WASHINGTON STATE SHORELANDS AND COASTAL ZONE MANAGEMENT PROGRAM: WETLANDS SECTION

SALINITY TOLERANCE OF PLANTS OF ESTUARINE WETLANDS AND ASSOCIATED UPLANDS

Dr. Ian Hutchinson
Department of Geography
Simon Fraser University
Burnaby, B.C., Canada
V5A 1S6

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PART I
INTRODUCTION

Intertidal marshes are interfacial communities; they occupy the transition zone between marine and terrestrial ecosystems in low-energy coastal areas supplied with sediment from either marine or riverine sources. The designation of the upper limit of a marsh community (the marsh-upland transition) has conventionally been based on hydrologic criteria (inundation frequency and duration) and/or vegetation (presence/absence of indicator plant species) (Boon et al. 1977; NOS 1975; Frenkel et al. 1978); although other criteria have been proposed (e.g. substrate salinity, water content, nutrient status or stratigraphy (Hawkes 1966) or the anatomy and distribution of underground organs of plants (Seliskar 1983)).

The criteria adopted by the State of Washington to define tidal wetlands in the state under the jurisdiction of the Shoreline Management Act represent a unique approach to wetland habitat designation. The Washington Administrative Code, Chapter 173-22, states: 'In low energy environments where the action of waves and currents is not sufficient to prevent vegetation establishment below mean higher high tide, the ordinary high water mark is coincident with the landward limit of salt-tolerant vegetation. "Salt-tolerant vegetation" means vegetation which is tolerant of interstitial salinities greater than or equal to 0.5 parts per thousand'.

The statute recognizes the fact that, whereas ground-water levels and soil salinity exhibit rapid temporal variation at a site, vegetation composition is relatively stable. It encapsulates the notion that the plant cover of an area is in equilibrium with the physical environment (in this case, the local tidal and salinity regime), and as such can serve to locate thresholds along an environmental gradient which are difficult to establish by temporally-varying parameters. In addition, the vegetation pattern along a transect can be assessed instantaneously, and can thereby allow critical soil salinity thresholds and tidal limits to be established in a short period of time.

This 'indicator plant' approach to landscape description and classification has a long tradition in ecology. The major characteristic of the approach is that individual species or ecological associations are used to indicate the biophysical status of a site. The application of this approach reached its apogee in the 1960's in the form of 'botanical prospecting' for mineral deposits. It also inspired the development of the "direct gradient" school of vegetation description and analysis led by Robert Whittaker in the same decade. The use of plants as indicators of the salinization status of soils is a widespread practice in agriculture (Farragher 1969; Alakhverdiev 1972; Ilyushina 1972; Worcester and Seelig 1976).

The other antecedent of the criteria embodied in the WAC definition can be found in the attempts by estuarine ecologists and limnologists over the last half-century to define the ecological (and geographical) boundary between freshwater and saline environments. The limiting salinity between these environments has been variously specified by individual researchers as 0.2 parts per thousand [ppt] (Redeke 1933) 0.3 ppt (Rawson and Moore 1944); 0.5 ppt (Hammer 1986), 1.0 ppt (Löffler 1956) and 3 ppt (Williams 1981). In 1959 the 'Venice System' was adopted as the international standard for brackish water classification (S.I.L 1959). In this classification the limiting salinity between freshwater and saline environments was defined as 0.5 ppt. Cowardin et al. (1979) modified the terminology of the Venice System slightly to allow it to be used as a basis for the classification of wetland environments in the U.S. They adopted 800 micromhos cm^{-1} specific conductance (0.5 ppt salinity) as the threshold between freshwater and saline environments, and WAC 173-22 continues the use of this definition.

Part II
THE ESTUARINE ENVIRONMENT AND SALT-TOLERANCE

II.1 Tidal Wetlands and the Estuarine Environment

WAC 173-22-040 (1) (b) defines tidal wetlands as "influenced by tidal water". The implicit assumption of this statement is that tidal limits are concordant with the landward limits of salt-tolerant vegetation in wetlands. In Washington State intertidal marshes are not extensive; the combined effects of tectonic and glacial activity have produced a coastline characterized by rocky shores and intervening beaches. Marshes are restricted to estuarine or deltaic settings where foreshore or channel-margin areas which are periodically inundated provide a suitable substrate for colonization by wetland plant species. The precise definition of the upper limit of marshes in such geomorphic settings is complicated by the presence of the river, which modulates water levels and salinity in the estuarine and deltaic environment. The problem can be clarified by categorizing the wetlands associated with the tidal reaches of a river into three zones (Figure 1).

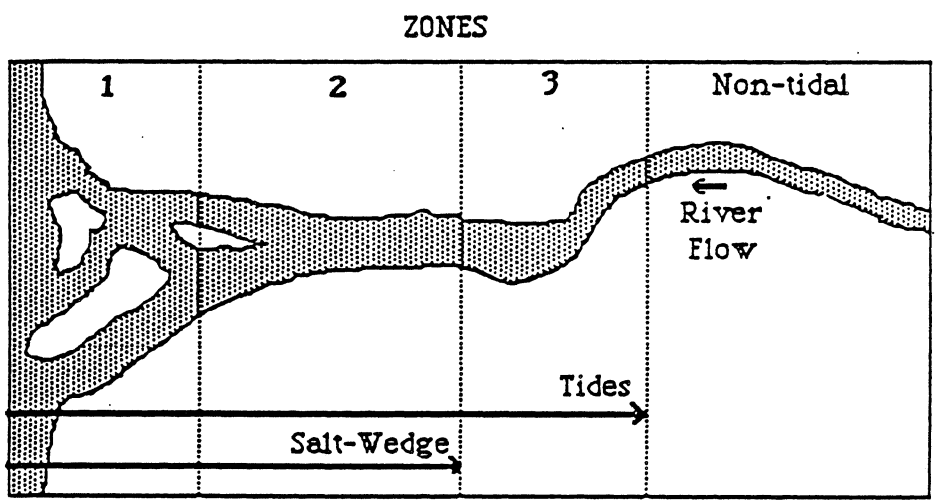


Figure 1. Model of an estuary

In this figure Zone 1 consists of the deltaic foreshore and the outer reaches of the estuary. The hydrology of these communities is completely under the influence of tidal fluctuations. Variations in river discharge will affect the salinity of inundating waters, but will not be an important control on water levels. The character of wetlands in this zone will reflect local salinity conditions, which in turn are dependent on the flow volumes and regime of the proximate river, and the distance from the river channel. Because of the predictable nature of the inundation regime in this zone, the distinctions between wetland and upland communities should be fairly clear-cut, and may be assessed on the basis of a number of biophysical criteria, including interstitial salinity regimes and the salt tolerance of member species. Tidal limits may be coincident with the landward limit of salt-tolerant vegetation in this zone.

Zone 1 grades into Zone 2, in which the inundation regime of channel-side and floodplain wetlands is controlled both by daily tidal cycles and variations in river level. Salinity regimes are in-phase with, but less-pronounced than those in Zone 1. During periods of high river flow the waters inundating the channel-side wetlands may be essentially fresh. The duration and frequency of inundation in this zone is far less predictable than in Zone 1, and for this reason, and also because of the reduced salinity of inundating waters, distinctions between wetland and upland vegetation are likely to be less clear-cut. In addition, the landward limit of salt-tolerant species may not coincide with the wetland-upland boundary in this zone, as freshwater wetland plants may occur at a higher elevation on the marsh platform.

The boundary between Zone 2 and Zone 3 coincides with the maximum penetration of the estuarine salt-wedge. Channel-margin marshes in this upstream zone (Zone 3) are freshwater wetlands influenced to some extent by the attenuated tidal regime, but predominantly by variations in river level. Differentiation between wetland and upland communities cannot be based on salinity regime or the salt-tolerance of member species.

In addition to the problems outlined above, the delineation of the wetland-upland transition in a particular locality is complicated by the dynamism of the upper intertidal environment. The upper intertidal zone is subject to physical disturbance and concomitant changes in community composition. In addition to the periodic changes in soil anoxia, salinity, and temperature which accompany tidal inundation, wave action during storms may produce considerable physical disturbance at the high tide mark, usually as a result of the transport and deposition of drift logs and wrack. During periods of tidal exposure rain may leach salts from the soil, or extended periods of drought may lead to evaporative concentration of salts in the soil. In estuarine environments low frequency, high-magnitude floods may leave substantial deposits of river-borne sediment on the marsh surface, effectively burying the emergent marsh plants. Such floods usually bring about considerable changes in soil salinity. As a result of these changes a salt-tolerant community may be replaced by a freshwater community, which then persists, despite the gradual return of saline conditions. (Beares and Zedler 1987).

II.2 Distributional Limits and the Salt-tolerance of Estuarine Plant Species

All salt-tolerant plant species (halophytes) will germinate and grow in non-saline conditions (Ungar 1978; 1982). The absence of halophytes from non-saline habitats in the field is usually taken as an indication of their reduced competitive ability in such habitats.compared to plants which are not tolerant of saline substrates (glycophytes) Reduced competitive ability is likely a product of the energetic costs of building and maintaining the cellular apparatus necessary to exclude or exude salt from the plant. Because there are likely inter-specific differences in the competitive ability of halophytes, variations in the location of the upland transition in the field may reflect the relative vigour of the halophyte occupying that location, not a salinity threshold.

The role of salt tolerance in limiting field distributions may be effectively assessed by integrating information from three sources of data:

1) Laboratory tests, which provide information on the performance of the species over a range of salinity conditions in the absence of competitors and predators;

2) Field data on the joint distribution of soil salinity and plant species in the presence of competitors and predators; and.

3) Transplant studies (marsh creation projects), which indicate the relative success of species populations moved into previously unoccupied habitats, usually in the absence of competitors. Data from these sources can be considered to provide a field test of the predictions derived from laboratory sources.

It is a relatively straightforward task to document the salinity tolerance of a species population in terms of seed viability, germination, and growth rate. The effects of exposure to saline solutions have been recorded in laboratory tests for a large number of wetland and upland (principally crop) plants. Unfortunately, such documentation is subject to several drawbacks which limits its interpretation in field situations:

1) Only a limited number of seed sources are usually tested. The total range of population variability usually remains unknown.

2) Only a limited number of life-stages are assessed. Data on the salt tolerance of germinating seeds of a large number of plant species are available; the information

on the tolerance characteristics of all life-stages is only available for a limited subset of this total.

3) A plant which is sensitive to salt exposure may be effectively protected in the field by its life-history strategy or phenological behaviour - the plant may be dormant or senescent during the periods of high salinity.

4) Salt-intolerance is not an absolute characteristic of the species population. Some species of glycophytes may become acclimated to low levels of salt in the soil solution by exposure.

5) Salt-tolerance is not independent of other environmental conditions; tolerance may be mediated, for example, by ambient temperature, thermoperiod , etc.

6) Salinity conditions in laboratory experiments are usually held constant throughout the course of the experiment. The effects of short-term excursions above a given value in the field may therefore be difficult to predict.

Data derived from field observations on plant distribution and salinity regimes also suffer from a number of drawbacks, primarily:

1) Plant distributions are dynamic; the absence of a species from a site may be unrelated to the presence or absence of a particular environmental condition.

2) Plant distributions may be curtailed by extreme, low-frequency events at a site, not by long-term averages.

3) Field distributions are almost always the result of a nexus of interactions between abiotic and biotic factors; the role of a single factor (e.g. salinity) may be extremely difficult to identify.

Data derived from transplant studies are probably ideal as a means of identifying the relative role of abiotic factors in plant distribution. Competitive effects are minimized, and the site conditions are usually monitored prior to, and after transplanting. Unfortunately only a few marsh creation projects have been attempted in the Pacific Northwest, and the approach in these projects has been very conservative; only a few species have been transplanted. In addition, most marsh creation projects have focussed on low elevation habitats; considerably less work has been undertaken at the marsh-upland interface.

Part III

METHODS

III.1 Salinity measurement and salinity thresholds

The budget and time allocation for this project were too limited to allow a field or laboratory investigation of the problem. Instead, the investigation was conducted by compiling a database on the salt tolerance of plant species occupying coastal wetland and nearshore habitats in the Pacific Northwest. The information for this database was derived entirely from the available literature.

The salt content of the soil, inundating water, or growing medium was expressed in the research literature by a variety of parameters (salinity, chlorinity, specific conductance, osmolality, osmotic pressure, moles NaCl, etc.) and a diversity of units (ppt, millimhos, Siemens, Pascals, etc.). In order to standardize the results of this survey all quantitative measurements of salt content have been expressed as 'salinity' in parts per thousand. Factors to convert the other measurement parameters to salinity in ppt are listed in Appendix 1.

III.2 Species as Indicators of Tidal Limits

The distribution of plants relative to local salinity gradients was graphed from data derived from field studies in the coastal wetlands of the Pacific Northwest (Oregon, Washington and British Columbia). The salinity range of each species, and the overall salinity domain in the marsh habitats in each estuary in the growing season were plotted (see Figure 2 for a typical case).

Two salinity levels are tested as potential thresholds marking the distributional limits of glycophytes (upland and freshwater wetland plant species). These are: 0.5 ppt, as embodied in WAC Chapter 173-22, and 5.0 ppt, the limit utilised by Cowardin et al. (1979) to mark the upper limit of slightly brackish (oligosaline) water. Those species which were restricted to freshwater habitats (peak growing season salinity of ≤0.5 ppt) or oligosaline habitats (≤5.0 ppt) were considered to be potential indicators of freshwater wetland or upland habitats. Freshwater wetland species were distinguished from upland species on the basis of habitat descriptions in the field reports. If the argument advanced by WAC Chapter 173-22 is correct, the seaward distributional limit of these salt-sensitive species should mark the position of OHWM, and conversely, this threshold should be marked by the landward limit of all other species (those which are salt-tolerant).

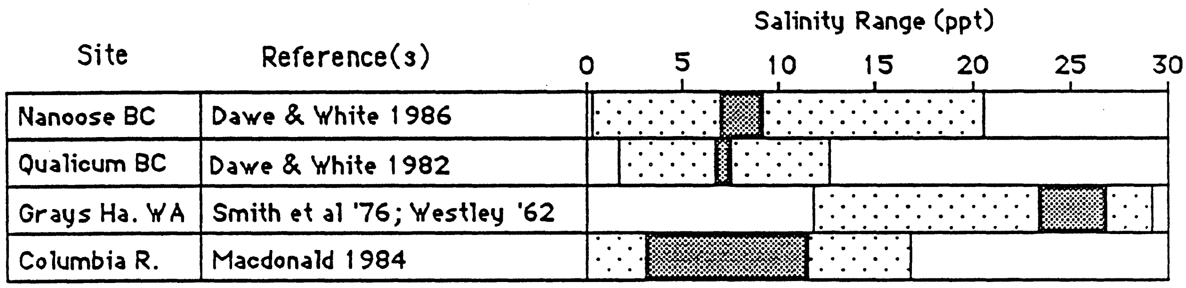


Figure 2. Field distribution of a plant species in four estuarine marshes in the Pacific Northwest. The heavily-shaded rectangles indicate the salinity range occupied by the species in question, the lightly-shaded portions of the figure indicate the salinity domain of other marsh habitats in the estuary.

Each species was given a letter code to specify its indicator status, the prefix representing salinity tolerance, the suffix representing wetland (W) or upland (U) status. The salt-tolerance coding was as follows: (the numeric values indicating the range of peak salinity experienced in the growing season).

VS	very sensitive	0 - 0.5 ppt
S	sensitive	0.5 - 5. ppt
MS	moderately sensitive	5-10 ppt
MT	moderately tolerant	10 - 15 ppt
T	tolerant	15 - 20 ppt
VT	very tolerant	>20 ppt

This terminology is derived from Maas (1986), who classified North American vegetable, forage, and fruit crops in terms of their characteristic sensitivity to salt in the rooting zone. Mass (1986) adopted a graphical model to define the limits of each class. The model (Figure 3) was based on yield-response curves of plants in the post-seedling stage derived from crop field trials. Yield-response curves were only available for a small percentage of the wetland and upland plant species reviewed in the present study, and consequently these data were supplemented by data derived from field distributional limits. A preliminary analysis of the few available yield-response curves indicated that the upper limit of field distribution coincided in the majority of cases with the salinity associated with 60% - 70 % yield reduction; these are the salinity values used to delimit salinity classes in the table above, and in Figure 3.

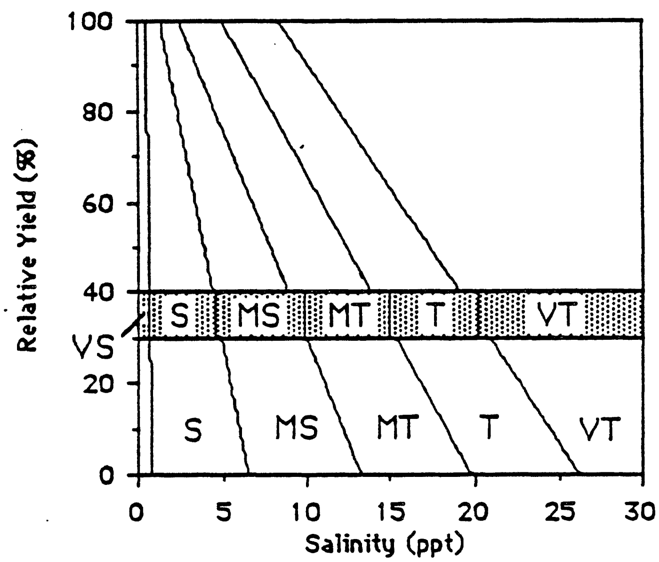


Figure 3. Divisions for classifying salinity tolerance. The diagonal lines are limiting yield-response values, the shaded boxes represent equivalent field distribution limits. See text for details.

III.3 Vegetation as an Indicator of Tidal Limits

Although a map of the distribution of limited number of indicator plant species may provide a robust descriptor of tidal limits in some estuarine situations, the absence of individual species may be a response to a wide variety of physical or biotic causes, and not just an indication that an elevational threshold has been reached. Rather than rely on a few species as sources of information on the upland-marsh boundary, it is conceptually preferable to integrate information from the complete plant assemblage in a sample plot.

A single score can be calculated for each sample plot across a suspected marsh-upland transition zone in order to detect the location of OHWM, which is considered to be equivalent to the limit of salt-tolerant vegetation. The percentage cover of constituent species is multiplied by the species salinity-tolerance score in order to calculate the salinity index for the sample plot. A rapid change in the magnitude of the index is indicative of an ecotone, and the location of OHWM is indicated by the balance between salt-tolerant and salt-sensitive species. At OHWM, in other words, the salinity index should equal zero.

The weightings given to individual species in the present study are as follows:

Salinity Class	Weighting
very sensitive	-3
sensitive	-2
moderately sensitive	-1
moderately tolerant	+1
tolerant	+2
very tolerant	+3

III.3 'Field' Test of the Indicator Species and Vegetation Index Methods.

Frenkel et al. (1978) surveyed the vegetation of 4292 sample plots along 190 marsh-upland transects in 20 marshes in coastal Oregon and Washington. They delimited the mid-transition zone (MTZ) location in each marsh and on the basis of vegetation change and related tidal data (NOS 1978, 1980), and tested the application of a marsh-upland vegetation index (the Multiple Occurrence Method) to the delimitation of this threshold. The MOM index weights each species by an elevation coefficient which indicates the primary zone of occurrence of that species: low marsh=+2, high marsh=+1, upland=-2, 0=non-indicator, and then calculates a sample plot score on the basis of relative species cover. The salinity-tolerance index developed in this study is conceptually the same as the MOM index used by Frenkel et al. (1978). The difference between the two approaches is that salt tolerance (on a scale of -3 to +3) has been substituted in the present study for an elevation coefficient.

The utility of the salt-tolerance approach will be examined by means of a 'field' test using the vegetation data provided by Frenkel et al. (1978). The test will :

1) examine the extent to which the distributional limits of species of differing salt tolerance coincides with MTZ (considered to be equivalent to OHWM), in a subsample of the transects surveyed in Washington State;

2) examine the extent to which the "vegetation salinity index" developed in the present study (henceforth refered to as SALTY) can locate MTZ; and

3) compare the relative accuracy and merits of the SALTY and MOM indices as estimators of the position of MTZ.

Part IV

INVENTORY OF SALT TOLERANCE

IV.1 Data Survey

Salinity-tolerance ratings were compiled for a total of 116 plant species from coastal wetland and associated upland environments in the Pacific Northwest. Maximum limits of distribution in the field with respect to salinity gradients were established for 79 species, and yield-response curves were constructed for 20 species.

Suprisingly, the relatively large data base on coastal plant communities in the Pacific Northwest which has developed within the the last decade or so (see Hutchinson 1986; 1988 for reviews), proved to contain a relatively small number of studies which incorporated in situ data on soil and water salinity regimes. In Washington State, only Ewing's Ph.D. thesis research on the plant communities of the Skagit River delta (Ewing 1982; 1983) and the study by Disraeli and Fonda (1979) on the Nooksack River marshes provided contemporaneous, in situ salinity readings. The latter study was limited by the very small range of salinities in the marsh domain. The work by Macdonald (1984) in the marshes of the Columbia River estuary contains detailed descriptions of marsh community structure and production, but salinity regimes for individual sites are derived from readings taken in the middle of the river channel. These values may be extrapolated to neigboring low marsh areas with some degree of confidence, but likely do not present an accurate picture of conditions in high marsh areas, in whih local patterns of drainage, seepage and evaporation create a more complex hydrological and vegetational mosaic. The same comment may be applied to the study by Smith et al. (1976). In this case I supplemented their descriptions of the vegetation of Gray's Harbor with mid-channel and bay salinity data compiled by Westley (1962). In some instances extrapolations of salinity regimes are made over a linear distance of 5 km. The results of this extrapolation are presented in the inventory that follows (Section IV.2), but are are so much at variance with other results that they are not used in the rating of salt-sensitivity characteristics.

Most of the studies undertaken in coastal marshes in Oregon, whilst providing valuable descriptions of species distributions, proved to contain little useful salinity data. Jefferson (1975) for instance, provides, amongst a wealth of vegetational information for a number of Oregon estuaries, only the most general description of salinity conditions at one site (Yaquina Bay). and the work undertaken by Eilers (1975) on the evolution and organization of the marsh communities of the Nehalem estuary, includes salinity data for the month of August, after plant growth in the estuary has virtually ceased.

Perhaps the most useful source of information as far as field distributional limits was concerned consisted of the work undertaken by Dawe and White (1982, 1986) on plant-environment relations in two estuaries of eastern Vancouver Island. These studies provided data, not only for species characteristic of low and high marsh environments, but also for some of the marsh-upland transition flora of the region. However, it must be noted that distributional data were primarily available for marsh plants, the limiting salinities for most of the upland flora (including important members of the forest resource such as Sitka spruce and western hemlock), remain unknown.

