.1±2.2	10.0±5.5
	Middle	*52.7±15.4*	*0*	*39.5±14.0*	*0*	68.8±0.0	30.9±14.3
	High	*11.1±4.2*	*39.2±14.8*	*20.9±4.4*	*11.0±11.0*	0.2±0.0	19.5±5.6
Triglochin maritimum	Low	1.4±1.4	2.5±1.6	*6.3±3.9*	*0.5±0.5*	*2.4±1.5*	*1.0±1.0*
	Middle	14.8±10.1	12.8±12.8	*15.9±3.5*	*0*	*24.3±0*	*12.9±8.4*
	High	5.6±4.3	14.75±8.0	*10.2±4.7*	*0*	*86.7±0*	*5.3±2.7*
Agrostis exarata	Low	*0*	*0*	0	0	0	0
	Middle	*0*	*3.2±3.2*	1.2±0.4	0	0	1.2±1.2
	High	*44.2±1.5*	*10.7±9.5*	30.6±7.7	51.4±13.7	0	36.1±7.0

NOTE: *Typha latifolia*, *Potentilla pacifica*, and *Distichlis spicata* are omitted from this table. All three species are influenced only by the marsh surface elevation.

salinity. The elevation – salinity – water content interaction is more marked in the case of *S. maritimus*. It is the dominant species in the middle marsh on sites which have poor drainage and restricted freshwater influx. Conversely, on sites with low salinities *Carex lyngbyei* and *Scirpus validus* are the dominant species (Table 2). Furthermore, *C. lyngbyei* is also associated with well-drained, fine-grained substrates in this zone, which it shares with *Triglochin maritimum*. These species form fairly dense stands and build substantial root mats in the surface sediment. Transpiration rates are apparently very high in this zone; cracking and compaction of the surface of the substrate is noticeable on sunny summer days. Moody (1978) considers that these patches of compacted sediment and root mats are virtually immune to erosion, and there is therefore preferential tidal erosion around the edge of the colony, resulting in the growth of a steep-sided hummock. The middle marsh zone is a chaotic mosaic of small hummocks, separated from each other by deep, narrow ditches which are floored with soft muds and occupied by vigorous patches of *S. maritimus*. Outliers of this hummocky marsh surface occur in the lower marsh particularly in the northern sector. If these are relics of a previously more extensive middle marsh zone they indicate that the successional process in the Lulu marsh may be quite complex.

Scirpus validus is a prominent member of the middle marsh community in areas close to the Fraser River where freshwater influences are greatest. Table 2 demonstrates the importance of the elevation–salinity interaction for this species. *Scirpus validus* is also a minor element in the low and high marsh zones, typically occupying shallow ponds in areas of low salinity.

The high marsh is a complex mosaic of clones of *Typha latifolia*, *Potentilla pacifica*, *Agrostis exarata*, *Distichlis spicata*, and *Carex lyngbyei*, with an admixture of ruderals in disturbed sites. According to the ANOVA results, of the species which are restricted to the high marsh, only *Agrostis exarata* is responding to physical controls in addition to that of the submergence regime (Table 1). This grass forms extensive mats with an admixture of *Typha latifolia* in the immediate vicinity of pumphouse culverts in the dyke. Salinity values in these areas are lower than elsewhere on the marsh, and the soil moisture regime and vegetation in these areas have presumably been considerably modified in the postsettlement period as a result of flushing of drainage water into the marsh. *Typha latifolia* forms large, almost pure stands in areas close to the freshwater influence of the South and Middle arms of the Fraser River in the high marsh. Intervening areas experience a slightly higher salinity status and consists of meadows of *Distichlis spicata*, *Potentilla pacifica*, *Carex lyngbyei*, and *Scirpus validus*, with *Atriplex patula* and *Lathyrus palustris* as minor components.

Discussion

The pattern of vegetation zonation on the Fraser River foreshore marshes is clearly linked to the elevation of the marsh platform, with salinity, substrate texture, and soil moisture content being of secondary importance as determinants of species distribution.

As Moody (1978) notes, it is impossible to make a direct comparison between the elevational ranges of marsh plants in the Fraser system with those elsewhere in the Pacific Northwest because of the differences in tidal datum between the United States and Canada. Until we have comparable submergence–exposure data available, only qualitative comparisons can be made. It is clear, however, that the marsh described here has strong floristic and ecological affinities with those examined by Jefferson (1975) and Eilers (1975) in Oregon, and Disraeli and Fonda (1979) and Burg et al. (1980) in Washington. The dominance of *Carex lyngbyei* and *Scirpus americanus* places all these marshes into the Temperate Pacific biogeographic group, extending from northern California to southern Alaska (MacDonald 1977).

Jefferson (1975) outlined an elaborate successional model for coastal marshes in Oregon, and by extension, the entire Temperate Pacific phytogeographic zone. In her schema, pioneering *S. americanus* is succeeded on sandy substrates by *C. lyngbyei*, followed by a *Deschampsia–Potentilla–Trifolium–Juncus* high marsh community. On silts the pioneer species is *S. maritimus*, which is again followed by pure stands of *Carex*, which is in turn succeeded by a *Carex – S. validus – Triglochin* association. The Fraser River foreshore marshes show affinities with both these models, and presumably represent an intermediate type. The major differences in the early and building phases of marsh succession are the roles played by *S. maritimus* and *S. validus*. There are also some differences in high marsh community structure.

Coastal marshes in the Pacific Northwest are restricted almost entirely to estuarine and deltaic situations. Hence the physical environment of the marsh, both that of the substrate and the tidal floodwaters, will be influenced to a considerable extent by the discharge volume, seasonal regime, and suspended sediment load of the proximate river. Variations in successional patterns may be attributable to this cause, although the oceanic setting of the estuary and the local atmospheric climate will also be contributing factors. On the Lulu Island foreshore the reduction in tidal energy as a result of the hydraulic resistance of the dense stands of *S. americanus* (growing on sandy silts) leads to an increased deposition of fines, which are stabilized by the growth of the sedge root systems and surface microalgae. The accretion of silts and the incorporation of plant detritus into the substrate leads to an increased retention of water at low tide, and an invasion by *S. maritimus*. One of the contrasts between the Fraser delta marshes and those of the Nooksack delta in northern Puget Sound examined by Disraeli and Fonda (1979) is the complete absence of *S. maritimus* in the latter. This may be due to differences in sediment texture, but is more likely a result of the higher salinities experienced on the Fraser River foreshore. On the Nisqually delta in the southern part of Puget Sound, both *S. americanus* and *S. maritimus* are absent. Pioneer species here are true halophytes: *Spergularia marina* and *Salicornia virginica*. Clearly these variations in pioneer species and successional patterns must be related to the volume of freshwater discharge into the estuary, the texture of the suspended load, and the pattern of dispersal of the river plume under maritime influences.

A latitudinal gradient in high marsh communities also appears to exist in the Temperate Pacific marsh group. True salt marsh species (e.g., *Jaumea carnosa*, *Plantago maritima*) are prominent members of estuarine high marshes in Oregon, but are absent in northern Washington and British Columbia. Again, this may be linked to the fluvial regime. In Oregon, interstitial salinities are highest during the summer as a result of predominantly winter discharge. In contrast, the Fraser foreshore marshes experience the lowest salinities in early summer, reflecting the impact of the later melt season.

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