

VEGETATION-ENVIRONMENT RELATIONSHIPS IN A SUBALPINE WET MEADOW
AND A BRACKISH TIDAL MARSH

By

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B.Sc., The University of British Columbia, 1989

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES
(Department of Botany)

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

April 1992

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ABSTRACT

Community structure, community-environment relationships, the role of land surface elevation as a determinant of plant species composition, and aspects of scale were examined and compared between a brackish tidal marsh in the Squamish estuary and a subalpine wet meadow in Garibaldi Park in southwestern British Columbia. Vegetation abundance, soil variables, and ground elevation data were collected from 225, 0.5 X 0.5 m quadrats systematically located at five metre intervals in a 40 X 120 m sampling grid in both sites. The effect of changing the sampling scale was examined through simulation rather than by resampling in the field using different quadrat sizes. Larger quadrat sizes were simulated by aggregating adjacent quadrats in the grid and calculating average values for species and environmental variables. Five aggregation scales (referred to as 'agg' levels) were formed: agg1 (0.5 X 0.5 m), agg4 (5 X 5 m), agg6a (5 X 10 m), agg6b (10 X 5 m), and agg9 (10 X 10 m). At each scale, minimum variance cluster analysis and canonical correlation analysis were used to describe community structure by selecting a dendrogram level to segregate the vegetation data into subcommunities. Vegetation data were correlated with environmental data using canonical correspondence analysis. To evaluate which scale provided the clearest picture of community structure (yielded the largest between and smallest within-cluster variability estimate), an analysis of variance was performed on canonical correspondence

analysis first and second axis scores using the selected dendrogram level for stratification at each scale. This helped to provide an overall between and within-cluster variability estimate for each scale. The role of elevation as a determinant of vegetation pattern was investigated by regressing a canonical axis representing species variables against a canonical axis representing elevation. Residuals, representing that proportion of the variation in vegetation unexplained by elevation, were saved and correlated with the environmental variables to examine if other variables unrelated to elevation shared strong relationships.

At most scales the marsh study site is composed of two subcommunities: upper and lower. The upper zone, characterized by soils of greater sand and organic content but less clay than the lower, is resident to many species common to Pacific coastal marshes. The lower zone is a monospecific stand of Carex lyngbyei that is exposed to high-low tide alternation which may remove organic content, sand, and deposit clay. Salinity did not share strong correlative relationships with the vertical distribution of plant species. However, soils were most saline and acidic in a low area near the upper marsh that was apparently not exposed to tidal flushing. Strong correlations between residuals and carbon, sand, and clay content suggest sources other than elevation such as tides and the species themselves may influence edaphic factors which in turn share relationships with vegetation pattern.

Generally, the subalpine meadow is composed of three subcommunities: forb meadow (upper), heath (middle), and sedge meadow (lower). Greater sand and electrical conductivity in upper meadow soils suggest a well-exposed and well-drained area. The lower subcommunity characterized by mostly Carex nigricans, possess soils of greater clay and organic content. Soils generally tend to be less acidic than the upper zone suggesting that leaching may be occurring as water drains from the upper meadow into the lower.

Simulation sampling with a rectangular quadrat positioned perpendicular to vegetational banding (agg6b), defined eight subcommunities in both sites. In addition, overall within-assemblage variability was least and between-assemblage variability was greatest suggesting that observation clarity is maximized at agg6b. Correlations among environmental variables and species axes generally become stronger at progressively coarser scales. In particular, subcommunity-pH relations were unnoticeable at agg1 but strengthened at agg4 in both sites. However, a strong agg4 correlation weakened at agg9 in the tidal marsh, recognizing exceptions. An hierarchical approach reminds one to be cautious when assessing the 'importance' of environmental variables. Results of this study suggest the importance of environmental factors, estimated by their correlations with vegetation pattern, may depend on the scale at which the data are analyzed.

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ACKNOWLEDGEMENTS

The author expresses sincerest thanks to committee members Dr. G.E. Bradfield, Department of Botany, University of British Columbia, for his assistance, advice, and encouragement; Dr. W.B. Schofield, Department of Botany, University of British Columbia, for his encouragement and help with bryophyte identification; and Dr. R.E. Foreman, Department of Botany, University of British Columbia, for his valuable suggestions and encouragement.

Special thanks to Dr. L.M. Lavkulich, Department of Soil Science, University of British Columbia, for permission to use his laboratory facilities as well as Mr. B.W. von Spindler, Department of Soil Science, University of British Columbia, for help with laboratory soil analyses.

The author is indebted to Drs. G.B. Straley, Department of Botany, University of British Columbia, and A. Ceska, Royal British Columbia Museum, for their help in identifying vascular plant species.

Sincerest thanks also goes to the British Columbia Ministry of Parks for granting permission to work in Garibaldi Provincial Park and to Miss J. Lawrence for her help in collecting field data as well as my wife, Mrs. A.S. Drewa, for her help in collecting field data and encouragement.

CHAPTER 1: INTRODUCTION

1.1 Prelude

Plant community ecology is concerned largely with the description and explanation of plant distribution patterns in the field. Moreover, plant ecology attempts to interpret the relationship of plants to their environments (Billings 1964). An environment is a complex of many factors that interact not only with an organism but also among themselves, changing continuously through time (Billings 1964; Greig-Smith 1983). The difficulties in studying communities are twofold: 1) the number and uniqueness of communities and community components far exceed the number of individual items that an ecologist considers for investigation, and 2) communities and their components are integrated, yet our minds approach communities by a succession of individual thoughts (Simon 1962; Daubenmire 1968; Elsassner 1969; Gauch 1982).

Recognizing that plant ecology is a "product of interaction between communities and ecologists through observations and analysis" (Gauch 1982), a study was undertaken to examine and briefly compare vegetation-environment relationships in the context of a brackish tidal marsh and a subalpine wet meadow. Alpine/subalpine habitats have provided excellent opportunities to study species and community pattern. Vegetation pattern is usually sharply accentuated in subalpine/alpine regions because of topographic diversity and often changes abruptly related to rapid

shifts in environmental gradients (Douglas and Bliss 1977). Though marsh systems tend to have fewer environmental gradients and, therefore, fewer species, vegetation pattern tends to be more distinctive. Marsh habitats also tend to be highly productive providing critical habitats for large numbers of bird, fish, and mammalian species. Their easy accessibility also provide excellent opportunities to study vegetation pattern. The benefits of studying these habitats are threefold. First, issues concerning vegetation pattern and vegetation-environment relationships can be examined in both systems within the confines of a relatively small area and within the limited time frame allotted for a MSc. thesis. Second, valuable contributions already exist in the scientific literature, providing helpful insights and suggestions for future research. Third, results from this study may provide new insights into marsh as well as subalpine/alpine park management. Despite the differences between the two habitat types, a brief comparison between a brackish tidal marsh and a subalpine wet meadow may be in order since they are both influenced by fresh water and may, in fact, represent opposite ends of a fresh water gradient. Different species of the same genus such as Carex, Potentilla, Agrostis, Deschampsia, and Juncus may be found in most subalpine meadow and brackish tidal marsh systems in the Pacific Northwest.

1.2 Marsh Literature Review

Topography directly controls the submergence/emergence ratio

of a marsh through its interaction with tides. Dawe and White (1982) emphasized elevation as playing a major role in determining vegetation zonation in the Little Qualicum River estuary, British Columbia. While soil texture, type, and salinity were mentioned as playing relatively important roles, all were dependent on elevation and its interaction with tides. Vegetation pattern was also concluded to be controlled primarily by elevation in the Nanoose-Bonell estuary on Vancouver Island, British Columbia. Once again, Dawe and White (1986) stressed the interaction between elevation and tides and how elevation is responsible for controlling the submergence/emergence ratio of the marsh. Elevation as well as soil texture controlled species distribution along the vertical gradient of the marsh while inundating water salinities determined the species' horizontal distribution. Three major plant communities were identified along a vertical gradient of a tide influenced meadow on Chichagof Island, Alaska (Stephens and Billings 1967). Communities were clearly dependent on elevation and its interaction with tides. Soil characteristics such as pH, cation exchange capacity, and exchangeable sodium, calcium, magnesium, and potassium were also deemed important. Campbell and Bradfield (1989) recognized vegetation-elevation relationships in two estuarine marshes of northern British Columbia. The Yakoun marsh showed a closer connection between vegetation pattern and elevation and a clearer zonation of communities than the Dala marsh. The Yakoun marsh experiences steeper gradients in submergence time and flooding frequency, offering an explanation

for the difference in vegetation-elevation relationships between the two.

Despite other researchers' emphasis on topography/elevation as primarily determining vegetation distribution, Disraeli and Fonda (1979) have stated that elevation shows not a direct but instead, an indirect effect on vegetation distribution. Through its effect on other environmental factors like tidal inundation, sand and silt content of the soil, and soil moisture, elevation indirectly caused the Nooksack delta marsh species to be broadly zoned into two marsh types at Bellingham Bay, Washington. Mahall and Park (1976) attempted to investigate why two distinct zones of Salicornia virginica and Spartina foliosa were prominent in salt marshes of northern San Francisco Bay. Experiments in which Salicornia and Spartina plants were exposed to artificial tides indicated that inhibition of growth through reduced daylight, inhibition of re-rooting and the production of new branches prevented Salicornia seedlings from advancing seaward to the Spartina zone. Major portions of two monotypic stands were found to have different tidal relationships, frequency, and duration of flooding in a salt marsh in Davis Bay, Mississippi (Eleuterius and Eleuterius 1979). Tidal phenomena per se could not be shown to account for salt marsh zonation and the clear demarcation between zones. Eleuterius and Eleuterius (1979) urged that other environmental factors, especially edaphic conditions and possibly biotic interactions, need to be investigated.

Vince and Snow (1984) described patterns of plant species distribution, plant abundance, and environmental factors on Susitna Flats, an Alaskan subarctic marsh. Though there was little topographic relief and soil texture was similar throughout the Flats, vegetation zones differed with respect to flooding frequency, rate of siltation, soil organic content, moisture content, redox potential, and salinity. Waterlogging and soil salinity were found to segregate most of the vegetation zones. Vince and Snow (1984) emphasized that it is unlikely that tidal inundation per se determines plant distribution on Susitna Flats. Dawson and Bliss (1987) recognized a salinity and soil extractable-ion gradient on a high arctic brackish marsh. They concluded that plant zonation exists at least in part as a function of plant response to gradients in edaphic characteristics. A study was conducted at the brackish tidal marsh along the shore of Skagit Bay near Mt. Vernon, Washington by Ewing (1983). Principal components analysis indicated that salinity and soil texture were strongly correlated with the first generated factor while elevation and soil redox potential with the second and third respectively. Ewing (1983) concluded that brackish intertidal marshes of the Pacific Northwest are most profoundly affected by water salinity. Community composition is also affected by soil texture, soil redox potential, and elevation. Conversely, Disraeli and Fonda (1979) clearly stated that "salinity played no significant role" on a brackish marsh at Bellingham Bay, Washington.

An experimental study of the role of edaphic conditions was conducted by Snow and Vince (1984). Salt tolerance of each species corresponded with the soil salinity in the zone of occurrence. Snow and Vince (1984) also emphasized that the results from a two year reciprocal transplant experiment demonstrated the influence of between-species competition on zonation. Bertness and Ellison (1987) concluded physical disturbance and interspecific competition to be major determinants of spatial pattern in a salt marsh community in New England. Interspecific competition was cited as a major determinant of pattern by 1) transplant studies, 2) distribution and rapid recruitment of rare high marsh plants in areas where dominant high marsh plants are numerically lacking, and 3) the rapid closure of disturbance-generated bare patches and relative rarity of early colonists in undisturbed vegetation. Patterning of New England salt marsh plant communities is an interactive product of physical constraints on plant success, predation pressure, physical disturbance, and interspecific competition (Bertness and Ellison 1987). Resource competition for soil nitrogen and light was examined in a brackish tidal marsh located at Brunswick Point, British Columbia by Pidwirny (1990). Two vegetation zones of Scirpus americanus and Carex lyngbyei were identified. Pidwirny suggested that Scirpus is dominant in the low marsh because it is a better competitor for nitrogen. Conversely, Carex may be dominant in the high marsh because of its greater biomass and height, thus making it a superior competitor for light.

1.3 Alpine/Subalpine Literature Review

Snow distribution in alpine/subalpine systems is nonuniform because of the interaction between wind and topography (Billings and Bliss 1959). Topographic diversity in conjunction with wind not only affect snow cover depth but the rate of snowmelt which in turn is often responsible for steep and abrupt environmental gradients (Douglas and Bliss 1977; Oberbauer and Billings 1981; Olyphant 1984; Evans and Fonda 1990). Abrupt changes in species composition occur resulting in a mosaic of plant communities. In the North Cascade Range of both British Columbia and Washington, phenological patterns of vegetation shared strong correlative relationships with the snowmelt date and early season temperature regimes (Douglas and Bliss 1977). At Rocky Mountain National Park, vegetational and phenological differences were also correlated with the melting back of late season snowbanks (Holway and Ward 1963). In their study, persistent snow cover delayed normal plant development, replaced certain species by different ones and may have contributed to the failure to complete certain life cycle phases. Length of the growing season differed by two to three weeks between successive communities along a snow depth gradient, a function of topography, in the Olympic Mountains, Washington (Kuramoto and Bliss 1970). In an area of New Zealand alpine herbfield, Weir and Wilson (1987) examined micro-zonation pattern. Discriminant functions analysis suggested snow cover, slope, and exposure as important correlates of vegetation pattern. Bray-

Curtis ordination was used to analyze vegetation pattern on Signal Mountain in the Canadian Rockies (Hrapko and La Roi 1978). Again, snow depth and duration, correlated with topography, were concluded as being primarily responsible for species composition. Such microtopographic factors as aspect, slope, and drainage patterns were critical determinants of nineteen plant communities in the southern Chilcotin Mountains (Selby and Pitt 1984). In the alpine tundra of the Colorado Front Range, topographic changes were responsible for a mosaic of snow cover conditions, resulting in sharp contrasts in moisture conditions. Moisture conditions, in turn, were found to be strongly related to bryophyte distribution patterns (Flock 1978).

Snow depth and duration may influence soil conditions, such as soil type (Knapik et al. 1973), moisture, and temperature (Douglas and Bliss 1977). Many biological processes are dependent on soil temperature. Processes include the decomposition of organic matter, release of nutrients as well as their uptake by plant roots. Growth, development, and life cycle characteristics of soil organisms can all be related to soil temperature (Brown et al. 1980). Soil temperatures are also of importance because of their impact upon carbon and nitrogen cycles (Nimlos et al. 1965). Though soil temperature was believed to have little effect on vegetation pattern, soil moisture was emphasized as being the most critical factor affecting vegetational differences above and below a snow bank in the Snowy Range of the Medicine Bow Mountains,

Wyoming (Billings and Bliss 1959). Within an alpine ecosystem on the Beartooth Plateau, approximately thirty miles southwest of Red Lodge, Montana, soil moisture was the dominant environmental factor in determining the distribution of three stand types (Nimlos et al. 1965).

Interactions between topography, precipitation, wind, insolation, soil texture and other factors ultimately govern water relations (Isard 1986). The distribution of water in space and time has been emphasized as largely controlling the spatial pattern of vegetation (Isard 1986; de Molenaar 1987). De Molenaar (1987) emphasized that water has a direct causal effect on vegetation as a "nutrient" and acts as a solvent for all other plant nutrients. Water has an influence on aeration, redox conditions, and acidity, nitrogen and phosphorous supply as well as metal ion availability in the rhizosphere. Humus formation and breakdown, nutrient cycling, leaching, and other aspects of soil formation depend on the interaction of the water regime and relayed phenomena with plant cover (de Molenaar 1987).

Holway and Ward (1963) demonstrated the importance of surface meltwater as a thermoregulator on the microclimate in a study involving the artificial application of meltwater to many species. Results showed a delay in flowering for the majority of species ranging from a week to as much as one month. Water availability does not simply differ horizontally along topographic gradients.

It also varies temporally and vertically (Oberbauer and Billings 1981). Groundwater flow was investigated in fen meadows in Dutch stream valleys where they are influenced by both deep (calcium rich) and shallow (calcium poor) groundwater flows (Grootjans et al. 1988). They found that distribution of groundwater patterns influenced plant species and showed distinct relationships with the distribution of different groundwater types. Trophic gradients in virgin mires are mainly responses to differences in the ionic content of the groundwater as well as the flow rate.

1.4 Hierarchy Theory

Ecologists have generally recognized ecosystems as possessing specific levels of organization or exhibiting hierarchic structure (Simon 1962; Allen and Starr 1982; O'Neill et al. 1986). Ecosystem complexity is attributed to vegetation-environment relationships operating at varying spatial and temporal scales (Allen 1987). Our understanding of ecological complexity depends critically on methods used to describe it (Simon 1962). In general, the sampling strategy, quadrat size, data transformations, and preferred statistical tools influence not only the collection of ecological data but also its subsequent interpretation. In particular, quadrat size is of critical importance when examining ecological attributes of a system. Choosing a quadrat of certain size and dimensions to sample a system is equivalent to choosing a specific scale to observe relationships. By selecting only one scale (ie.

quadrat size) to observe ecological relationships, an anthropocentric bias is introduced. "An ecosystem's attributes, perhaps the most critical in terms of its proper functioning, may be virtually unobservable because the chosen scale may have suppressed them" (Allen and Starr 1982).

Hierarchy theory leads to observational approaches that attempt to circumvent the anthropocentric bias by recognizing the need to examine ecosystem relationships at different scales. Hierarchy theory uses the concept of level as one of its organizing principles (Allen 1987) and relies on the use of multivariate statistical methods for examining different scales within a vegetation community. In conjunction with multivariate statistical methods, various kinds of data transformation are used to change the scale at which dominant processes that are reflected in the data structure may be observed. As the scale of perception is changed through the use of these tools, the ecologist's eye moves either up or down through the hierarchy (Allen and Starr 1982).

Despite the intuitive appeal of hierarchy theory in relation to ecosystem organization, few published studies exist. Allen and Wyleto (1983) used an hierarchical approach to investigate the role of fire from 1951 to 1972 on vegetation of the Curtis Prairie of the Arboretum of the University of Wisconsin. Two levels of organization were displayed in two separate principal component analyses. At a fine-grained scale, analyses of species cover data

revealed fire to act as a disturbance with the potential to alter greatly the individual patterns of species cover within the vegetation. At a coarse-grained scale, derived by transforming the cover data to presence/absence data, the analysis indicated that fire was acting as a stabilizing factor, maintaining species diversity within the vegetation. Allen and Wyleto (1983) concluded that the removal of fire would, in fact, represent a coarse-scale disturbance in the grassland system just as the presence of fire was acting as a disturbance at a fine scale. Allen et al. (1984) investigated the effects of data transformation on phytoplankton daily abundance data over two years, for thirty species from a temperate lake in Llyn Maelog, North Wales. Using this approach led to an improved understanding of the dynamics of the lake ecosystem in terms of species turnover, seasonal areas of attraction, and uniqueness of individual sample dates. Maintaining the scale but altering the reference or observation point is another strategy which can be used to improve understanding on how ecosystems are organized. For example, Bradfield and Orloci (1975) used cluster analysis to generate a classification of some open beach vegetation in southwestern Ontario, and then used discriminant analysis to assign a separate set of quadrats, obtained at the same sampling scale, to the pre-established groups. Such repositioning within a level of an hierarchy allows greater insight into the effects of inferred processes operating at that scale.

An hierarchical approach does not completely eliminate an anthropocentric perspective since the different levels of organization within a community are defined by observer-chosen criteria (Allen et al. 1984). Based on experience, however, it seems logical to examine various processes at different scales than at only one. Examination of different levels can only enhance our understanding of vegetation pattern. The hierarchical concept results in a sharpening of the concepts and issues involved (Bossort et al. 1977).

1.5 Objectives

Before the ecological investigation was initiated, a number of objectives were established. The first objective was to describe and compare community pattern/structure in a subalpine wet meadow and a brackish tidal marsh. The second objective was to examine relationships between measured environmental variables and community pattern/structure in both marsh and subalpine meadow study sites. Given the emphasis in the marsh and subalpine/alpine scientific literature on topography and its influence on species distribution patterns, a closer examination of the role of land surface elevation as a determinant of plant species composition in both systems constituted a third objective. The use of quadrats of specific size and dimensions during field sampling introduces an anthropocentric bias when observing ecological relationships. Thus, a fourth objective was an attempt to alleviate some of this

bias by investigating what effect different quadrat sizes (scales) have on the perception of community structure and community-environment relationships. Here, the underlying hypothesis was that environmental factor 'importance', estimated by their correlations with vegetation pattern, as well as perception of community structure, are dependent on the scale at which the data are analyzed.

CHAPTER 2: METHODS

2.1 Study Sites

2.1.1 Tidal Marsh

The marsh study was conducted in a brackish tidal marsh at the Squamish estuary. Adjacent to the town of Squamish, located approximately 45 km north of Vancouver, British Columbia, the Squamish Marsh is influenced by glacially fed water from the Squamish River and by Howe Sound, a saltwater source (Figure 1). In reference to Table I, a weather station adjacent to the marsh in Squamish, B.C., recorded 2247 mm as an average of the total annual precipitation from 1951-1980. Most of the precipitation occurs during the fall and winter months in the form of rain (2109.5 mm). Temperatures tend to be mild during the spring-summer growing season (approximately 16°C) and colder during the fall and winter (October to April) (4.6°C) (Environment Canada 1980). While the lower marsh is characterized by vast stands of Carex lyngbyei, the upper is a mixture of marsh species common to other coastal marshes of the Pacific Northwest such as Potentilla pacifica, Deschampsia cespitosa, and Triglochin maritimum (Hutchinson et al. 1989) (Photograph I).

2.1.2 Subalpine Wet Meadow

Approximately 37 km north of Squamish, is the Black Tusk recreation area of Garibaldi Provincial Park. A wet meadow area

Figure 1: Maps showing the location of the tidal marsh and the subalpine wet meadow study sites.