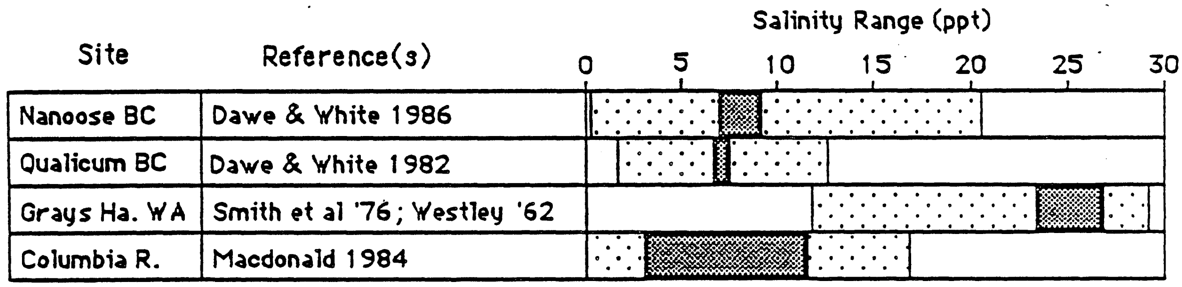
The major weakness detected in the experimental data sources was the relatively limited number of species investigated. Most of the available data were derived from work on cosmopolitan halophytes; relatively little work has been undertaken on the limits and mechanisms of salt tolerance (or sensitivity) in the freshwater-brackish wetland or upland floras. In addition, most research has been conducted on non-local populations of these halophytes; the extrapolation of data derived, for instance, from Dutch populations of Juncus gerardii, to populations in the Pacific Northwest, must be viewed with caution.

The least satisfactory data base for information on salinity tolerance comprised the set of transplantation projects examined. In some cases no post-transplant monitoring of the success or failure of the transplanted material had been undertaken, in others the failure of a project was a result of a combination of factors (e.g. mobile substrates or excessive wave action, or herbivory) and the role of salinity in limiting transplantation success could usually not be determined with any accuracy.

IV.2 Inventory of Salinity Tolerance

In the following section a species-by species description of salinity tolerance characteristics is compiled. Nomenclature follows Hitchcock et al. (1969), and the species are listed in alphabetical order.

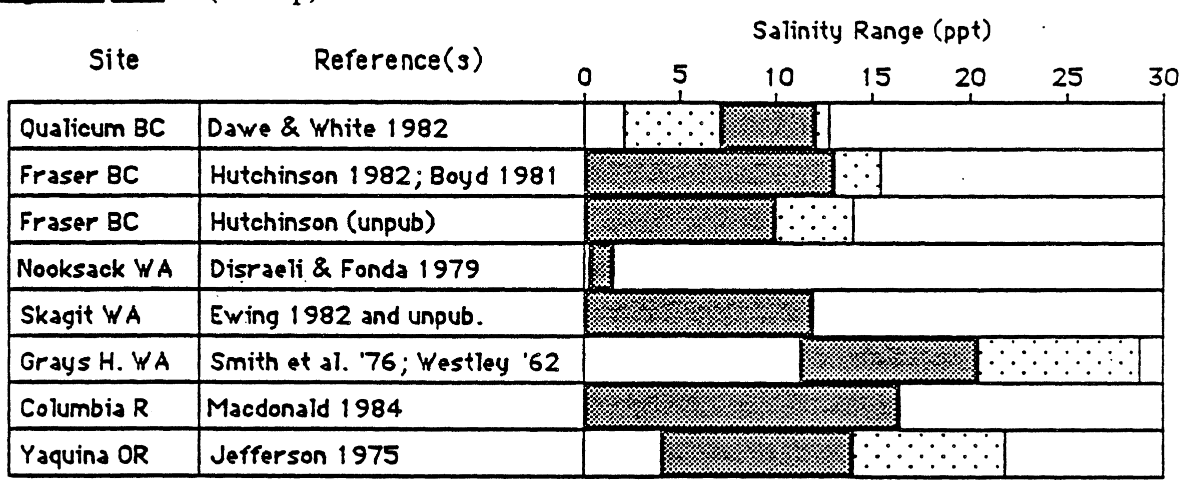
Achillea millefolium L. (Common Yarrow)

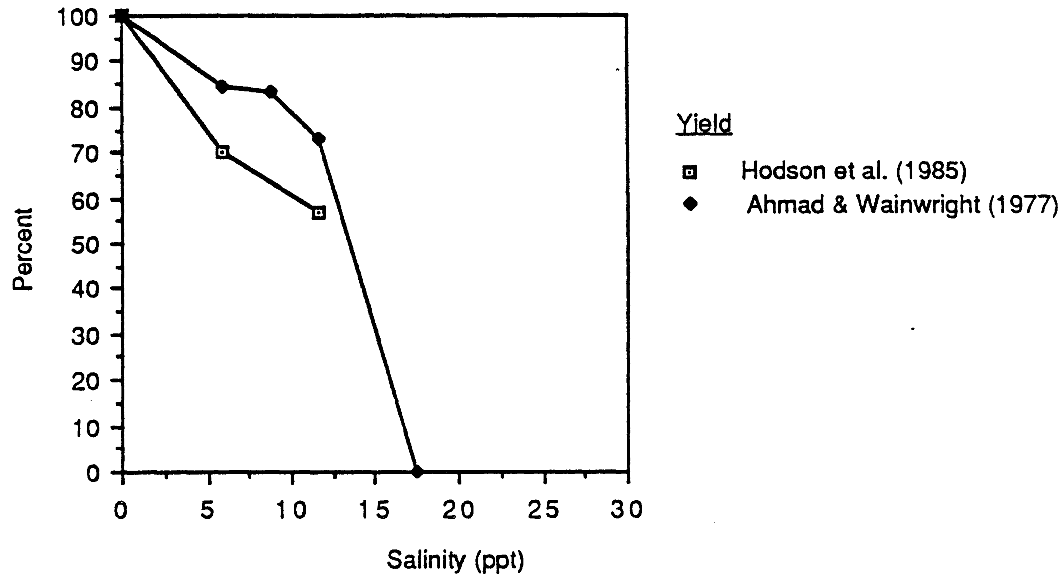


A. millefolium is widely distributed in the Pacific Northwest. The coastal variety is a common member of the marsh-upland transition zone flora. The available field data indicate that coastal populations in the study area are associated with reasonably well-drained and moderately saline microhabitats (3-12 ppt).

Agropyron repens (L.) Beauv. (Couch-grass)
A. repens is widespread in meadows and waste places in the Paçific Northwest. Populations in the saline meadows of the Qualicum River and Nanoose estuaries on the east coast of Vancouver Island are exposed to soil salinities in the 5 - 10 ppt range (Dawe and White 1982; 1986). Venables and Wilkins (1980) indicate that root growth of some British populations of this species is enhanced as a result of exposure to saline media (NaCl concentrations up to 200 mM (11 ppt)).

Agrostis alba L. (Redtop)



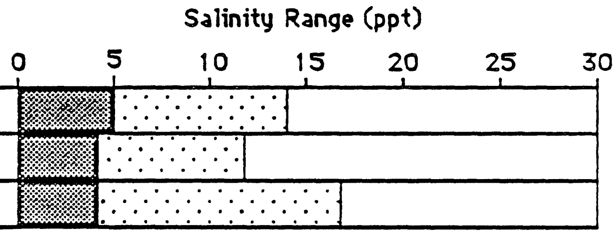


A. alba (=A. stolonifera var. alba) is a common member of the flora of meadowlands from low elevations to treeline. Coastal populations are found on a variety of substrates and in a wide range of salinity conditions. This species is a dominant element of brackish intertidal meadows where interstitial salinities in the growing season are commonly below 5 ppt, but the species can tolerate salinities up to 15 ppt. The general character of the germination response of this species was established by Bartolomaeus and Heerkloss (1980), who noted that germination declined to ca. 60% of the value in freshwater at a salinity of 12 ppt. Experimental data (Ahmad and Wainwright 1977; Hodson et al. 1985) indicate a 10 % reduction in the relative yield of intertidal marsh populations of A. stolonifera at a salinity of 3 ppt. Wu (1981) contrasted the germination and growth responses of shore, coastal dyke, and inland populations of A. stolonifera and A. tenuis from Oregon and Britain. The A. stolonifera material derived from Oregon shore populations was considerably more salt tolerant than A. stolonifera and A. tenuis from the adjacent dyke. Similar results were obtained by Ahmad and Wainwright (1977), who compared the growth of salt marsh, spray zone, and inland populations of A. stolonifera in Britain. Differences in the ecological performance of these populations were slight at 6 ppt, but the salt marsh population grew more rapidly than the spray zone and inland populations at 9 ppt. Venables and Wilkins (1980) indicated that the relative root growth of A. stolonifera increased by 75% at salinities between 3 - 6 ppt, and was 20% more rapid at 11 ppt than in freshwater treatments. Their data are derived from plants taken from a recently salinized meadow in England, and indicate the rapid action of selection for salt tolerance in this and co-occurring species. The role of selection in producing salt-tolerant lines of A. stolonifera was also examined by Ashraf et al. (1986).

Aira praecox L. (Little hairgrass)
No accounts of distribution in the field relative to salinity gradients or experimental data on the salinity tolerance of this species were found in the literature reviewed.

Alisma plantago-aquatica L. (American waterplantain)

Site	Reference(s)
Fraser BC	Hutchinson (unpub)
Skagit WA	Ewing 1982 and unpub.
Columbia R.	Macdonald 1984



A. plantago-aquatica is a widespread, but generally minor component of the brackish and freshwater coastal marsh flora in the Pacific Northwest. It is usually found growing along the margins or bottoms of shallow ponds or ditches at higher elevations on the marsh platform. The available field data indicate that salinities above 3 ppt may persist in these habitats for short periods of time (usually early in the growing season).

Alnus rubra Bong. (Red alder)
No accounts of distribution in the field relative to salinity gradients or experimental data on the salinity tolerance of this species were found in the literature reviewed. On the basis of injury ratings and leaf chloride content following exposure to highway de-icing salt, Shortle and Rich (1970) considered Alnus rugosa, an ecologically similar species in eastern North America, to be salt-intolerant. Alnus tenuifolia was rated as having low salt tolerance by Kirkpatrick et al. (1978), i.e. 10% reduction in yield at 1 - 2 ppt; 50% reduction in yield at 2 - 5 ppt. The resistance of various North European tree and shrub species to seawater flooding was described by Richardson (1955). He noted that alder was considered by most authorities to be one of the least tolerant of trees to seawater exposure.

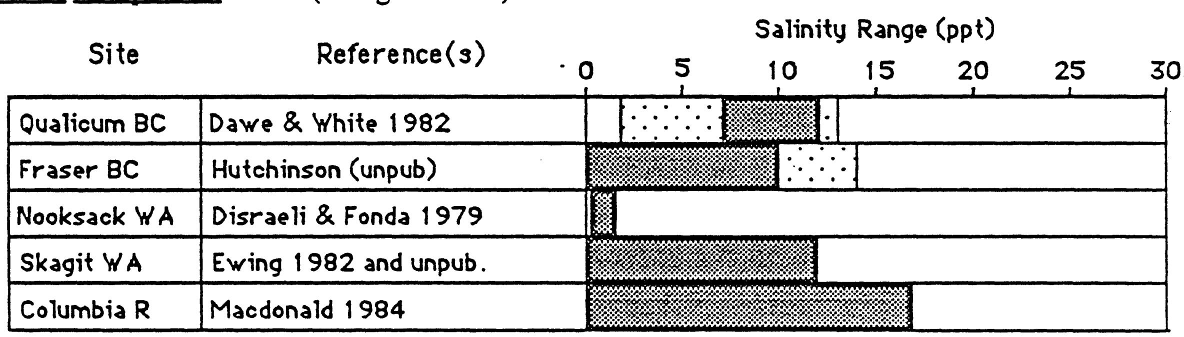
Ammophila arenaria (L.) Link. (European beachgrass)
European beachgrass is a fairly common plant of coastal dunes, spits, and associated wetland margins. No accounts of the distribution in the field of this species relative to salinity gradients were found in the literature reviewed. Woodell (1985) attempted to germinate caryopses of A. arenaria in distilled water and seawater. He obtained poor germination in fresh water, and no germination at the three salinity levels tested (17 ppt, 35 ppt, 54 ppt)

Angelica arguta Nutt. (Sharptooth angelica)
This species is a minor component of freshwater marshes. Data collected over the course of one year in the Fraser River estuary (Hutchinson, unpub.) indicate that salinities in the habitats occupied by A. arguta remain below 0.5 ppt in the growing season.

Angelica lucida L. (Seawatch)
A. lucida is a relatively common plant of the marsh-upland transition flora; however, no accounts of distribution in the field relative to salinity gradients, or experimental data on the salinity tolerance of this species were found in the literature reviewed.

Anthoxanthum odoratum L. (Sweet vernalgrass)
This is a widespread and relatively common grass species in upland meadows, and in the marsh-upland transition flora. No accounts of distribution in the field relative to salinity gradients, or experimental data on the salinity tolerance of this species were found in the literature reviewed.

Aster subspicatus Nees (Douglas' aster)



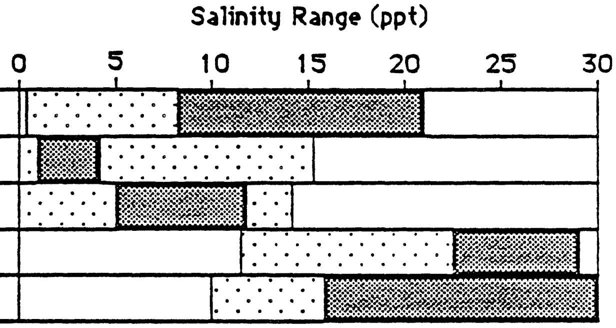
A. subspicatus is a common element of the high marsh flora in brackish marshes in the field area. The available field data indicate that the species is distributed over a 0 - 12 ppt salinity range. The salinity values cited in the study by Macdonald (1984) are derived from readings in mid-channel, and are likely not representative of conditions in the high marsh sites occupied by this species. The only available experimental data on the salinity tolerance of members of this genus are derived from research on Aster tripolium, (widely distributed in saline marshes in Europe). Such data are not considered relevant to the ecological responses or tolerance limits of A. subspicatus.

Athyrium filix-femina (L.) Roth. (Lady fern)
Lady fern is a widespread and relatively common plant in coastal forest communities, coastal swamps, and in the upper zone of some freshwater marshes. Its distribution would

indicate that it is salt-sensitive, but no field or experimental data on the salinity tolerance of this species were found in the literature reviewed.

Atriplex patula L. (Orache)

Site	Reference(s)
Nanoose BC	Dawe & White 1986
Fraser BC	Hutchinson 1982; Boyd 1981
Fraser BC	Hutchinson (unpub.)
Grays H. WA	Smith et al. '76; Westley '62
Suisun CA	Mall 1969



A. patula is a morphologically variable annual species that is common in saline intertidal marshes, and is less frequently encountered in the brackish marshes of the study area. It occupies a broad range of elevations, substrates and salinity conditions (from sub-saline to hypersaline), but it is dominant only in saline microhabitats subject to frequent physical disturbance, (e.g. drift-lines). No experimental data on the ecological response of this species to variable salinity conditions were found.

Berberis aquifolium Pursh. (Shining Oregon grape)
Oregon grape is a widespread and common species in the coastal forest understorey, particularly on relatively dry sites. Its distribution would indicate that it is not salt tolerant, and Maas (1986) classed it as "very sensitive" (i.e. limit of tolerance ca 0.5 - 1.5 ppt).

Bidens cernua L. (Nodding beggars-tick)
This species occurs infrequently in high brackish and fresh intertidal marshes of the study area, generally on organic substrates. In the Fraser River estuary it is limited to sites which have growing season salinities <2 ppt.

Bromus mollis L. (Soft brome)
Dawe and White (1982, 1986) reported this species as a minor component of high marshes in their study areas. Soft brome was limited to sites with soil salinities <3 ppt.

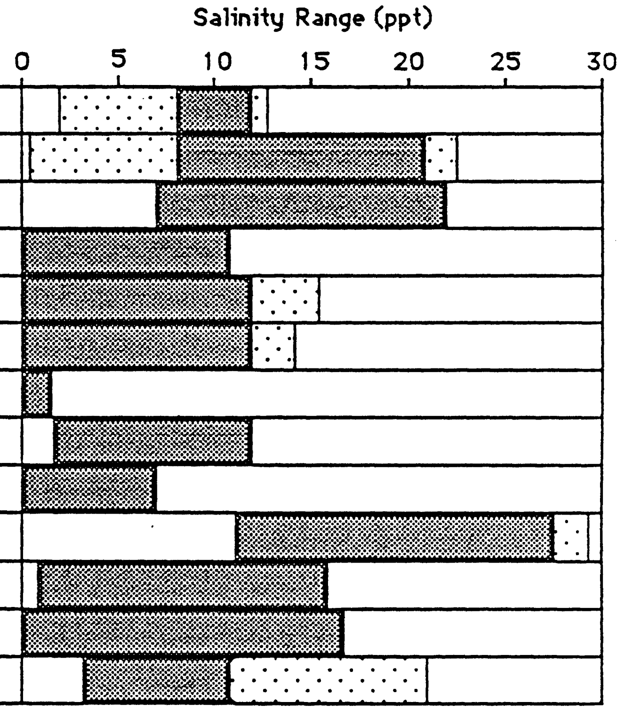
Calamagrostis nutkaensis (Presl.) Steud. (Pacific reedgrass)
Pacific reedgrass is a fairly common plant in the uplan-marsh transition zone. No field or experimental data on the ecological response of this species to variable salinity conditions were found in the literature reviewed.

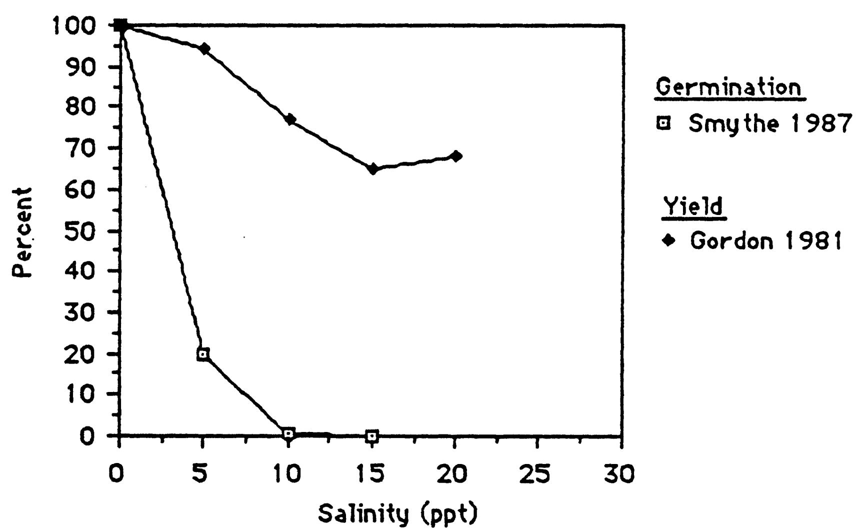
Caltha asarifolia DC. (Yellow marshmarigold)

This species is a widespread, but minor component of shallow freshwater marshes in the estuaries of the Pacific Northwest. Macdonald (1984) documented a salinity range of 0 - 0.5 ppt for this species in the Columbia River estuary, and it occupies the same range in the estuary of the Fraser River (Hutchinson, unpub. data).

Carex lyngbyei Hornem. (Sea sedge)

Site	Reference(s)
Qualicum BC	Dawe & White 1982
Nanoose BC	Dawe & White 1986
Nanaimo BC	Smythe 1987
Squamish BC	Smythe 1987
Fraser BC	Hutchinson 1982; Boyd 1981
Fraser BC	Hutchinson (unpub.)
Nooksack WA	Disraeli and Fonda 1979
Skagit WA	Ewing 1982; (unpub.)
Skagit WA	Smythe 1987
Grays H. WA	Smith et al. '76; Westley '62
Grays H. WA	Thom 1981
Columbia R.	Macdonald 1984
Yaquina OR	Jefferson 1976





Sea (or Lyngbye's) sedge is the dominant plant of brackish intertidal marsh communities in the Pacific Northwest. It is absent from marshes where soil salinities above 20 ppt persist for most of the growing season, but may achieve dominance on a wide variety of substrates in the appropriate salinity range (0 - 20 ppt; Knudson and Woodhouse 1982). Flushing of the substrate by freshwater is apparently required to promote germination (Hutchinson and Smythe 1986, Smythe 1987), but mature plants can tolerate a wide range of salinities (Gordon 1981).

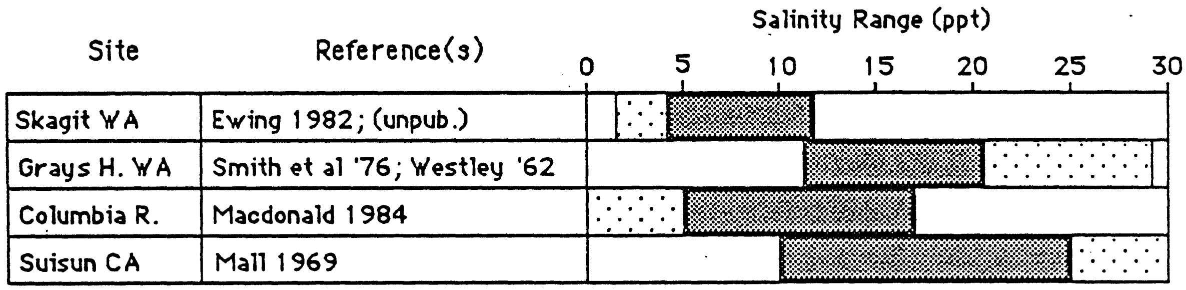
Carex obnupta Bailey (Slough sedge)
Boulé et al. (n.d.) note that slough sedge is 'typical' of freshwater habitats such as coastal swamps, but is a common member of the flora of 'high salt/brackish marsh'. Macdonald (1984) records this species at one high marsh site in the Columbia River estuary. This site has an associated salinity (in mid-channel) of 4 - 13 ppt. In my experience this species is restricted to freshwater marshes (or swamps) or freshwater seeps in high brackish marshes, and Frenkel et al. (1978) consider it to be a freshwater indicator species.

Carex rostrata Stokes (Beaked sedge)
Beaked sedge is a very common species in freshwater marshes. In the Fraser River estuary it is restricted to channel-side marshes in which soil salinities never exceed 0.5 ppt (Hutchinson, unpub. data). No experimental data on the salinity tolerance of this species were found in the literature reviewed.