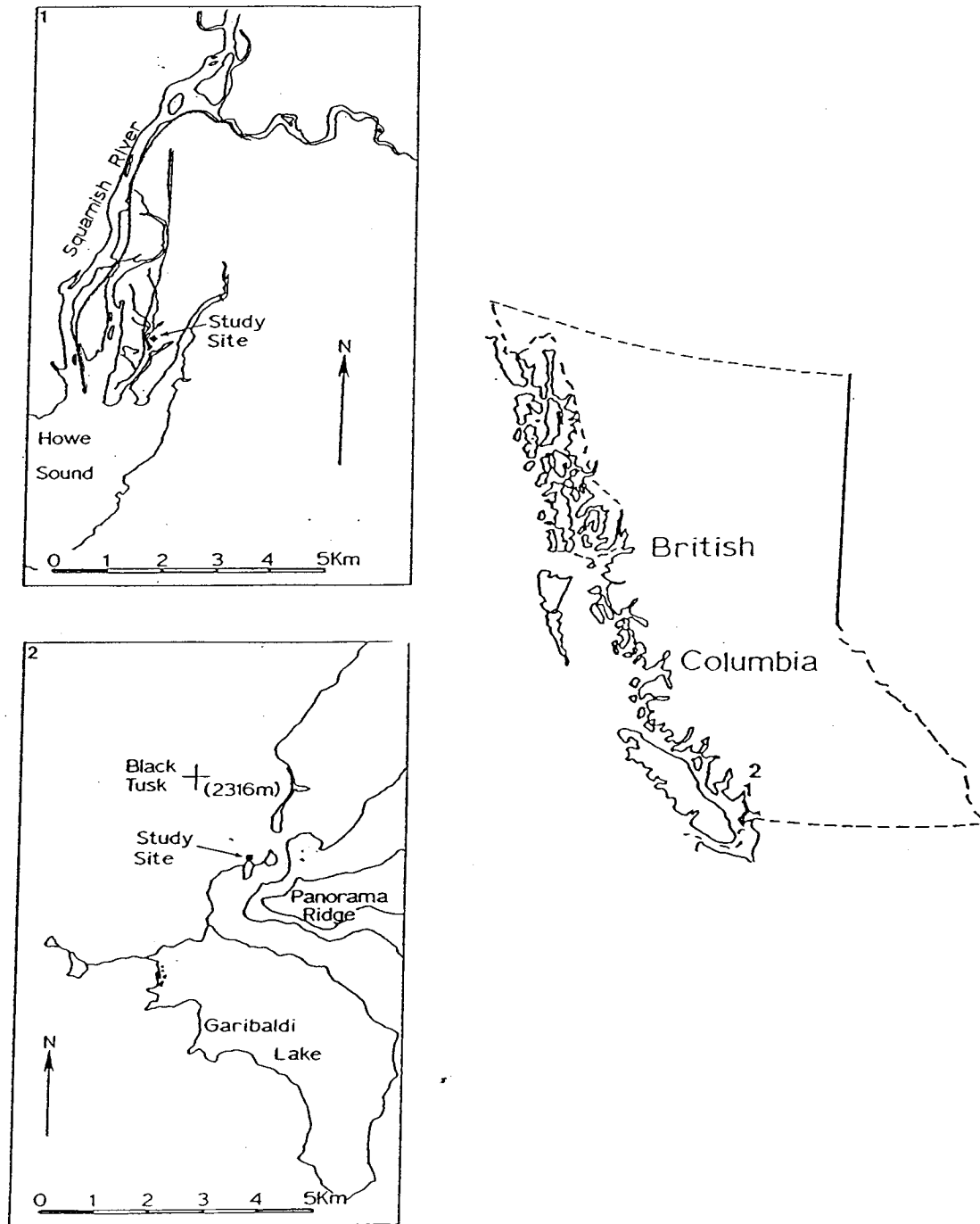


Table I: Mean precipitation and temperature data, 1951-1980, for Squamish (tidal marsh) and Alta Lake (subalpine wet meadow) (Environment Canada 1980).

	Squamish		Alta Lake	
	Mean	Std. Dev.	Mean	Std. Dev.
<u>Precipitation (mm)</u>				
May-September	79.6	50.1	53.04	30.32
October-April	264.1	99.7	164.3	69.2
Total Annual	2247.0	244.3	1415.4	226.1
Total Annual Rainfall	2109.5		800.6	
Total Annual Snowfall	177.1		657.4	
<u>Temperature (°C)</u>				
May	11.5	1.0	9.0	1.1
June	14.3	1.3	12.5	1.8
July	16.6	0.9	15.3	1.5
August	16.3	1.3	14.9	1.5
September	13.7	1.2	11.9	1.4
October-April	4.6	1.3	0.6	1.9

Photograph I: Photograph of the Squamish Marsh.



adjacent to Mimulus Lake in the Black Tusk meadows was deemed suitable for study. The wet meadow site has an aspect of 135° (southeast) and is located well within the Coast Mountain Range at an elevation of approximately 1700 m (Figure 1). A nearby weather station at Alta Lake, adjacent to the town of Whistler, B.C., has recorded total mean annual precipitation as being approximately half (1415.4 mm) of that in Squamish. However, Alta Lake, more representative of the subalpine study site, receives almost six times the amount of snow per year (657.4 mm as opposed to 177.1 mm at Squamish) (Table I). Though temperatures are comparably mild, compared to Squamish during the spring and summer months, freezing temperatures, or at least temperatures close to freezing are typical of the Black Tusk area during the winter (Table I) (Environment Canada 1980). While the lower portion of the site is characterized by a virtually monospecific stand of Carex nigricans other species such as Phyllodoce empetriformis, Cassiope mertensiana, Lupinus latifolius, and Luetkea pectinata become more abundant in the middle and upper portions of the study area (Photograph II). All of these species are common throughout Garibaldi Provincial Park (Brink 1959; Archer 1963).

2.2 Field Data Collection

During July and August of 1990, field data were collected using 0.5 X 0.5 m quadrats systematically located every 5 m along transects arranged in a 40 X 120 m "systematic grid" at both meadow

Photograph II: Photograph of the subalpine wet meadow adjacent to Mimulus Lake in Garibaldi Park, British Columbia.



and marsh sites (Figure 2). Within the 225 quadrats of each sampling grid, vascular plant species were identified and assigned values of 1, 2, 3, 4, or 5 designating their occurrence in one of five aerial coverage classes (<5%, 6-25%, 26-50%, 51-75%, 76-100%). Nomenclature followed Hitchcock and Cronquist (1973). If a large log, rock or some other obstacle prevented data collection at a specific location, then the quadrat was positioned to allow appropriate data collection adjacent to the obstacle. Ground level elevation, relative to the lowest quadrat location (EL), was also recorded for each quadrat by using a survey level. Bryophytes and lichens were recorded in the meadow area but, except for Sphagnum warnstorffii and Cetraria subalpina, were not included in data analyses. Bryophyte identification followed the nomenclature of Stotler and Stotler (1977) and Ireland et al. (1987). Bryophytes and lichens were not encountered during sampling in the marsh.

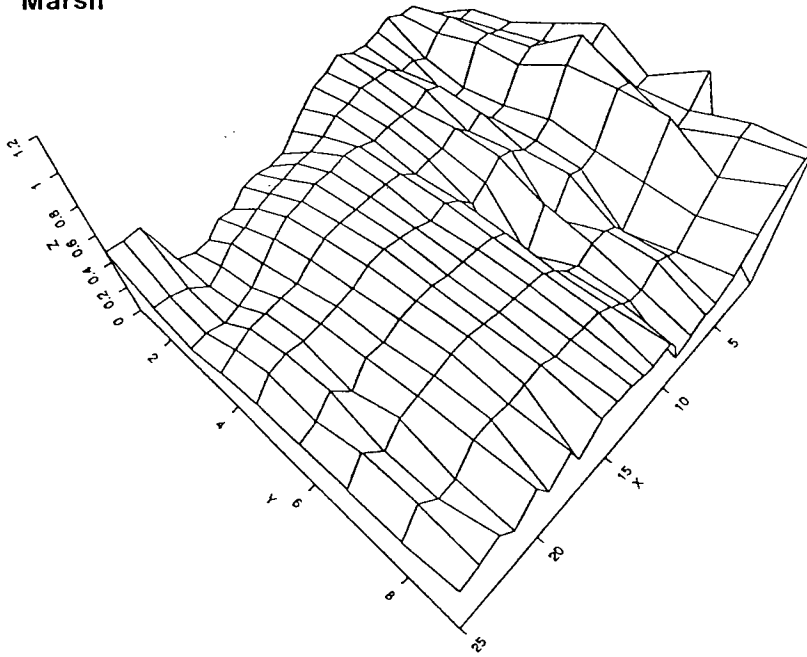
In addition to the vegetation data, soil samples were collected from every other quadrat along alternate transects within the sampling grid. In this fashion, sixty-five soil samples of approximate dimensions, 15 x 15 x 15 cm, were collected from both marsh and meadow sites.

2.3 Laboratory Data Collection

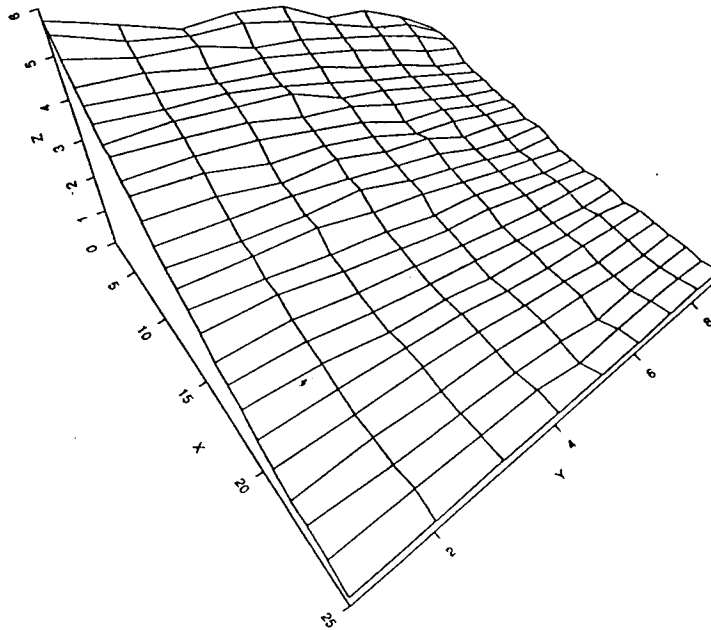
Soil samples were air dried (Jackson 1958; Davidescu and Davidescu 1982) in individual plastic trays at approximately 20°C.

Figure 2: "Systematic grid" sampling design superimposed on topographic profiles of marsh and subalpine meadow study sites. Numbers along the X and Y axes refer to transects; the Z axis denotes elevation in metres.

Marsh



Meadow



After drying, the samples were gently crushed with a rolling pin to break up aggregate soil particles and were subsequently passed through a 2 mm sieve. That fraction of soil samples failing to pass through the sieve (meadow soils only) was weighed and used to determine a separate variable (FI) for data analysis (FI = the percentage of "fines" (particles <2 mm) in the total). All 130 soil samples from meadow and marsh sites were analyzed for pH, electrical conductivity (EC), carbon content (C), and percent sand (SA) and clay (CY) using procedures outlined by Lavkulich (1981). Soil pH was measured using a 1:2, soil:distilled water ratio, whereas EC measurements were recorded from a 1:2 volume extract following the recommendation of Rhoades (1982).

2.4 Data Analysis

2.4.1 Altering the Scale of Observation

Interpretation of community structure as well as community-environment relationships may be a function of scale. The scale of observation is dependent on the quadrat size used during field sampling. Raw vegetation and environmental data matrices represent the most detailed scale of observation (agg1). Neighbouring cases in both matrices were aggregated in groups of four (agg4), six (width-wise) (agg6a), six (length-wise) (agg6b), and nine (agg9) to simulate sampling with larger quadrat sizes (5 X 5 metres, 5 X 10 metres, 10 X 5 metres, and 10 X 10 metres respectively) (Figure 3). This was equivalent to examining a system at progressively coarser

Figure 3: Simulation sampling with larger quadrat sizes by aggregating neighbouring 0.5 X 0.5 m quadrats (agg1 level): agg4 (a); agg9 (b); agg6a (c); agg6b (d). '99' denotes omitted quadrats because of an unavailability of neighbouring quadrats to group with.

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b

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c

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d

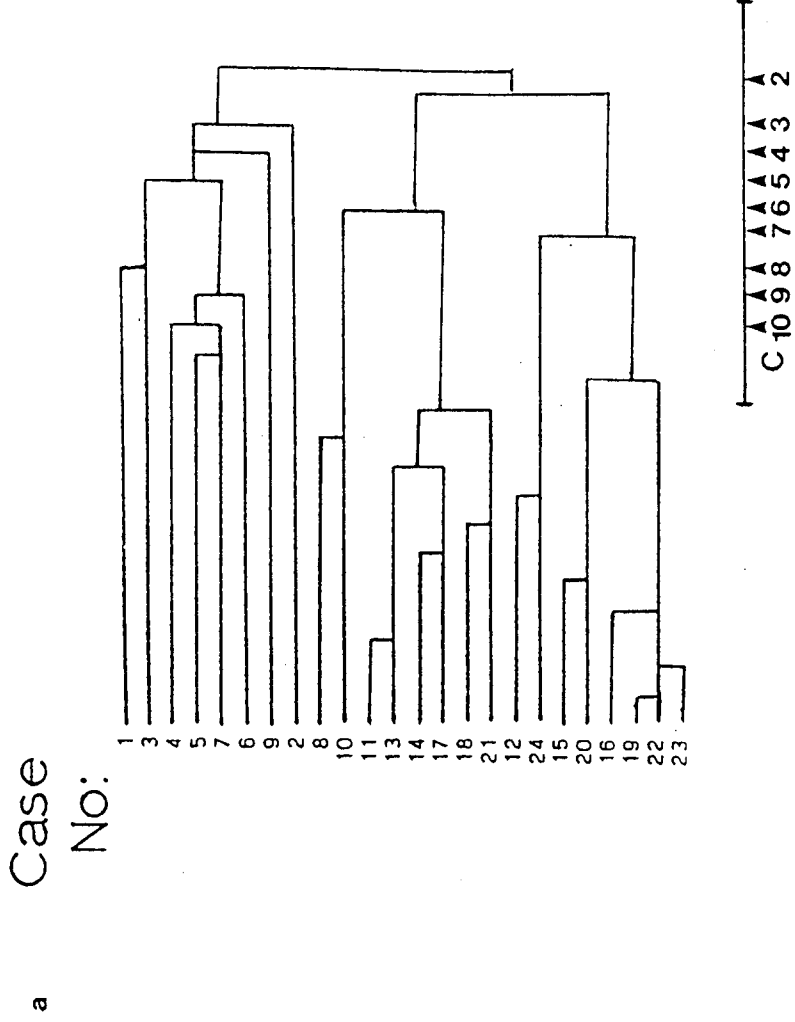
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29. 29. 30. 30. 31. 31. 32. 32. 99.
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scales. Regrettably, it was impossible to aggregate all quadrats for each aggregation scheme because of an unavailability of neighbouring quadrats to group with. Where quadrats were aggregated in groups of four and six (length-wise), the last quadrat of each transect as well as the last transect itself were omitted. The last transect was omitted from data analyses where cases were grouped by nine and six (width-wise). At each aggregation level or observation scale, mean values of species aerial coverage and environmental variables were used to assess community structure and its relationships with environmental variables.

2.4.2 Classification of Subcommunities

In order to examine community structure and how the perception of community structure may change at different scales, minimum variance cluster analysis (MVCA) was performed on both marsh and meadow vegetation matrices using the MIDAS statistical program (Fox and Guire 1976) on the Amdahl 470 V6-II mainframe computer at the University of British Columbia. Using Euclidean distance as a dissimilarity measure, MVCA provided a dendrogram and nine grouping variables for each scale (Figure 4). Categorical grouping variables offer an alternative way of presenting MVCA results. Organized in a matrix, each quadrat was assigned a number depending on which subcommunity it belonged to at a particular dendrogram level. For this purpose, canonical correlation analysis (CCorA)

Figure 4: A dendrogram (a) and grouping variables (b) offering alternative means of presenting MVCA results. C2-C10 refer to different dendrogram levels in (a) and respective grouping variables in (b).



(Gittins 1985) was used to provide quantitative guidelines for selecting among the nine possible partitionings of the vegetation in the dendrogram for each aggregation level. Application of CCorA, using MIDAS, involved correlating the covariance relationships of species with grouping variables corresponding to each of the nine dendrogram levels. The useful statistics generated from these analyses included canonical correlation coefficients (R_c), which provided an overall measure of the relationships between species and the grouping variables, and redundancy, defined as the proportion of variation in the species variables explained by a particular grouping variable. Because the R_c -values are sensitive to distributional peculiarities in a data set (Kowalski 1972; Thissen et al. 1981), redundancy estimates were used to help describe subcommunity zonation.

2.4.3 Interpolation of Soil Variables

Given logistic constraints during the field work, it was possible to obtain soil samples for only 65 of the 225 quadrats in the marsh and meadow sampling grids. In order to estimate the values of soil variables (pH, EC, C, SA, CY, and FI (meadow only)) at quadrat locations where soil samples had not been obtained, an interpolation technique known as kriging (Krige 1966) was used. Kriging, based on regionalized variable theory, is one of the most reliable interpolation techniques available because it provides not only an optimal interpolation estimate but also a complementary

variance estimate (Webster 1985; Robertson 1987). Semivariance and best fit anisotropic model analyses, performed on the untransformed soil data by program GS+ (Gamma Design Software 1991) provided punctual kriged soil variable estimates, and two dimensional isopleths displaying the zonation pattern of each soil variable. Before proceeding with further multivariate analyses of the soil data, the soil variables were tested for normality with both a Kolmogorov-Smirnov one-sample test (Kolmogorov 1933; Smirnov 1939) and a more robust Lilliefors test (Lilliefors 1967). Transformations of soil variables that did not conform to a normal distribution (log, square root, winsorizing and trimmed means) were attempted but provided isopleths that were less meaningful and lacked the desirable map details provided by those obtained with the untransformed data. Two dimensional isopleths, showing the extent of topographic variation within the sampling grids, were also generated.

2.4.4 Vegetation-Environment Relationships

Vegetation-environment relationships were examined with canonical correspondence analysis (CCA) (Ter Braak 1986, 1987a, 1987b). CCA determines the major axes of compositional variation that are also constrained to be linear combinations of the environmental variables. For each of the marsh and meadow data sets, a Monte Carlo permutation test was used to evaluate the significance of the first canonical axis and the trace statistic

(summation of eigenvalues of the first four canonical axes). The CCA's and Monte Carlo permutation tests were performed using program CANOCO (Ter Braak 1987b). Ordination diagrams were produced to illustrate graphically the extent of vegetation-environment relationships. The locations of the previously determined subcommunities were shown by superimposing 50% confidence ellipses on the ordination diagrams. CANOCO also calculated Pearson correlation coefficients among the environmental variables and the CCA axes which greatly assisted interpretation of the ordination axes. Correlative relationships were deemed relevant for those variables with $r \geq 0.3$.

2.4.5 Overall Between-Within Cluster Variability Assessment

A subcommunity-environment biplot with subcommunities represented as 50% confidence ellipses provides a qualitative assessment of between and within-cluster (subcommunity) variability. In order to evaluate which observation scale provided the clearest picture of community structure, a quantitative assessment was deemed necessary. An analysis of variance was performed on CCA first and second axis scores using the selected grouping variable for stratification. This provided a between, within, and total sum of squares estimate for each axis. For each axis, the between sum of squares estimate was divided by the total sum of squares. The quotient was subsequently multiplied by the axis eigenvalue with the understanding that each axis did not

account for 100% of the variation in the data sets. Between sum of squares, expressed as a percentage for each axis, were subsequently added together providing an overall between sum of squares value. This value was subtracted from the sum of CCA axes I and II eigenvalues, ultimately providing an overall percentage of within sum of squares. For each scale overall percentage estimates of between and within-cluster variability were standardized for purposes of comparing community structure clarity across scales. Scales that possessed relatively greater between and less within-cluster variability values segregated quadrats into relatively tighter and more independent groups. This was judged to give a clearer picture of community structure as opposed to scales of relatively less between and greater within-group estimates since subcommunities are not as compact and tend to overlap more.

2.4.6 Closer Examining the Effect of EL

EL has been recognized as a major determinant of species composition through its interaction with the tidal regime in many marsh systems. Through its interaction with wind, and their joint influence on snow distribution and soil variables, EL has also been recognized as a major determinant of species composition in meadow systems. In view of past findings, it was deemed necessary to closer examine whether other environmental variables unrelated to EL shared strong correlative relationships with species composition. Using a method outlined by Bradfield and Campbell

(1986), principal components analysis (PCA) was performed on both marsh and meadow vegetation data sets. CCorA was then used to examine relationships among the first three PCA axes and EL. Canonical axis scores, summarizing the PCA axes, were subsequently regressed against the quadrat scores along the canonical axis of EL. This not only examined the relationship between EL and the vegetation data summarized by the canonical axis but provided residuals as well. Residuals represent that proportion of the variation in vegetation unexplained by EL. Residuals were saved and subsequently correlated with the environmental variables to examine if other variables unrelated to EL shared strong relationships. This set of correlations was compared to a set between the canonical axis scores representing the vegetation data and environmental variables. Similar correlations between the two sets would suggest a strong lack of EL influence on vegetation pattern.

CHAPTER 3: RESULTS

3.1 Tidal Marsh and Wet Meadow: A Brief Comparison

In reference to Figure 5, Whittaker diversity curves indicate the greater diversity of species in the wet meadow (36 species) compared to the tidal marsh (19 species). The diversity curve representing the tidal marsh possesses a steeper slope than the meadow because of the overwhelming dominance of Carex lyngbyei, Potentilla pacifica, and Triglochin maritimum. As in the tidal marsh, the genus Carex is a predominant constituent of the wet meadow vegetation. Specifically, Carex nigricans and Carex spectabilis are the main species. The more gradually sloping diversity curve and greater number of species in the subalpine meadow may suggest the presence of more microhabitats than in the marsh. The names of marsh and meadow species shown in order of decreasing abundance of each species, as well as encountered bryophytes in the wet meadow may be found in Appendix A.

3.2 Brackish Tidal Marsh

3.2.1 Aggl Scale (0.5 X 0.5 Metre Observation Unit)

3.2.1.1 Community Structure

Table II summarizes the results of applying CCorA to dendrogram levels C2-C10 obtained with cluster analysis of the aggl scale marsh vegetation data. Dendrogram level C2 provided the largest redundancy (15.60%) and R_c (0.9309) estimates; thus, two

Figure 5: Whittaker diversity curves for the marsh and subalpine meadow study areas.