Cicuta douglasii (DC.) Coult & Rose (Douglas' water-hemlock)
This species is a member of the flora of high brackish and freshwater marshes. Ewing (1982, unpub. data) records a soil salinity range of 3 - 6 ppt associated with sites occupied by water-hemlock on the Skagit River delta, which corresponds with observations on its distribution in southern British Columbia (Hutchinson, unpub. data)

Cornus stolonifera Michx. (Red-osier dogwood)
This shrub species is common in channel-side swamps, and in partially-shaded gaps in floodplain forests. In the Fraser River estuary it is restricted to freshwater marsh and upland environments. Kirkpatrick et al. (1978) state that this species has "low" salt tolerance.

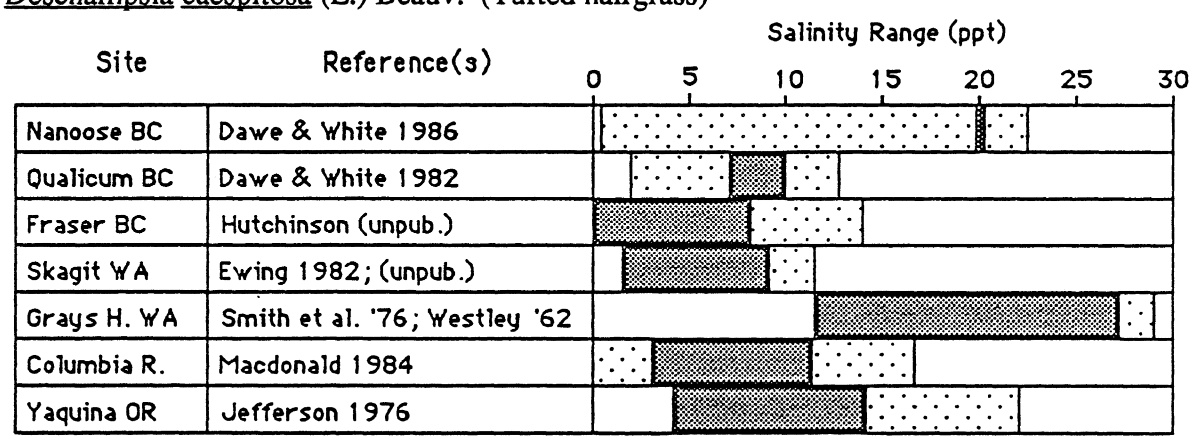
Cotula coronopifolia L. (Brass buttons)
This species is common along the margins of pannes or ditches in saline and brackish water environments. It occurs in sites which have growing season salinities in the 0 - 25 ppt range.



Cuscuta salina Engelm. (Saltmarsh dodder)
Saltmarsh dodder is a parasite, particularly of Chenopodiaceae and Compositae. It is primarily restricted to sites in which salinities above 20 ppt persist for much of the growing season. For example, Smith et al. (1976) record it as occurring in Gray's Harbor on the most saline substrates (bay salinities: 24-29 ppt; Westley 1962).

Dactylis glomerata L. (Orchard-grass)
The germination respnse of orchard-grass was characterized in a general fashion by Heerkloss and Bartolomaeus (1980), who established that germination declined to 50% of the freshwater total at ca. 6 ppt, and 20% at 12 ppt. Ashraf et al. (1986a) noted that this species "does not normally occur in habitats with high salt concentration in the rooting medium", and recorded a 65% reduction in yield at 6 ppt Ashraf et al. (1986b) . Bernstein (1964) classed it as of "moderate" salt tolerance (equivalent to ca.10% yield reduction at 2 ppt; ca. 50% reduction in yield at 6 ppt), and Maas (1986) noted that reductions in yield can be expected at 1.5 dS/m (1.2 ppt) with a yield reduction slope value of 6.2

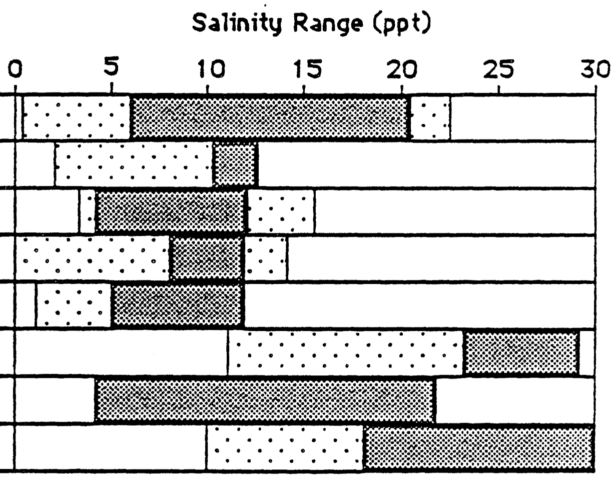
Deschampsia caespitosa (L.) Beauv. (Tufted hairgrass)

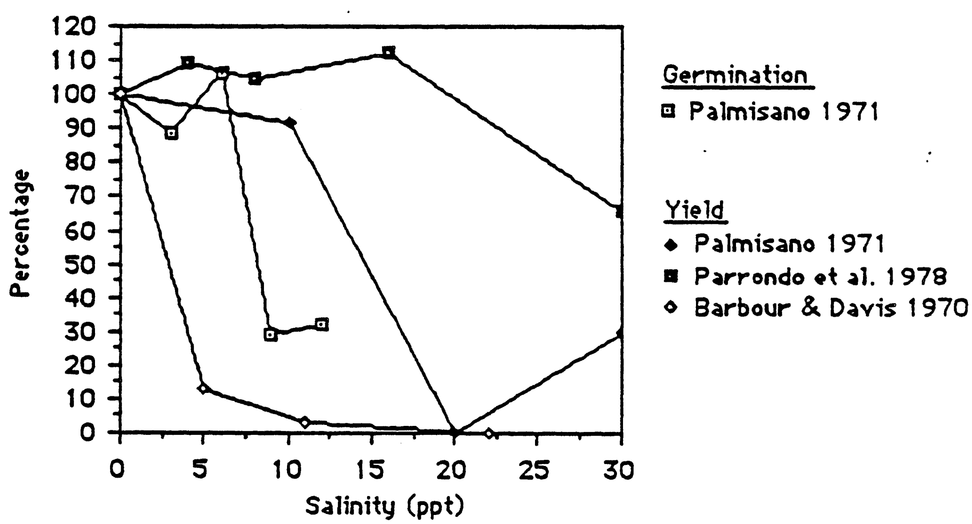


D. caespitosa is common in brackish high marshes throughout the Pacific Northwest. The field distribution data confirm the contention of Knudson and Woodhouse (1982) that this species "is found in freshwater and in brackish waters up to about 20 ppt". No experimental data on the ecological response of this species to variable salinity conditions were found.

Distichlis spicata (L.) Greene (Saltgrass)

Site	Reference(s)
Nanoose BC	Dawe & White 1986
Qualicum BC	Dawe & White 1982
Fraser BC	Hutchinson 1982; Boyd 1981
Fraser BC	Hutchinson (unpub.)
Skagit WA	Ewing 1982; unpub.
Grays H. WA	Smith et al. '76; Westley '62
Yaquina OR	Jefferson 1976
Suisun CA	Mall 1969

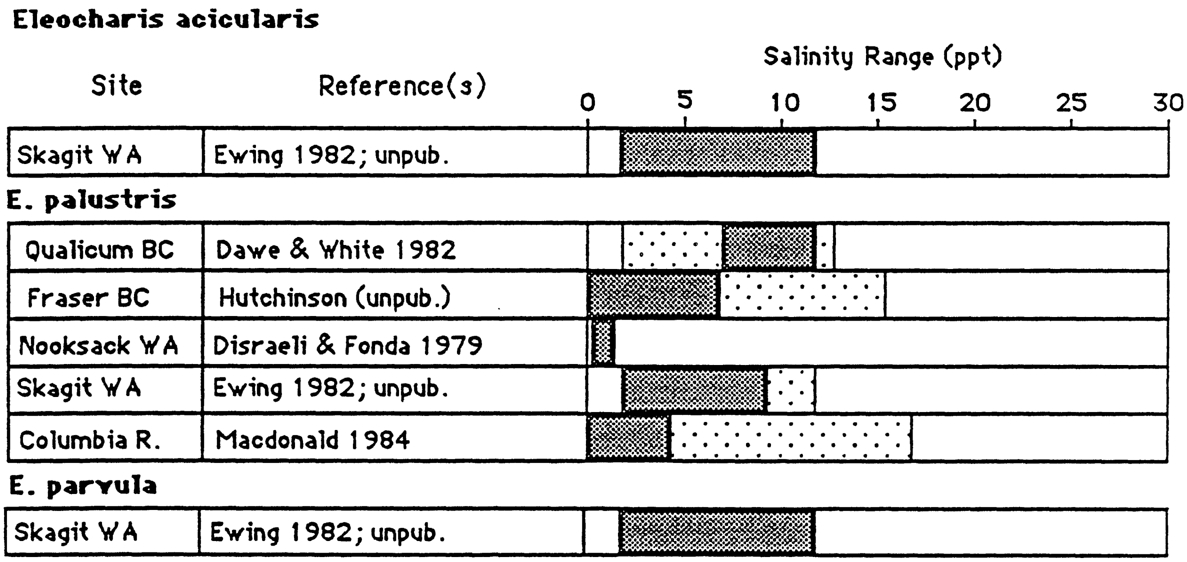




Saltgrass is common and widespread in saline and brackish marshes in the study area. It is often the dominant species in high saline marshes, and can withstand hypersaline conditions up to 50 ppt, according to Knudson and Woodhouse (1982), although Hansen et al. (1976) recorded it on soils with surface salinities >120 ppt, and subsurface slinity values up to 70 ppt. Germination is apparently inhibited by salinities >6 ppt (Palmisano 1971), but the growth of mature plants may be stimulated by moderately saline media

(Parrondo et al. 1978; Smart and Barko 1980; Kemp and Cunningham 1981). The inconsistent results reported by Barbour and Davis (1970) are a result of the fact that their experimental material was derived from a brackish, rather than a salt marsh environment.

Eleocharis spp. (Spike-rush)



Several species of spike-rush occur in local wetlands. The data provided by Ewing (1982; unpub.) indicate that the three most frequntly encountered species have similar distributions with respect to salinity gradients. It should be noted however, that the most common and widespread species (E. palustris), is a very complex taxon (Hitchcock et al. 1969), and may well comprise several distinct populations with respect to salt tolerance.

Elymus mollis Trin. (Dune wildrye)

This is a plant of sand dune, upper beach, and gravel spit habitats above the range of tidal influence. No accounts of distribution in the field relative to salinity gradients or experimental data on the salinity tolerance of this species were found in the literature reviewed, however, data on related, and possibly ecologically similar species do exist. Macdonald (1984) recorded Elymus glaucus (Western wildrye) in the marshes of the Columbia River estuary. Mid-channel salinities offshore of these sites were 3 - 11.5 ppt. Gorham et al. (1986) noted that plants of Elymus canadensis (Canadian wildrye) grown from seed had a 93% reduction in yield at 14.5 ppt compared to a freshwater control, and Bernstein (1964) characterises this latter species as having "good" salt tolerance, and E. triticoides (Creeping wildrye) as having "moderate" salt tolerance. It should perhaps be assumed (until more precise data are available) that E. mollis also has relatively high tolerance of salt.

Epilobium watsonii Barbey (Watson's willow-herb)
A species of infrequent occurrence in the upland-marsh transition zone. No field or experimental data on salinity tolerance were found in the literature reviewed.

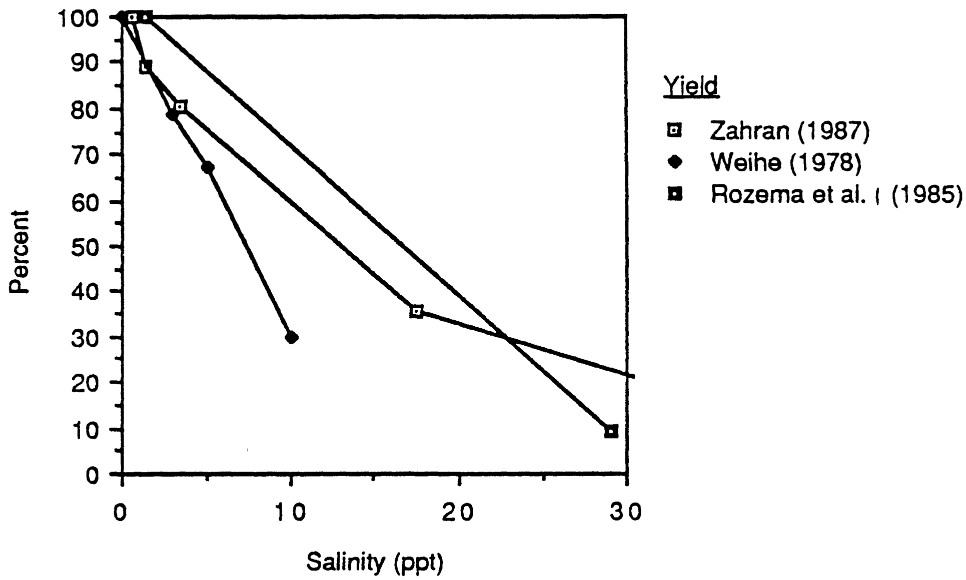
Equisetum arvense L. (Common horsetail)
No field or experimental data on the salinity tolerance of this species were found in the literature reviewed.

Equisetum fluviatile L. (Water horsetail)
This species is common at low and high elevations in shallow freshwater marshes. In the Columbia River estuary Macdonald (1984) recorded it only in freshwater habitats (mid-channel salinity range 0 - 0.5 ppt), whereas in the Fraser River estuary it occupied a broader salinity range (Hutchinson, unpub. data). Downstream channel-edge marshes with substantial beds of E. fluviatile in this estuary may experience salinities up to 5 ppt early in the growing season (April - early May).

Festuca arundinacea Schreb. (Tall fescue)
Tall fescue is a widespread, but not particularly common member of the flora of high brackish and freshwater marshes. Bernstein (1964) considers that it has "good" salt tolerance: i.e. 50% reduction in yield at 12 ppt, and Macdonald (1984) records it over the full range of salinity conditions recorded in marshes in the Columbia River estuary (0 - 17 ppt). In the Fraser River estuary it is most common in freshwater and subsaline marshes where salinities remain below 3 ppt for most of the growing season, occasionally rising to 5 ppt.

Festuca rubra L. (Red fescue)
Red fescue is a widespread and common plant of meadowlands in the study area, but is only infrequently found in wetland habitats. It forms a minor component of the transition zone flora between high marshes and uplands of some saline marshes in the Puget Trough (Hutchinson 1988) and Smith et al. (1976) recorded it from the most saline marshes in Gray's Harbor. Bulow-Olsen (1983) recorded 50-100% germination of caryopses of this species in freshwater; 10-75% in seawater diluted to 9 ppt, 10% in seawater diluted to 17.5 ppt, and negligible germination in full-strength seawater (35 ppt). Rhebergen and Nelissen (1985) documented the variable salt tolerance of salt marsh, dune and polder populations of this species, and note that salt marsh populations had the highest salt tolerance. The experimental results graphed above (all derived from European salt marsh populations of F.

rubra var. littoralis) indicate that it has relatively high tolerance of salt in the rooting zone.



Galium spp. (Bedstraw)

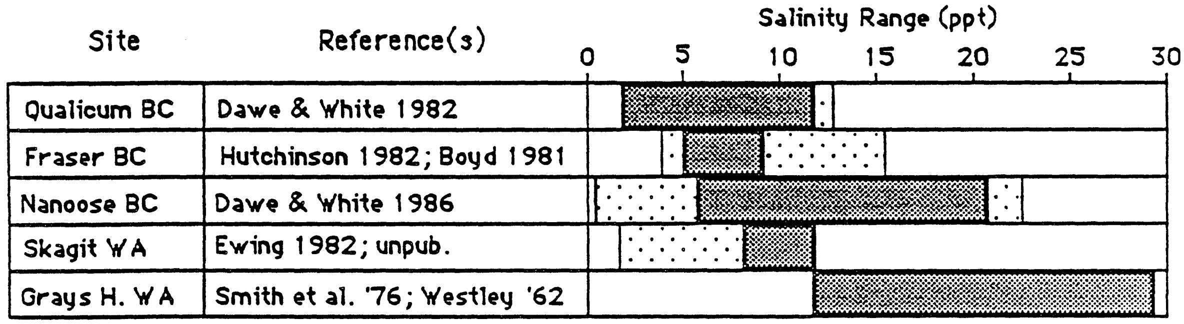
Three species in this genus (G. aparine, G. cymosum and G. trifidum) are known to occur as minor elements of the wetland flora in the Pacific Northwest. Data on field distribution with respect to substrate salinity are only available for G. cymosum. This species is restricted in wetland environments to the upper elevations of freshwater marshes. In both the Columbia and Fraser River estuaries the effective growing season salinity range in sites occupied by the species is 0 - 0.5 ppt (Macdonald 1984; Hutchinson, unpub. data). It may be assumed, until more precise data are available, that other members of the genus are equally salt-sensitive.

Gaultheria shallon Pursh (Salal)

Salal is a very common understorey sub-shrub in coastal forests, in dry upland sites, and upland-marsh transition zones. No field or experimental data on salinity tolerance were found in the literature reviewed, but its associates (e.g. western hemlock, Douglas fir) would suggest that it is salt-sensitive.

Glaux maritima L. (Saltwort)

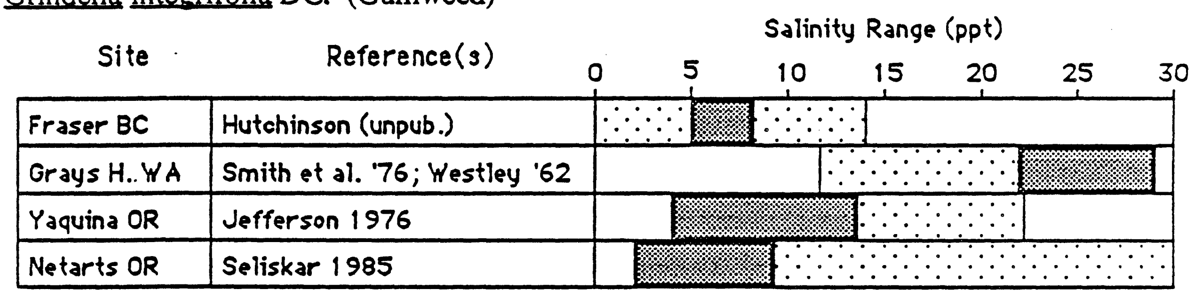
This species is a widespread, but not particularly common member of the coastal marsh flora of the Pacific Northwest. It is most frequently found on reasonably well-drained substrates in fairly open, brackish marshes at low elevations. The salinity range in these habitats is 3 -20 ppt. Rozema et al. (1985) note that the relative growth rate of this species at 29 ppt salinity is 30% of that in subsaline water (1.5 ppt).



Glyceria grandis Wats. (American mannagrass)

This species is most frequently encountered in wetland environments as a member of the upland-marsh transiiton zone in freshwater environments. No accounts of distribution in the field relative to salinity gradients or experimental data on the salinity tolerance of this genus were found in the literature reviewed.

Grindelia integrifolia DC. (Gumweed)



G. integrifolia is a common member of saline marsh communities at or above the high water mark, and may be found at somewhat lower elevations in well-drained microhabitats (e.g. along the levees of tidal channels). Although the field data indicate that it is primarily restricted to sites with salinities below 15 ppt, it is known to occcur in marshes in which soil salinities may on occasion rise to hypersaline levels.

Habenaria dilatata (Pursh.) Hook. (Bog-candle)

This species is restricted to high freshwater marshes on organic substrates and coastal swamps. Macdonald's (1984) data from the Columbia River estuary indicate that it is restricted to sites with salinities <0.5 ppt.

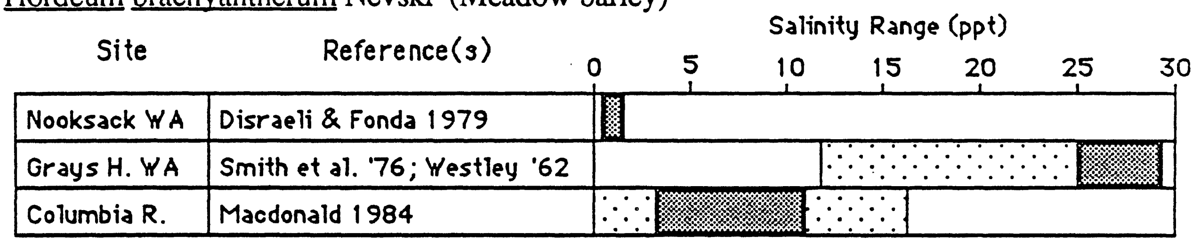
Heracleum lanatum Michx. (Cow-parsnip)

This species is found in the upland transition zone, and at the highest levels of freshwater marshes. Macdonald's (1984) data from the Columbia River estuary indicate that it is restricted to sites with salinities <0.5 ppt.

Holcus lanatus L. (Yorkshire fog)

Ashraf et al. (1986a) commented that H. lanatus "does not normally occur in habitats with high salt concentration in the rooting medium", and that germination and growth is inhibited by NaCl. They noted that root growth was severely inhibited by salinities of 16 ppt (Ashraf et al. 1986a), and that mean dry weight declined by 35% at 6 ppt (Ashraf et al. 1986b).

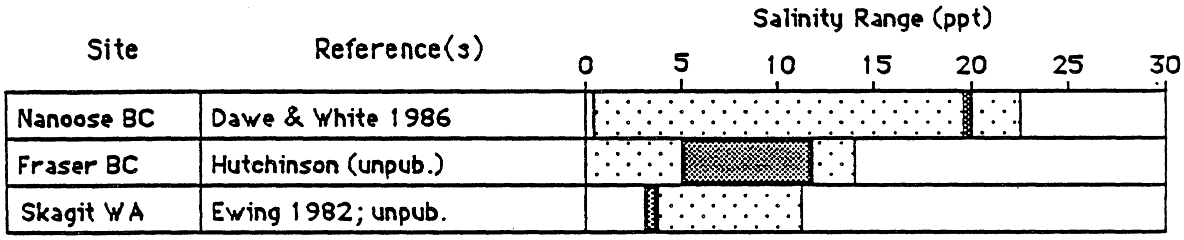
Hordeum brachyantherum Nevski (Meadow barley)

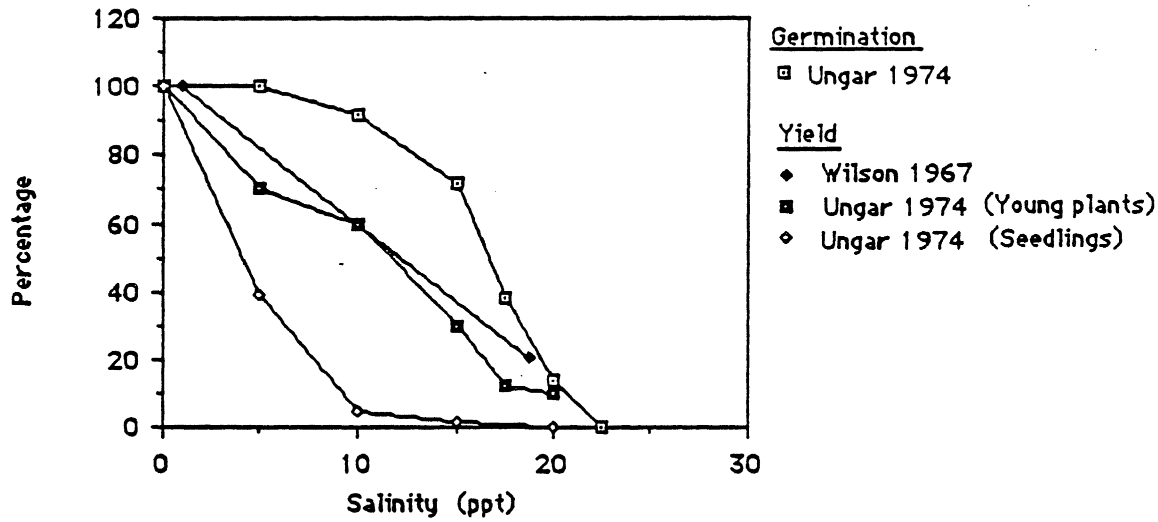


The two common species of barley in coastal marshes of the Pacific Northwest are most commonly encountered in brackish and saline high marsh meadows. The available field data indicate that H. brachyantherum may have a somewhat narrower salinity range than H. jubatum. No experimental data were found on the salinity tolerance of the former species.

Hordeum jubatum L. (Foxtail barley)

Whilst seed germination of H. jubatum is only slightly inhibited by salinities below 15 ppt, the growth of seedlings is substantially inhibited at these levels (Ungar 1974). More mature plants are better able to withstand salinities above 5 ppt (Wilson 1967; Ungar 1974), but complete mortality occurs in hypersaline media (Orton 1980).



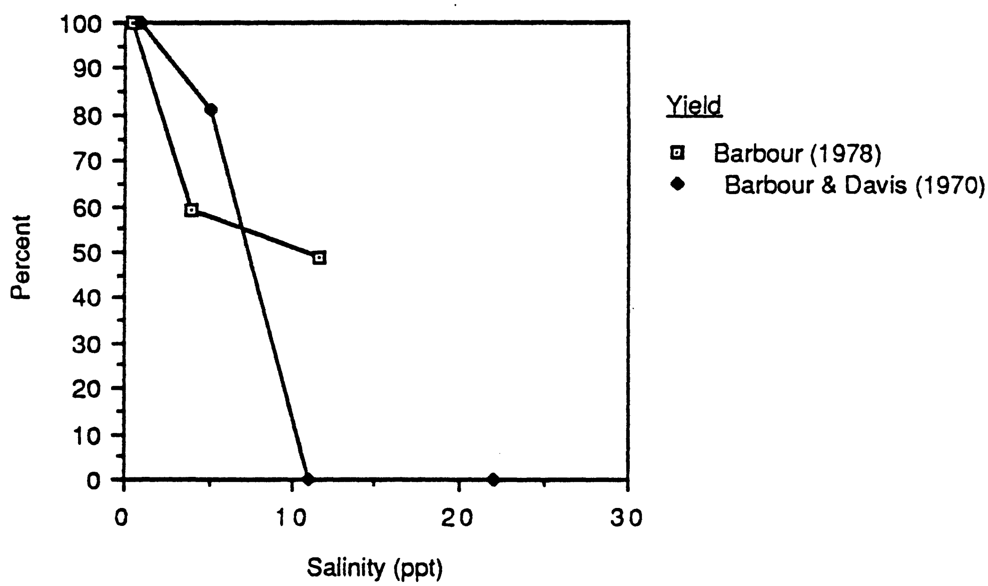


Hypericum formosum H.B.K. (Western St. John's wort)
This species is found in the upland transition zone, and at the highest levels of freshwater marshes. Macdonald's (1984) data from the Columbia River estuary indicate that it is restricted to sites with salinities <0.5 ppt.

Hypochaeris radicata (Hairy cats-ear)
This weed is a fairly common member of the marsh-upland transition flora. Turkington and Aarsen (1983) conclude from its occupance of exposed coastal cliff sites in western Britain that this species "has some degree of salt tolerance". In the estuaries of eastern Vancouver island it is found on gravel substrates that experience salinities up to 3ppt (Dawe and White 1982).

Iris pseudoacorus L. (Yellow flag)
Isolated individuals of Iris spp. are found along the margins of shallow ponds or muddy ditches towards the upper margins of freshwater marshes in estuarine habitats. Macdonald's (1984) data from the Columbia River estuary indicate that it this species is restricted to sites with salinities <0.5 ppt.

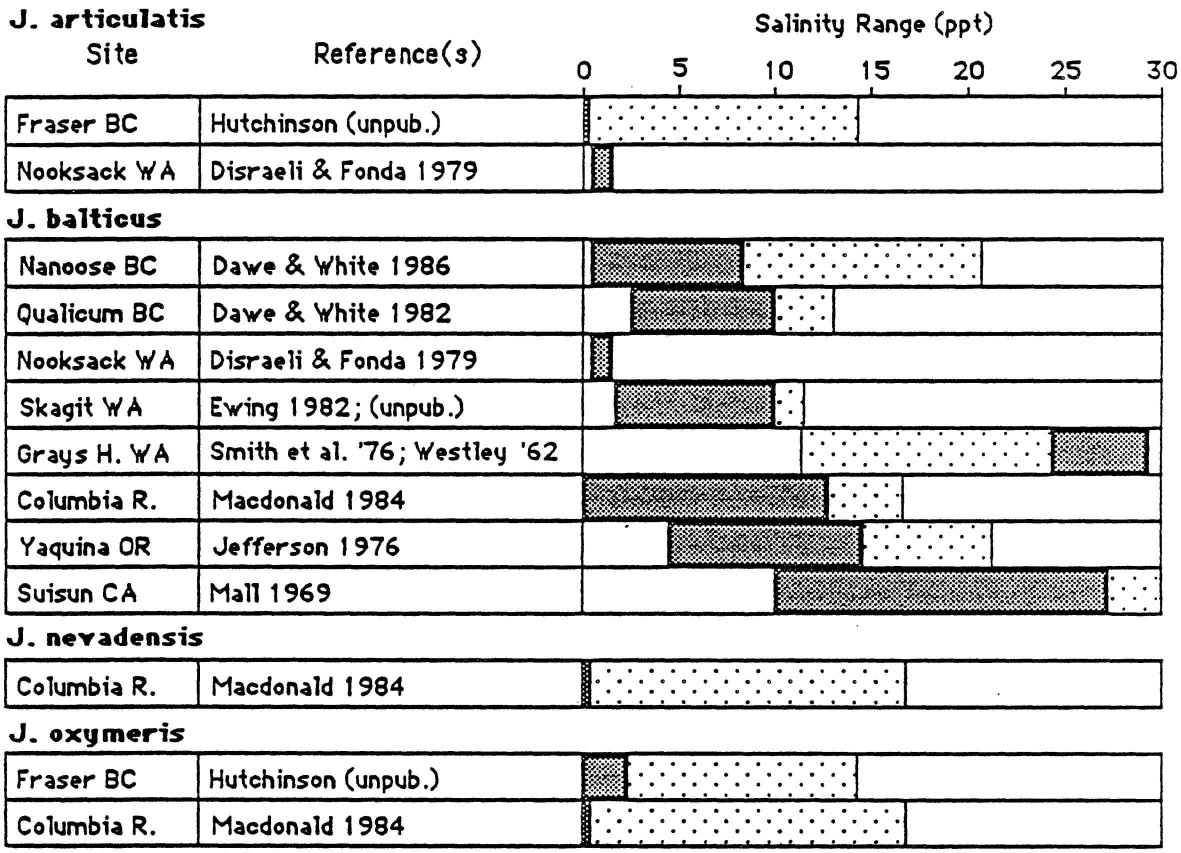
Jaumea carnosa (Less.) Gray (Fleshy jaumea)



This species is a common, sometimes dominant element in the flora of the middle and upper zones of saline marshes from Vancouver Island south to California. Seliskar (1985) notes that it is found in the most saline habitats in Netarts Bay (Oregon), where salinities may rise to 39 ppt in the growing season. Experimental data on the ecological performance of fleshy jaumea is provided by Barbour and Davis (1970), Barbour (1978), and St. Omer and Schlesinger (1980). Barbour (1978) contended that 11.6 ppt salinity was the limit of tolerance for Jaumea, based on experimental material that he obtained from a brackish marsh at Bodega Head, California. St. Omer and Schlesinger (1980) concluded that optimal growth occured at ca. 9 ppt, and that the limit of tolerance was ca. 35 ppt for material from Santa Barbara, California. These values are likely more representative of the tolerance ranges of salt marsh populations of this species in the Pacific Northwest.

Juncus spp. (Rush)
Several species of the common rush occur in the marshes of the Pacific Northwest. With the exception of J. balticus and J. gerardii, all are limited to fresh or subsaline conditions.J. balticus is a complex and variable taxon whose populations occupy a broad range of habitats in Pacific Northwest marshes, from poorly-drained, low-elevation muds in brackish and freshwater environments to the upper limits of saline meadows, where it may coexist with J. gerardii. The ecological characteristics of J. balticus and its varieties require study. Rozema (1976) and Rozema et al (1985) analysed the relative growth of Dutch stocks of J. gerardii at varying salinity levels. They demonstrated that there is little growth

depression at salinities below 3.5 ppt, but that there is a 52% reduction in yield at 9 ppt, and that yields may be reduced by 87% at salinities from 17.5 ppt (Rozema 1976) to 29 ppt (Rozema et al 1985). Juncus leseurii and J. effusus are common species in freshwater marshes, wet meadows and bogs in the Pacific Northwest, but no data were found on the salinity limits of these species in the literature reviewed.



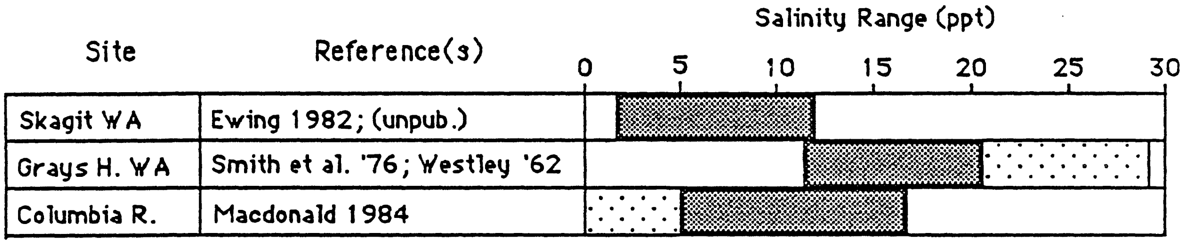
Lathyrus japonicus Willd. (Beach peavine)

Beach peavine is a plant of sand dune, upper beach, and gravel spit habitats above the range of tidal influence. It is found occasionally in the marsh-upland transition flora in sites with salinities ranging from 0 - 4 ppt (Hutchinson 1982).

Lathyrus palustris L. (Marsh peavine)

This species is an infrequent member of the brackish marsh flora, usually associated with sloughs and ditches in the upper marsh. Macdonald (1984) records L. palustris in the marshes of the Columbia River estuary. Mid-channel salinities offshore of these sites were 3 - 13 ppt.

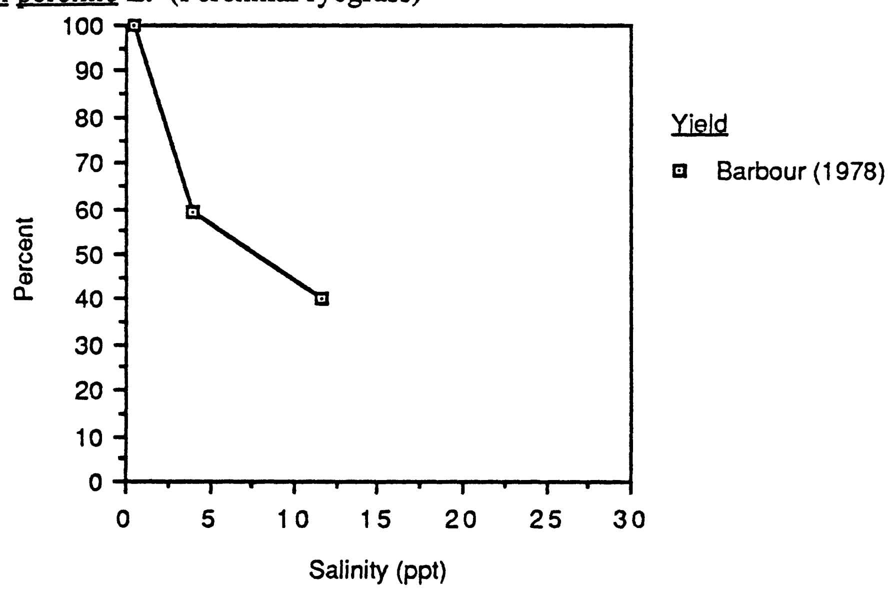
Lilaeopsis occidentalis Coult & Rose (Lilaeopsis)



L. occidentalis is a species of muddy substrates, particularly at low elevation in freshwater and brackish marshes.

Limosella aquatica L. (Mudwort)
Mudwort is characteristically found in fairly open habitats in freshwater and brackish marshes. Ewing (1982, and unpub. data) recorded this plant from low salinity environments (3 - 6 ppt) in the Skagit River delta marshes, and I have recorded it from freshwater sites only (0 - 0.5 ppt) in the FRaser River estuary.

Lolium perenne L. (Perennial ryegrass)



This is a widespread and common plant of wet meadows and the marsh-upland transition zone. Bernstein (1964) listed perennial ryegrass as "moderately" salt-tolerant and Mass (1986) stated that yield reductions occured above 5.6 dS/m (4.6 ppt), with a slope of 7.6% per dS. Venables and Wilkins (1980) noted that it was absent only from the most saline soils of a salinized pasture in Britain. These authors recorded uniform root growth from 0 - 6 ppt in experimental treatments, but a substantial decrease in root production over the salinity range 6 - 12 ppt. Although comparisons of root vs. whole-plant yield must be tentative, these results indicate that the U.K. populations may be somewhat more salt-tolerant than those from a brackish marsh in California examined by Barbour (1978).

Lonicera involucrata (Rich.) Banks (Black twinberry)
This shrub species is characteristic of partially shaded marsh-upland transition communities and floodplain forests. No accounts of distribution in the field relative to salinity gradients or quantitative data on the salinity tolerance of this species were found in the literature reviewed, although Kirkpatrick et al. (1978) noted that it has "low" salt-tolerance.

Lotus corniculatus L. (Birdsfoot-trefoil)
The trefoil species are relatively common plants in high marsh and upland-marsh transition zone floras. Bernstein (1964) ranked this species towards the lower boundary of those that he considered to have "good" salt-tolerance. Maas (1986), citing Bernstein (1964), listed L. corniculatus as being moderately salt-tolerant. He stated that yield reductions occured above 5.0 dS/m (4.2 ppt), with a slope of 10% per dS. In the Columbia River estuary birdsfoot-trefoil ranges over the entire spectrum of salinity conditions, from 0 - 17 ppt. (mid-channel salinity data presented by Macdonald 1984).

Lotus ulignosus L. (Big trefoil)
Maas (1986) listed big trefoil as being moderately salt-sensitive. He stated that yield reductions occured above 2.3 dS/m (1.9 ppt), with a slope of 19% per dS

Lysichitum americanum Hultén & St. John (Skunk cabbage)
Common in coastal swamps, skunk cabbage may occasionally be found as a minor component of freshwater high marshes, particularly on boggy organic substrates. Macdonald (1984) noted this species only in the upstream reaches of the Columbia River estuary, where salinity values never exceed 0.5 ppt..

Lythrum salicaria L. (Purple loosestrife)
This species is rapidly invading freshwater and subsaline marshes in the Pacific Northwest. In the habitats that it occupies on the Fraser River delta foreshore, salinity values up to 8 ppt may be experienced early in the growing season for short periods of time (Hutchinson unpub. data). There are no quantitative data from elsewhere in the Pacific Northwest on distribution relative to salinity gradients.

Maianthemum dilatatum (Wood) Nels. & Macbr. (May-lily)
A common member of the plant communities of moist streambanks, floodplain forests, etc., this species may invade the shaded margins of freshwater marshes in estuarine

environments No quantitative data on distribution in the field relative to salinity gradients or the salinity tolerance of this species were found in the literature reviewed.

Mentha spp. (Mint)
Individuals of M. arvensis and M. piperata are occasionally encountered in freshwater marshes in the study area. In the Columbia and Fraser estuaries they are restricted to sites having salinities <0.5 ppt (Macdonald 1984; Hutchinson, unpub. data).

Menyanthes trifoliata L. (Buckbean)
Buckbean is commonly found in freshwater marshes on wet organic substrates. In the Fraser delta the salinity conditions in these soils is usually in the fresh to subsaline range (<3 ppt), but may rise to 5 ppt in sites near the delta foreshore for short periods at the beginning of the growing season (Hutchinson, unpub. data).

Myosotis laxa Lehm. (Forget-me-not)
M. laxa is a minor element in the flora of high freshwater marshes. In the Columbia and Fraser estuaries it is restricted to sites having salinities <0.5 ppt (Macdonald 1984; Hutchinson, unpub. data).

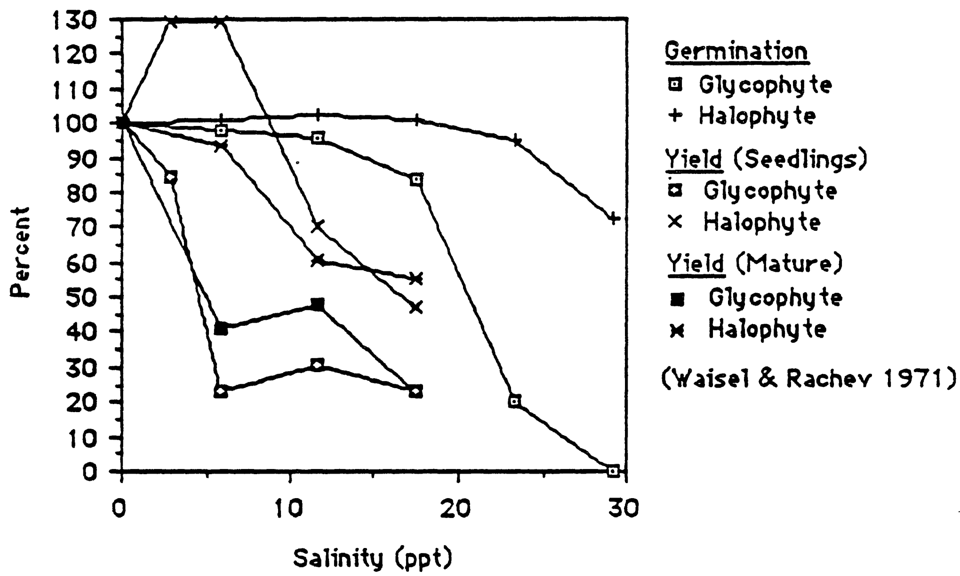
Oenanthe sarmentosa Presl. (Water-parsley)
This species is an infrequent member of high fresh (predominantly) and brackish marsh communities. In the Columbia estuary it is found over sites with a salinity range of 0 - 13 ppt (Macdonald 1984).

Orthocarpus castillejoides Benth. (Paint-brush owl-clover)
An infrequently-encountered plant of high brackish marshes, O. castillejoides appears to have a high salt tolerance. Macdonald (1984) records it over a salinity range of 5 - 17 ppt in the Columbia River estuary.

Phalaris arunidacea L. (Reed canary-grass)
Bernstein (1964), and Kirkpatrick et al. (1978) note that reed canary-grass has a "moderate" salt tolerance. This term indicates that a 10% reduction in yield may be expected between 2.5 - 5 ppt; a 50 % reduction in yield between 6 - 9 ppt.

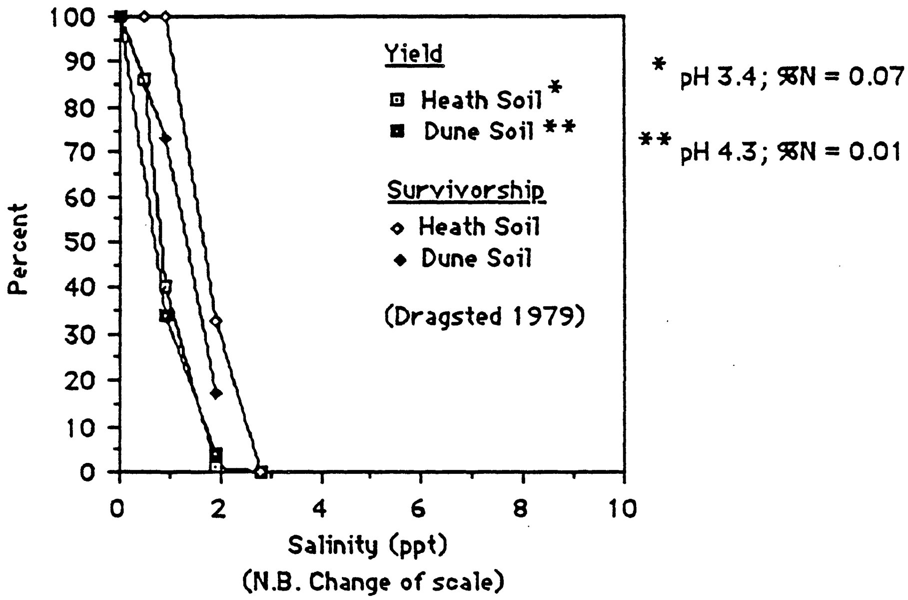
Phragmites communis (L.) Trin. (Common reed)
Common reed is infrequently found in the high freshwater and brackish marshes of the Pacific Northwest. Waisel and Rachev (1971) documented the ecological performance of glycophytic and halophytic ecotypes of this species (from Israel) across a broad range of salinity conditions. They noted that seedlings of this species are found in the field (in

Israel) only on soils with salinities <6 ppt, and even though mature plants of halophytic ecotypes can withstand 30 ppt salinity in laboratory culture, they are never found at this salinity level in the field.