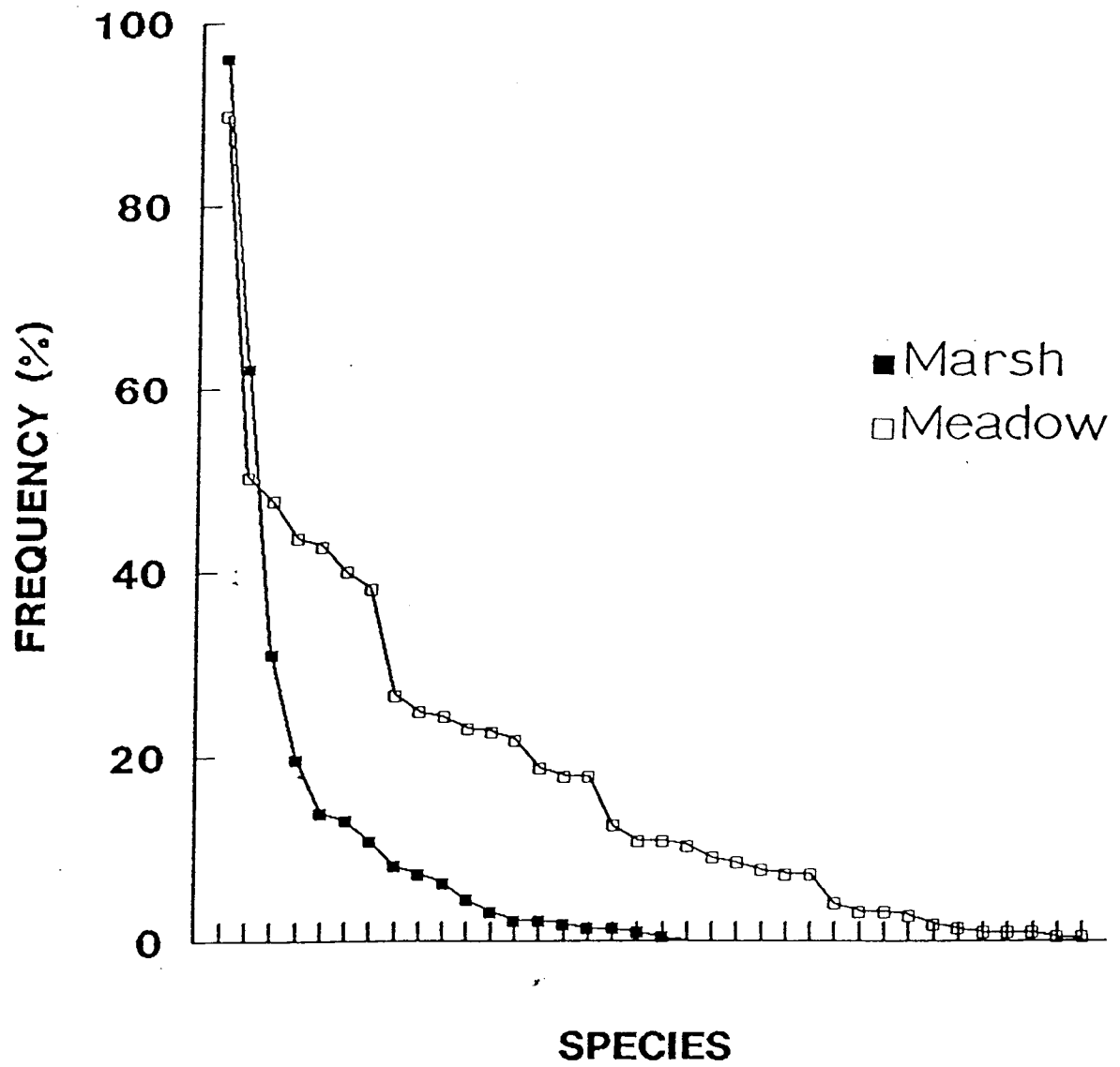


Table II: Redundancy and R_c estimates for dendrogram levels C2-C10 at different scales in the Squamish Marsh. Highest redundancy and R_c estimates at each scale are marked with an '*'.

Agg1 Scale

	<u>Redundancy (%)</u>	<u>R_c</u>
C 2	*15.60	*0.9309
C 3	8.71	0.8684
C 4	6.75	0.862
C 5	5.51	0.8424
C 6	5.56	0.8569
C 7	6.9	0.8778
C 8	7.98	0.8826
C 9	7.43	0.8644
C10	6.76	0.8551

Agg4 Scale

	<u>Redundancy (%)</u>	<u>R_c</u>
C 2	*29.21	*0.9943
C 3	12.45	0.9646
C 4	8.19	0.9615
C 5	6.45	0.9576
C 6	6.09	0.9553
C 7	4.88	0.9609
C 8	6.03	0.9760
C 9	6.66	0.9740
C10	6.13	0.9765

Agg6a Scale

	<u>Redundancy (%)</u>	<u>R_c</u>
C 2	*44.38	*0.9797
C 3	37.07	0.9382
C 4	29.86	0.9307
C 5	34.63	0.9625
C 6	37.8	0.9599
C 7	40.84	0.9743
C 8	41.6	0.9744
C 9	41.6	0.9736
C10	38.81	0.9661

Agg6b Scale

	<u>Redundancy (%)</u>	<u>R_c</u>
C 2	45.92	0.9694
C 3	42.5	0.9607
C 4	45.34	0.9851
C 5	44.68	0.9799
C 6	45.15	0.9897
C 7	46.22	0.9912
C 8	*47.22	0.9921
C 9	46.97	*0.9932
C10	46.43	0.9925

Agg9 Scale

	<u>Redundancy (%)</u>	<u>R_c</u>
C 2	*39.55	0.9686
C 3	34.0	0.9479
C 4	33.11	0.9493
C 5	33.05	0.9606
C 6	34.76	0.9521
C 7	36.96	*0.9692
C 8	36.48	0.9677
C 9	37.58	0.9640
C10	37.5	0.9688

subcommunities may be recognized (Figure 6a). Subcommunity 1 represents the lower marsh and is virtually a monospecific stand of Carex lyngbyei. Potentilla pacifica also characterizes subcommunity 1 but tends to occur mainly in close proximity to the boundary with subcommunity 2. Subcommunity 2, representative of the upper marsh, is characterized by C. lyngbyei, P. pacifica, as well as Triglochin maritimum, Deschampsia cespitosa, and Agrostis alba (Table III). Because P. pacifica, as a member of subcommunity 1, is found only in the vicinity of subcommunity 2, the transition between the two subcommunities tends to be gradual.

3.2.1.2 Environmental Variable Relationships

EL interacts with many of the measured environmental variables in the marsh study area. In reference to Table IV, EL is positively correlated with C (0.58) and SA (0.46) and negatively correlated with CY (-0.44). C and SA share a positive correlative relationship of 0.78 and share negative correlative relationships with CY (-0.54 and -0.68 respectively). Because the study site was located on a slight incline, more SA and C are prevalent in the upper marsh area compared to the lower marsh where soils contain more CY. Though protected by a dyke, the lower marsh is adjacent to a water channel that overflows into the lower marsh zone during high tide. High-low tide alternation may act as a flushing mechanism that may remove much organic content (C) and contribute to CY accumulation in the lower marsh. Because it is relatively

Figure 6: Grid maps showing subcommunity layout at different scales in the tidal marsh study site: agg1 (a), agg4 (b), agg9 (c), agg6a (d), and agg6b (e).

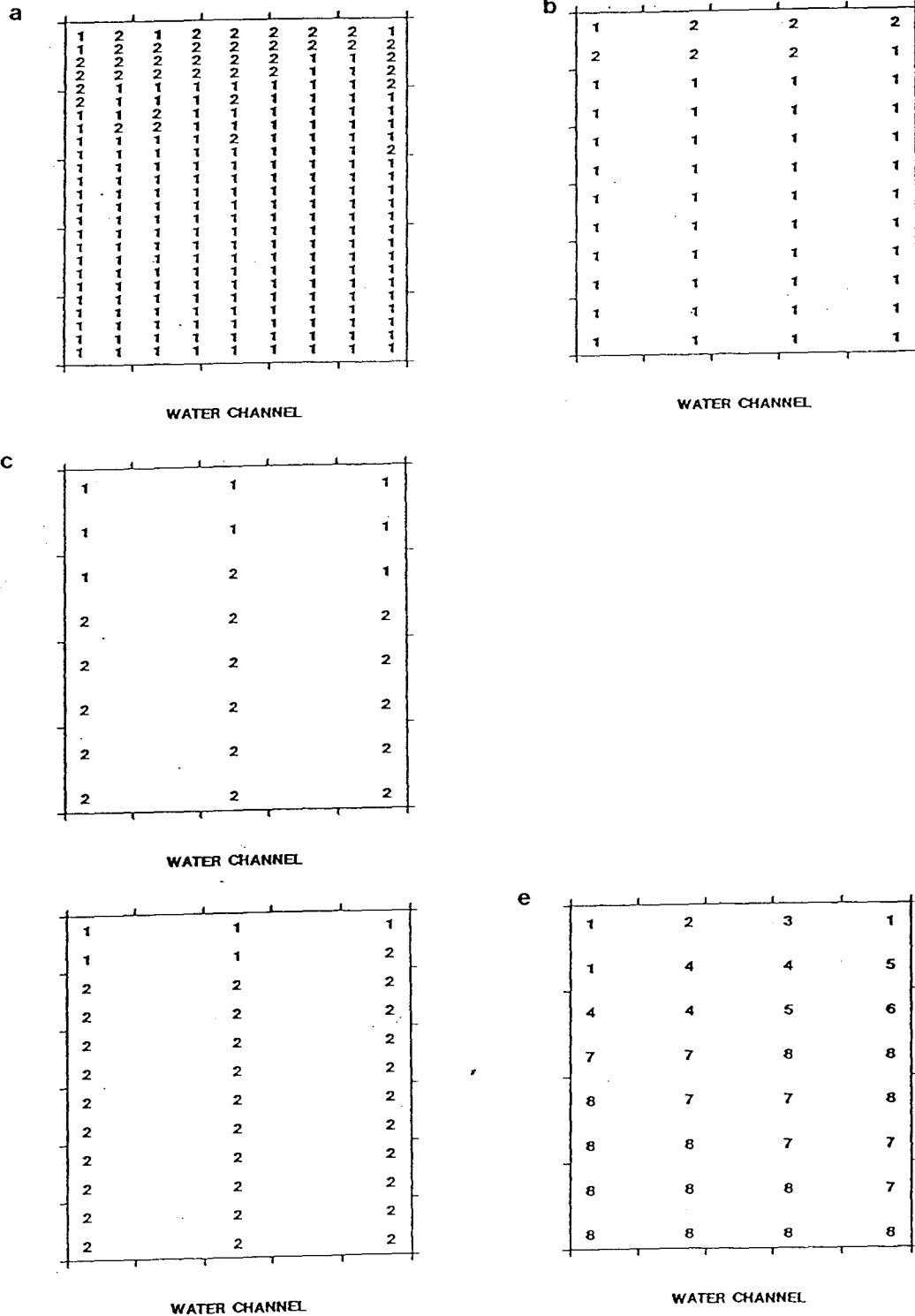


Table III: Species mean aerial coverage class data for subcommunities at different scales in the Squamish Marsh. Those species with a mean aerial coverage class estimate ≥ 1 were deemed to be representative of a particular subcommunity. Species names corresponding to the codes used below may be found in Appendix A. Integers directly above mean and standard deviation estimates represent subcommunities at each scale.

Aggl Scale

	1		2	
	Mean	Std Dev	Mean	Std Dev
CARLYN	4.36	1.01	1.22	0.85
POTPAC	1.12	1.15	1.73	0.61
TRIMAR	0.36	0.79	1.97	1.14
DESCES	0.04	0.24	1.19	1.45
STEHUM	0.10	0.37	0.76	1.12
AGRALB	0.09	0.40	2.65	1.34
ASTEAT	0.01	0.15	0.22	0.53
TRIWOR	0		0.11	0.39
LATPAL	0		0.16	0.44
JUNBAL	0.02	0.13	0.78	1.21
HORBRA	0.01	0.10	0.56	0.99
SONARV	0.01	0.07	0.05	0.23
RANCYM	0.12	0.46	0.03	0.16
SIUSUA	0.19	0.45	0.03	0.16
ELYMSP	0.01	0.10	0.22	0.75
CONPAC	0		0.03	0.16
ATRPAT	0.06	0.30	0.03	0.16
PLAMAR	0.02	0.16	0	
SCIMAR	0.07	0.54	0	

Table III: (Continued)

Agg4 Scale

	1		2	
	Mean	Std Dev	Mean	Std Dev
CARLYN	4.21	0.88	1.17	0.47
POTPAC	1.26	1.01	1.75	0.55
TRIMAR	0.40	0.57	1.96	0.62
DESCES	0.06	0.25	1.54	0.73
STEHUM	0.12	0.27	0.92	0.82
AGRALB	0.27	0.59	2.46	0.49
ASTEAT	0.01	0.08	0.33	0.49
TRIWOR	0		0.17	0.20
LATPAL	0		0.25	0.27
JUNBAL	0.04	0.13	1.00	0.74
HORBRA	0.02	0.12	0.83	0.66
SONARV	0.01	0.04	0.08	0.20
RANCYM	0.13	0.30	0.04	0.10
SIUSUA	0.18	0.32	0.04	0.10
ELYMSP	0.01	0.05	0.33	0.61
CONPAC	0		0.04	0.10
ATRPAT	0.07	0.16	0.04	0.10
PLAMAR	0.02	0.09	0	
SCIMAR	0.01	0.04	0	

Agg6a Scale

	1		2	
	Mean	Std Dev	Mean	Std Dev
CARLYN	1.57	0.91	4.16	0.93
POTPAC	1.67	0.57	1.20	0.95
TRIMAR	1.93	0.63	0.45	0.54
DESCES	1.50	0.72	0.03	0.09
STEHUM	0.90	0.69	0.10	0.15
AGRALB	2.20	0.52	0.26	0.60
ASTEAT	0.27	0.43	0.01	0.06
TRIWOR	0.13	0.22	0	
LATPAL	0.20	0.28	0	
JUNBAL	0.97	0.57	0.02	0.05
HORBRA	0.77	0.45	0	
SONARV	0.07	0.15	0.01	0.03
RANCYM	0.03	0.08	0.12	0.24
SIUSUA	0.07	0.09	0.18	0.28
ELYMSP	0.27	0.43	0.01	0.04
CONPAC	0.03	0.08	0	
ATRPAT	0.03	0.08	0.06	0.13
PLAMAR	0		0.02	0.07
SCIMAR	0		0.07	0.30

Table III: (Continued)

Agg6b Scale

	1		2		3	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
CARLYN	2.33	0.17	1.00		0.50	
POTPAC	1.72	0.19	2.17		1.67	
TRIMAR	1.94	0.54	2.33		1.50	
DESCES	0.94	0.54	2.33		1.50	
STEHUM	1.00	0.58	0.83		0.33	
AGRALB	2.17	0.44	2.33		2.00	
ASTEAT	0		0.17		1.00	
TRIWOR	0.06	0.10	0.33		0.17	
LATPAL	0.06	0.10	0.17		0.50	
JUNBAL	0.50	0.44	1.33		1.50	
HORBRA	0.44	0.42	1.00		1.50	
SONARV	0.11	0.19	0		0	
RANCYM	0.11	0.10	0		0	
SIUSUA	0.11	0.10	0		0	
ELYMSP	0.06	0.10	0		1.33	
CONPAC	0.06	0.10	0		0	
ATRPAT	0.06	0.10	0		0	
PLAMAR	0		0		0	
SCIMAR	0		0		0	

	4		5		6	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
CARLYN	3.00	0.43	3.17	0.23	2.67	
POTPAC	2.37	0.09	1.58	0.35	0	
TRIMAR	0.92	0.29	0.33		1.67	
DESCES	0.25	0.32	0.09	0.12	0	
STEHUM	0.38	0.31	0.25	0.11	0.17	
AGRALB	1.25	0.35	0.58	0.35	0	
ASTEAT	0.04	0.09	0.17	0.23	0	
TRIWOR	0		0		0	
LATPAL	0.04	0.09	0		0	
JUNBAL	0.04	0.09	0		0	
HORBRA	0		0		0	
SONARV	0		0.09	0.12	0	
RANCYM	0.13	0.09	0.75	0.35	1.00	
SIUSUA	0.04	0.09	0.09	0.12	0.17	
ELYMSP	0.04	0.09	0		0	
CONPAC	0		0		0	
ATRPAT	0.13	0.16	0.50	0.24	0	
PLAMAR	0		0.25	0.11	0	
SCIMAR	0.04	0.09	0		0	

Table III: (Continued)

Agg6b Scale (Continued)

	7		8	
	Mean	Std Dev	Mean	Std Dev
CARLYN	4.31	0.46	4.83	0.27
POTPAC	2.19	0.42	0.40	0.43
TRIMAR	0.33	0.33	0.08	0.20
DESCES	0		0	
STEHUM	0.02	0.06	0.04	0.10
AGRALB	0.05	0.12	0.01	0.05
ASTEAT	0		0	
TRIWOR	0		0	
LATPAL	0		0	
JUNBAL	0.05	0.08	0.01	0.05
HORBRA	0		0	
SONARV	0		0	
RANCYM	0		0.03	0.06
SIUSUA	0.38	0.21	0.14	0.20
ELYMSP	0		0	
CONPAC	0		0	
ATRPAT	0		0.03	0.06
PLAMAR	0		0	
SCIMAR	0		0	

Agg9 Scale

	1		2	
	Mean	Std Dev	Mean	Std Dev
CARLYN	1.56	0.84	3.56	0.84
POTPAC	1.75	0.46	1.72	0.99
TRIMAR	1.97	0.54	0.61	0.53
DESCES	1.38	0.77	0.05	0.14
STEHUM	0.88	0.74	0.16	0.27
AGRALB	2.25	0.60	0.48	0.73
ASTEAT	0.25	0.44	0.03	0.13
TRIWOR	0.13	0.19	0	
LATPAL	0.19	0.26	0	
JUNBAL	0.84	0.72	0	
HORBRA	0.72	0.63	0	
SONARV	0.06	0.18	0.02	0.06
RANCYM	0.06	0.12	0.28	0.45
SIUSUA	0.06	0.12	0.09	0.15
ELYMSP	0.25	0.53	0.03	0.09
CONPAC	0.03	0.09	0	
ATRPAT	0.03	0.09	0.16	0.22
PLAMAR	0		0.05	0.14
SCIMAR	0		0.02	0.06

Table IV: Pearson correlations between environmental variables at different scales in the Squamish Marsh. EL, relative ground level elevation; C, carbon content; EC, electrical conductivity; SA, sand content; CY, clay content; pH, soil acidity.

Agg1 Scale

	EL	C	pH	EC	SA
C	0.5766				
pH	0.1421	0.0104			
EC	-0.0993	0.1655	-0.2036		
SA	0.4565	0.7788	0.0310	0.2550	
CY	-0.4437	-0.5377	-0.0040	-0.2670	-0.6802

Agg4 Scale

	EL	C	pH	EC	SA
C	0.6541				
pH	0.4130	0.1470			
EC	0.0869	0.3973	-0.3510		
SA	0.6523	0.9100	0.2358	0.2913	
CY	-0.6811	-0.8241	-0.1916	-0.4066	-0.8904

Agg6a Scale

	EL	C	pH	EC	SA
C	0.6932				
pH	0.3426	0.0459			
EC	-0.0168	0.3652	-0.4231		
SA	0.6093	0.8955	0.0404	0.3940	
CY	-0.6669	-0.8268	-0.0150	-0.4781	-0.9051

Agg6b Scale

	EL	C	pH	EC	SA
C	0.7170				
pH	0.4882	0.0839			
EC	0.1186	0.4446	-0.3634		
SA	0.6982	0.9292	0.1161	0.3499	
CY	-0.7211	-0.8585	-0.1014	-0.4440	-0.9245

Agg9 Scale

	EL	C	pH	EC	SA
C	0.7457				
pH	0.4646	0.0285			
EC	0.0405	0.4092	-0.5524		
SA	0.6545	0.9147	-0.0999	0.4489	
CY	-0.6933	-0.8437	0.0781	-0.5219	-0.9321

higher and farther away from a main water channel, the upper zone may be less disturbed, allowing organic content accumulation and receiving relatively less CY.

3.2.1.3 Community-Environment Relationships

The results from CCA are summarized as a subcommunity-environment biplot in Figure 7a. The arrangement of subcommunities indicates their similarities in relation to the main axes summarizing variation in vegetation and environmental conditions. Biplot interpretation also involves examination and comparison of the environmental vectors whose lengths indicate the relative importance of the different variables. The greater the vector length, the stronger the correlative relationship between that environmental variable and subcommunity(ies), relative to other environmental variables. Each environmental vector points in the direction of maximum change of that environmental variable (Ter Braak 1987a, 1987b).

The first and second ordination axes of the CCA have eigenvalues of 0.38 and 0.13 respectively. The first canonical ordination axis eigenvalue and trace statistic are both significant ($p < 0.05$). Figure 7a shows two very distinct subcommunities. Vector CY is the only environmental variable that points in the direction of subcommunity 1. Its direction as well as its length emphasize the relationship between subcommunity 1 and CY. CY is a

Figure 7: Subcommunity-environment biplots at different scales for the marsh study site: agg1 (a), agg4 (b), agg9 (c), agg6a (d), and agg6b (e). Subcommunities are represented by 50% confidence ellipses. Ellipses were unable to be produced where those subcommunities were represented by three or fewer sampling units. Each environmental variable is represented by a vector. EL, relative ground level elevation; C, carbon content; EC, electrical conductivity; SA, sand content; CY, clay content; pH, soil acidity.