Physocarpus capitatus (Pursh) Kuntze (Pacific ninebark)
This woody shrub is common in coastal swamps and along streambanks. No field or experimental data on salinity tolerance were found in the literature reviewed, but its associates (e.g. Sitka spruce, red osier dogwood) would suggest that it is salt-sensitive.

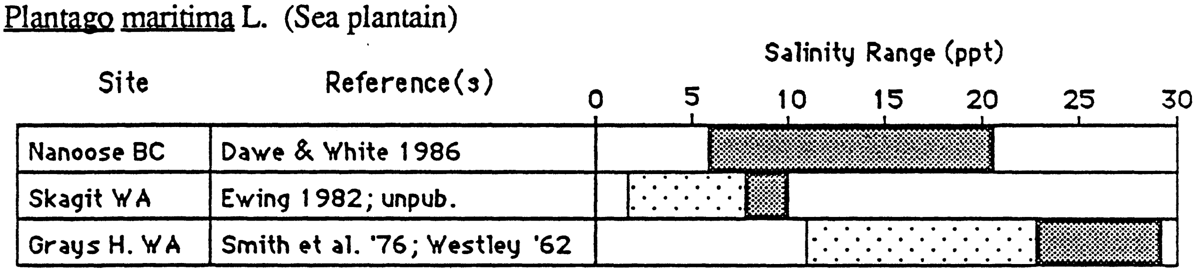
Picea sitchensis (Bong.) Carr. (Sitka spruce)
Sitka spruce is one of the prominent members of the arboreal stratum in tidal floodplain forest, and may form pure stands on fixed coastal dunes. Despite its ecological and commercial importance in the forest resource of the Pacific Northwest, no quantitative data are available on the salinity characteristics of the sites on which it grows. The only data on tolerance of salts in soil culture are from growth experiments on 3-year old plants derived from Scandinavia plantations (Dragsted 1979). These indicate that the yield of Sitka spruce is severely inhibited at 1 ppt salinity, and survivorship is negligible above 2 ppt. The North American provenance of the material used in these experiments is unknown. It may be derived from inland populations with inherently low salt-tolerance characteristics, and these results may not therefore be directly applicable to spruce populations in near-shore environments.



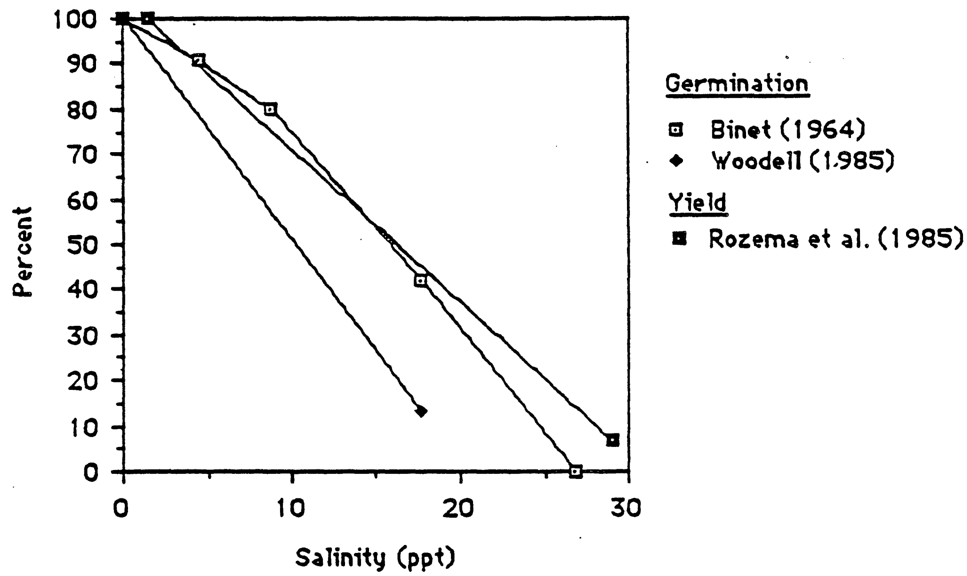
Plantago lanceolata L. (Ribwort plantain)

Ribwort plantain is a common member of the marsh-upland transition flora, particularly in disturbed habitats. Data presented by Dawe and White (1986) indicate that it has a moderate degree of salt tolerance; in Nanoose Harbour it grows on substrates with soil salinities in the 0.4 - 8 ppt range.

Plantago maritima L. (Sea plantain)

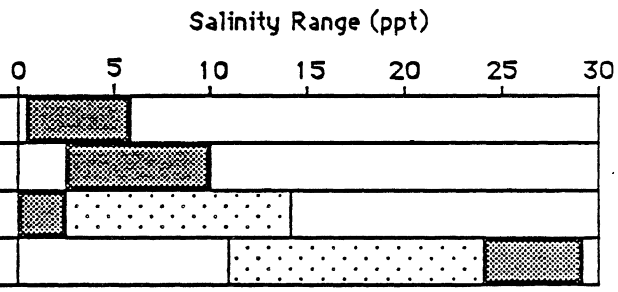


This species is a common, but usually a minor component of the saline marsh flora in the Pacific Northwest. It is most frequently encountered in the low marsh on relatively well-drained substrates. Habitats occupied in the field have a salinity range of 5 - 25 ppt in the growing season. Binet (1964) and Woodell (1985) indicated that germination rate decreases linearly with increasing salinity , and Binet (1964) concluded that germination was influenced by temperature and salinity pre-treatments. He obtained highest germination rates at 25 C, in light, and in fresh water. The graph above is for seed floated in seawater at 5 C in the dark prior to the germination experiment. Rozema et al. (1985) compared the relative growth rate of plants derived from Dutch salt marshes at two salinity levels. Their data indicated that the upper tolerance limit for P. maritima was ca. 30 ppt.



Poa pratensis L. (Kentucky bluegrass)

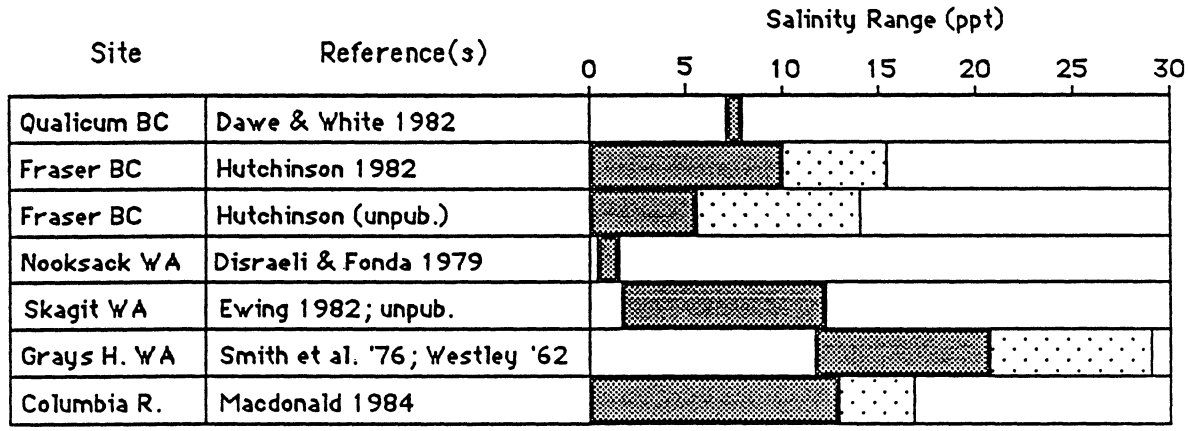
Site	Reference(s)
Nanoose BC	Dawe & White 1986
Qualicum BC	Dawe & White 1982
Fraser BC	Bradfield & Porter 1982
Grays H. WA	Smith et al. '76; Westley '62



Kentucky bluegrass is an infrequent species in fresh and brackish marshes in the study area. It occupies substrates with a salinity range of 0 - 10 ppt.

Polystichum munitum (Kaulf.) Presl. (Sword-fern)
Sword-ferns are a common plant in the coastal forest understorey on a variety of substrates, and may occasionally be found in the marsh-upland transition zone in shaded situations. No data were found on the field distribution of this species in relation to salinity gradients, or tolerance of salinity in experimental treatments in the literature reviewed.

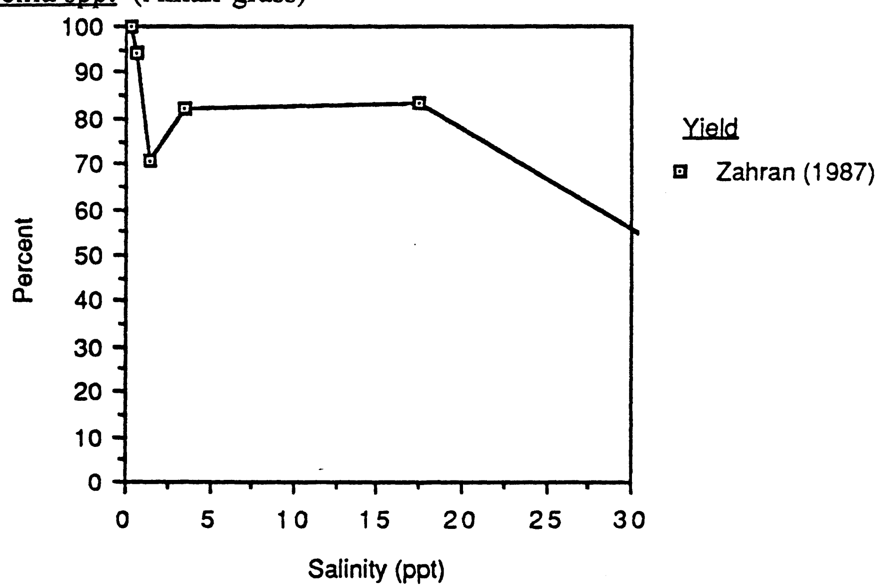
Potentilla pacifica Howell (Pacific silverweed)
Pacific silverweed is a common member of the high marsh flora of brackish and fresh marshes in the Pacific Northwest. It is commonly found in association with Carex lyngbyei and Deschampsia caespitosa on substrates with salinities from 0 - 12 ppt. No experimental data on the salinity tolerance of this species were found in the literature reviewed.



Potentilla palustris (L.) Scop. (Marsh cinquefoil)
No accounts of distribution in the field relative to salinity gradients or experimental data on the salinity tolerance of this species were found in the literature reviewed.

Pteridium aquilinum (L.) Kuhn. (Bracken)
No accounts of the salinity limits of this common upland fern in the field, or experimental data on its salinity tolerance, were found in the literature reviewed.

Puccinellia spp. (Alkali-grass)



Isolated individuals of P. pumila and P. nutkaensis are commonly encountered in high saline marshes in the Pacific Northwest in asociation with Salicornia virginica and Distichlis spicata. Dawe and White (1986) indicated that this species is found over a salinity range of 6 - 21 ppt (the highest value recorded) in the marshes of Nanoose Harbour. Tolerance limits for these species may be equivalent to that of their more dominant European counterpart (P. maritima), which recorded 50% germination at 40 ppt. salinity (Zahran 1987). Venables and Wilkins (1980) showed that root growth of P. maritima was stimulated over a salinity range of 3 - 12 ppt compared to fresh water. Rozema et al. (1985) indicated that Dutch plants of this species had a 66% reduction in relative growth rate at 29 ppt compared to fresh water in flooded treatments; the British material used by Zahran (1987) (see graph) was even more tolerant of these extreme conditions.

Pyrus fusca Raf. (Western crabapple)

Crabapples are common members of the marsh-upland transition flora, and stands are also frequently found in floodplain meadows and along streambanks. No data on the salinity conditions associated with habitats occupied by this species were found in the literature reviewed, but flowering crabapples (cultivated varieties of P. fusca) are classified as having "low" salt tolerance by Kirkpartick et al. (1978), and cultivated varieties of P. malus are also known to be salt-sensitive (Maas 1986). Dilley et al. (1958) indicated that Cl concentrations of 355 ppm (approx. 0.6 ppt salinity) reduced the growth of "Delicious" seedlings by 15%, and 665 ppm (approx 1.1 ppt salinity) resulted in an 80% reduction. Bernstein (1980) noted that 10% reductions in crop yield occurred in cultivated apples at 1.2 - 2.0 ppt salinity.

Ranunculus cymbalaria Pursh (Shore buttercup)

This species is a minor element of brackish marshes in the study area. Dawe and White (1982) and Ewing (1982) provide data that indicate that the species occupies sites with a maximum salinity of 12 ppt.

Ribes sanguineum Pursh (Red currant)

R. sanguineum is a fairly common species in open floodplain forests and in the marsh - upland transition flora. No data exist on the salinity conditions in these habitats. Kirkpatrick et al. (1978) stated that Ribes spp. possess "moderate" salinity tolerance; i.e. a likely reduction of 10% in relative growth at 2 - 5 ppt salinity; 50 % reduction at 6 - 9 ppt., and Maas (1986) considers members of the genus to be salt-sensitive.

Rosa gymnocarpa Nutt. (Baldhip rose)

According to Kirkpatrick et al. (1978) R. gymnocarpa has "low" salt tolerance: i.e. a likely reduction of 10% in relative growth at 1 - 2 ppt salinity; 50 % reduction at 2.5 - 5 ppt. Cultivated roses are known to have similarly low tolerance of salts in the root zone. Bernstein, Francois and Clark (1972) recorded 50 % reduction in yield at 2.6 ppt, burning effects on the leaves at this salinity level, and 50% mortality at 3.3 ppt.

Rosa nutkana Presl. (Nootka rose)

Nootka rose seems to share the low salt tolerance of its congenerics. Dawe and White (1982, 1986) recorded Rosa communities on gravel bars in subsaline portions of the Qualicum River and Nanoose estuaries. These substrates had associated salinities of 2 - 3 ppt and 0.3 - 0.5 ppt respectively.

Rubus spp. (Blackberry)

Blackberries (R. discolor, R. lacianatus, R. spectabilis, R. ursinus) are common in marsh-upland transition communities and in disturbed an semi-open habitats in floodplain forest. Bernstein (1980) indicated that members of this genus have "low" salt tolerance. This term is used to indicate species which exhibit 10 % reduction in yield at 1.2 - 2 ppt, and 50 % reduction in yield at 3 - 5 ppt.

Rumex acetosella L. (Sheep sorrel)

Fairly common in wetland communities at or above the marsh-upland transition, the salinity tolerance limits of this species are unknown. Dawe and White (1986) indicated that it is restricted to freshwater (>0.5 ppt) habitats in the marshes of the Nanoose estuary.

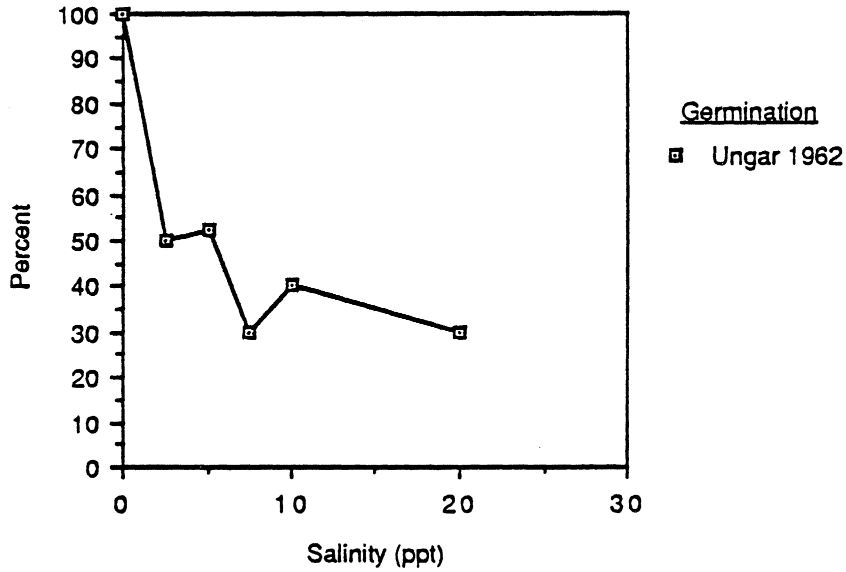
Rumex crispus L. (Curly dock)

A common, but ususally minor element in high brackish and freshwater marsh communities in the Pacific Northwest, Macdonald (1984) recorded curly dock across a salinity range of 0 - 13 ppt in the Columbia River estuary (mid-channel data). In contrast, on salinized soils of the mid-West it is restricted to sites with salinities <6 ppt (Worcester and Seelig 1976). Woodell (1985) obtained virtually complete germination of seeds of this species in freshwater, but negligible germination (<1 %) at the lowest salinity level that he tested (17.5 ppt).

Sagittaria latifolia Willd. (Wapato)

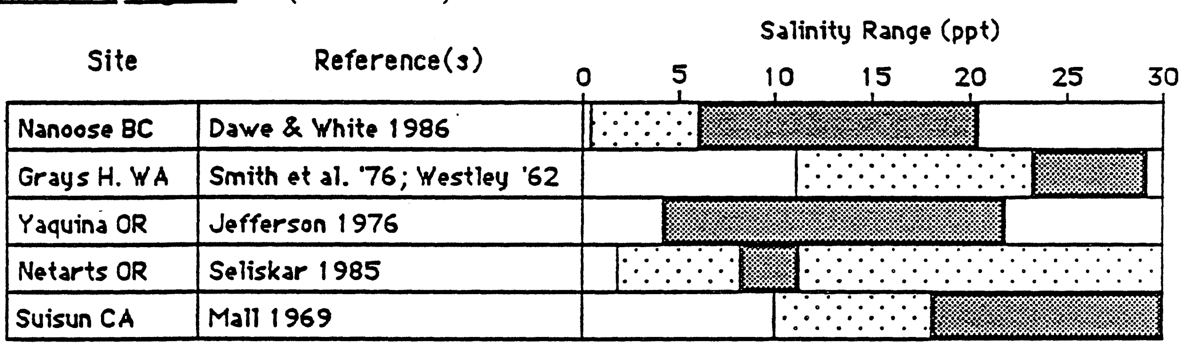
Wapato is a common member of the freshwater marsh community. It is associated with ponds and mucky substrates in shallow freshwater marshes. Macdonald (1984) recorded wapato only in freshwater habitats (< 0.5 ppt) in the Columbia River estuary (mid-channel data), but the species is known to occur in the foreshore marshes of the Fraser River delta in sites in which salinities may, on occasion, be as high as 5 ppt in the early part of the growing season (Hutchinson, unpub. data).

Salicornia europea L. (European glasswort)



Members of this complex taxon of annual halophytes are rarely encountered in undisturbed marshes. However, large numbers of seedlings of may colonize a saline marsh following disturbance. Their tenure on such sites is relatively limited. Rozema et al. (1985) noted that the growth of Dutch material was more rapid at 29 ppt than in freshwater, and they have been recorded in the Pacific Northwest in habitats in which interstitial salinities exceeded 45 ppt. Growth in such conditions is likely slow (Hutchinson, unpub data). Ungar (1962), working with seeds derived from populations from the east coast of North America, indicated that germination was severely inhibited in saline culture, but this result was not confirmed by later work on material from inland salt lakes (Ungar 1974).

Salicornia virginica L. (Pickleweed)



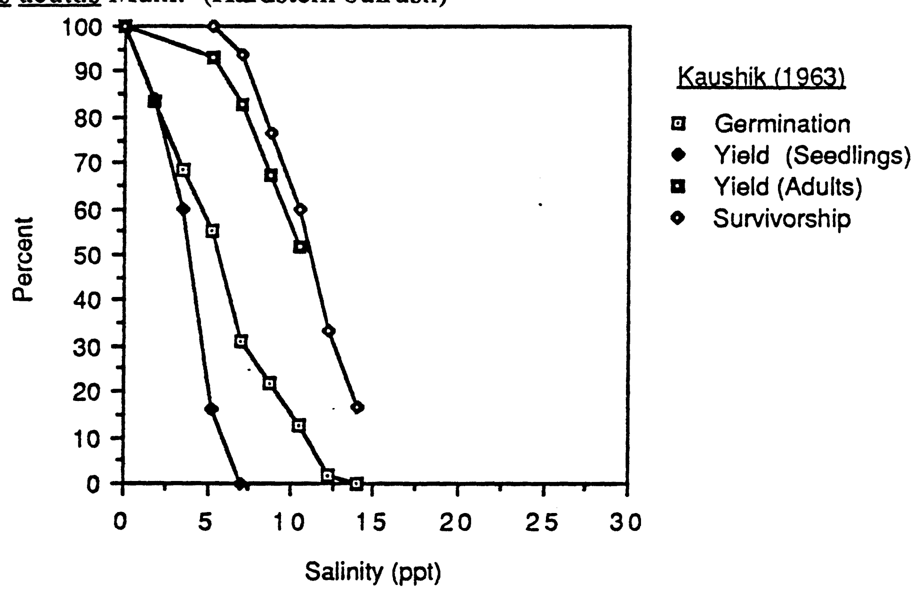
This is the dominant plant in many saline marshes along the northwest Pacific littoral, particularly at low elevations. It occupies a broad salinity range; Knudson and Woodhouse (1982), citing Mall (1969), note that it is found over a salinity range of 20 - 80 ppt in

California. Whilst salinities in the marshes of Washington State probably rarely exceed 50 ppt, the species has been recorded from our area from sites with peak salinities of 45 ppt (Hutchinson, unpub. data). Pickleweed may also occur as a rare component of the high brackish marsh flora, growing on sites with mean growing season salinities as low as 5 ppt. Pearcy and Ustin (1984) noted that the highest relative growth rates of this species occurred at salinities between 9 - 18 ppt, with a modest decline between 18 - 27 ppt. These results contrast with those obtained by Barbour and Davis (1970), who worked with brackish marsh material. They recorded a linear decline in growth between 1 - 11 ppt, and complete mortality of the experimental cohort at 22 ppt salinity. They noted that these results likely reflect the low inherent tolerance of this S. virginica population.

Salix spp. (Willow)

Stands of willows are found along streambanks, around the upper margins of freshwater and brackish marshes, and in moist swales in coastal dunefields. In their compilation of the salinity tolerance of trees and shrubs of Nevada, Kirkpatrick et al. (1978) documented the salt tolerance of all four willows that they survey as "moderate"; i.e. a likely reduction of 10% in relative growth at 2 - 5 ppt salinity; 50 % reduction at 6 - 9 ppt.. The resistance of various North European tree and shrub species to seawater flooding was described by Richardson (1955). He noted that willows were considered by most authorities to be relatively resistant to seawater exposure. In the absence of other data, it may be assumed that the willow species associated with coastal habitats (principally S. hookeriana Barratt, commonly found on stabilized dunes) share this trait.

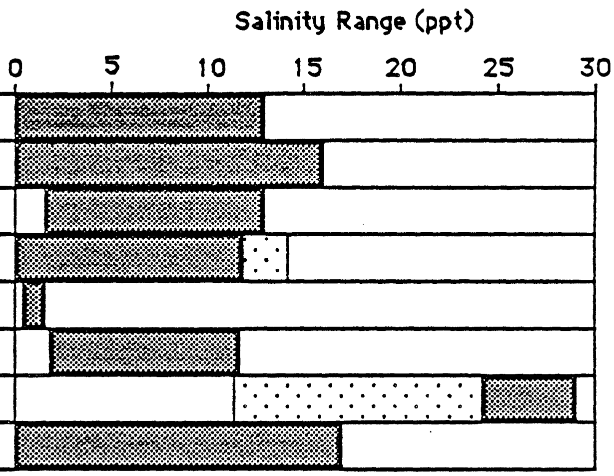
Scirpus acutus Muhl. (Hardstem bulrush)

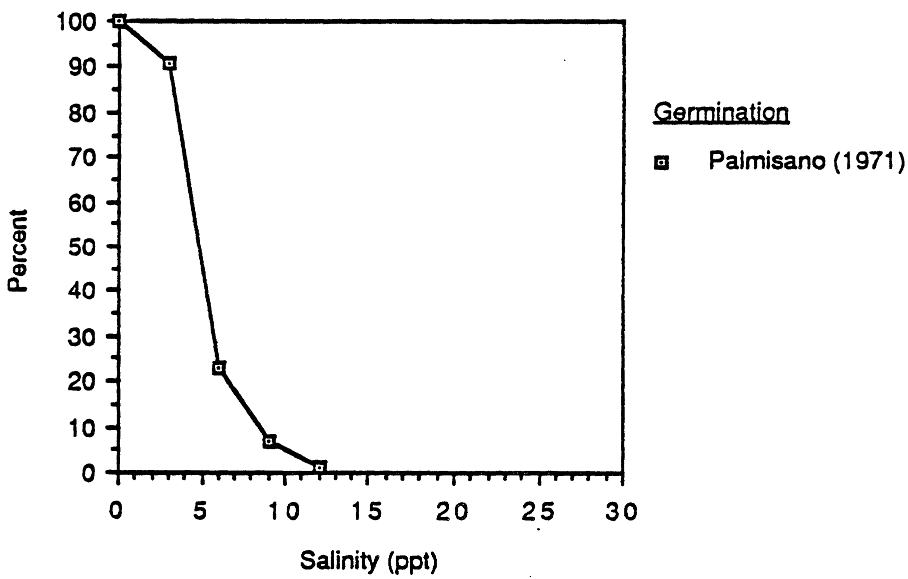


In the Fraser River estuary S. acutus is limited to freshwater and subsaline marshes along the river distribuatries, and areas of freshwater seepage in the foreshore marshes. These habitats have salinities genrally below 3 ppt, but salinities up to 6 ppt may persist for short periods of time early in the growing season (Hutchinson, unpub. data). This distribution appears to match the experimental results obtained by Kaushik (1963), who used material derived from the Great Salt Lake, Utah. He demonstrated that germination in this species is negligible above 10 ppt, and the seedlings are stongly inhibited by salinities above 5 ppt. As might be expected, adult plants were more robust at higher salinities, but mortality in media >7 ppt was very high. The mean life-expectancy at this salinity level was 23 d, and 4 d at 14 ppt.

Scirpus americanus Pers. (Three-square bulrush)

Site	Reference(s)
Fraser BC	Moody 1978
Fraser BC	Hutchinson 1982; Boyd 1981
Fraser BC	Karagatzides 1987
Fraser BC	Hutchinson (unpub.)
Nooksack WA	Disraeli & Fonda 1979
Skagit WA	Ewing 1982; unpub.
Grays H. WA	Smith et al. '76; Westley 62
Columbia R.	Macdonald 1984



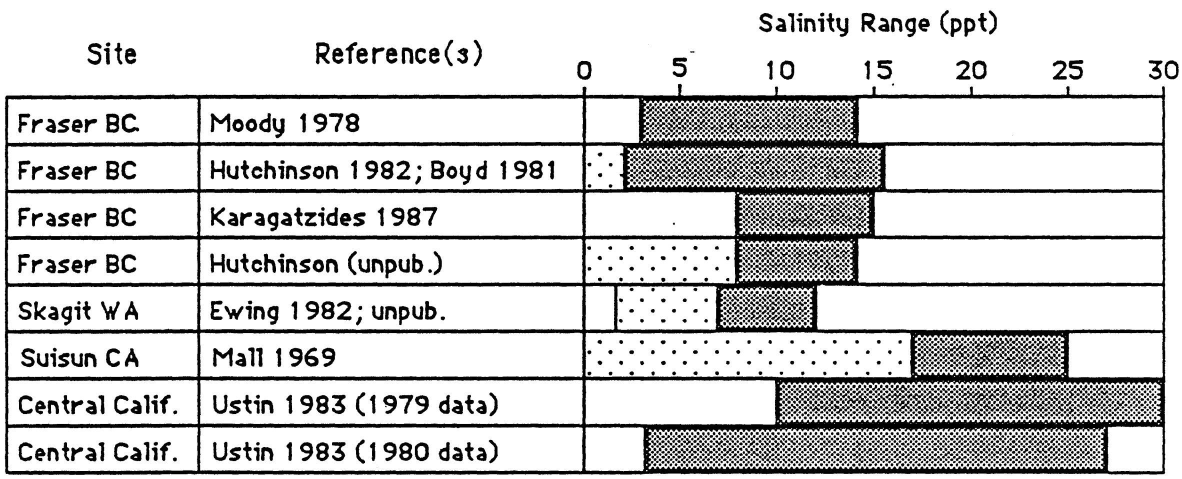


S. americanus is the dominant species along this littoral at low elevations in brackish marshes in which salinities remain relatively low throughout the growing season (Hutchinson 1988). Palmisano (1971) noted that germination rates were highest in fresh and subsaline media , and mean growing-season salinities in the 5 - 10 ppt range are apparently required to maintain competitive dominance by this species. The upper distributional limit for the species is ca. 15 ppt in local marshes, but Gordon (1981) demonstrated that plants derived from a subsaline reach of the Fraser River estuary can tolerate salinities of 20 ppt. At 15 ppt they experienced a yield reduction of 62% compared to plants grown in freshwater.

Scirpus cernuus Vahl (Low clubrush)

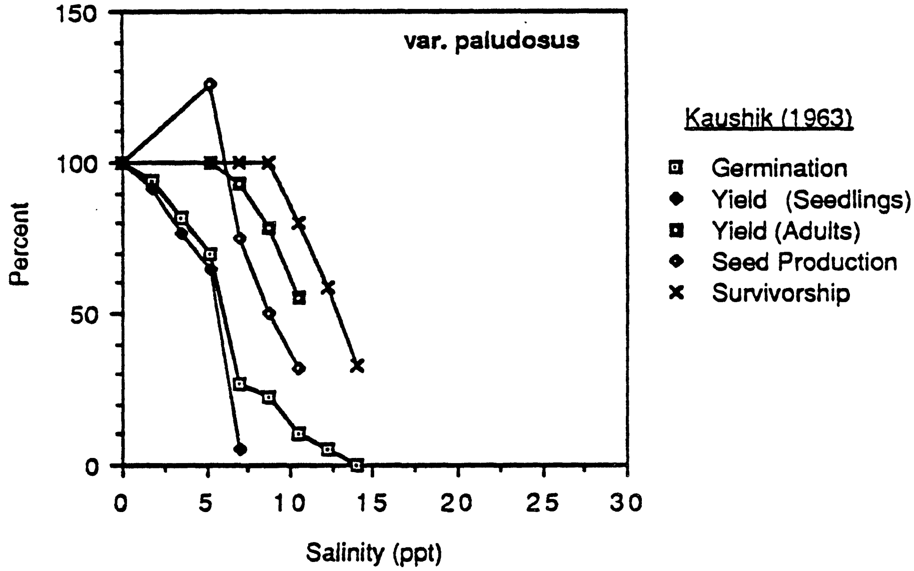
S. cernuus co-occurs with S. americanus and S. maritimus in the brackish marshes of the Pacific Northwest, and likely has a congruent tolerance range. No experimental data on the ecological response of this species to variable salinity levels were found in the literature reviewed.

Scirpus maritimus L. (Seacoast bulrush)



This species is dominant on anoxic muds in moderately saline marsh environments, and is absent from freshwater habitats. The ill-defined variety that is characteristic of the marshes of the Pacific Northwest (var. paludosus) is restricted to sites with salinities between 3 - 15 ppt; the coastal sub-species in California (var. robustus), is found on more saline substrates. The var. paludosus material examined by Kaushik (1963) may be less salt-tolerant than coastal material from the Pacific Northwest.. The mean life-expectancy at

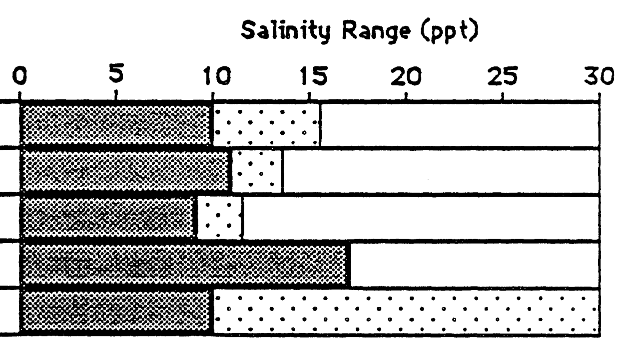
10.5 ppt for plants from a marsh on the Great Salt Lake was only 49 d



Scirpus microcarpus Presl. (Small-fruited bulrush)
This sedge is characteristic of freshwater marsh-upland transition communities, particularly in shaded situations. It is also common in the understorey of deciduous woodlands in coastal floodplains. In the Fraser River estuary it is restricted to freshwater (<0.5 ppt) environments (Hutchinson, unpub. data). In the Columbia River estuary it is associated with sites having a 0 - 4 ppt salinity range (mid-channel data; Macdonald 1984). Hutchinson (unpublished) noted 100% mortality of seedlings over the course of a growing season in flooded treatments with a mean salinity of 10 ppt, 72 % in 5 ppt, and 0 % in freshwater. The 5 ppt treatment exhibited a reduction in yield of 88% compared to freshwater.

Scirpus validus Vahl (Tule)

Site	Reference(s)
Fraser BC	Hutchinson 1982; Boyd 1981
Fraser BC	Hutchinson unpub.
Skagit WA	Ewing 1982; unpub.
Columbia R.	Macdonald 1984
Suisun CA	Mall 1969

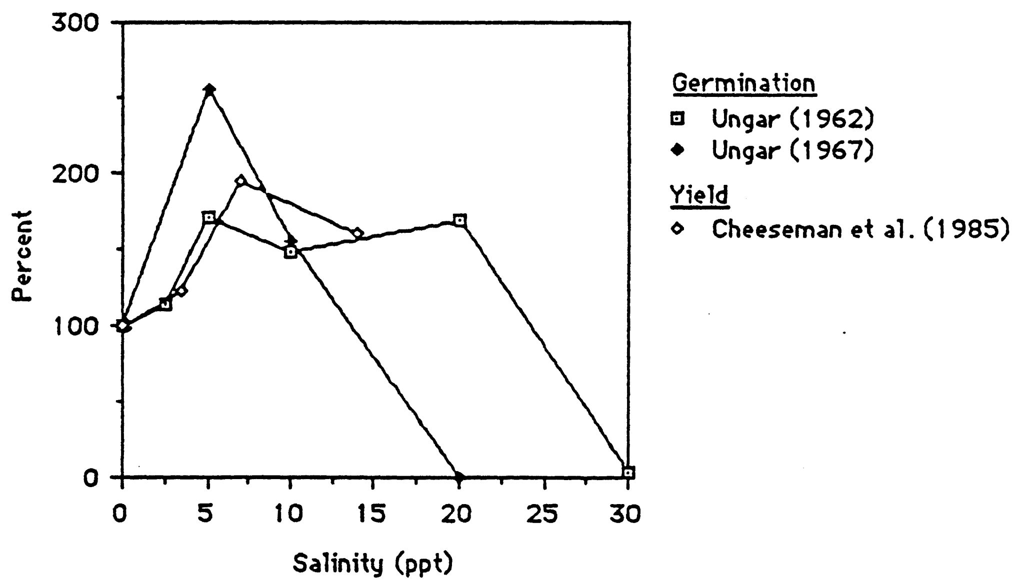


Tule, or soft-stem bulrush, is a major component of low freshwater and brackish marshes in the region. It is primarily associated with sites in which mean growing season salinities are <5 ppt, but can withstand exposure to water up to 10 ppt for short periods of time. The data presented by Macdonald (1984) indicated a range of 0 - 17 ppt, were based upon readings in mid-channel in the Columbia River, and may not be representative of occupied sites. Hutchinson (unpublished) noted that 83% of the seedlings died in flooded treatments with a mean salinity of 10 ppt over the course of a growing season, compared to 25 % in freshwater. The 10ppt treatment also exhibited a reduction in yield of 73% compared to freshwater.

Sium suave L. (Water-parsnip)
This species is fairly common in freshwater and high brackish marshes. In the Fraser River estuary it is restricted to sites with salinities in the range 0 - 5 ppt (Hutchinson, unpub. data); in the Columbia River estuary it is found in channel-side marshes with salinities in the range 0 -0.5 ppt (Macdonald 1984)

Sonchus arvensis L. (Perennial sow-thistle)
Perennial sow-thistle is fairly common in the saline marsh-upland transition zone. Pegtel (1972) described coastal and arable ecotypes in the Netherlands which likely have differing salinity tolerances, although no specific data on the salinity tolerance of this species or its varieties were found in the literature reviewed.

Spergularia spp (Sandspurry)

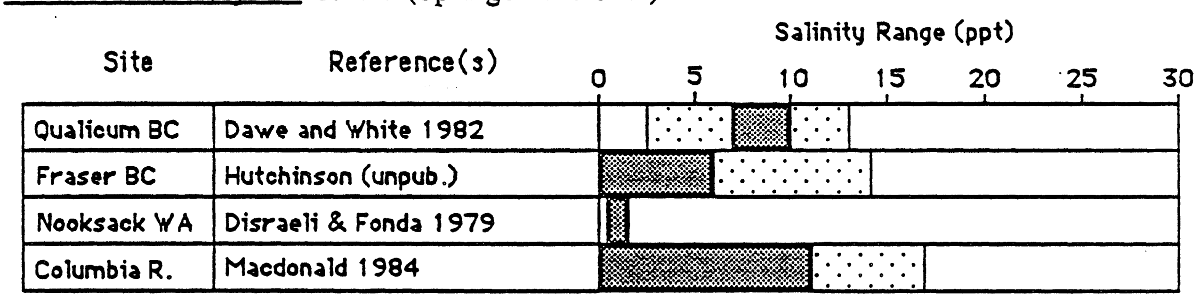


These species (S. canadensis, S. marina) are frequent, but rarely dominate the brackish and saline marsh communities along our coast. The data provided by Smith et al. (1976), Boyd (1981); Ewing (1982, and unpublished), Hutchinson (1982), and Dawe and White (1986) indicate that the niches of the two species overlap on the estuarine salinity gradient. In both cases the range of salinities occupied by these species is ca. 6 - ca. 20 ppt. In the case of S. marina, the experimental data provided by Ungar (1962, 1967) indicate that (depending on the origin of the popuulation) germination may be stimulated by exposure to saline media in the range 5 - 20 ppt. Cheeseman et al. (1985) showed that relative growth of the species is greater over the range of salinities tested than in freshwater.

Suaeda maritima (L.) Dumort. (Herbaceous seablite)
This annual species is infrequently encountered in west coast marshes. It is most common in saline wetlands developed on coarse substrates (e.g. sandy gravel). Woodell (1985) recorded 33% germination compared to freshwater at 17.5 ppt salinity, and 11% at 35 ppt. Yeo and Flowers (1980) noted that growth was increased by 40% at 19 ppt compared to freshwater, and Clipson and Flowers (1987) commented that optimal growth was in media with a salinity of approx. 12 ppt.

Trifolium spp (except T. wormsjioldii) (Clover)
Various species of clover may be found in upland and upland-marsh transition zones. Maas (1986) characterizes the clovers as being salt-sensitive, and Heerkloss and Bartolomaeus (1980) noted that germination was severely inhibited by exposure to salt.

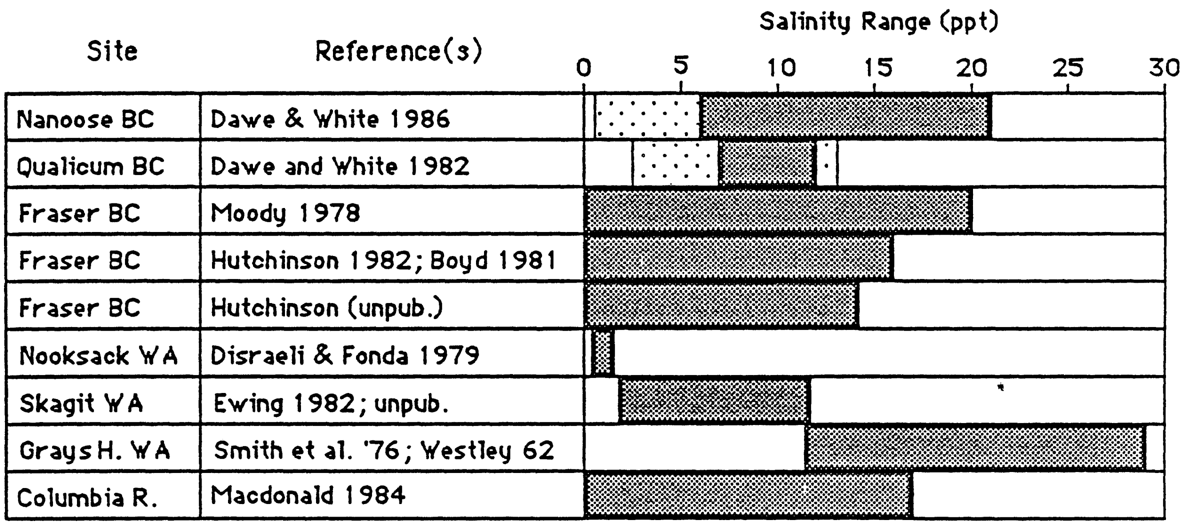
Trifolium wormskioldii Lehm. (Springbank clover)

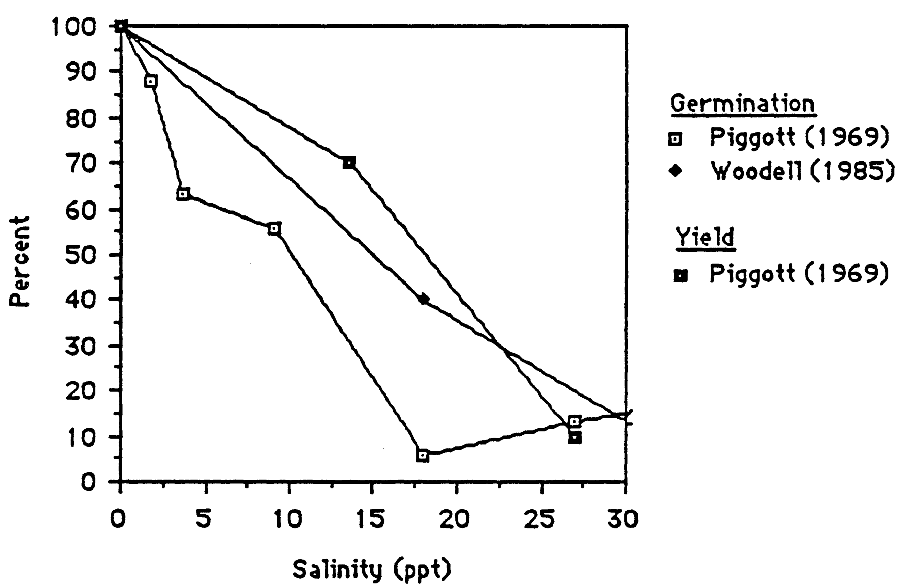


This is a characteristic plant of the high brackish marsh. The available field data indicate that it occurs over a salinity range of 0-10 ppt, and is absent from more saline habitats.

Triglochin maritimum L. (Seaside arrowgrass)
This species is found over a broad salinity range. The available field data indicate an occupance of sites varying in salinity from 0 - 21 ppt in the Pacific Northwest, but T. maritima is also found in more saline habitats than those represented here, and may be able to tolerate hypersaline conditions for brief periods (Hutchinson, unpub. data). The rarer T. concinnum (graceful arrow-grass) is found towards the upper end (in salinity) of the range

of habitats occupied by T. maritima in Grays Harbor, Washington (Smith et al. 1976). Seeds of T. maritima planted by Piggott (1969) germinated over the range of salinities tested (0 - 36 ppt), but germination was substantially reduced on media >10 ppt. Woodell (1985), achieved very low germination totals with Triglochin, as with all the other species he tested. In Piggott's experiment yields declined virtually linearly between 0 - 27 ppt. Rozema et al. (1985) apparently dealt with a somewhat more salt-tolerant ecotype. They recorded only a 60 % reduction in yield at 29 ppt compared to freshwater.



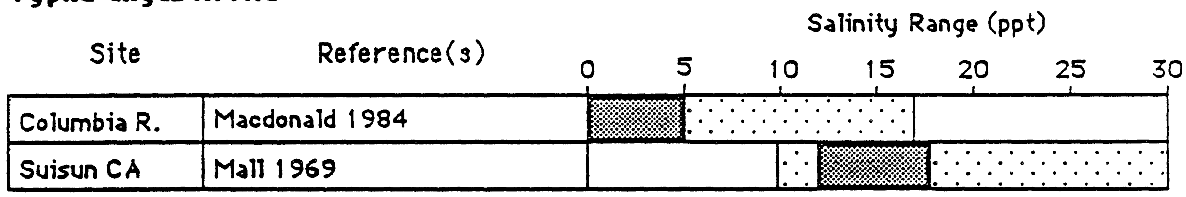


Tsuga heterophylla (Raf.) Sarg. (Western hemlock)

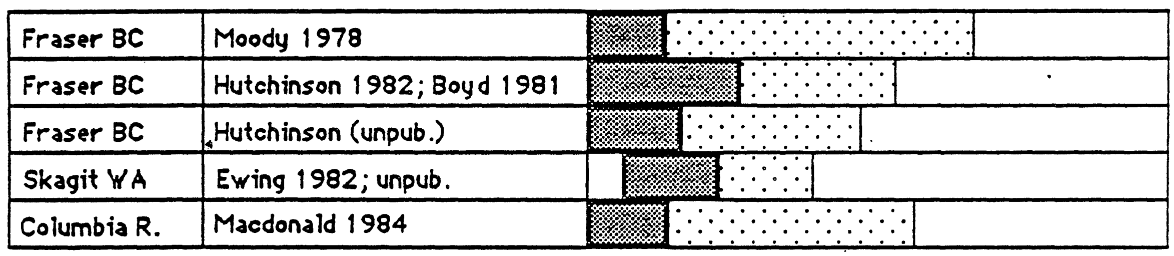
Wsetern hemlock is a dominant member of tideland or floodplain forest, often in association with Sitka spruce. No data on the salinity conditions associated with habitats occupied by this species were found in the literature reviewed, but eastern hemlock (T. canadensis) is classified as being susceptible to highway de-icing salt damage by Shortle and Rich (1970), and Richardson (1955) classified conifers generally as very susceptible to seawater flooding.