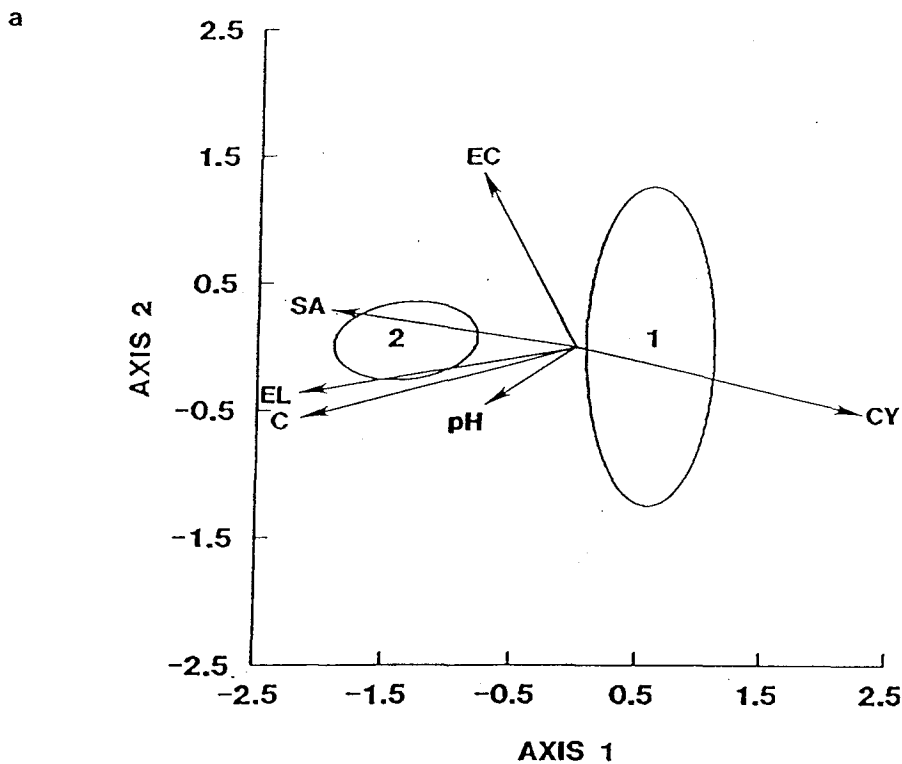


Figure 7: (Continued)

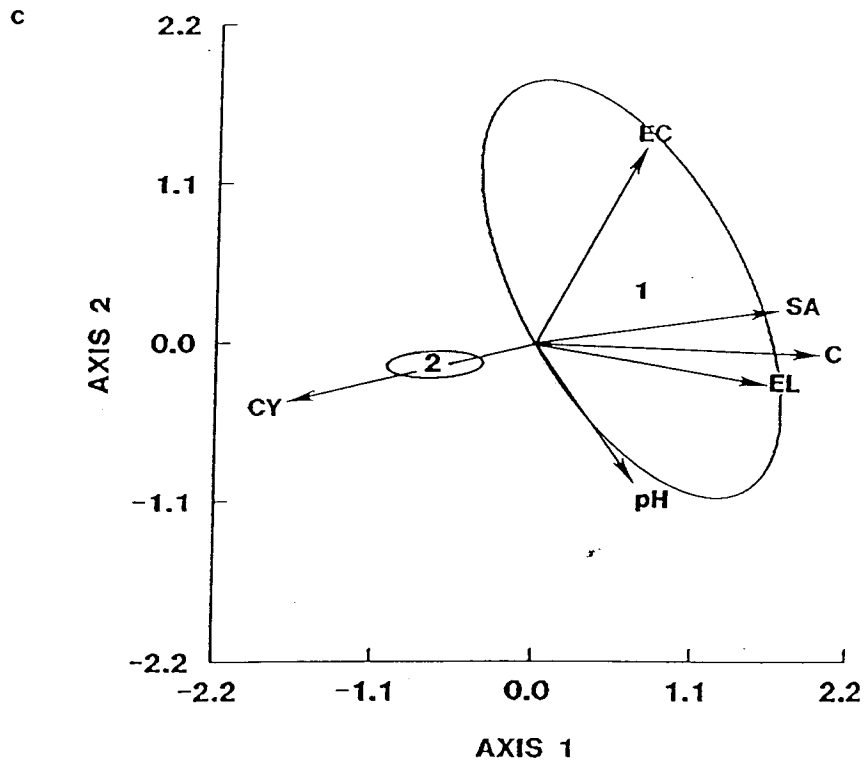
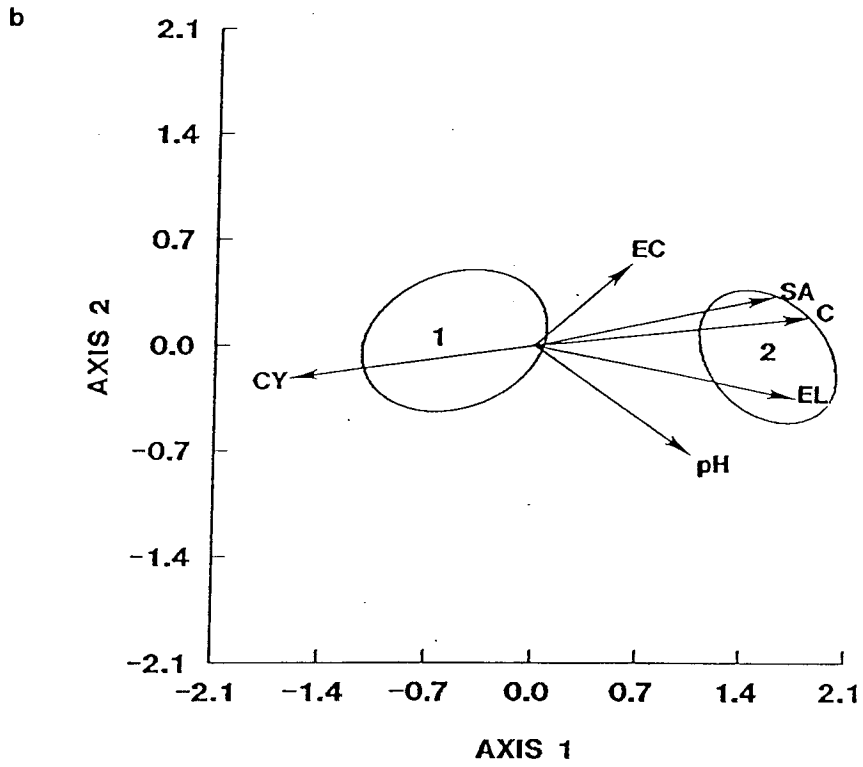
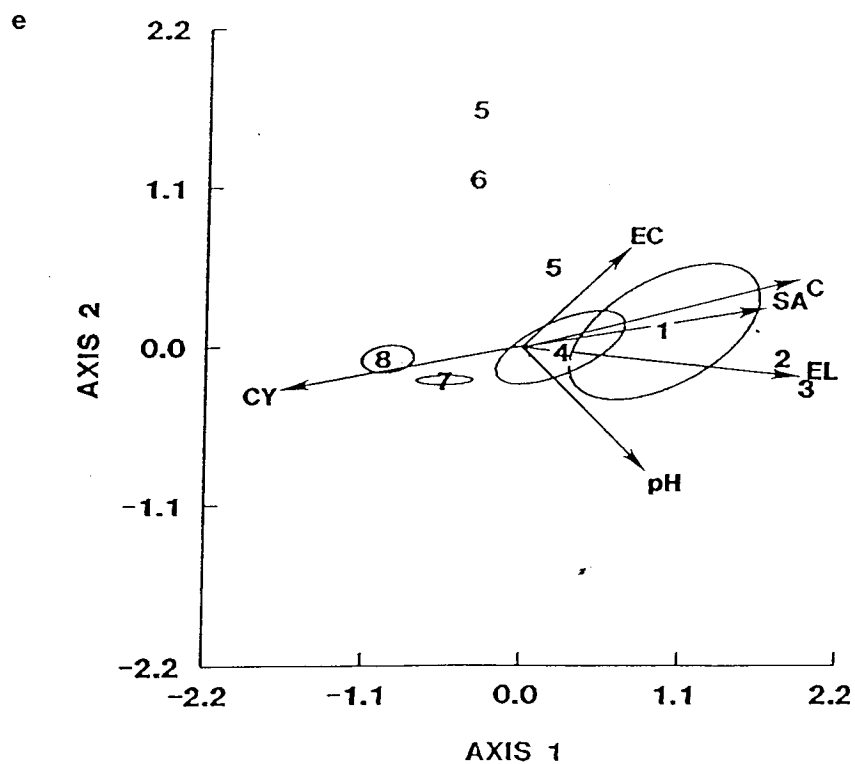
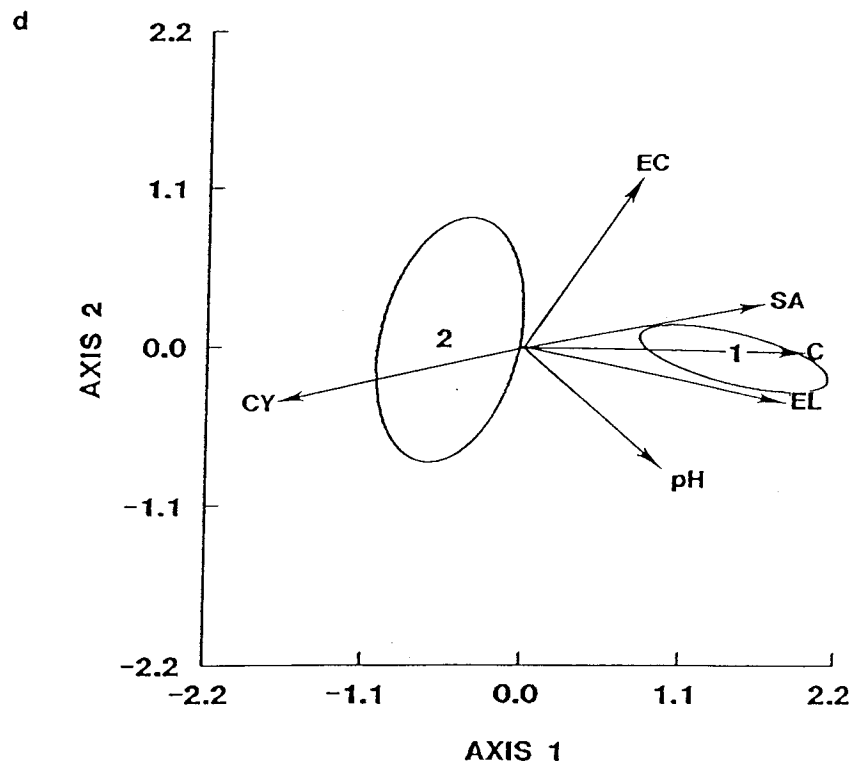


Figure 7: (Continued)



positive correlate of the first species axis (0.64) (Table V). Referring to Table VI, average CY content found in subcommunity 1 is 29.7% as opposed to 21.2% in subcommunity 2 (upper marsh). However, subcommunity 2 soils possess relatively more SA (24.0%) and C (11.6%) compared to the lower marsh (15.3% and 8.5% respectively). In Figure 7a, vectors representing EL, C, and SA are also relatively long and point in the direction of subcommunity 2; moreover, they share negative correlative relationships with the first species axis (-0.63, -0.67, and -0.70 respectively) (Table V). Figures 8a, b, and c display CY, SA, and C zonation patterns respectively, reaffirming upper marsh soils as possessing greater SA and C content and lower marsh soils possessing more CY.

While EL is an important determinant of species axis 1, it may also be responsible for the positive correlative relationship between EC and species axis 2 (0.34) (Table V). The EL gradient in the marsh lacks consistent step-wise elevation change. Figure 8d displays a low area near the upper marsh where EL is approximately equivalent to that of the lower marsh (0.42-0.61 m). As a result, the low area near the upper marsh receives more salt water per se relative to most of the study site, but is not exposed to the flushing process unique to the lower marsh. Hence, this area has a preponderance of salt deposits (Figure 8e).

Table V: Pearson correlations between environmental variables and species axes I and II at different scales in the Squamish Marsh. EL, relative ground level elevation; C, carbon content; EC, electrical conductivity; SA, sand content; CY, clay content; pH, soil acidity.

Agg1 Scale

	<u>SPP AXIS 1</u>	<u>SPP AXIS 2</u>
EL	-0.6274	-0.1067
C	-0.6667	-0.1310
pH	-0.1806	-0.1491
EC	-0.1643	0.3390
SA	-0.7003	0.0602
CY	0.6444	-0.1420

Agg4 Scale

	<u>SPP AXIS 1</u>	<u>SPP AXIS 2</u>
	0.7479	-0.2881
	0.8004	0.1881
	0.4354	-0.5772
	0.2395	0.4055
	0.8735	0.2110
	-0.8813	-0.2023

Agg6a Scale

	<u>SPP AXIS 1</u>	<u>SPP AXIS 2</u>
EL	0.7337	-0.1934
C	0.7820	-0.0403
pH	0.3822	-0.4472
EC	0.2728	0.5489
SA	0.8536	0.1206
CY	-0.8655	-0.1992

Agg6b Scale

	<u>SPP AXIS 1</u>	<u>SPP AXIS 2</u>
	0.8305	-0.1697
	0.8228	0.2254
	0.3434	-0.6612
	0.2778	0.4595
	0.9098	0.1656
	-0.9071	-0.2612

Agg9 Scale

	<u>SPP AXIS 1</u>	<u>SPP AXIS 2</u>
EL	0.8405	-0.1648
C	0.8175	-0.0640
pH	0.2596	-0.5401
EC	0.2489	0.6638
SA	0.8797	0.0940
CY	-0.8898	-0.2421

Table VI: Summarized environmental data for the main subcommunities recognized at the different scales of analysis (agg levels) in the tidal marsh. Integers directly above mean and standard deviation estimates represent subcommunities at each scale. EL, relative ground level elevation; C, carbon content; EC, electrical conductivity; SA, sand content; CY, clay content; pH, soil acidity.

Agg1 Scale

	1		2	
	Mean	Std Dev	Mean	Std Dev
EL (m)	0.57	0.17	0.84	0.23
C (%)	8.48	1.96	11.61	2.35
pH	5.31	1.11	5.80	1.02
EC (mmhos/cm)	4.25	1.40	4.74	1.09
SA (%)	15.25	4.73	24.00	4.24
CY (%)	29.67	6.11	21.21	3.13

Agg4 Scale

	1		2	
	Mean	Std Dev	Mean	Std Dev
EL (m)	0.60	0.15	0.88	0.16
C (%)	8.72	1.74	12.04	1.46
pH	5.37	0.59	6.07	0.14
EC (mmhos/cm)	4.27	0.87	4.65	0.24
SA (%)	15.26	3.89	25.00	2.66
CY (%)	29.82	4.17	20.11	1.72

Agg6a Scale

	1		2	
	Mean	Std Dev	Mean	Std Dev
EL (m)	0.84	0.18	0.59	0.14
C (%)	11.81	1.07	8.66	1.70
pH	5.98	0.24	5.29	0.58
EC (mmhos/cm)	4.70	0.50	4.36	1.02
SA (%)	25.16	2.91	15.46	3.75
CY (%)	20.43	1.39	29.52	4.14

Table VI: (Continued)

Agg6b Scale

	1		2		3	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
EL (m)	0.76	0.06	0.92		1.01	
C (%)	11.50	2.36	12.40		12.07	
pH	5.57	0.60	6.09		6.23	
EC (mmhos/cm)	4.13	0.28	4.72		4.82	
SA (%)	23.87	5.63	25.01		25.27	
CY (%)	21.36	3.23	20.83		18.37	

	4		5		6	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
EL (m)	0.76	0.03	0.65	0.01	0.51	
C (%)	10.49	0.98	11.22	1.12	8.61	
pH	5.69	0.51	5.03	0.74	3.95	
EC (mmhos/cm)	4.58	0.63	5.21	0.36	6.29	
SA (%)	20.00	1.90	19.66	0.43	16.46	
CY (%)	25.54	2.65	24.28	1.67	24.45	

	7		8	
	Mean	Std Dev	Mean	Std Dev
EL (m)	0.70	0.02	0.49	0.13
C (%)	8.67	0.88	7.67	1.26
pH	5.65	0.08	5.34	0.37
EC (mmhos/cm)	3.83	0.54	4.18	0.73
SA (%)	14.11	1.48	13.15	1.84
CY (%)	30.70	1.90	32.46	2.50

Agg9 Scale

	1		2	
	Mean	Std Dev	Mean	Std Dev
EL (m)	0.75	0.15	0.57	0.13
C (%)	10.89	1.80	8.21	1.27
pH	5.29	0.86	5.43	0.36
EC (mmhos/cm)	4.93	0.99	4.15	0.78
SA (%)	22.17	4.10	14.13	2.24
CY (%)	22.55	3.03	31.11	2.84

Figure 8: Two-dimensional isopleths displaying EL and soil variable zonation patterns at the aggl scale in the marsh study site: CY, clay content (a); SA, sand content (b); C, carbon content (c), EL, relative ground level elevation (d); EC, electrical conductivity (e); and pH, soil acidity (f).

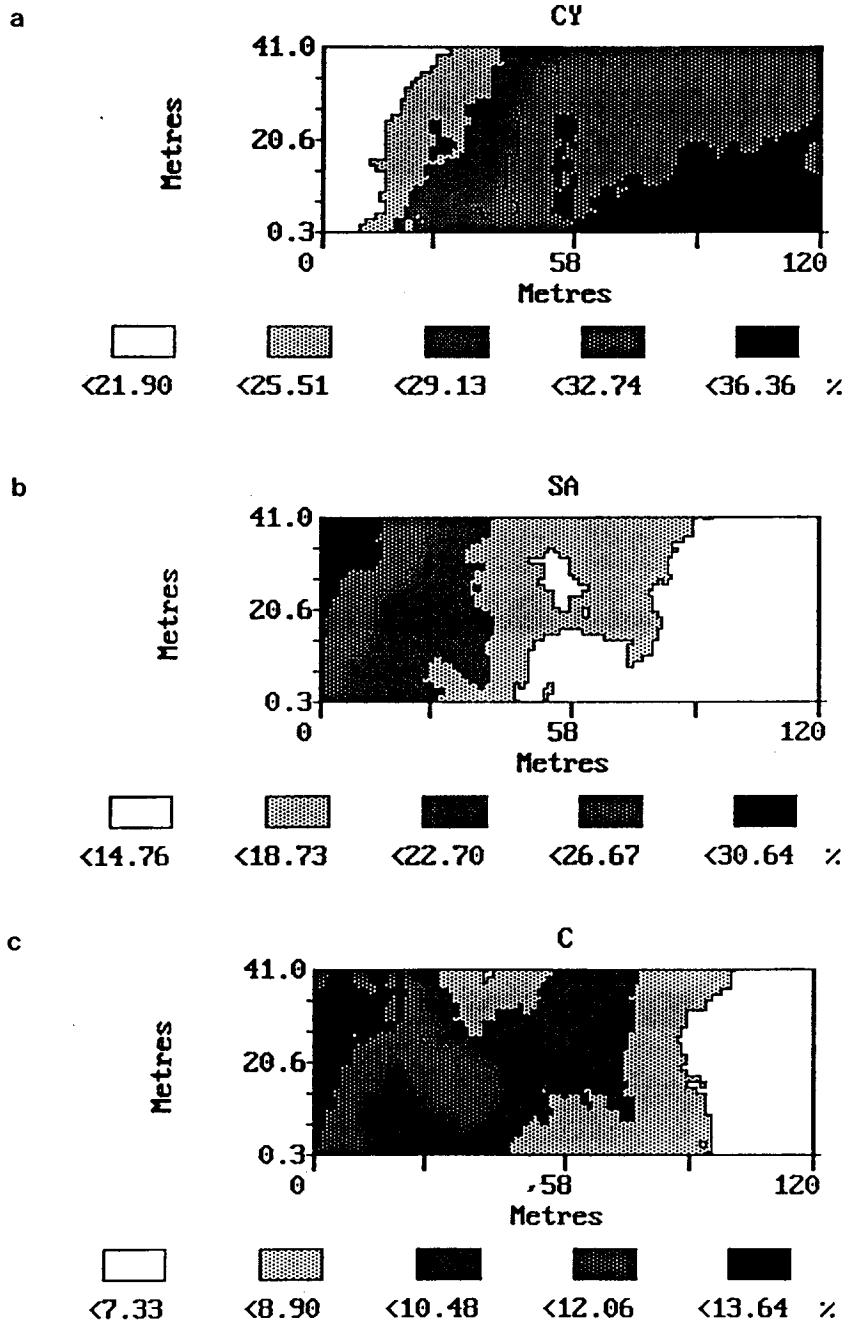
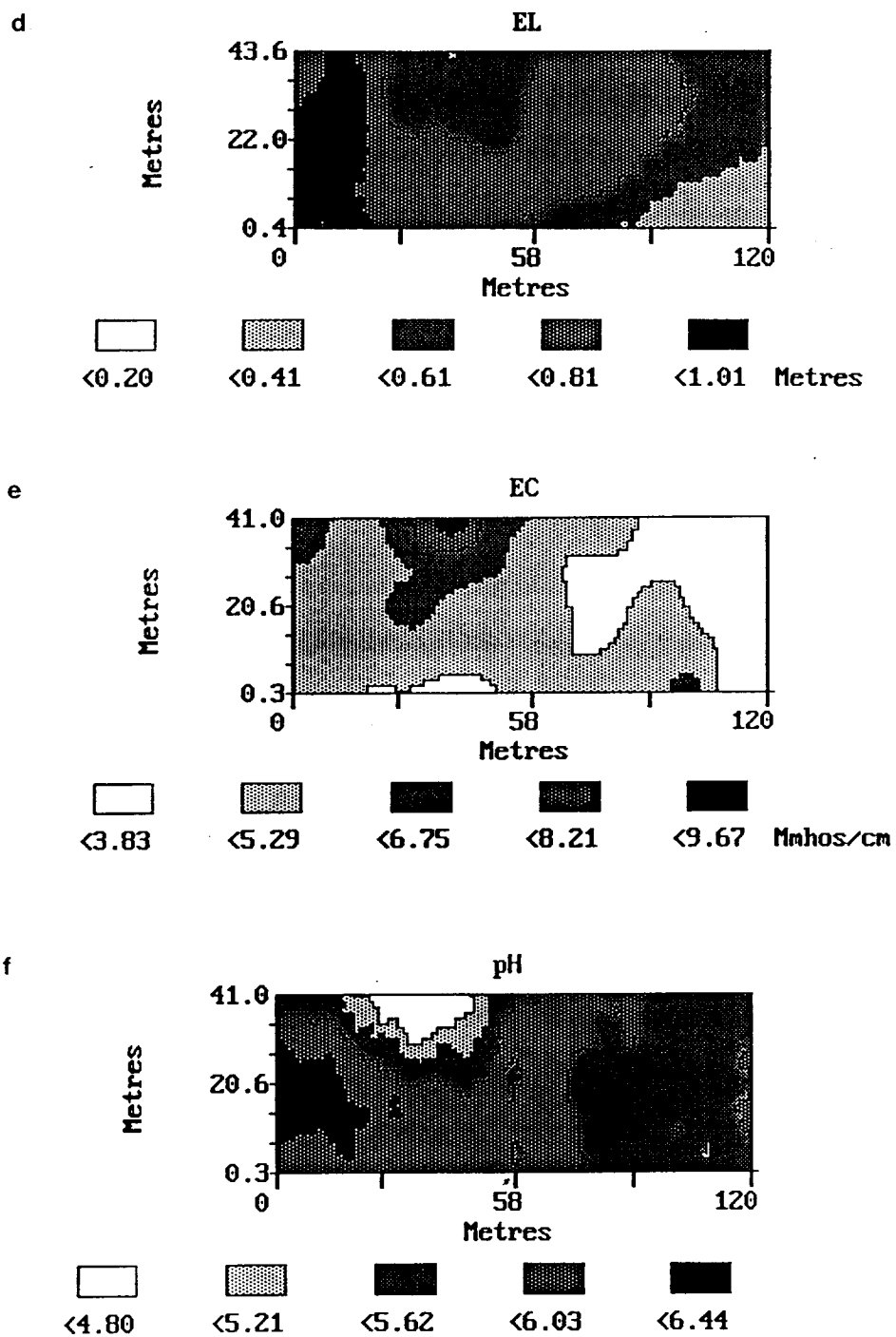


Figure 8: (Continued)



3.2.2 Agg4 Scale (5 X 5 Metre Observation Unit)

3.2.2.1 Community Structure

At agg4, level C2 in the dendrogram yields the highest redundancy (29.21%) and R_c (0.9943) values (Table II). Again, two subcommunities are recognized in the marsh (Figure 6b). While Carex lyngbyei and Potentilla pacifica continue to be representative species of subcommunity 1 (lower marsh), the same species mentioned at agg1 as well as Juncus balticus characterize the upper marsh (Table III).

3.2.2.2 Environmental Variable Relationships

In reference to Table IV, EL shares stronger correlative relationships with C, SA, and CY (0.65, 0.65, and -0.68 respectively) compared to agg1. At this scale, EL clearly shares a positive correlative relationship with pH (0.41) as well. While SA and CY maintain stronger relationships with C (0.91 and -0.82 respectively), EC is well correlated not only with C (0.40) but with pH (-0.35) as well. In addition, EC as well as SA share negative correlative relationships with CY (-0.41 and -0.89 respectively).

An EL gradient is also recognized at agg4 where greater SA, C and less acidic soils are found in the upper marsh. Conversely, the lower end of the gradient contains relatively more CY.

3.2.2.3 Community-Environment Relationships

The first and second ordination axes of the CCA have eigenvalues of 0.45 and 0.08 respectively. The first canonical ordination axis eigenvalue and trace statistic are significant ($p < 0.05$).

Figure 7b tells an almost identical story to that previously described at agg1. Stronger correlations between CY, SA, EL, C, and the first species axis are apparent at this scale (-0.88, 0.87, 0.75, and 0.80 respectively) (Table V). All three environmental vectors representing SA, EL, and C pass through subcommunity 2 (Figure 7b). Moreover, subcommunity 2 contains more C and SA and less CY than subcommunity 1 (Table VI).