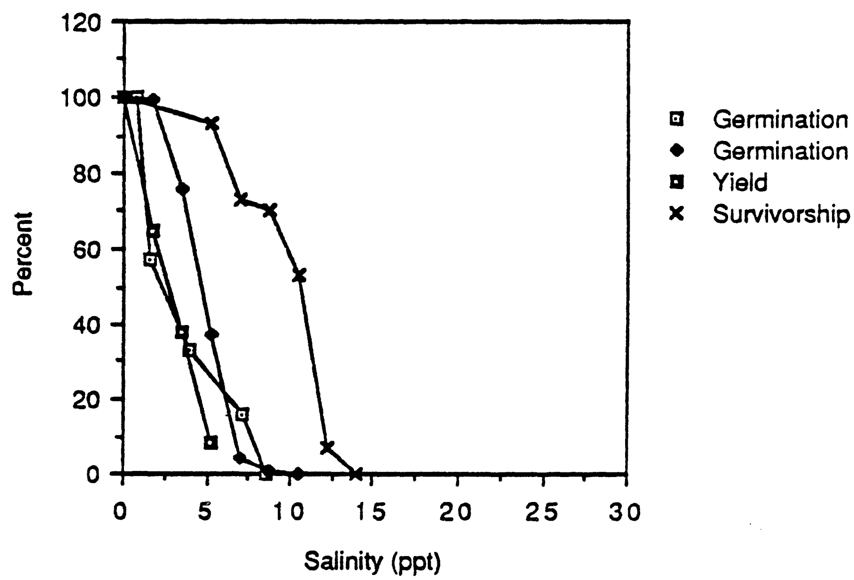
Typha spp. (Cat-tail)

Typha angustifolia



Typha latifolia





Two species of cat-tail occur in the coastal marshes of the Pacific Northwest (T. angustifolia, the narrowleaf cat-tail, and T. latifolia, the common cat-tail). Within the study area both are restricted to freshwater marshes or high brackish marshes, particularly in areas of considerable freshwater influence. For the most part these sites experience salinities in the fresh and sub-saline range, but there may be short periods during which salinities may reach up to 8 ppt. The data provided by Mall (1969) indicate that stands of T. angustifolia in California occupy more saline habitats than those colonized by this species in the Pacific Northwest. The ecological range of the species in the San Francisco Bay area thus seems more akin to some of that of T. domingensis in southern California (Beare and Zedler 1987). The limiting effect of salinity on germination in T. latifolia was documented by Kaushik (1963) and Choudhuri (1968), the former working with material from Utah, the latter with material of an eastern Washington provenance. The effects of salinity on yield and survivorhip were recorded by Kaushik (1963). He indicated that plants exposed to a medium containing 10.5 ppt salt have a mean life-expectancy of only 26 d, and this declined to 6 d at 13 ppt.

Vaccinium spp. (Huckleberry)
No data on the salinity conditions associated with habitats occupied by these species were found in the literature reviewed.

Vicia gigantea Hook. (Giant vetch)
The only data available on the salinity conditions associated with habitats occupied by this species are derived from Macdonald (1984). The single site from which this species was recorded in the Columbia River estuary has a nominal salinity range (from mid-channel data) of 4 - 13 ppt. These figures do not seem to mirror the floristic character of this site, which appears to be much 'fresher' than these values would indicate.

Part V

INDICATOR SPECIES, VEGETATION, AND TIDAL LIMITS: FIELD TESTS

V.I. Indicator Plants as Delimiters of OHWM

The field and experimental database on salinity tolerance that was described in Part IV is summarised in Appendix 2. This lists species alphabetically in terms of their field distributional limits, yield thresholds, and yield reduction slopes. These data form the basis for a classification of species into salinity-tolerance classes, based on the criteria outlined in Figure 3 (p. 9). Table 1 is a further summary of these data, and comprises a list of species by tolerance class.

In order to test whether OHWM formed a critical upper (landward) limit for the distribution of salt-tolerant plants, the number of occurrences of species in the tolerance classes MT, T, and VT (i.e. species whose field distribution encompasses habitats with peak growing season salinities >10 ppt) in plots above MTZ was enumerated from 26 vegetation transects in four of the coastal marsh areas examined by Frenkel et al. (1978) in Washington State. These 26 transects comprised the subsample of coastal marshes in the state that were surveyed topographically by NOS (1980), and in which the position of the mid-transition zone (MTZ) stake (MTZ is assumed to be equivalent to OHWM) was marked.

To test the hypothesis that OHWM (or MTZ) formed a critical lower (seaward) limit for salt-sensitive species the number of occurrences of species in the tolerance classes VS and S (i.e. species whose field distribution is limited to habitats with peak growing season salinities <5 ppt)was enumerated in the plots below MTZ in this same sample of 26.transects.

The results for individual marsh areas and transects are given in Appendix 3. In sum there were 657 occurrences of salt-tolerant species out of a total of 950 species-occurrences in 214 plots located on the upland side of MTZ. Species in the MT,T, and VT classes therefore comprised 69% of the total species-occurrences, at an average density of 3.1 species-occurrences per plot. In contrast, salt-sensitive species were comparatively rare in the marsh habitats below MTZ. An enumeration of 295 plots revealed 45 occurrences of species in the VS and S classes out of a total of 1414 species-occurrences. Salt-sensitive species comprised 3.1% of the total occurrences with an average density of <0.2 species-

Table 1. Salt sensitivity rating of the estuarine wetlands and associated uplands flora of the Pacific Northwest. (* =estimated)

Very Sensitive

- *Tsuga heterophylla
- Angelica arguta
- Berberis aquifolium
- Caltha asarifolia
- Carex rostrata
- Equisetum fluviatile
- Galium cymosum
- Habenaria dilatata
- Heracleum lanatum
- Hypericum formosum
- Iris pseudoacorus
- Juncus nevadensis
- Lysichitum americanum
- Mentha arvensis
- Mentha piperata
- Myosotis laxa
- Picea sitchensis
- Rumex acetosella

Sensitive

- *Aira praecox
- *Alnus rubra
- *Angelica lucida
- *Anthoxanthum odoratum
- *Athyrium felix-femina
- *Calamagrostis nutkaensis
- *Carex obnupta
- *Cornus stolonifera
- *Equisetum arvense
- *Glyceria grandis
- *Holcus lanatus
- *Hypochaeris radicata
- *Lonicera involucrata
- *Maianthemum dilatatum
- *Physocarpus capitatus
- *Polystichum munitum
- *Potentilla palustris
- *Pteridium aquilinum
- *Ribes sanguineum
- *Vaccinium spp.
- Alisma plantago-aquatica
- Bidens cernua
- Bromus mollis
- Juncus articulatis
- Juncus oxymeris
- Lathyrus japonicus
- Menyanthes trifoliata
- Pyrus fusca
- Rosa gymnocarpa
- Rosa nutkana
- Rubus spp.
- Rumex conglomeratus
- Sagittaria latifolia
- Scirpus microcarpus
- Sium suave
- Typha latifolia

Moderately Sensitive

- *Ammophila arenaria
- *Lathyrus palustris
- *Phragmites communis
- *Rumex crispus
- *Salix hookeriana
- *Vicia gigantea
- Achillea millefolium
- Agropyron repens
- Cicuta douglasii
- Dactylis glomerata
- Limosella aquatica
- Lotus ulignosus
- Lythrum salicaria
- Plantago lanceolata
- Poa pratensis
- Scirpus acutus
- Scirpus validus
- Sonchus arvensis
- Trifolium spp.

Moderately Tolerant

- *Elymus mollis
- *Hordeum brachyantherum
- *Oenanthe sarmentosa
- *Phalaris arunidacea
- *Scirpus cernuus
- Agrostis alba
- Aster subspicatus
- Eleocharis acicularis
- Eleocharis palustris
- Eleocharis parvula
- Festuca arundinacea
- Festuca rubra
- Lolium perenne
- Lotus corniculatus
- Potentilla pacifica
- Ranunculus cymbalaria
- Scirpus americanus
- Trifolium wormskjoldii

Tolerant

- *Orthocarpus castillejoides
- *Typha angustifolia
- Carex lyngbyei
- Deschampsia caespitosa
- Glaux maritima
- Hordeum jubatum
- Juncus gerardii
- Liliaeopsis occidentalis
- Scirpus maritimus
- Stellaria humifusa

Very Tolerant

- *Grindelia integrifolia
- *Suaeda maritima
- *Triglochin concinnum
- *Triglochin maritimum
- Atriplex patula
- Cotula coronopifolia
- Distichlis spicata
- Jaumea carnosa
- Juncus balticus
- Plantago maritima
- Puccinellia pumila
- Salicornia europea
- Salicornia virginica
- Spergularia canadensis
- Spergularia marina

occurrences per plot. It would appear that MTZ is much more permeable to salt-tolerant species than it is to those that are salt-sensitive.

V.I. Vegetation Indices as Delimiters of OHWM.

SALTY and MOM indices were calculated by a computer program for each of sample plots along the 26 marsh-upland transects in Washington State. The ouput from this program is listed as Appendix 4. For each of the transects the location of MTZ (NOS 1980), and the upper limit (UL) of marsh vegetation as defined by the MOM index, and the upper limit of salt-tolerant vegetation as defined by the SALTY index are also given. These latter were located using the methods outlined by Frenkel et al (1978). Briefly, these are:

a) in cases where the sign of the index changes monotonically, UL locations will be coincident with the point at which the index changes from positive (marsh or salt-tolerant vegetation) to negative (upland, or salt-sensitive vegetation).

b) in cases where the sign of the index fluctuates from positive to negative, UL locations will be midway between the first and last instances at which the index changes sign.

Table 2 summarises the output from the computer program and gives the relative location of MTZ from the upland end of each transect as determined topographically, by the MOM index, and by SALTY. It is apparent from the data in Appendix 4 and Table 2 that the MOM method provides a more precise index of the true location of MTZ. Of the transects surveyed, the estimate of MTZ location from the MOM index was closer to the true position in 18 of the 26 cases. The mean error in position was 7.4 m (range = -17 m to +35.2 m) in the case of the MOM index, and the 'sign' of the error was approximately equal between positive and negative occurrences. In 12 instances the predicted position according to the MOM index was on the upland side of the true MTZ position, in the remaining 14 the predicted position was on the marsh side. In the case of the SALTY index the mean error in position was 12.1 m (range=-49.5 m to +11.9 m), but in virtually all cases (22 out of 26) the predicted upper limit of salt-tolerant vegetation was on the upland side of the MTZ location.

The two field tests of salt-tolerance as a predictor of upper marsh limits gave consistent results. Salt-tolerant species occur frequently at elevations above MTZ, and their presence influences the magnitude of the index of salt-tolerance of the vegetation as a whole, so that MTZ cannot be precisely located by this technique. The upper distributional limit of salt-tolerant vegetation appears to lie landward of MTZ; the two do not coincide

Table 2. Location of the mid upland-marsh transition zone as delimited by a vegetational-topographic survey (MTZ) and the MOM and SALTY indices.

Marsh	Transect	MTZ	MOM	SALTY
Willapa Bay (WB-2)	1A	29.9	24.5	20.
	2	15.5	11.5	8.5
	3	21.0	19.	11.5
	5	12.5	24	22.
	6	21.9	23.	19.5
	8	14.0	17.	9.5
	9	32.0	29.	21.
	10B	25.3	21	9.5
Grays Harbor (GH-1)	3	28.0	34.5	11.5
	5	34.1	53.	46.
	6B	40.5	41.	33.
	7	35.4	35	10.5
	8	17.7	22.5	13.
	9	69.5	75.	30.
	10	41.8	77	10.5
	11C	60.0	43.	11.5
Grays Harbor (GH-3)	2	15.8	13.8	9.5
	3	19.8	15.2	9.5
	4	16.2	13.5	9.5
	5	15.5	13.8	9.5
	6	16.5	13.8	10.
Quilceda Creek (EP-1)	2	10.5	21	14.3
	3	10.1	28	21.5
	4	11.3	16	9.
	5B	11.9	29.5	9.8
	6	11.6	15.5	9.

Part VI
CONCLUSIONS AND RECOMMENDATIONS

There are several distinct advantages to the use of individual plant species and vegetation as indicators of critical tidal limits such as OHWM in the estuarine environment. Plants, as sedentary organisms, represent an adapted and integrated response to the local physical environment, and may therefore serve to indicate the longer-term, average conditions at a site. Whereas sea-surface levels, water-table depths, and soil salinity characteristics are subject to rapid periodic and stochastic fluctuations, and are therefore of little use for establishing critical tidal limits in reconnaissance fieldwork, vegetation, although dynamic, represents a relatively stable reponse to these locally and temporally varying factors. In addition, vegetation surveys can be performed fairly rapidly and precisely, they can be replicated, and they require virtually no instrumentation.

Plants along a marsh-upland transition can be categorized in various ways in order to facilitate the analysis of ecological and physical boundaries. Such a classification should share the same qualities as the vegetation survey: it should be simple, precise, capable of standardization so that relatively-untrained personnel can perform it, and be ecologically meaningful. The proposal in the WAC that salt-tolerance forms a satisfactory metric for such a classification, and for establishing the location of a boundary such as OHWM, has been shown to have several drawbacks. These are:

1) The data base on the field distributional limits of the local estuarine wetland and associated upland flora with respect to salt tolerance, and germination and yield response in laboratrory or field experiments, is relatively meagre. Whilst the tolerance limits of many low marsh and halophytic species are known with some precision, for a large proportion of the upland flora no equivalent data exist.

2) Responses to salt in the growing medium are not absolute. Plant response varies with environment, length of exposure, and growth-stage. The response of germinating seeds differs from that of young seedlings, and both usually differ from that of adult plants (see Part IV for examples). Shoot growth is usually more susceptible than root growth, and yield responses, reproductive responses, and mortality rates may all be different. It is therefore very difficult to characterise the response of a species to salinity with a single index.

3) Variability is a primary characteristic of all biological populations. A plant species population in a saline environment will likely have an enhanced tolerance of salts in the

rooting medium compared to its counterpart in a non-saline environment. As such traits are heritable, the species as a whole will exhibit a wide ranging response to salinity, depending upon the provenance of the plant material tested (see Part IV for examples). Again, it is therefore difficult to characterise the response of a species to salinity with a single index.

4) With the exception of the obligate halophytes (essentially equivalent to the VT group in this report), that require sodium, all salt-tolerant species are capable of enhanced growth in non-saline than in saline substrates. They are excluded from non-saline substrates primarily by the better-adapted glycophyte flora, not by intolerance of these conditions. The landward limit of a salt-tolerant flora therefore represents a boundary of relative competitive dominance, not a well-defined physical limit.

5) Even though populational and growth stage variability mean that no absolute index of salinity-tolerance can be developed for individual species, it is possible to assign species to categories along a gradient of salt tolerance (see Table1; Appendix 2). A total of 116 species were surveyed (Part IV), and for most of these a specific assignment to a salinity-tolerance category was possible on the basis of the field and experimental data analysed.

6) The categorization of species in this fashion allowed a 'field test' of the hypothesis that OHWM can be located on the basis of the landward limit of salt-tolerant vegetation to be examined. The data are derived from Frenkel et al.(1978) and consist of records of species abundance along 26 marsh-upland transects in Washington State, with the location of a surrogate for OHWM (mid-transition zone: MTZ) specified. The results (Part V; Appendix 3) indicate that transgression of the salt-tolerant flora into 'upland' areas above OHWM is common (69% of species-occurrences), and the tidal limit (MTZ) is not coincident with the geographical limit of this flora.

7) The converse hypothesis, that OHWM can be located on the basis of the seaward limit of salt-sensitive vegetation, was substantiated. OHWM represents an essentially impermeable barrier to this flora; only 3% of species-occurrences in the marsh consisted of salt-sensitive species.

8) A salinity index (SALTY) which calculates a "salinity-score" for the vegetation in each of the sample plots was developed.. The behaviour of this index in the 26 transects was examined to determine whether MTZ could be reliably and precisely located, and to assess the utility of this index versus the MOM index developed by Frenkel et al.

(1978). The MOM method estimates the true location of MTZ more reliably and precisely than SALTY (Table 2; Appendix 4). The MOM index was closer to the true position of MTZ in 18 of the 26 cases, and the mean error of position was 7.4 m (compared to 12.1 m for SALTY).

Recommendations

On the basis of the findings of this report I would make two recomendations:

1) That the criterion for OHWM delimitation in WAC Chapter 173-22; viz: that this tidal limit is demarcated by 'the landward limit of salt-tolerant vegetation', be eliminated.

2) That in the place of this criterion the Washington State Dapartment of Ecology consider one of two alternatives:
   a) that WAC Chapter 173-22 be changed to reflect the reality that OHWM is demarcated by the seaward limit of salt-sensitive vegetation, rater than the landward limit of salt-tolerant vegetation. An inventory of salt-sensitive species in upland habitats associated with estuarine wetlands is compiled in Table 1.. This inventory should be updated as further information on the salinity response characteristics of the upland and wetland flora becomes available.

   b) that the reliance on indicator species be replaced by a vegetation index. This has the advantage of being far less sensitive to the localized distribution of individual species. Based upon the results reported in Part V, the MOM index, or something conceptually similar, should be preferred to the more complex and less precise salinity index generated here. The MOM index, based upon a division of the estuarine wetland and associated upland flora into 'marsh', 'upland' and 'non-indicator' elements, is simpler, and proved to be more precise than its salinity-tolerance counterpart .

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Appendix 1

Conversion factors for salinity and associated measures of saline water chemistry for standard seawater at 15⁰C

Salinity = 35.0 ppt (or 35.0 g/L)
Chlorinity = 19.4 ppt
Specific conductance = 42.9 mmhos/cm (or 42.9 dS/m)
Nominal density = 1.028
Osmotic pressure = -2.2 MPa
Osmolality = 1.13 Os/kg
Salinity equivalent to 600 mM/L NaCl

Appendix 2

Salinity Tolerance Ratings of Plants from Pacific Northwest Coastal Marshes and Associated Uplands

(Unless otherwise stated, all values are in ppt salt)

Species	Max. Salinity in Field	Yield Threshold	Yield Slope (%)	Tolerance Rating
Achillea millefolium	9	-	-	MS
Agropyron repens	9	-	-	MS
Agrostis alba	14	4	6.2	MT
Aira praecox	-	-	-	S*
Alisma plantago-aquatica	5	-	-	S
Alnus rubra	-	-	-	S*
Ammophila arenaria	-	-	-	MS*
Angelica arguta	0.5	-	-	VS
Angelica lucida	-	-	-	S*
Anthoxanthum odoratum	-	-	-	S*
Aster subspicatus	13	-	-	MT
Athyrium felix-femina	-	-	-	S*
Atriplex patula	45	-	-	VT
Berberis aquifolium	-	-	-	VS
Bidens cernua	2	-	-	S
Bromus mollis	3	-	-	S
Calamagrostis nutkaensis	-	-	-	S*
Caltha asarifolia	0.5	-	-	VS
Carex lyngbyei	20	3	3.3	T
Carex obnupta	-	-	-	S*
Carex rostrata	0.5	-	-	VS
Cicuta douglasii	6	-	-	MS
Cornus stolonifera	-	-	-	S*
Cotula coronopifolia	25	-	-	VT
Dactylis glomerata	-	1.5	6.2	MS
Deschampsia caespitosa	20	-	-	T
Distichlis spicata	50	13	3.3	VT
Eleocharis acicularis	12	-	-	MT
Eleocharis palustris	12	-	-	MT
Eleocharis parvula	12	-	-	MT
Elymus mollis	12?	-	-	MT*
Equisetum arvense	-	-	-	S*
Equisetum fluviatile	0.5	-	-	VS
Festuca arundinacea	17?	-	-	MT
Festuca rubra	-	2	4.3	MT
Galium cymosum	0.5	-	-	VS
Glaux maritima	20	-	-	T
Glyceria grandis	-	-	-	S*
Grindelia integrifolia	14	-	-	VT*
Habenaria dilatata	0.5	-	-	VS
Heracleum lanatum	0.5	-	-	VS
Holcus lanatus	-	-	-	S*
Hordeum brachyantherum	11?	-	-	MT*
Hordeum jubatum	20	1.5	5.0	T
Hypericum formosum	0.5	-	-	VS

Hypochaeris radicata	3	-	-	S*
Iris pseudoacorus	0.5	-	-	VS
Jaumea carnosa	39	0.5?	7.7?	VT
Juncus articulatis	1.5	-	-	S
Juncus balticus	27	-	-	VT
Juncus effusus	-	-	-	S*
Juncus gerardii	-	3.5	5?	T
Juncus leseurii	-	-	-	S*
Juncus nevadensis	0.5	-	-	VS
Juncus oxymeris	2	-	-	S
Lathyrus japonicus	4	-	-	S
Lathyrus japonicus	13?	-	-	MS*
Liliaeopsis occidentalis	17?	-	-	T
Limosella aquatica	6	-	-	MS
Lolium perenne	-	5.6	7.6	MT
Lonicera involucrata	-	-	-	S*
Lotus corniculatus	17?	5	10.	MT
Lysichitum americanum	0.5	-	-	VS
Lythrum salicaria	8	-	-	MS
Maianthemum dilatatum	-	-	-	S*
Mentha arvensis	0.5	-	-	VS
Mentha piperata	0.5	-	-	VS
Menyanthes trifoliata	5	-	-	S
Myosotis laxa	0.5	-	-	VS
Oenanthe sarmentosa	13?	-	-	MT*
Orthocarpus castillejoides	17?	-	-	T*
Phalaris arunidacea	-	-	-	MT*
Phragmites communis	-	-	-	MS*
Physocarpus capitatus	-	-	-	S*
Picea sitchensis	-	0.2	62.5	VS
Plantago lanceolata	8	-	-	MS
Plantago maritima	21?	1.5	3.3	VT
Polystichum munitum	-	-	-	S*
Poa pratensis	10	-	-	MS
Potentilla pacifica	13?	-	-	MT
Potentilla palustris	-	-	-	S*
Pteridium aquilinum	-	-	-	S*
Puccinellia pumila	21?	-	-	VT
Pyrus fusca	-	-	-	S
Ranunculus cymbalaria	12	-	-	MT
Ribes sanguineum	-	-	-	S*
Rosa gymnocarpa	-	-	-	S
Rosa nutkana	3	-	-	S
Rubus spp.	-	1.5	22	S
Rumex acetosella	0.5	-	-	VS
Rumex conglomeratus	4?	-	-	S
Rumex crispus	13?	-	-	MS*
Sagittaria latifolia	5	-	-	S
Salicornia europea	80	-	-	VT
Salicornia virginica	80	20?	-	VT
Salix hookeriana	-	-	-	MS*
Scirpus acutus	6	1	14.2	MS
Scirpus americanus	15	-	-	MT
Scirpus cernuus	-	-	-	MT*

Scirpus maritimus	15?	1.5	10	T
Scirpus microcarpus	4?	-	-	S
Scirpus validus	10	-	-	MS
Sium suave	5	-	-	S
Sonchus arvensis	10	-	-	MS
Spergularia canadensis	21	-	-	VT
Spergularia marina	12?	23	14.2	VT
Stellaria humifusa	19	-	-	T
Suaeda maritima	-	-	-	VT*
Trifolium spp.	-	1.5	12.	MS
Trifolium wormskjoldii	11?	-	-	MT
Triglochin concinnum	-	-	-	VT*
Triglochin maritimum	21?	7	4.5	VT*
Tsuga heterophylla	-	-	-	VS*
Typha angustifolia	18?	-	-	T*
Typha latifolia	8	0.5	20	S
Vaccinium spp.	-	-	-	S*
Vicia gigantea	13?	-	-	MS*

Tolerance Ratings are as follows:

VS	very sensitive
S	sensitive
MS	moderately sensitive
MT	moderately tolerant
T	tolerant
VT	very tolerant

* = estmate

Appendix 3

Output of a computer program to enumerate the number of occurrences of salt-tolerant species above MTZ and salt-sensitive species below MTZ.