A positive correlative relationship between pH and species axis 1 is stronger at this scale (0.44) (Table V). Figure 7b suggests that the relative importance of pH is better observed at agg4. The length of the pH vector is not as short in relation to SA, C, and EL vectors as opposed to Figure 7a. Differences in pH between subcommunities are not as clear at a finer scale (agg1) (Table VI) mostly because pH measurements within each subcommunity are quite variable (high standard deviation estimates). At agg4 a more noticeable difference between subcommunities is evident (relatively lower standard deviation estimates). While subcommunity 2 is located in relatively less acidic soils (6.1),

lower marsh soils are slightly lower (5.4) (Table VI).

Though EC is a weak correlate of species axis 1 (0.24) (Table V), a slight salinity difference between subcommunity 1 and 2 is apparent (4.3 mmhos/cm and 4.7 mmhos/cm respectively) (Table VI). As in agg1, EC shares a stronger correlative relationship, however, with species axis 2 (0.41) (Table V), emphasizing the effect of the low area near the upper marsh on EC. At agg4, pH is also clearly recognized as a correlate of species axis 2 (-0.58) (Table V). Though Figure 8f displays how pH is clearly affected by the low area near the upper marsh at agg1, pH and the second species axis shared a rather weak correlative relationship (0.15) (Table V). Changing observation graininess from agg1 to agg4 has brought out an important feature whose view may have been obstructed among much noise and clutter at agg1. CY is not well correlated with the second species axis (-0.20) perhaps suggesting that its distribution remains for the most part unaffected by a lack of consistency in EL change (Figure 8a). Nevertheless, the unique low area near the upper marsh possesses soils of relatively less CY possibly suggesting the absence of a flushing mechanism.

At agg4 ellipses 1 (lower marsh) and 2 (upper marsh) (Figure 7b) are respectively smaller and larger than the corresponding ellipses at agg1 (Figure 7a). More variability is included in the lower marsh at agg1 whereas within-assemblage variability for ellipse 2 appears to be less. Because of simulation sampling at a

coarser scale (agg4), some of the variability has been transferred from the low marsh at agg1, to what is now defined as the upper marsh at agg4 possibly better defining a gradual transition between upper and lower subcommunities (Figure 7b). In reference to Figure 9, standardized estimates of (overall) between and within-cluster variability suggest that agg4 defines community structure marginally better than agg1. Between-assemblage variability is slightly greater (57.9%) and within-assemblage variability is less (42.1%) at agg4 as opposed to agg1 (54.4% and 45.6% respectively).

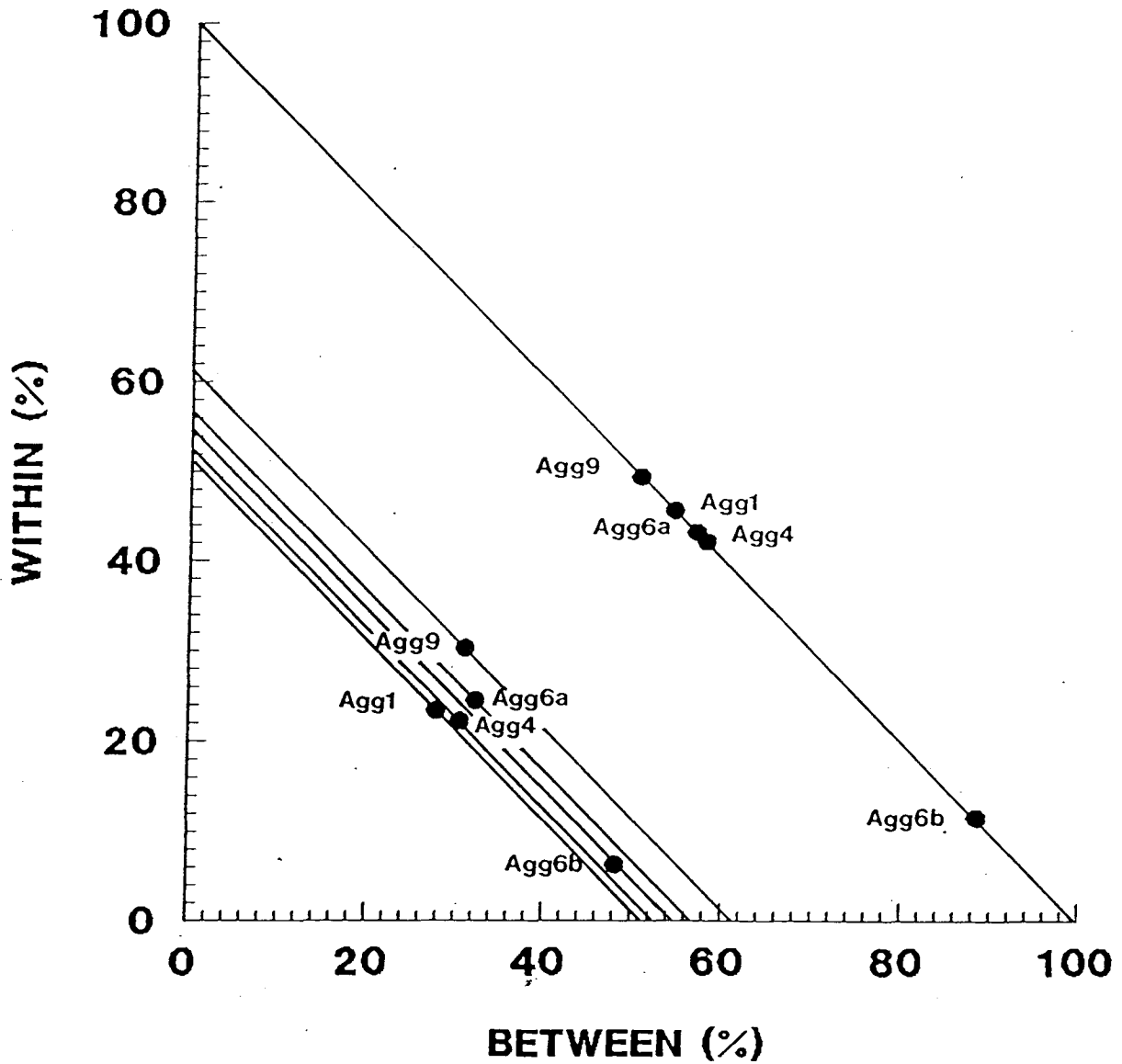
Noteworthy is a close association between C and SA vectors in Figure 7b and a close association between EL and C vectors in Figure 7a. To suggest that C and SA variables have a close relationship at agg4 but less so at agg1 should be supported by Pearson correlations showing the same trend. Such evidence is lacking. At both scales, SA always has a stronger correlative relationship with C than C and EL (Table IV).

3.2.3 Agg9 Scale (10 X 10 Metre Observation Unit)

3.2.3.1 Community Structure

At agg9, C2 (39.55%) and C7 (0.9692) provide the highest redundancy and R_c estimates respectively (Table II). Similar to agg1 and agg4, the marsh study site is divided into two subcommunities (Figure 6c). Both Carex lynqbyei and Potentilla pacifica characterize the lower marsh (subcommunity 2) and the same

Figure 9: Overall between and within-cluster variability estimates for all scales in the marsh study site. Unstandardized estimates shown along inner isoclines; standardized estimates shown along outer isocline.



species excluding Juncus balticus described at agg1 and agg4 characterize the upper (subcommunity 1) (Table III).

3.2.3.2 Environmental Variable Relationships

Environmental interactions at this scale reinforce what has been revealed at agg4. Generally, correlations are stronger to the extent of emphasizing an additional interaction. SA and EC share a positive correlative relationship (0.45) perhaps due to the low elevated area located close to the upper marsh where there is relatively greater SA, EC, and less CY (Table IV).

3.2.3.3 Community-Environment Relationships

CCA reported eigenvalues of 0.45 and 0.08 for the first and second ordination axes. The first canonical ordination and trace statistic are significant ($p < 0.05$) as well.

Figure 7c reveals an almost identical story to that described in agg1 and agg4. Supported by stronger correlations with species axis 1 (Table V), SA, EL, and C vectors are associated with subcommunity 1, and subcommunity 2 (lower) is associated with vector CY. Relatively more SA and C are found in the upper marsh and more CY is characteristic of the lower (Table VI).

At agg4 pH was noticeably well correlated with species axis 1

(0.44). At agg9, however, the correlative relationship has weakened (0.26) (Table V). The upper marsh possessed slightly less acidic soils at agg4 compared to the lower (6.1 and 5.4 respectively). At agg9, however, the difference between upper and lower subcommunities is more subtle (5.3 and 5.4 respectively) (Table VI). Ellipses representing the upper marsh have consistently increased, and ellipses representing the lower marsh have consistently decreased at progressively coarser scales (agg1, 4, to agg9) (compare a, b, and c of Figure 7). At agg9 (Figure 7c), ellipse 1 (upper marsh) has ballooned in size compared to ellipse 2 (upper marsh) (Figure 7b). In contrast is ellipse 2 at agg9 (lower marsh) (Figure 7c) which is better defined as a monospecific stand of Carex lyngbyei. Its within-assemblage variability is considerably less compared to ellipse 1, representative of the lower marsh at agg4 (Figure 7b). Because variability is disproportionately distributed to a greater degree at agg9 as opposed to agg1 and agg4, overall, standardized within-assemblage variability is greater (49.40%) than agg1 and agg4 estimates, which in turn has decreased variability between groups (50.60%) (Figure 9). Sampling with a larger quadrat (agg9) has incorporated more variability into the upper zone. Variability may be attributed mostly to vegetation structure affected by the low elevated area described at finer scales as being located near the upper marsh. This may also disrupt the correlative relationship between pH and species axis 1 (Table V) and explain a subtle pH difference between upper and lower zone soils (Table VI).

3.2.4 Agg6a and Agg6b Scales (5 X 10 Metre and 10 X 5 Metre)

Observation Units

3.2.4.1 Community Structure and Environmental Variable Relationships

When a 5 X 10 meter quadrat (agg6a) is imposed on the study site, dendrogram level C2 provides the highest redundancy (44.38%) and R_c (0.9797) values (Table II). Thus, the marsh is partitioned in two subcommunities (Figure 6d). Similar to agg1, agg4, and agg9 scales, the two subcommunities represent upper and lower marsh zones, and are well represented by the same species at agg9 (Table III).

Simulation sampling with a quadrat of same dimensions but positioned length-wise (agg6b) provides the highest redundancy and R_c values at C8 (47.22%) and C9 (0.9932) respectively (Table II). At this scale, the marsh is composed of eight distinctive groups (Figure 6e). In reference to Table III, subcommunities 1 to 3 are characterized by Potentilla pacifica, Triglochin maritimum, and Agrostis alba. While Carex lyngbyei and Stellaria humifusa are found in 1, C. lyngbyei is also found in 2 along with Deschampsia cespitosa, Juncus balticus, and Hordeum brachyantherum. Subcommunity 3 is also well represented by J. balticus, H. brachyantherum, D. cespitosa, Elymus sp., and Aster eatonii. Subcommunities 4, 5, and 6 are characterized by C. lyngbyei. In addition, subcommunity 4 is also represented by Potentilla

pacifica, Triglochin maritimum, and Agrostis alba. P. pacifica is also found in subcommunity 5 and T. maritimum, and Ranunculus cymbalaria are found in subcommunity 6 as well. Subcommunities 7 and 8 represent the lower marsh: 7 characterized almost exclusively by C. lyngbyei and P. pacifica, and 8 characterized by C. lyngbyei.

Simulation sampling with both a 5 X 10 meter quadrat and a 10 X 5 meter quadrat reveal very similar environmental variable relationships to agg1, agg4, and agg9 scales (Table IV).

3.2.4.2 Community-Environment Relationships

First and second axes eigenvalues of 0.44, 0.13 for agg6a and 0.46, 0.08 for agg6b as well as a significant ($p < 0.05$) first canonical axis eigenvalue and trace statistic were reported from CCA. Environmental variable first and second species axes relationships are the same not only between agg6a and agg6b but also the same as that previously described for agg4 (Table V) (Figures 7d and e).

Simulation sampling at agg6a recognized the same subcommunity number as agg1, agg4, and agg9. However, at agg6b perception of only two subcommunities appears to be lost. Interestingly, agg6b provides the clearest overall perception of community structure. In reference to Figure 9 between-assemblage variability is much

greater (88.5%) and overall within-assemblage variability is much less (11.5%) than other scales.

3.2.5 EL Influence Verification

3.2.5.1 Agg1, 4, 6a, 6b, 9 Scales

Correlations between environmental variables and a canonical correlation axis representing species variables (summarized by three PCA axes) as well as residuals, confirm EL influence on soil characteristics (Table VII). Environmental variable-canonical axis correlations reveal very similar trends previously discussed at all scales. Environmental variable-residual correlations are not as strong as environmental variable-canonical axis correlations. However, several environmental variable-residual correlations are quite respectable perhaps suggesting the existence of an EL gradient with less influence on edaphic factors. Independent of EL, SA, CY (soil texture) and C (organic content) share noticeable correlative relationships with residuals for all scales (Table VII).

3.2.6 Tidal Marsh Discussion

The Squamish marsh study site is generally composed of two subcommunities: upper and lower. Generally, this corresponds with Hutchinson et al.'s (1989) general description of the Squamish estuary where the lower zone is virtually a monospecific stand of

Table VII: Pearson correlations at different scales between environmental variables, residuals, and a canonical axis representing species variables in the Squamish Marsh. AXIS, canonical correlation axis; RESD, residuals; EL, relative ground level elevation; C, carbon content; EC, electrical conductivity; SA, sand content; CY, clay content; pH, soil acidity.

Agg1 Scale

	EL	C	pH	EC	SA	CY
AXIS	0.7211	0.6363	0.1349	0.0377	0.5599	-0.4444
RESID	0	0.2879	0.0583	0.1667	0.3454	-0.2126

Agg4 Scale

	EL	C	pH	EC	SA	CY
AXIS	0.8466	0.7516	0.3923	0.0917	0.7340	-0.7275
RESID	0	0.3278	0.1580	0.1400	0.3210	-0.2928

Agg6a Scale

	EL	C	pH	EC	SA	CY
AXIS	0.8586	0.7561	0.3850	0.0161	0.6824	-0.6830
RESID	0	0.3051	0.2316	0.1387	0.3041	-0.2531

Agg6b Scale

	EL	C	pH	EC	SA	CY
AXIS	0.9103	0.7810	0.4536	0.0897	0.7791	-0.7332
RESID	0	0.2711	0.1914	0.0610	0.3448	-0.2178

Agg9 Scale

	EL	C	pH	EC	SA	CY
AXIS	0.9075	0.7844	0.4080	0.0295	0.7250	-0.7063
RESID	0	0.2542	0.1228	0.0640	0.3323	-0.2513

Carex lyngbyei and the upper zone is a mixture of wetland species such as Potentilla pacifica, C. lyngbyei, Triglochin maritimum, Juncus balticus, and Deschampsia cespitosa. Communities of similar species composition have been documented also in a brackish marsh on Lulu Island in Richmond, British Columbia (Hutchinson 1982) and in a fjord head marsh in northern coastal British Columbia (Campbell and Bradfield 1989). Furthermore, virtually monospecific stands of Carex lyngbyei have been extensively described along tidal marshes in the Pacific Northwest (Disraeli and Fonda 1979; Dawe and White 1982; Ewing 1983; Vince and Snow 1984). At all scales, upper marsh soils are associated with greater SA and C while lower marsh soils possess more CY. The predominance of C. lyngbyei on clayey soils has also been documented for a brackish intertidal marsh in the Puget Sound area of Washington (Ewing 1983). Because the lower zone is closest to a water channel, high-low tide alternation may be responsible for CY accumulation and C removal. In general, the vertical distribution of vegetation did not share strong correlative relationships with EC. This may be in disagreement with Hutchinson et al. (1989) since they found Deschampsia in more saline locations. However, this result is in agreement with similar marsh research done in a brackish marsh in Bellingham Bay, Washington (Disraeli and Fonda 1979) and the Little Qualicum River estuary, Vancouver Island, British Columbia (Dawe and White 1982) where salinity was found to play a very minor role in the vertical distribution of communities. Though community structure for the most part corresponds well with EL, a presumed EL

gradient lacked consistent step-wise elevation change. One such area was located near the upper marsh that shared approximately the same EL as the lower zone, yet lacked a tidal flushing mechanism. As a result, salt deposition and lower pH characterized this area. Generally, upper marsh soils had slightly greater pH than lower at most scales but can only be perceived as having a minor role in determining species composition. A somewhat "flawed" EL gradient may explain strong correlations between residuals data and edaphic factors. Specifically, tides and the decomposition of the organic material provided by the species themselves may contribute to differences in soil texture (SA and CY) and organic content (C) between upper and lower subcommunities which in turn share relationships with plant distribution patterns.

Employment of different sampling units as well as CCorA to select among nine possible subcommunity schemes per MVCA reveal different aspects of community structure. At agg1 the upper marsh is represented by ellipse 2 in Figure 7a which is smaller than ellipse 1. That is, within-assemblage variability is greater in the lower as opposed to the upper marsh. At agg4, (Figure 7b) ellipse 2, representing the upper, and ellipse 1, representing the lower, have increased and decreased in size respectively. Employing a square quadrat of larger area to sample the marsh site has included some of the variability inherent in the lower at agg1 into the upper at agg4. Perhaps at this scale, a smooth transition between upper and lower is best observed. Overall within-

assemblage variability is shown to be less and between-assemblage variability is greater at agg4 than agg1 (Figure 9), emphasizing the redistribution of variation from the lower to the upper ellipse between agg1 and agg4 scales. A monospecific stand of Carex lyngbyei is best represented at agg9 (Figure 7c). Here, within-assemblage variability is considerably less for the lower subcommunity (ellipse 2) as opposed to ellipse 1 where upper marsh boundaries have shifted seaward incorporating the aforementioned area of EL gradient inconsistency.

3.3 Subalpine Wet Meadow

3.3.1 Agg1 Scale (0.5 X 0.5 Metre Observation Unit)

3.3.1.1 Community Structure

At the agg1 observation scale, the two group level yields the highest R_c value(0.9426) and the five group level yields the highest redundancy value (8.86%) (Table VIII). Five reasonably distinct subcommunities may be recognized (Figure 10a). Subcommunities 1 and 2 are located in the lower meadow area beside Mimulus Lake. Whereas subcommunity 2 is predominately a monospecific stand of Carex nigricans, subcommunity 1 contains this species in mixture with Leptafrhena pyrolifolia, Caltha biflora, Epilobium anagallidifolium, and Agrostis thurbergiana (Table IX). Between high and low meadow areas is subcommunity 3 (Figure 10a) characterized by Carex nigricans, Caltha biflora, Luetkea pectinata, Erigeron peregrinus, Cassiope mertensiana, and

Table VIII: Redundancy and R_c estimates for dendrogram levels C2-C10 at different scales in the subalpine wet meadow. Highest redundancy and R_c estimates at each scale are marked with an '*'.

Agg1 Scale

	<u>Redundancy (%)</u>	<u>R_c</u>
C 2	8.34	*0.9426
C 3	8.82	0.9317
C 4	8.53	0.9407
C 5	*8.86	0.9404
C 6	7.89	0.9264
C 7	8.03	0.9247
C 8	8.43	0.9297
C 9	8.76	0.9329
C10	8.42	0.9265

Agg4 Scale

	<u>Redundancy (%)</u>	<u>R_c</u>
C 2	20.39	0.9723
C 3	*22.06	0.9725
C 4	20.40	0.9762
C 5	21.72	0.9745
C 6	21.28	0.9730
C 7	20.48	0.9685
C 8	21.34	0.9724
C 9	21.38	*0.9789
C10	21.04	0.9752

Agg6a Scale

	<u>Redundancy (%)</u>	<u>R_c</u>
C 2	23.14	0.9826
C 3	*26.08	0.9889
C 4	23.37	0.9899
C 5	25.40	0.9896
C 6	24.68	0.9896
C 7	25.26	0.9916
C 8	25.22	0.9924
C 9	24.79	0.9936
C10	25.47	*0.9948

Agg6b Scale

	<u>Redundancy (%)</u>	<u>R_c</u>
C 2	21.40	0.9907
C 3	24.10	0.9893
C 4	23.88	0.9853
C 5	22.10	0.9908
C 6	23.36	0.9929
C 7	24.38	0.9937
C 8	*24.69	0.9934
C 9	24.29	0.9937
C10	24.41	*0.9941

Agg9 Scale

	<u>Redundancy (%)</u>	<u>R_c</u>
C 2	26.06	0.9883
C 3	*28.71	0.9963
C 4	25.81	0.9987
C 5	26.87	*0.9994
C 6	28.36	0.9989
C 7	28.22	0.9989
C 8	28.14	0.9988
C 9	27.94	0.9984
C10	27.22	0.9978

Figure 10: Grid maps showing subcommunity layout at different scales in the subalpine wet meadow study site: agg1 (a), agg4 (b), agg9 (c), agg6a (d), agg6b (e).

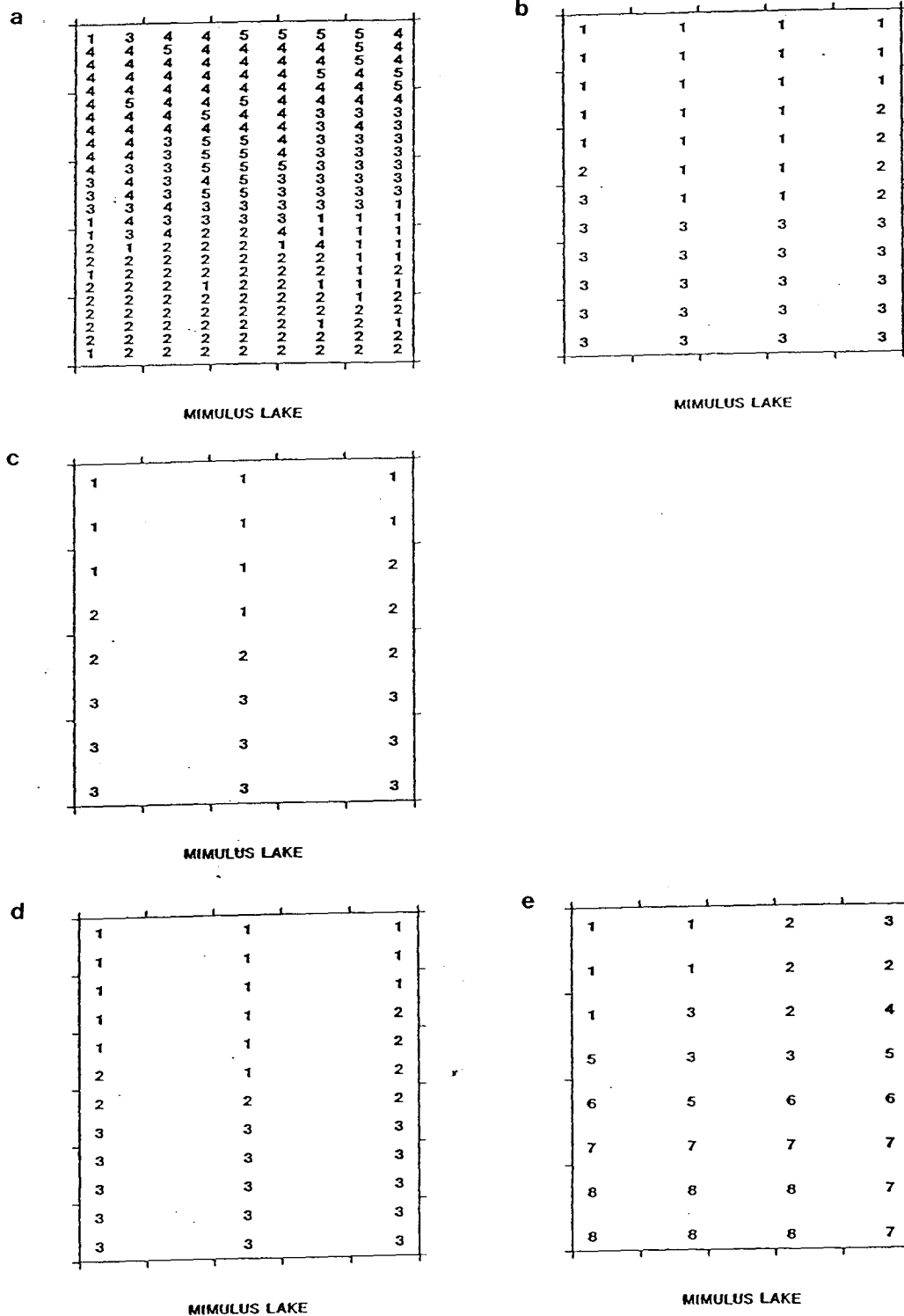


Table IX: Species mean aerial coverage class data for subcommunities at different scales in the subalpine wet meadow. Those species with a mean aerial coverage class estimate ≥ 1 were deemed to be representative of a particular subcommunity. Species names corresponding to the codes used below may be found in Appendix A. Integers directly above mean and standard deviation estimates represent subcommunities at each scale.

Aggl Scale

	1		2		3	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
SENTRI	0.04	0.20	0.02	0.12	0.09	0.29
CARNIG	3.08	0.56	4.12	1.07	1.21	1.03
LEPPYR	2.62	0.85	0.26	0.64	0.67	0.97
LUEPEC	0.54	0.81	0.14	0.46	1.98	1.10
ERIPER	0.69	0.79	0.10	0.29	1.21	0.97
HIEGRA	0		0		0.28	0.63
EPIANA	0.96	0.72	0.58	0.79	0.49	0.67
CALBIF	2.19	1.10	0.67	0.90	1.72	1.14
CASMER	0.27	0.53	0.02	0.12	2.37	1.09
POACUS	0.38	0.57	0.17	0.41	0.19	0.39
JUNCSP	0.31	0.47	0.10	0.34	0.79	0.86
PHYEMP	0.35	0.75	0.02	0.12	1.74	1.36
VERWOR	0.04	0.20	0.03	0.17	0.26	0.49
POTFLA	0.04	0.20	0.02	0.12	0	
CARSPE	0.04	0.20	0.26	0.59	0.53	0.70
PETFRI	0		0		0.02	0.15
LUPLAT	0		0		0.74	1.18
VALSIT	0		0.02	0.12	0.14	0.47
LUZPAR	0		0		0.07	0.34
PHLALP	0.04	0.20	0		0.02	0.15
ANEOCC	0		0		0.07	0.26
ABILAS	0		0		0	
ERYGRA	0		0		0	
CASPAR	0		0		0.09	0.29
POALEP	0		0		0	
RANESC	0		0		0.02	0.15
ANTALP	0.27	0.60	0.08	0.36	0.14	0.41
TRISPI	0		0		0.02	0.15
VACDEL	0		0		0.07	0.34
LYCSEL	0.04	0.20	0		0.12	0.32
KATMIC	0		0.03	0.17	0.19	0.45
AGRTHU	0.96	0.66	0.21	0.51	0.23	0.48
EQUARV	0.23	0.43	0.02	0.12	0	
CETSUB	0		0		0.37	0.79
SPHWAR	0.12	0.59	0.02	0.12	0	
PEDBRA	0		0		0	

Table IX: (Continued)

Aggl Scale (Continued)

	4		5	
	Mean	Std Dev	Mean	Std Dev
SENTRI	0.49	0.96	0.30	0.56
CARNIG	2.21	1.05	1.30	0.97
LEPPYR	0.04	0.27	0	
LUEPEC	0.66	1.23	1.22	1.13
ERIPER	1.22	1.04	0.70	0.82
HIEGRA	0.70	0.87	0.65	0.71
EPIANA	0.48	0.61	0.26	0.54
CALBIF	0.33	0.77	0.35	0.78
CASMER	0.15	0.47	0.13	0.46
POACUS	0.34	0.54	0.17	0.39
JUNCSP	0.93	0.88	0.91	0.90
PHYEMP	0.01	0.12	0.09	0.29
VERWOR	0.31	0.50	0.35	0.57
POTFLA	0.49	0.96	0.09	0.42
CARSPE	1.72	0.88	1.87	1.01
PETFRI	0.01	0.12	0	
LUPLAT	0.36	0.79	3.48	0.90
VALSIT	1.30	1.27	1.04	1.11
LUZPAR	0.19	0.47	0.13	0.34
PHLALP	0.01	0.12	0.04	0.21
ANEOCC	0.43	0.87	0.13	0.46
ABILAS	0.03	0.17	0	
ERYGRA	0.01	0.12	0	
CASPAR	0.33	0.64	0.17	0.49
POALEP	0.37	0.60	0.17	0.58
RANESC	0.28	0.49	0.26	0.54
ANTALP	0.06	0.24	0	
TRISPI	0.06	0.30	0.13	0.34
VACDEL	0		0.13	0.63
LYCSEL	0		0	
KATMIC	0		0	
AGRTHU	0.01	0.12	0.04	0.21
EQUARV	0		0	
CETSUB	0.12	0.41	0	
SPHWAR	0		0	
PEDBRA	0		0.04	0.21

Table IX: (Continued)

Agg4 Scale

	1		2		3	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
SENTRI	0.48	0.59	0		0.04	0.12
CARNIG	1.90	0.85	0.85	0.42	3.63	0.78
LEPPYR	0.11	0.30	0.60	0.84	0.76	0.74
LUEPEC	0.70	0.78	2.45	0.84	0.44	0.51
ERIPER	1.07	0.66	1.70	0.62	0.43	0.59
HIEGRA	0.64	0.48	0.20	0.33	0.01	0.05
EPIANA	0.42	0.38	0.30	0.21	0.65	0.55
CALBIF	0.51	0.70	1.25	0.64	1.17	0.99
CASMER	0.40	0.58	2.25	0.94	0.27	0.51
POACUS	0.28	0.32	0.30	0.21	0.13	0.15
JUNCSP	0.82	0.51	0.90	0.76	0.33	0.53
PHYEMP	0.22	0.48	1.40	0.58	0.29	0.48
VERWOR	0.38	0.30	0.15	0.14	0.08	0.14
POTFLA	0.40	0.55	0		0	
CARSPE	1.65	0.58	0.60	0.38	0.30	0.39
PETFRI	0.01	0.05	0		0.01	0.05
LUPLAT	1.33	1.18	0.20	0.27	0.04	0.16
VALSIT	1.25	0.66	0.20	0.21	0.01	0.05
LUZPAR	0.16	0.36	0.05	0.11	0	
PHLALP	0.02	0.07	0.05	0.11	0	
ANEOCC	0.40	0.54	0		0	
ABILAS	0.02	0.07	0		0	
ERYGRA	0.01	0.05	0		0	
CASPAR	0.26	0.36	0.25	0.31	0.02	0.08
POALEP	0.32	0.39	0		0	
RANESC	0.30	0.38	0		0	
ANTALP	0.02	0.07	0.20	0.21	0.18	0.30
TRISPI	0.08	0.18	0.05	0.11	0	
VACDEL	0.03	0.16	0		0	
LYCSEL	0		0.10	0.14	0.05	0.13
KATMIC	0.01	0.05	0.15	0.22	0.06	0.13
AGRTHU	0.03	0.16	0.20	0.45	0.39	0.41
EQUARV	0		0		0.05	0.10
CETSUB	0.17	0.33	0.20	0.21	0.01	0.05
SPHWAR	0		0		0	
PEDBRA	0.01	0.05	0		0	

Table IX: (Continued)

Agg6a Scale

	1		2		3	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
SENTRI	0.49	0.53	0.05	0.08	0.02	0.09
CARNIG	2.01	0.67	1.10	0.59	3.68	0.69
LEPPYR	0.06	0.22	0.57	0.57	0.94	0.86
LUEPEC	0.64	0.64	2.14	0.49	0.40	0.48
ERIPER	0.99	0.61	1.36	0.42	0.38	0.50
HIEGRA	0.70	0.44	0.33	0.32	0.01	0.04
EPIANA	0.37	0.28	0.48	0.40	0.70	0.51
CALBIF	0.32	0.54	1.43	0.71	1.23	1.00
CASMER	0.24	0.33	2.00	0.63	0.21	0.44
POACUS	0.32	0.32	0.17	0.17	0.19	0.18
JUNCSP	0.89	0.36	0.74	0.49	0.28	0.42
PHYEMP	0.04	0.10	1.60	0.53	0.20	0.28
VERWOR	0.33	0.32	0.21	0.21	0.07	0.11
POTFLA	0.42	0.51	0		0.02	0.09
CARSPE	1.76	0.28	0.64	0.35	0.26	0.36
PETFRI	0.01	0.04	0.02	0.06	0	
LUPLAT	1.19	0.88	0.86	0.82	0	
VALSIT	1.32	0.56	0.14	0.15	0	
LUZPAR	0.19	0.28	0.07	0.19	0	
PHLALP	0.02	0.09	0.02	0.06	0	
ANEOCC	0.39	0.48	0.05	0.08	0	
ABILAS	0.02	0.06	0		0	
ERYGRA	0.01	0.04	0		0	
CASPAR	0.24	0.36	0.21	0.19	0.01	0.04
POALEP	0.35	0.39	0		0	
RANESC	0.31	0.35	0		0	
ANTALP	0.01	0.04	0.14	0.18	0.17	0.21
TRISPI	0.07	0.14	0.05	0.08	0	
VACDEL	0.04	0.13	0.07	0.13	0	
LYCSEL	0		0.05	0.08	0.04	0.13
KATMIC	0		0.12	0.19	0.06	0.14
AGRTHU	0		0.24	0.38	0.41	0.40
EQUARV	0		0.02	0.06	0.07	0.11
CETSUB	0.11	0.17	0.33	0.40	0.01	0.04
SPHWAR	0		0		0.01	0.04
PEDBRA	0.01	0.04	0		0	

Table IX: (Continued)

Agg6b Scale

	1		2		3	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
SENTRI	1.13	0.38	0.04	0.08	0.25	0.22
CARNIG	1.97	0.62	2.58	0.55	1.42	0.78
LEPPYR	0.17	0.37	0		0.08	0.17
LUEPEC	0.17	0.24	0.71	0.72	0.75	0.59
ERIPER	1.40	0.55	0.46	0.53	1.08	0.63
HIEGRA	0.33	0.42	1.00		0.54	0.08
EPIANA	0.43	0.30	0.38	0.42	0.17	0.14
CALBIF	0.27	0.28	0.17	0.33	0.67	0.56
CASMER	0.17	0.37	0.17	0.19	0.54	0.42
POACUS	0.40	0.35	0.29	0.16	0.21	0.32
JUNCSP	0.53	0.25	1.38	0.39	0.58	0.29
PHYEMP	0.07	0.15	0		0.29	0.48
VERWOR	0.50	0.24	0.17	0.24	0.38	0.28
POTFLA	1.03	0.27	0.08	0.17	0.08	0.17
CARSPE	1.93	0.63	1.42	0.40	1.71	0.16
PETFRI	0.03	0.07	0		0	
LUPLAT	0.47	0.45	0.71	0.25	2.83	0.30
VALSIT	1.47	0.43	1.58	0.52	1.04	0.67
LUZPAR	0.03	0.07	0.50	0.43	0.04	0.08
PHLALP	0.07	0.09	0		0	
ANEOCC	0.57	0.58	0.21	0.25	0.50	0.64
ABILAS	0.03	0.07	0		0	
ERYGRA	0		0.04	0.08	0	
CASPAR	0.23	0.25	0.17	0.33	0.21	0.32
POALEP	0.60	0.42	0.29	0.34	0.13	0.25
RANESC	0.53	0.46	0.08	0.10	0.29	0.25
ANTALP	0		0.04	0.08	0.04	0.08
TRISPI	0.03	0.07	0		0.17	0.24
VACDEL	0		0.13	0.25	0	
LYCSEL	0		0		0	
KATMIC	0		0		0	
AGRTHU	0		0		0	
EQUARV	0		0		0	
CETSUB	0		0.17	0.33	0.25	0.50
SPHWAR	0		0		0	
PEDBRA	0		0		0.04	0.08

Table IX: (Continued)

Agg6b Scale (Continued)

	4		5		6	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
SENTRI	0		0.06	0.10	0.11	0.19
CARNIG	0.50		1.11	0.51	2.06	0.38
LEPPYR	0		0.56	0.59	1.28	0.51
LUEPEC	2.50		2.39	0.35	1.50	0.44
ERIPER	1.17		1.83	0.50	1.39	0.25
HIEGRA	0.17		0.56	0.69	0.11	0.19
EPIANA	0.33		0.56	0.35	0.94	0.42
CALBIF	0.83		1.28	0.35	2.50	0.17
CASMER	3.33		1.22	0.63	1.67	0.44
POACUS	0.50		0.22	0.10	0.22	0.10
JUNCSP	0.17		0.89	0.54	1.28	0.10
PHYEMP	0.33		1.67	0.76	1.17	0.33
VERWOR	0.17		0.22	0.10	0.39	0.25
POTFLA	0		0		0	
CARSPE	1.00		0.83	0.33	0.50	0.44
PETFRI	0		0		0.06	0.10
LUPLAT	0.33		0.67	0.88	0.61	0.67
VALSIT	0.33		0.28	0.19	0.06	0.10
LUZPAR	0.17		0		0	
PHLALP	0		0		0.06	0.10
ANEOCC	0		0.06	0.10	0	
ABILAS	0		0.06	0.10	0	
ERYGRA	0		0		0	
CASPAR	0.17		0.56	0.59	0.11	0.10
POALEP	0		0		0	
RANESC	0		0.06	0.10	0	
ANTALP	0		0.28	0.10	0.17	0.29
TRISPI	0		0.17		0	
VACDEL	0		0		0	
LYCSEL	0		0.11	0.10	0.22	0.19
KATMIC	0		0.17	0.17	0.17	0.17
AGRTHU	0		0.06	0.10	0.83	0.33
EQUARV	0		0		0	
CETSUB	0.17		0.44	0.25	0.06	0.10
SPHWAR	0		0		0	
PEDBRA	0		0		0	

Table IX: (Continued)

Agg6b Scale (Continued)

	7		8	
	Mean	Std Dev	Mean	Std Dev
SENTRI	0.03	0.07	0	
CARNIG	3.44	0.66	4.17	0.48
LEPPYR	1.08	0.58	0.19	0.27
LUEPEC	0.50	0.21	0.14	0.22
ERIPER	0.56	0.46	0	
HIEGRA	0.03	0.07	0	
EPIANA	0.92	0.53	0.28	0.20
CALBIF	1.64	0.39	0.22	0.17
CASMER	0.25	0.31	0	
POACUS	0.06	0.09	0.14	0.16
JUNCSP	0.39	0.39	0.03	0.07
PHYEMP	0.17	0.15	0.08	0.20
VERWOR	0.08	0.09	0	
POTFLA	0		0	
CARSPE	0.14	0.13	0.39	0.46
PETFRI	0		0	
LUPLAT	0		0	
VALSIT	0		0	
LUZPAR	0		0	
PHLALP	0		0	
ANEOCC	0		0	
ABILAS	0		0	
ERYGRA	0		0	
CASPAR	0.03	0.07	0	
POALEP	0		0	
RANESC	0		0	
ANTALP	0.25	0.31	0.06	0.14
TRISPI	0		0	
VACDEL	0		0	
LYCSEL	0		0	
KATMIC	0.08	0.14	0	
AGRTHU	0.61	0.23	0.06	0.14
EQUARV	0.11	0.14	0	
CETSUB	0		0	
SPHWAR	0		0	
PEDBRA	0		0	

Table IX: (Continued)

Agg9 Scale

	1		2		3	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
SENTRI	0.49	0.53	0.07	0.09	0.01	0.04
CARNIG	2.05	0.61	1.35	0.72	3.79	0.62
LEPPYR	0.06	0.19	0.78	0.64	0.83	0.81
LUEPEC	0.62	0.67	1.96	0.44	0.30	0.22
ERIPER	0.94	0.59	1.39	0.38	0.28	0.42
HIEGRA	0.67	0.36	0.35	0.40	0.01	0.04
EPIANA	0.35	0.26	0.61	0.40	0.65	0.46
CALBIF	0.28	0.36	1.63	0.77	1.07	0.89
CASMER	0.22	0.20	1.78	0.67	0.11	0.18
POACUS	0.32	0.29	0.26	0.13	0.14	0.11
JUNCSP	0.86	0.27	0.80	0.45	0.22	0.29
PHYEMP	0.04	0.08	1.39	0.71	0.12	0.14
VERWOR	0.33	0.30	0.24	0.16	0.04	0.06
POTFLA	0.43	0.48	0		0.02	0.07
CARSPE	1.75	0.13	0.67	0.44	0.25	0.29
PETFRI	0.01	0.04	0.02	0.05	0	
LUPLAT	1.21	0.83	0.70	0.58	0	
VALSIT	1.35	0.48	0.15	0.13	0	
LUZPAR	0.20	0.27	0.06	0.14	0	
PHLALP	0.02	0.07	0.02	0.05	0	
ANEOCC	0.40	0.44	0.06	0.09	0	
ABILAS	0.01	0.04	0.02	0.05	0	
ERYGRA	0.01	0.04	0		0	
CASPAR	0.19	0.27	0.26	0.32	0.01	0.04
POALEP	0.36	0.37	0		0	
RANESC	0.30	0.32	0.04	0.09	0	
ANTALP	0.01	0.04	0.19	0.15	0.14	0.20
TRISPI	0.06	0.11	0.06	0.06	0	
VACDEL	0.04	0.11	0.06	0.09	0	
LYCSEL	0		0.11	0.14	0	
KATMIC	0		0.13	0.16	0.04	0.08
AGRTHU	0		0.35	0.45	0.35	0.34
EQUARV	0		0.02	0.05	0.07	0.12
CETSUB	0.09	0.15	0.31	0.35	0	
SPHWAR	0		0		0.01	0.04
PEDBRA	0.01	0.04	0		0	

Phyllodoce empetriformis (Table IX). Subcommunities 4 and 5 are found mostly in the high meadow. Both are represented by Juncus sp., Carex spectabilis, Valeriana sitchensis, and Carex nigricans. However, 4 is also well represented by Erigeron peregrinus, and 5 is represented by Luetkea pectinata and Lupinus latifolius (Table IX).

3.3.1.2 Environmental Variable Relationships

Similar to the marsh, EL interacts with many of the measured environmental variables in the subalpine meadow study area. In reference to Table X, EL is positively correlated with EC and SA (0.69 and 0.34 respectively), and is negatively correlated with CY (-0.71). Relatively higher EC values are present where soil contains relatively more SA (0.32) and relatively less CY (-0.49). Considering that the study site was located on an incline, areas of greater CY are found near the lower end, adjacent to Mimulus Lake, possibly resulting from CY being carried by water flow during snow melt. Higher areas within the community are well-drained (greater SA content) and receive more exposure. Better drainage as well as more evaporation on the higher areas may explain greater EC and SA presence.

3.3.1.3 Community-Environment Relationships

The first and second ordination axes of the CCA have

Table X: Pearson correlations between environmental variables at different scales in the subalpine wet meadow. EL, relative ground level elevation; C, carbon content; EC, electrical conductivity; SA, sand content; CY, clay content; pH, soil acidity; FI, soil sample particles < 2 mm.

Agg1 Scale

	EL	C	pH	EC	SA	CY
C	-0.1481					
pH	-0.2765	0.1269				
EC	0.6931	0.2452	-0.1223			
SA	0.3419	-0.0024	0.2453	0.3238		
CY	-0.7094	-0.0434	0.1436	-0.4918	-0.2607	
FI	0.1685	0.0893	0.0397	0.1597	-0.0682	-0.0791

Agg4 Scale

	EL	C	pH	EC	SA	CY
C	-0.1668					
pH	-0.5336	0.1414				
EC	0.9008	-0.1653	-0.4870			
SA	0.5681	-0.0990	-0.1987	0.5741		
CY	-0.8377	-0.0072	0.4167	-0.6836	-0.5209	
FI	0.3369	0.2708	0.0554	0.2518	0.0568	-0.3757

Agg6a Scale

	EL	C	pH	EC	SA	CY
C	-0.1461					
pH	-0.6656	0.1947				
EC	0.9093	-0.1959	-0.6221			
SA	0.6148	-0.1487	-0.3359	0.5792		
CY	-0.8198	-0.0416	0.4754	-0.6671	-0.6440	
FI	0.2983	0.2107	0.0104	0.2169	-0.1149	-0.2675

Agg6b Scale

	EL	C	pH	EC	SA	CY
C	-0.2040					
pH	-0.5819	0.3326				
EC	0.9348	-0.2631	-0.5103			
SA	0.5825	-0.1027	-0.1076	0.5565		
CY	-0.8573	0.0179	0.4283	-0.7397	-0.5949	
FI	0.3298	0.3760	0.0653	0.2567	0.0708	-0.4128

Table X: (Continued)

Agg9 Scale

	EL	C	pH	EC	SA	CY
C	-0.1809					
pH	-0.7255	0.3193				
EC	0.9429	-0.3186	-0.6888			
SA	0.6004	-0.1257	-0.2487	0.5746		
CY	-0.8405	-0.0258	0.4650	-0.7315	-0.6939	
FI	0.2968	0.3104	-0.0249	0.1920	-0.0620	-0.3054

eigenvalues of 0.33 and 0.14 respectively. The first canonical axis eigenvalue and trace statistic are significant ($p \leq 0.05$). Figure 11a shows five subcommunities, arranged in an arch or horseshoe shape. This suggests an environmental variable has a strong effect on the ordination (Ter Braak 1987b). EL is not only strongly correlated with species axis one (-0.84) (Table XI), but is represented in Figure 11a by a vector of considerable length, suggesting that EL is a major determinant of the first species axis. Moreover, axis 2 is simply a quadratic function of the first. Figure 12a confirms the presence of what appears to be a definite EL gradient. EC and SA are also negatively correlated with the first species axis (-0.66 and -0.33 respectively) (Table XI). All three vectors pass directly through subcommunities 4 and 5 located in the high meadow area (Figure 11a). Table XII shows subcommunities 4 and 5 are located in soils of greater SA and EC as opposed to subcommunities 1 and 2, located at the low end of the meadow. Subcommunities 1 and 2, however, are associated with soils that have slightly more CY (12.5% and 13.4% respectively) than subcommunities 3, 4, and 5 (11.9%, 7.8%, and 7.8% respectively) offering an interpretation of a CY-species axis 1 correlative relationship of 0.57 (Table XI). Figures 12b, c, and d reaffirm the presence of greater EC and SA as well as less CY respectively in upper as opposed to lower meadow soils. C, the highest correlate with species axis 2 (0.37) (Table XI), is mostly associated with predominantly monospecific stands of Carex nigricans (subcommunity 2) (11.4%). Other subcommunities contain

Figure 11: Subcommunity-environment biplots at different scales for the subalpine meadow study site: agg1 (a), agg4 (b), agg9 (c), agg6a (d), and agg6b (e). Subcommunities are represented by 50% confidence ellipses. Ellipses were unable to be produced where those subcommunities were represented by three or fewer sampling units. Each environmental variable is represented by a vector. EL, relative ground level elevation; C, carbon content; EC, electrical conductivity; SA, sand content; CY, clay content; pH, soil acidity; FI, soil sample particles < 2 mm.