Marshes are: 09 - Willapa Bay (WB2);
11 - Grays Harbor (GH1);
12 - Grays Harbor (GH3);
17 - Quilceda Creek (EP1).

Variables are: VAR1 - Total No. of species occurrences above MTZ (species x plots)
VAR2 - No. of salt-tolerant species occurrences above MTZ
VAR3 - Total No. of species occurrences below MTZ
VAR4 - No. of salt-sensitive species occurrences below MTZ

MARSH	TRANS	VAR1	VAR2	VAR3	VAR4
9	1	36	33	69	1
9	2	45	39	50	0
9	3	35	25	48	0
9	5	3	0	50	5
9	6	26	19	34	0
9	8	36	24	37	0
9	9	43	31	79	0
9	10	65	59	77	0

MARSH	TRANS	VAR1	VAR2	VAR3	VAR4
11	3	44	27	98	7
11	5	57	30	98	11
11	6	47	20	114	1
11	7	42	26	36	1
11	8	26	12	49	4
11	9	33	13	60	9
11	10	69	41	64	4
11	11	58	41	137	0

MARSH	TRANS	VAR1	VAR2	VAR3	VAR4
12	2	32	29	30	0
12	3	57	47	28	0
12	4	39	33	42	0
12	5	33	27	37	0
12	6	28	24	65	1

MARSH	TRANS	VAR1	VAR2	VAR3	VAR4
17	2	12	7	29	1
17	3	11	2	12	0
17	4	22	15	23	0
17	5	20	12	28	0
17	6	31	21	20	0

Appendix 4

Output of a computer program to calculate MOM and SALTY indices along marsh-upland gradients.

Marshes are: 09 - Willapa Bay (WB2);
11 - Grays Harbor (GH1);
12 - Grays Harbor (GH3);
17 - Quilceda Creek (EP1).

Variables are: D1 - Distance from low end of transect (m)
D2 - Distance from upper end of transect (m)

Arrows indicate the actual location of MTZ (with respect to D2), and the predicted positions of MTZ from the MOM and SALTY indices.

OUTPUT FROM PGM.FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
9	1	0	57	10.	15.
9	1	2	55	8.	12.
9	1	4	53	8.	12.
9	1	6	51	18.	27.
9	1	8	49	17.	28.
9	1	10	47	13.	21.
9	1	12	45	9.	17.
9	1	14	43	14.	21.
9	1	16	41	7.	24.
9	1	18	39	5.	22.
9	1	20	37	3.	20.
9	1	22	35	4.	20.
9	1	24	33	4.	20.
9	1	26	31 ←	6.	22.
9	1	28	29	4.	20.
9	1	30	27	1.	18.
9	1	31	26	1.	10.
9	1	32	25	-4.	12.
9	1	33	24	1. ←	13.
9	1	34	23	-2.	11.
9	1	35	22	2.	11.
9	1	36	21	2.	8.
9	1	37	23	-2.	1. ←
9	1	38	22	-4.	-4.
9	1	39	21	-4.	-4.

OUTPUT FROM PGM.FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
9	2	0	41	12.	14.
9	2	3	38	8.	6.
9	2	6	35	8.	6.
9	2	9	32	10.	11.
9	2	12	29	10.	13.
9	2	15	26	12.	12.
9	2	16	25	18.	27.
9	2	18	23	11.	22.
9	2	20	21	14.	18.
9	2	22	19	7.	19.
9	2	24	17	3.	26.
9	2	26	15 ←	4.	20.
9	2	27	14	1.	11.
9	2	28	13	-9.	15.
9	2	29	12	-10.	9.
9	2	30	11	-10. ←	2.
9	2	31	10	2.	6.
9	2	32	9	-10.	11. ←
9	2	33	8	-8.	-5.
9	2	34	7	-8.	-8.

OUTPUT FROM PGM.FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
9	3	0	38	4.	5.
9	3	2	36	8.	8.
9	3	4	34	12.	13.
9	3	6	32	15.	19.
9	3	8	30	21.	29.
9	3	10	28	13.	28.
9	3	12	26	7.	23.
9	3	14	24	1.	13.
9	3	16	22 ←	4.	20.
9	3	18	20	-1 ←	23.
9	3	20	18	5.	18.
9	3	22	16	-19.	9.
9	3	24	14	-10.	8.
9	3	26	12	-10.	8.
9	3	27	11	-12.	-10. ←
9	3	28	10	-14.	-12.
9	3	29	9	-6.	-6.

OUTPUT FROM PGM.FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
9	5	0	43	2.	3.
9	5	2	41	2.	3.
9	5	4	39	12.	18.
9	5	6	37	14.	21.
9	5	8	35	19.	29.
9	5	10	33	20.	29.
9	5	12	31	12.	15.
9	5	14	29	15.	19.
9	5	16	27	14.	19.
9	5	18	25	11 ←	13.
9	5	20	23	-6.	-4.
9	5	22	21	-2.	2. ←
9	5	24	19	-8.	-6.
9	5	26	17	-8.	-5.
9	5	28	15 ←	-2.	12.
9	5	34	9	-8.	-12.
9	5	35	8	-8.	-12.
9	5	36	7	-8.	-12.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
9	6	0	36	10.	15.
9	6	2	34	8.	12.
9	6	4	32	2.	3.
9	6	6	30	6.	9.
9	6	8	28	12.	15.
9	6	10	26	11.	25.
9	6	12	24	9.	24.
9	6	14	22	-4.	28.
9	6	15	21	-9.	15.
9	6	16	20	-14.	-1.
9	6	17	19	-10.	4.
9	6	18	18	-10.	-2.
9	6	19	17	-12.	-6.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
9	8	0	30	6.	8.
9	8	2	28	10.	15.
9	8	4	26	6.	9.
9	8	6	24	14.	19.
9	8	8	22	12.	13.
9	8	10	20	6.	17.
9	8	12	18	10.	30.
9	8	14	16	-1.	21.
9	8	16	14	-13.	24.
9	8	17	13	-20.	7.
9	8	18	12	-18.	2.
9	8	19	11	-16.	4.
9	8	20	10	-10.	2.
9	8	21	9	-8.	-5.
9	8	22	8	-10.	-6.
9	8	23	7	-10.	-10.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
9	9	0	64	12.	18.
9	9	2	62	8.	12.
9	9	4	60	10.	15.
9	9	6	58	8.	12.
9	9	8	56	8.	12.
9	9	10	54	6.	9.
9	9	12	52	8.	12.
9	9	14	50	9.	14.
9	9	16	48	19.	26.
9	9	18	46	16.	24.
9	9	20	44	9.	15.
9	9	22	42	15.	27.
9	9	24	40	9.	17.
9	9	26	38	9.	18.
9	9	28	36	10.	23.
9	9	30	34	3.	14.
9	9	32	32	8.	20.
9	9	34	30	10.	21.
9	9	36	28	0.	22.
9	9	38	26	-8.	18.
9	9	40	24	-16.	11.
9	9	42	22	-18.	4.
9	9	44	20	-20.	-2.
9	9	50	19	-20.	-20.
9	9	51	18	-16.	-16.
9	9	52	17	-10.	-10.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
9	10	0	97	8.	20.
9	10	10	87	4.	15.
9	10	20	77	8.	25.
9	10	30	67	4.	16.
9	10	40	57	5.	19.
9	10	50	47	3.	11.
9	10	60	37	3.	25.
9	10	63	34	1.	22.
9	10	65	32	-3.	25.
9	10	67	30	7.	26.
9	10	69	28	5.	26.
9	10	71	26	8.	30.
9	10	73	24	8.	30.
9	10	75	22	8.	20.
9	10	77	20	6.	22.
9	10	79	18	7.	25.
9	10	81	16	4.	19.
9	10	83	14	6.	19.
9	10	85	12	7.	28.
9	10	87	10	3.	19.
9	10	88	9	-12.	-17.
9	10	89	8	-10.	-13.
9	10	90	7	-4.	-6.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
11	3	0	158	22.	33.
11	3	3	155	26.	37.
11	3	6	152	12.	20.
11	3	9	149	20.	29.
11	3	12	146	22.	26.
11	3	32	126	26.	36.
11	3	52	106	24.	34.
11	3	72	86	12.	17.
11	3	92	66	10.	17.
11	3	104	54	7.	25.
11	3	107	51	5.	25.
11	3	110	48	7.	16.
11	3	113	45	4.	9.
11	3	116	42	2.	9.
11	3	119	39	-1.	10.
11	3	122	36	-2.	9.
11	3	125	33	0.	13.
11	3	128	30	4.	11.
11	3	131	27	-4.	7.
11	3	134	24	-8.	4.
11	3	137	21	-2.	16.
11	3	140	18	-6.	3.
11	3	143	15	-12.	2.
11	3	146	12	-10.	2.
11	3	149	9	-8.	-6.
11	3	152	6	-10.	-9.
11	3	155	3	-4.	-4.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
11	5	0	166	30.	41.
11	5	3	163	28.	38.
11	5	6	160	24.	32.
11	5	9	158	12.	19.
11	5	12	154	22.	29.
11	5	32	134	10.	18.
11	5	52	114	20.	28.
11	5	72	94	-11.	-8.
11	5	92	74	10.	17.
11	5	112	54	7.	12.
11	5	118	48	-1.	4.
11	5	121	45	-2.	10.
11	5	124	42	-2.	3.
11	5	127	39	-3.	3.
11	5	130	36	2.	11.
11	5	133	33	0.	5.
11	5	136	30	-9.	0.
11	5	139	27	-3.	3.
11	5	142	24	-2.	3.
11	5	145	21	-2.	1.
11	5	148	18	-8.	4.
11	5	151	15	0.	12.
11	5	154	12	-6.	6.
11	5	157	9	4.	15.
11	5	160	6	2.	2.
11	5	163	3	-12.	-8.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
11	6	0	718	6.	9.
11	6	30	688	12.	18.
11	6	60	658	12.	18.
11	6	90	628	14.	21.
11	6	120	598	14.	21.
11	6	150	568	18.	27.
11	6	180	538	2.	3.
11	6	210	508	12.	18.
11	6	240	478	12.	18.
11	6	270	448	26.	40.
11	6	300	418	16.	24.
11	6	330	388	11.	18.
11	6	360	358	20.	30.
11	6	390	328	22.	33.
11	6	420	298	16.	24.
11	6	450	268	16.	24.
11	6	480	238	20.	28.
11	6	510	208	17.	24.
11	6	540	178	14.	20.
11	6	570	148	18.	26.
11	6	600	118	14.	23.
11	6	630	88	12.	18.
11	6	660	58	6.	9.
11	6	668	50	0.	15.
11	6	670	48	2.	16.
11	6	672	46	4.	15.
11	6	674	44	5.	19.
11	6	676	42	3.	7.
11	6	678	40 ←	-6. ←	0.
11	6	682	36	-10.	-8.
11	6	686	32	-9.	-3. ←
11	6	690	28	-4.	2.
11	6	694	24	-7.	-2.
11	6	698	20	-9.	-5.
11	6	702	16	-8.	-5.
11	6	706	12	-18.	-11.
11	6	709	9	-20.	-14.
11	6	712	6	-22.	-19.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
11	7	0	176	28.	41.
11	7	30	146	18.	25.
11	7	60	116	8.	14.
11	7	90	86	11.	16.
11	7	120	56	12.	16.
11	7	130	46	0.	19.
11	7	140	36	0.	21.
11	7	141	35 ←	0. ←	19.
11	7	146	30	0.	14.
11	7	151	25	0.	21.
11	7	156	20	-2.	14.
11	7	161	15	-6.	10.
11	7	164	12	-16.	-4. ←
11	7	167	9	-16.	2.
11	7	170	6	-24.	-13.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
11	8	0	180	30.	42.
11	8	30	150	32.	46.
11	8	60	120	26.	38.
11	8	90	90	5.	12.
11	8	120	60	5.	11.
11	8	135	45	2.	17.
11	8	150	30	0.	17.
11	8	155	25	1. ←	23.
11	8	160	20	0.	19.
11	8	162	18 ←	0.	17.
11	8	164	16	-4.	14.
11	8	166	14	-8.	14. ←
11	8	168	12	-10.	-2.
11	8	171	9	-26.	-9.
11	8	174	6	-16.	-11.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
11	10	0	275	38.	52.
11	10	30	245	34.	51.
11	10	60	215	32.	47.
11	10	90	185	19.	33.
11	10	120	155	12.	18.
11	10	150	125	3.	10.
11	10	180	95	-1. ←	16.
11	10	210	65	-6.	1.
11	10	220	55	-2.	15.
11	10	230	45	-2.	15.
11	10	235	40 ←	8.	13.
11	10	238	37	10.	26.
11	10	241	34	-3.	18.
11	10	244	31	-8.	11.
11	10	247	28	-8.	9.
11	10	250	25	-12.	4.
11	10	253	22	-6.	8.
11	10	256	19	-6.	12.
11	10	259	16	-2.	18.
11	10	262	13	-10.	11.
11	10	263	12	-10.	3. ←
11	10	266	9	-10.	-8.
11	10	269	6	-10.	-9.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
11	9	0	256	30.	44.
11	9	30	226	16.	26.
11	9	60	196	16.	25.
11	9	90	166	12.	19.
11	9	120	136	-6.	3.
11	9	150	106	10.	13.
11	9	160	96	0.	21.
11	9	170	86	-2.	15.
11	9	176	80	-6 ←	11.
11	9	186	70 ←	-10.	5.
11	9	196	60	-14.	-1.
11	9	206	50	-11.	-3.
11	9	216	40	-8.	14.
11	9	226	30	-8.	9. ←
11	9	244	13	-24.	-18.
11	9	247	10	-6.	-6.
11	9	250	7	0.	0.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
11	11	0	757	2.	3.
11	11	10	747	4.	6.
11	11	20	737	0.	0.
11	11	30	727	2.	3.
11	11	40	717	8.	12.
11	11	50	707	14.	21.
11	11	80	677	0.	0.
11	11	110	647	16.	24.
11	11	140	617	18.	27.
11	11	170	587	20.	30.
11	11	200	557	20.	30.
11	11	230	527	14.	21.
11	11	260	497	24.	36.
11	11	290	467	23.	36.
11	11	320	437	22.	33.
11	11	350	407	25.	39.
11	11	380	377	32.	48.
11	11	410	347	30.	44.
11	11	440	317	26.	38.
11	11	470	287	25.	39.
11	11	500	257	19.	34.
11	11	530	227	23.	45.
11	11	560	197	14.	28.
11	11	590	167	10.	20.
11	11	620	137	11.	21.
11	11	650	107	4.	23.
11	11	680	77	3.	12.
11	11	690	67	5.	13.
11	11	697	60	-1.	11.
11	11	702	55	1.	10.
11	11	707	50	5.	10.
11	11	712	45	1.	22.
11	11	717	40	1.	21.
11	11	722	35	-2.	18.
11	11	727	30	4.	23.
11	11	732	25	2.	23.
11	11	737	20	-2.	21.
11	11	742	15	-6.	16.
11	11	744	13	-6.	15.
11	11	747	10	-18.	-6.
11	11	750	7	-18.	-3.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
12	2	0	26	8.	16.
12	2	2	24	8.	17.
12	2	4	22	7.	27.
12	2	6	20	5.	19.
12	2	8	18	6.	15.
12	2	10	16	-2.	16.
12	2	11	15	-3.	12.
12	2	12	14	-3.	19.
12	2	13	13	0.	21
12	2	14	12	-2.	17.
12	2	15	11	2.	13.
12	2	16	10	-4.	5.
12	2	17	9	-4.	-1.
12	2	18	8	-8.	-7.
12	2	19	7	0.	0.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
12	3	0	37	10.	17.
12	3	4	33	3.	17.
12	3	8	29	4.	15.
12	3	12	25	5.	20.
12	3	16	21	2.	25.
12	3	17	20	-2.	26.
12	3	18	19	-2.	25.
12	3	19	18	-2.	16.
12	3	20	17	-3.	13.
12	3	21	16	-6.	15.
12	3	22	15	-1.	19.
12	3	23	14	-5.	20.
12	3	24	13	-2.	16.
12	3	25	12	-1.	18.
12	3	26	11	1.	7.
12	3	27	10	-1.	8.
12	3	28	9	-12.	-5.
12	3	29	8	-14.	-12.
12	3	30	7	-20.	-23.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
12	4	0	33	9.	14.
12	4	2	31	9.	17.
12	4	4	29	13.	23.
12	4	8	25	10.	18.
12	4	12	21	16.	38.
12	4	14	19	9.	28.
12	4	16	17	7.	28.
12	4	17	16	12.	38.
12	4	18	15	6.	25.
12	4	19	14	-2.	17.
12	4	20	13	0.	17.
12	4	21	12	-4.	5.
12	4	22	11	-4.	2.
12	4	23	10	-2.	1.
12	4	24	9	-4.	-4.
12	4	25	8	-12.	-12.
12	4	26	7	-8.	-6.

OUTPUT FROM PGM. FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
12	5	0	40	10.	15.
12	5	4	36	9.	15.
12	5	8	32	18.	30.
12	5	12	28	12.	20.
12	5	16	24	9.	15.
12	5	20	20	11.	29.
12	5	24	16	-6.	20.
12	5	25	15	2.	18.
12	5	26	14	-2.	20.
12	5	27	13	-3.	20.
12	5	28	12	4.	22.
12	5	29	11	0.	8.
12	5	30	10	0.	6.
12	5	31	9	-6.	-9.
12	5	32	8	-18.	-17.
12	5	33	7	-22.	-19.

OUTPUT FROM PGM.FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
12	6	0	68	12.	18.
12	6	2	66	6.	9.
12	6	4	64	14.	21.
12	6	8	60	6.	9.
12	6	12	56	14.	21.
12	6	16	52	20.	30.
12	6	20	48	20.	30.
12	6	24	44	13.	25.
12	6	28	40	14.	29.
12	6	32	36	17.	28.
12	6	36	32	13.	22.
12	6	40	28	11.	26.
12	6	44	24	14.	32.
12	6	48	20	3.	26.
12	6	52	16	-2.	22.
12	6	53	15	2.	18.
12	6	54	14	3.	20.
12	6	55	13	0.	7.
12	6	56	12	0.	7.
12	6	57	11	2.	6.
12	6	58	10	0.	0.
12	6	59	9	-4.	-6.
12	6	60	8	-6.	-9.
12	6	61	7	-10.	-11.

OUTPUT FROM PGM.FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
17	2	0	41	13.	22.
17	2	5	36	15.	27.
17	2	10	31	12.	24.
17	2	15	26	12.	16.
17	2	20	21	0.	0.
17	2	25	16	-3.	0.
17	2	30	11	-8.	7.
17	2	31	10	-8.	2.
17	2	32	9	-14.	-3.
17	2	33	8	-6.	3.
17	2	34	7	-8.	-4.

OUTPUT FROM PGM.FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
17	4	0	42	13.	20.
17	4	5	37	15.	23.
17	4	10	32	12.	16.
17	4	15	27	12.	17.
17	4	20	22	13.	19.
17	4	25	17	4.	4.
17	4	30	12	-12.	10.
17	4	31	11	-6.	9.
17	4	32	10	-6.	7.
17	4	33	9	-10.	0.
17	4	34	8	-14.	-7.
17	4	35	7	-8.	-4.

OUTPUT FROM PGM.FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
17	3	0	41	14.	26.
17	3	5	36	1.	2.
17	3	10	31	-4.	-2.
17	3	15	26	-2.	-1.
17	3	20	21	0.	0.
17	3	25	16	-6.	3.
17	3	30	11	-4.	4.
17	3	31	10	-10.	-2.
17	3	32	9	-16.	-18.
17	3	33	8	-20.	-27.
17	3	34	7	-18.	-27.

OUTPUT FROM PGM.FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
17	6	0	39	14.	23.
17	6	5	34	14.	19.
17	6	10	29	13.	19.
17	6	15	24	16.	24.
17	6	20	19	7.	10.
17	6	25	14	-4.	-2.
17	6	30	9	-12.	7.
17	6	31	8	-4.	4.
17	6	32	7	-14.	6.
17	6	33	6	-12.	4.
17	6	34	5	-8.	2.
17	6	35	4	-6.	7.
17	6	36	3	-10.	1.

OUTPUT FROM PGM.FRENKEL

MARSH	TRANS.	D1	D2	MOM	SALTY
17	5	0	105	10.	10.
17	5	30	75	15.	19.
17	5	60	45	12.	26.
17	5	63	42	12.	19.
17	5	68	37	0.	0.
17	5	73	32	17.	24.
17	5	78	27	16.	23.
17	5	83	22	0.	0.
17	5	88	17	-1.	3.
17	5	93	12	-10.	6.
17	5	94	11.	-14.	8.
17	5	95	10	-10.	6.
17	5	96	9	-14.	-18.
17	5	97	8	-10.	-11.
17	5	98	7	-18.	-1.