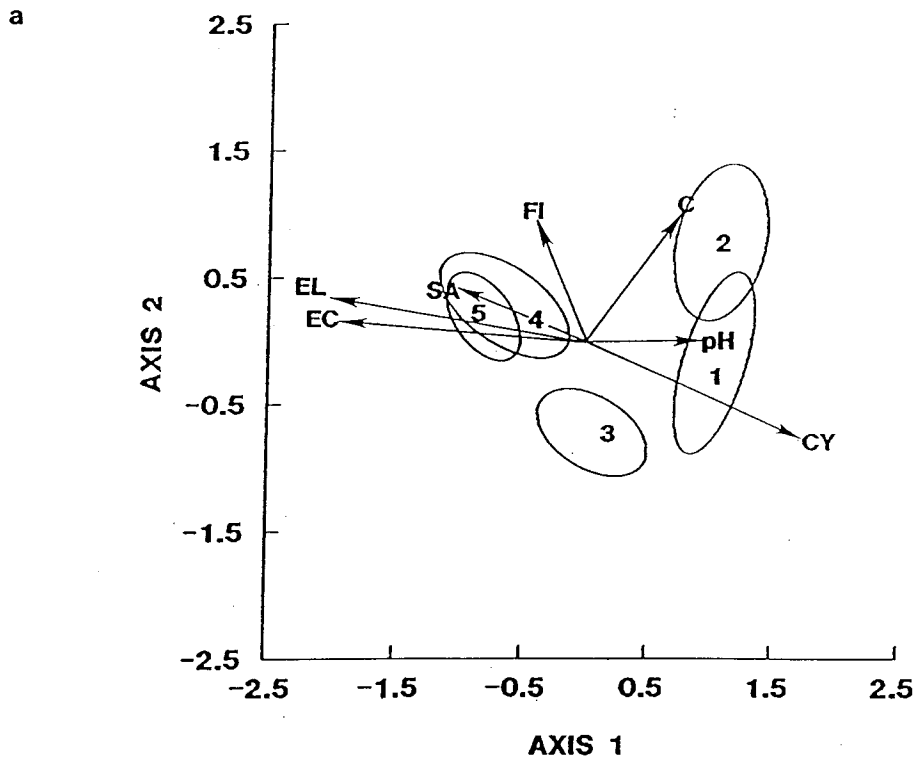


Figure 11: (Continued)

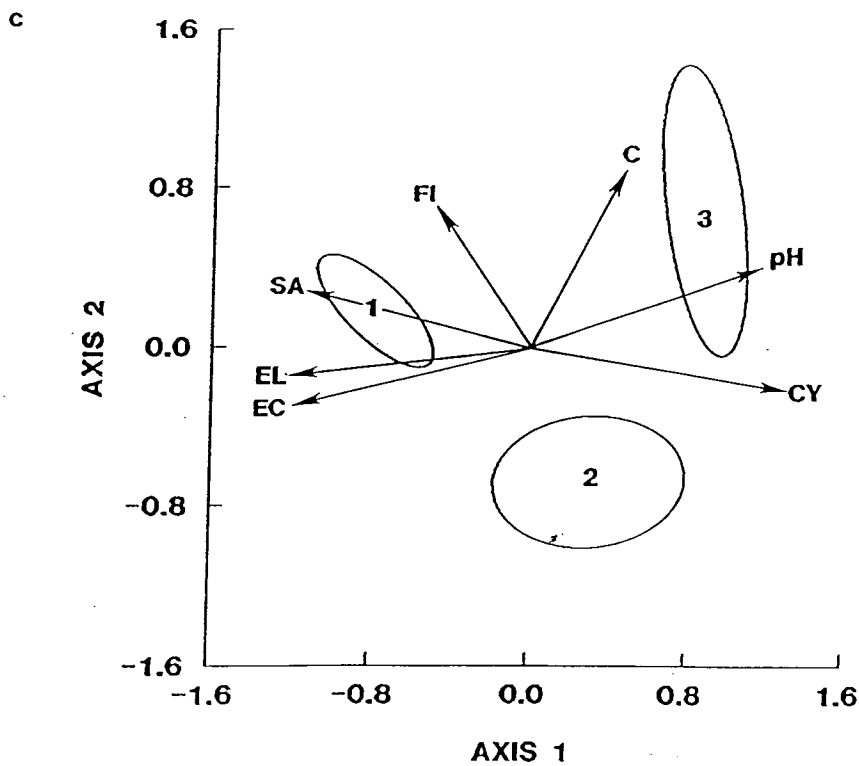
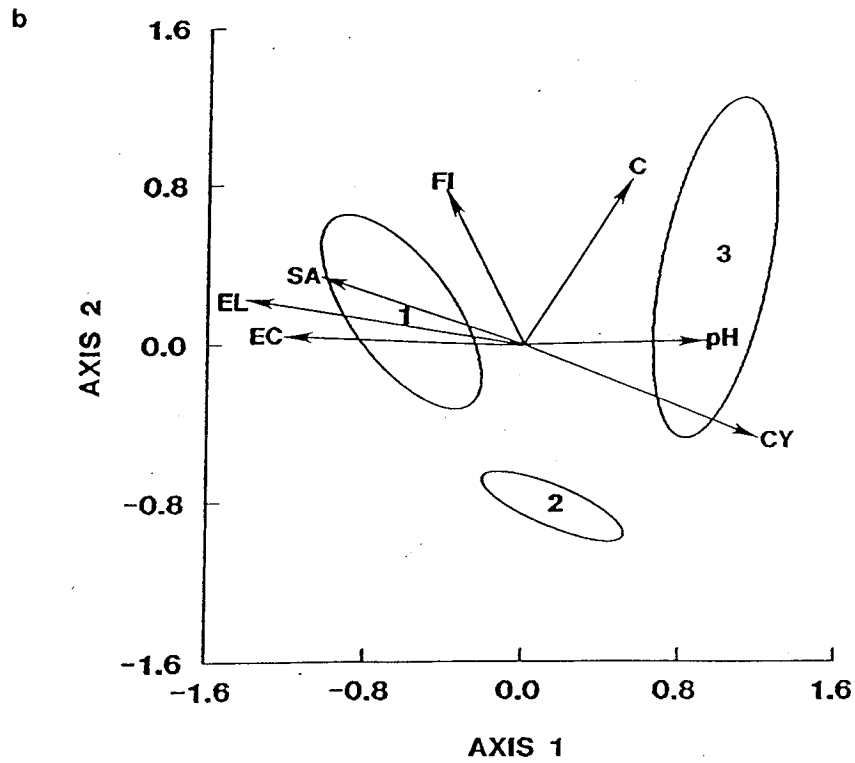
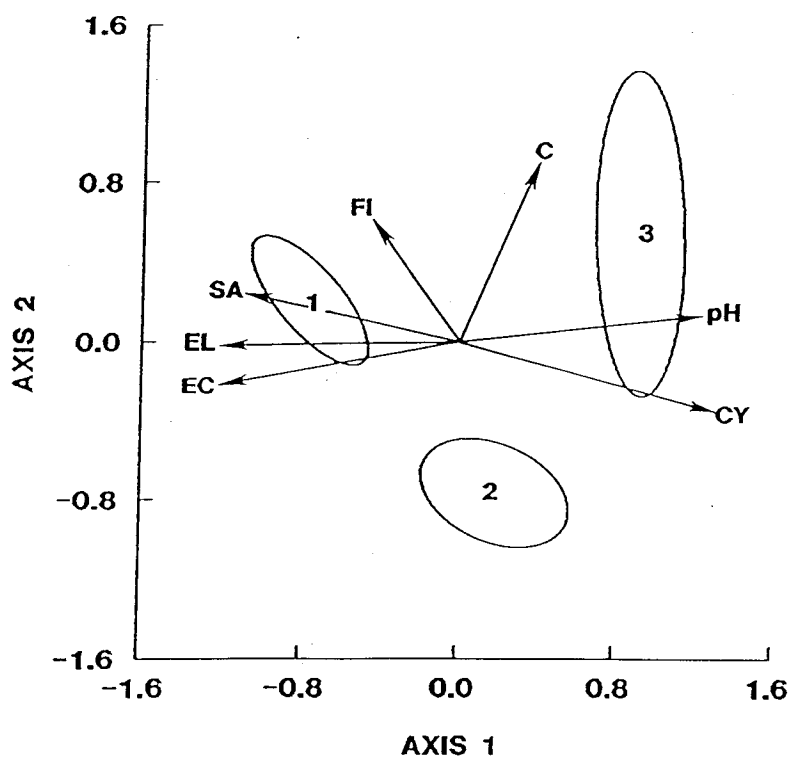


Figure 11: (Continued)

d



e

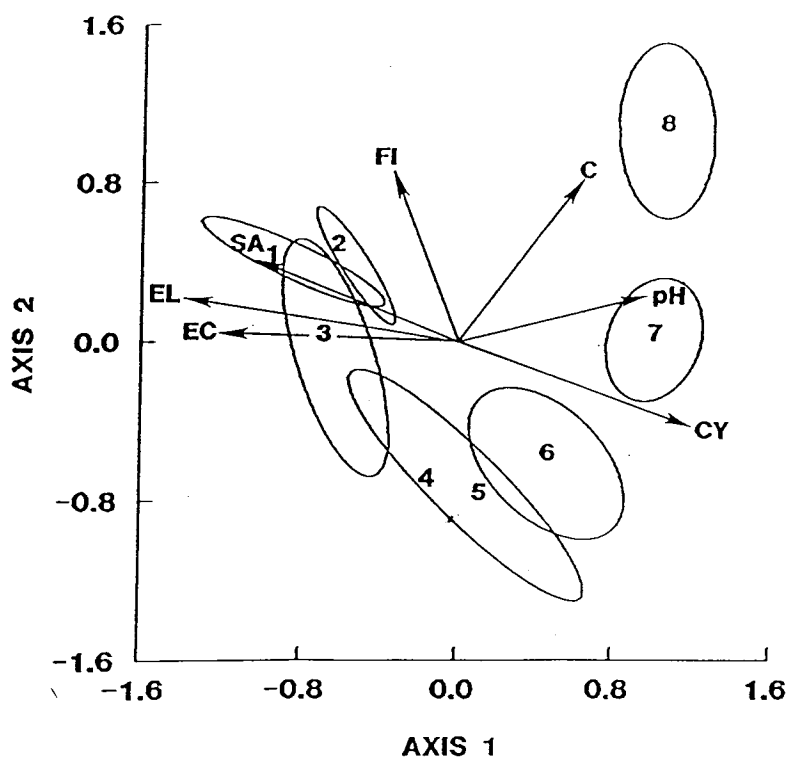


Table XI: Pearson correlations between environmental variables and species axes I and II at different scales in the subalpine wet meadow. EL, relative ground level elevation; C, carbon content; EC, electrical conductivity; SA, sand content; CY, clay content; pH, soil acidity; FI, soil sample particles < 2 mm.

Agg1 Scale

	<u>SPP AXIS 1</u>	<u>SPP AXIS 2</u>
EL	-0.8366	0.0896
C	0.2080	0.3689
pH	0.2810	-0.0230
EC	-0.6616	0.0407
SA	-0.3266	0.1222
CY	0.5716	-0.3166
FI	-0.0954	0.3520

Agg4 Scale

	<u>SPP AXIS 1</u>	<u>SPP AXIS 2</u>
	-0.8671	0.1324
	0.2803	0.5604
	0.5312	-0.0099
	-0.9048	0.0031
	-0.6027	0.2015
	0.7069	-0.3512
	-0.1935	0.5162

Agg6a Scale

	<u>SPP AXIS 1</u>	<u>SPP AXIS 2</u>
EL	-0.8756	-0.0422
C	0.1753	0.6065
pH	0.7002	0.0723
EC	-0.8828	-0.1747
SA	-0.6257	0.1435
CY	0.7361	-0.2712
FI	-0.2448	0.4200

Agg6b Scale

	<u>SPP AXIS 1</u>	<u>SPP AXIS 2</u>
	-0.8847	0.1286
	0.3412	0.5514
	0.5863	0.1446
	-0.9316	0.0094
	-0.5968	0.3038
	0.7233	-0.3286
	-0.1763	0.5981

Agg9 Scale

	<u>SPP AXIS 1</u>	<u>SPP AXIS 2</u>
EL	-0.8763	-0.1211
C	0.2295	0.6260
pH	0.6871	0.2662
EC	-0.8927	-0.2365
SA	-0.6644	0.1781
CY	0.7545	-0.1807
FI	-0.2696	0.4895

Figure 12: Two-dimensional isopleths displaying EL and soil variable zonation patterns at the aggl scale in the subalpine meadow study site: EL, relative ground level elevation (a); EC, electrical conductivity (b); SA, sand content (c); CY, clay content (d); carbon content C (e); FI, soil sample particles < 2 mm (f); and pH, soil acidity (g).

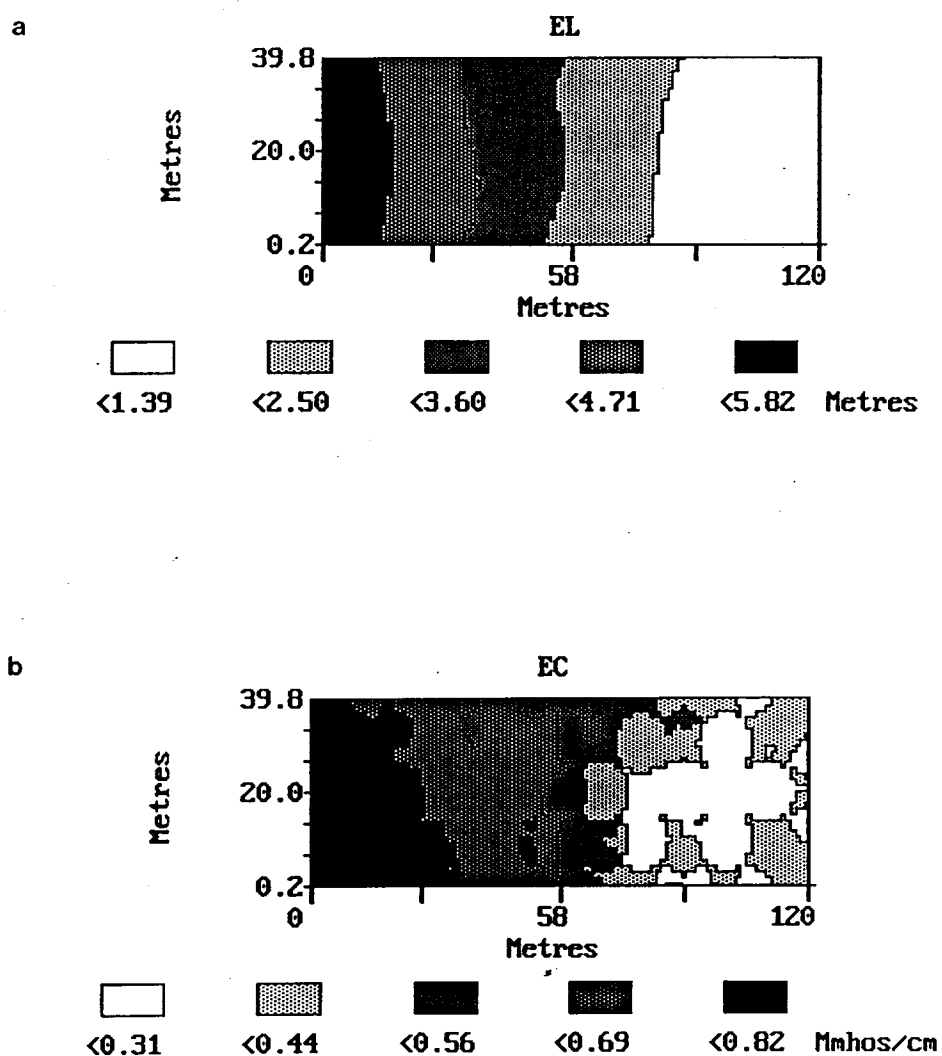


Figure 12: (Continued)

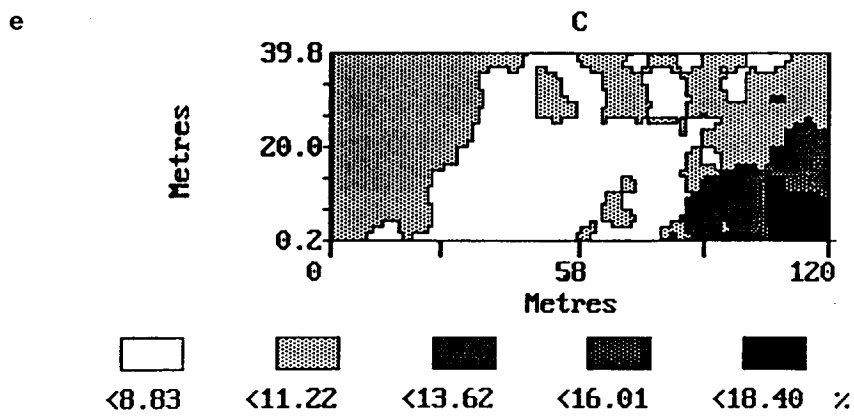
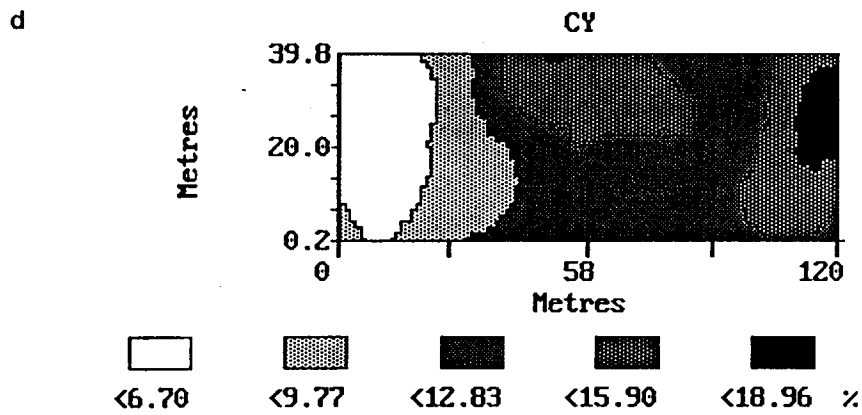
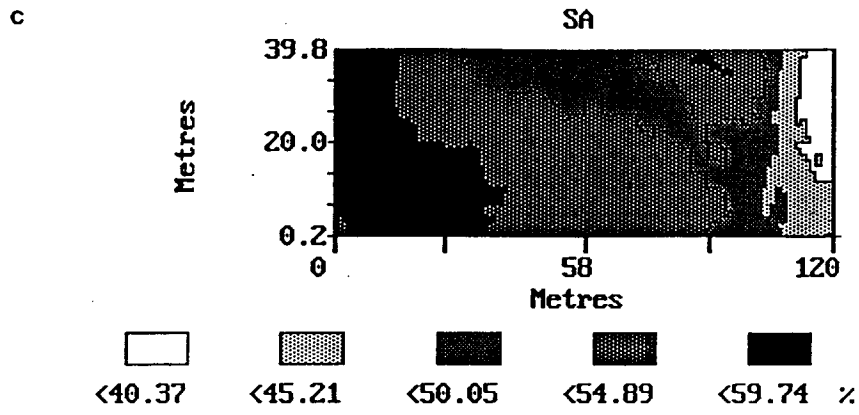
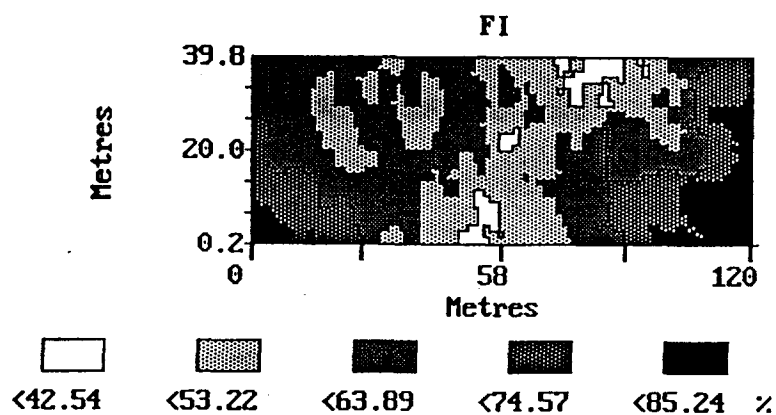


Figure 12: (Continued)

f



g

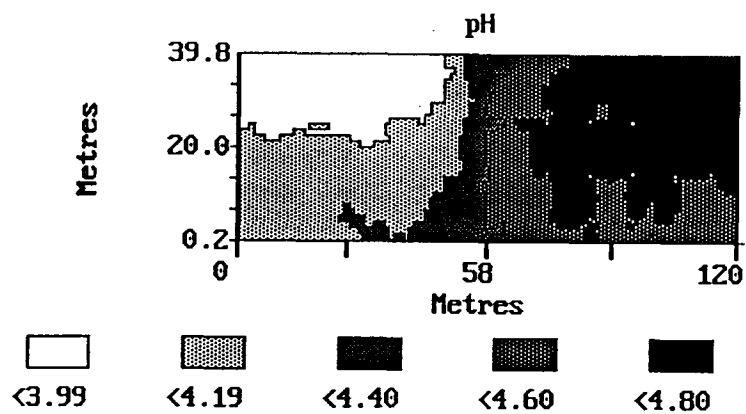


Table XII: Summarized environmental data for the main subcommunities recognized at the different scales of analysis (agg levels) in the subalpine wet meadow. Integers directly above mean and standard deviation estimates represent subcommunities at each scale. EL, relative ground level elevation; C, carbon content; EC, electrical conductivity; SA, sand content; CY, clay content; pH, soil acidity; FI, soil sample particles < 2 mm.

Agg1 Scale

	1		2		3	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
EL (m)	1.54	0.98	0.77	0.37	2.71	0.74
C (%)	9.66	3.63	11.39	4.89	8.31	1.72
pH	4.39	0.91	4.55	0.58	4.01	0.93
EC (mmhos/cm)	0.42	0.28	0.31	0.16	0.55	0.14
SA (%)	50.12	5.17	46.57	7.15	47.03	13.41
CY (%)	12.49	2.63	13.36	2.60	11.86	4.10
FI (%)	51.43	19.77	62.13	22.85	50.32	11.77

	4		5	
	Mean	Std Dev	Mean	Std Dev
EL (m)	4.09	1.05	4.09	1.14
C (%)	8.99	1.06	9.41	1.86
pH	3.80	1.10	3.87	0.85
EC (mmhos/cm)	0.69	0.13	0.71	0.12
SA (%)	54.37	7.66	54.72	3.08
CY (%)	7.83	2.95	7.75	3.76
FI (%)	57.63	13.89	58.84	12.49

Agg4 Scale

	1		2		3	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
EL (m)	4.09	1.06	2.86	0.56	1.10	0.52
C (%)	8.86	1.10	8.55	1.07	10.39	2.73
pH	3.78	0.50	4.12	0.25	4.51	0.37
EC (mmhos/cm)	0.70	0.08	0.56	0.05	0.33	0.10
SA (%)	54.18	3.47	48.61	5.85	47.35	4.95
CY (%)	7.88	2.73	12.78	2.96	12.81	1.91
FI (%)	59.15	9.92	48.24	7.35	57.00	12.75

Agg6a Scale

	1		2		3	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
EL (m)	4.33	0.90	2.69	0.54	1.07	0.49
C (%)	9.05	1.09	8.69	0.72	10.32	2.47
pH	3.76	0.34	4.08	0.27	4.53	0.29
EC (mmhos/cm)	0.71	0.06	0.59	0.04	0.33	0.08
SA (%)	54.71	3.17	49.14	3.88	47.67	4.98
CY (%)	7.29	2.57	12.59	2.59	12.70	1.90
FI (%)	59.18	9.92	50.17	6.68	56.81	13.02

Table XII: (Continued)

Agg6b Scale

	1		2		3	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
EL (m)	4.63	0.77	4.46	0.76	3.71	1.16
C (%)	8.63	0.48	9.79	0.98	8.46	1.28
pH	4.01	0.31	3.45	0.26	3.76	0.37
EC (mmhos/cm)	0.77	0.04	0.70	0.05	0.66	0.03
SA (%)	54.38	4.91	54.56	2.10	54.44	2.82
CY (%)	7.13	1.65	6.37	2.08	9.06	3.69
FI (%)	68.25	10.55	56.01	4.11	53.46	3.55

	4		5		6	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
EL (m)	3.52		2.57	0.37	2.08	0.09
C (%)	9.54		7.66	0.89	8.76	0.53
pH	3.84		3.79	0.68	4.22	0.47
EC (mmhos/cm)	0.56		0.54	0.10	0.52	0.04
SA (%)	50.03		49.55	5.00	44.32	5.10
CY (%)	9.75		12.52	1.95	12.42	3.11
FI (%)	53.67		44.77	4.93	48.22	9.13

	7		8	
	Mean	Std Dev	Mean	Std Dev
EL (m)	1.22	0.38	0.70	0.23
C (%)	8.95	1.02	12.55	1.97
pH	4.62	0.09	4.63	0.09
EC (mmhos/cm)	0.35	0.08	0.27	0.04
SA (%)	50.54	3.96	46.15	4.02
CY (%)	12.35	1.53	13.59	1.69
FI (%)	54.52	9.07	64.56	12.25

Agg9 Scale

	1		2		3	
	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
EL (m)	4.37	0.87	2.57	0.57	0.98	0.42
C (%)	9.11	1.05	8.40	0.58	10.65	2.01
pH	3.74	0.20	4.01	0.35	4.63	0.07
EC (mmhos/cm)	0.71	0.06	0.54	0.05	0.33	0.09
SA (%)	54.73	3.37	47.83	3.54	48.57	4.99
CY (%)	7.16	2.48	12.36	2.36	12.80	1.75
FI (%)	59.54	9.39	48.96	5.60	58.33	12.73

slightly less (Table XII) (also see Figure 12e).

Subcommunity 3, though well represented by species unique to it, may serve as a transition belt between high and low meadow areas. SA content in subcommunity 3 (47.0%), for example, is very similar to that in subcommunities 1 and 2 (50.1% and 46.6% respectively) (Table XII). Also, subcommunity 3 shares four representative species found in high and low meadow areas: Caltha biflora, Carex nigricans, Erigeron peregrinus, and Luetkea pectinata (Table IX).

FI shares a strong correlative relationship with species axis 2 (Table XI), yet Figure 12f confirms the difficulty in providing a possible explanation.

3.3.2 Agg4 Scale (5 X 5 Metre Observation Unit)

3.3.2.1 Community Structure

At agg4, the highest redundancy and R_c values are found at levels C3 (22.06%) and C9 (0.9789) respectively (Table VIII). Thus, the study site is divided into fewer zones than agg1: high meadow, mid-meadow, and low meadow (Figure 10b). Subcommunity 1, representative of the high meadow, is characterized in Table IX by Carex nigricans, Erigeron peregrinus, Carex spectabilis, Lupinus latifolius, and Valeriana sitchensis.

Erigeron peregrinus is also found in subcommunity 2 (Figure 10b), but is largely represented by Cassiope mertensiana and Phyllodoce empetriformis as well as Luetkea pectinata, and Caltha biflora (Table IX). Its representation as a transition belt between upper and lower meadow subcommunities is not as defined at this scale as opposed to subcommunity 3 at agg1 (Figure 10a).

Subcommunity 3, shown in Table IX is predominately a low meadow stand of Carex nigricans interspersed with Caltha biflora.

3.3.2.2 Environmental Variable Relationships

In reference to Table X, EL shares stronger correlative relationships with EC, SA, and CY (0.90, 0.57, and -0.84 respectively) compared to agg1. EC also shares stronger positive and negative relationships with SA and CY (0.57 and -0.68 respectively) as opposed to agg1.

Again referring to Table X, relationships between pH and other environmental variables are more pronounced at this scale. While EL and EC are negatively correlated with pH (-0.53 and -0.49 respectively), CY shares a positive correlative relationship of 0.42. Of interest is a negative correlative relationship between pH and SA (-0.20). Though this relationship is rather weak, it is, nevertheless, negative--unlike a positive relationship at agg1 (0.25) (Table X). Soils are slightly less acidic in the low meadow

area. Since lower meadow soils contain relatively more CY and relatively less SA, lower meadow soils have presumably greater water holding capacity and are less susceptible to leaching compared to upper meadow soils. In addition, the low meadow area is located at the bottom of a slope: an ideal location for a decrease in water flow rate and subsequent water settlement.

EL is also positively correlated with FI (0.34). Conversely, FI is negatively correlated with CY (-0.38) (Table X).

3.3.2.3 Community-Environment Relationships

CCA reported first and second axes eigenvalues of 0.33 and 0.16 respectively, and a significant ($p < 0.05$) trace statistic and first canonical ordination axis eigenvalue.

The subcommunity-environment biplot shown in Figure 11b tells an almost identical story to that previously described at a finer scale (agg1). Mostly monospecific stands of Carex nigricans (subcommunity 3) in Table XII are found in soils of slightly greater CY and C but contain less SA and EC as in subcommunity 1. Subcommunity 2 represents a community between two different extremes, is distinctive in species composition, and contains environmental variable values that are, again, usually similar to or between those values of subcommunities 1 and 3.

Differences in vector length are not as variable at this scale (Figure 11b). Generally, environmental variables have stronger correlative relationships with species axes 1 and 2. Referring to Table XI, SA and pH, for example, have stronger correlative relationships with species axis one (-0.60 and 0.53 respectively). In addition, pH vector length is not as short in relation to vector CY in Figure 11b as opposed to Figure 11a, possibly better recognizing pH-subcommunity relationships at this scale. Despite what appears to be clear pH zonation pattern at agg1 (Figure 12g), relative pH differences between subcommunities are not very clear at a finer scale (agg1) (Table XII) mostly because pH measurements within each subcommunity are quite variable (rather high standard deviation estimates). At a coarser scale, however, a more noticeable trend is evident (lower standard deviation estimates). Subcommunity 3 is located in slightly less acidic soils (4.5) as opposed to subcommunities 1 and 2 (3.8 and 4.1 respectively) (Table XII).

Interestingly, FI shares a strong correlative relationship with species axis 2 (Table XI). A definitive trend, however, appears to be lacking along a height gradient (Table XII).

3.3.3 Agg9 Scale (10 X 10 Metre Observation Unit)

3.3.3.1 Community Structure

At agg9, redundancy and R_c estimates are highest at levels C3

(28.71%) and C5 (0.9994) respectively (Table VIII). Here, the meadow is divided into three subcommunities (Figure 10c) characterized by the aforementioned species at agg4. One subtle difference, however, is the improved representation (aerial coverage class greater or equal to one) of Carex nigricans in subcommunity 2 (Table IX).

3.3.3.2 Environmental Variable Relationships

Environmental variable interactions at this observation scale reinforce what was revealed at agg4. Generally, correlations between environmental variables are stronger, to the extent of emphasizing additional interactions. The most noticeable interaction is between C and pH (0.32) as well as C and EC (-0.32) (Table X). Greater C is found in the low meadow areas where soils tend to be less acidic. Organic content may also be contributing to relatively better water holding capacity in soils resulting in less leaching.

3.3.3.3 Community-Environment Relationships

First and second axes' eigenvalues of 0.33 and 0.20 respectively and a first canonical ordination axis eigenvalue and trace statistic significant at 0.05 were reported from CCA. As reported at the agg4 scale, same subcommunity-environment relationships are relevant at this scale except that correlations

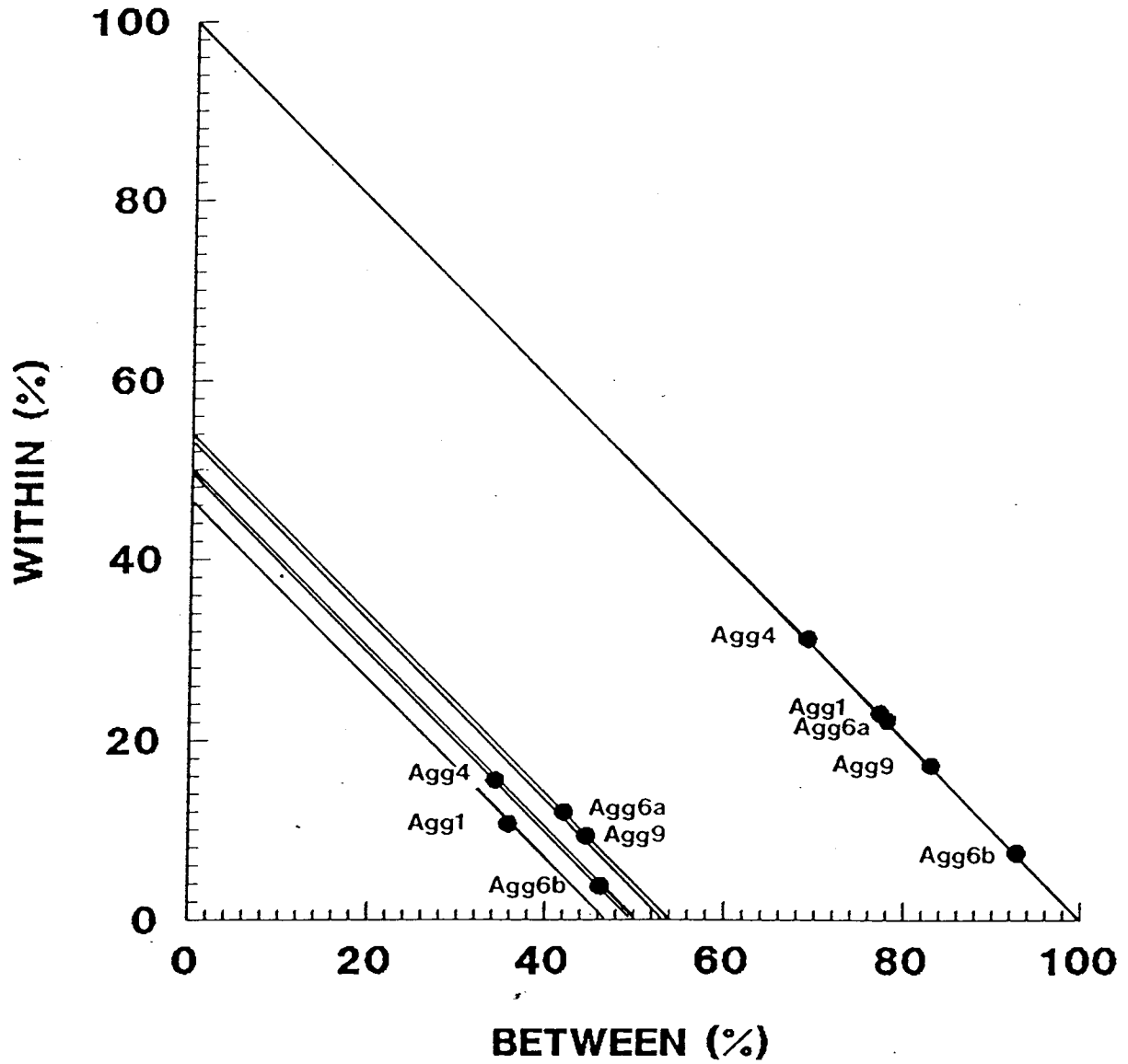
between relevant environmental variables and the first two species axes are generally stronger (Table XI). Of interest is the increased ellipse size of subcommunity 2 and decreased ellipse size of 1 and 3 in Figure 11c compared to Figure 11b. This may suggest that the distinctiveness of all three communities can be more clearly defined at agg9 as opposed to agg4. Within-assemblage variability of subcommunities 1 and 3 appears to be less at agg9 (Figure 11c) as opposed to agg4 (Figure 11b), clearly redefining upper and lower meadow zones. Conversely, within-assemblage variability in ellipse 2 has increased from agg4 (Figure 11b) to agg9 (Figure 11c). Perhaps this more clearly defines subcommunity 2 as a transition belt between upper and lower zones (Figure 10c), compared to agg4 (Figure 10b) and agg1 (Figure 10a). Referring to Figure 13, agg4 has a larger overall estimate of within-cluster variability (31.10%) and smaller estimate of between-cluster variability (68.90%) compared to agg1 (22.87% and 77.13% respectively). At agg9 community structure is more clearly defined than both agg1 and agg4 since overall between-assemblage variability is 82.88% and within-assemblage variability is 17.12%.

3.3.4 Agg6a and Agg6b Scales (5 X 10 Metre and 10 X 5 Metre Observation Units)

3.3.4.1 Community Structure and Environmental Variable Relationships

At agg6a, levels C3 (26.08%) and C10 (0.9948) yield the

Figure 13: Overall between and within-cluster variability estimates for all scales in the subalpine meadow. Unstandardized estimates shown along inner isoclines; standardized estimates shown along outer isocline.



highest redundancy and R_c values respectively (Table VIII). When field sampling is simulated with a rectangular quadrat positioned width-wise (agg6a), the wet meadow is, therefore, partitioned into three zones: upper, middle, and lower subcommunities (Figure 10d). The same representative species at agg9 also characterize the three subcommunities at agg6a (Table IX). At agg6b, levels C8 (24.69%) and C10 (0.9941) yield the highest redundancy and R_c (Table VIII). Hence, simulation sampling with a quadrat of the same area but positioned length-wise, divides the meadow into eight subcommunities (Figure 10e). In reference to Table IX, upper zone subcommunities 1, 2, and 3 are characterized by Carex nigricans, Carex spectabilis, and Valeriana sitchensis. Subcommunity 1 is also represented by Senecio triangularis, Erigeron peregrinus, and Potentilla flabellifolia. Hieracium gracile and Juncus sp. also characterize subcommunity 2. Subcommunity 3 also has a preponderance of E. peregrinus and Lupinus latifolius. The middle zone subcommunities 4, 5, and 6 are well represented by E. peregrinus, Luetkea pectinata, and Cassiope mertensiana. While C. spectabilis is another representative of subcommunity 4, Caltha biflora, Phyllodoce empetrifomis, and C. nigricans also characterize subcommunity 5, and C. biflora, C. nigricans, P. empetrifomis, Juncus sp., and Leptarrhena pyrolifolia also represent subcommunity 6. The lower zone comprises two subcommunities: 7 characterized by C. nigricans, C. biflora, and L. pyrolifolia, and 8, composed mostly of C. nigricans.

When scale is maintained but rectangular quadrat placement is altered during simulation field sampling, environmental variable interactions at both agg6a and agg6b levels reveal similar trends to those at the agg4 and agg9 scales (Table X).

3.3.4.2 Community-Environment Relationships

First and second axes eigenvalues of 0.34, 0.20 for agg6a, 0.33, 0.17 for agg6b, as well as a significant ($p < 0.05$) first canonical axis eigenvalue and trace statistic significant were reported from a CCA. Environmental variable-first and second species axes relationships are the same not only between agg6a and agg6b, but also the same as that previously described for agg4 and agg9 scales (Table XI).

Ellipses 1 and 3 in Figure 11d are smaller than ellipses 1 and 3 at agg4 (Figure 11b) yet larger than corresponding ellipses at agg9 (Figure 11c). Conversely, ellipse 2 in Figure 11d is larger than ellipse 2 at agg4 (Figure 11b) but smaller than agg9 (Figure 11c). Thus, within-assemblage variability consistently decreases in subcommunities 1 and 3 and increases in subcommunity 2 as progressively larger sampling units (agg4, agg6a, to agg9) are used. The distinctiveness of upper and lower zones and the interpretation of subcommunity 2 as a transition belt may become increasingly clearer at progressively coarser scales (agg4, agg6a, and agg9). Standardized between and within-variability estimates

at agg4, 6a, and 9 support this notion where between-assemblage variability gradually increases and within-assemblage variability gradually decreases. Similar to the marsh, largest between (92.7%) and smallest within (7.4%) estimates are provided at agg6b (Figure 13).

3.3.5 EL Influence Verification

3.3.5.1 Agg1, 4, 6a, 6b, 9 Scales

Correlations between environmental variables and a canonical correlation axis representing species variables (summarized by three PCA axes) as well as residuals confirm EL influence on vegetation pattern (Table XIII). Environmental variable-canonical axis correlations reveal very similar trends previously discussed at all scales. Independent of EL, environmental variable-residual correlations are generally not as strong as environmental variable-canonical axis correlations perhaps confirming the presence of a well-defined EL gradient, influencing species variables in the wet meadow study area. However, at agg6b and agg9, correlative relationships between C and residuals are quite strong (-0.27 and -0.26 respectively). This may suggest that relationships between organic content and vegetation are independent of EL to some degree. At these scales, vegetation (specifically Carex nigricans) may be clearly observed to contribute to the (C) organic content in lower meadow soils.

Table XIII: Pearson correlations at different scales between environmental variables, residuals, and a canonical axis representing species variables in the subalpine wet meadow. AXIS, canonical correlation axis; RESD, residuals; EL, relative ground level elevation; C, carbon content; EC, electrical conductivity; SA, sand content; CY, clay content; pH, soil acidity; FI, soil sample particles < 2 mm.

Aggl Scale

	EL	C	pH	EC	SA	CY	FI
AXIS	0.7563	-0.2322	-0.2969	0.6606	0.3375	-0.5103	0.0062
RESD	0	-0.0837	-0.0555	0.1511	0.0496	0.0776	-0.0180

Aggl4 Scale

	EL	C	pH	EC	SA	CY	FI
AXIS	0.8504	-0.3974	-0.5475	0.8924	0.5990	-0.6684	0.0756
RESD	0	-0.2344	-0.0320	0.2041	0.1457	0.1136	-0.0815

Aggl6a Scale

	EL	C	pH	EC	SA	CY	FI
AXIS	0.8693	-0.3660	-0.7307	0.9001	0.6162	-0.6812	0.0309
RESD	0	-0.1913	-0.1782	0.1833	0.1198	0.0900	-0.1244

Aggl6b Scale

	EL	C	pH	EC	SA	CY	FI
AXIS	0.8715	-0.4469	-0.6392	0.9110	0.5672	-0.6886	0.0528
RESD	0	-0.2719	-0.0628	0.1746	0.0648	0.1554	-0.1175

Aggl9 Scale

	EL	C	pH	EC	SA	CY	FI
AXIS	0.8865	-0.4342	-0.7968	0.9136	0.6055	-0.7067	0.0154
RESD	0	-0.2632	-0.1790	0.1465	0.1047	0.1095	-0.1514

3.3.6 Subalpine Wet Meadow Discussion

The wet meadow study site is generally composed of three zones: upper, middle, and lower. These three zones may correspond to major vegetation types in Garibaldi Provincial Park: forb meadow (upper), heath (middle), and sedge meadow (lower) (Brink 1959; Archer 1963; Brooke et al. 1970). Similar vegetation types have been documented in other alpine/subalpine regions of the Pacific Northwest. The upper subcommunity represented in the meadow site by such species as Valeriana sitchensis, Carex spectabilis, Lupinus latifolius, and Erigeron peregrinus have been extensively described by Kuramoto and Bliss (1970) in the Olympic Mountains, Douglas and Bliss (1977) on steep well-drained slopes in the North Cascade Range, and Evans and Fonda (1990) on windward slopes of Excelsior Ridge in the North Cascades. The heath subcommunity dominated by Phyllodoce empetriformis, Cassiope mertensiana, and Luetkea pectinata has also been identified as a common community type by Kuramoto and Bliss (1970) in the Olympic Mountains and Douglas and Bliss (1977) and Evans and Fonda (1990) in the North Cascades. Of all the major vegetation zones in the wet meadow study area, the Carex nigricans dominated subcommunity (lower meadow) is the most widespread. It has been found in the Olympic Mountains (Kuramoto and Bliss, 1970), east to the Canadian Rockies (Knapik et al. 1973); Hrapko and La Roi 1978), and North Cascades (Douglas and Bliss, 1977; Evans and Fonda 1990). C. nigricans snowbed communities have also been found by del Moral

(1979) in the Enchantment Lakes Basin, Washington.

At all scales, subcommunities found in the upper zone share strong correlative relationships with SA and EC while lower zone subcommunities share strong correlative relationships with CY and C. Lower meadow-pH relations are also apparent at most scales. The upper meadow may receive more exposure to climatic factors such as insolation than the middle and lower meadow. Also, Phyllodoce empetriformis and Carex nigricans, dominant species in middle and lower subcommunities respectively, were found to better insulate soil from solar radiation and higher temperatures on Excelsior Ridge in the North Cascades than Valeriana sitchensis, representative of the upper meadow (Evans and Fonda 1990). Though soil temperature was not recorded in this study, Evans and Fondas' (1990) findings may offer an hypothesis as to why EC values were found to be higher in the upper meadow (possibly a result of higher temperatures and thus higher evaporation rates leading to greater deposition of salts in upper soil horizons), than in the middle and lower subcommunities. The upper meadow is also well-drained because of greater sand content allowing water to flow easily into a catch basin (lower meadow) where soils possess relatively greater CY and C. Rapid water percolation through slightly more acidic soils in the upper meadow may be promoting a leaching process; superior water holding capacity a result of greater CY and (C) organic accumulation from Carex nigricans in the lower may help to slow this process. Relatively less acidic soils may help retain

the distinctiveness of the lower sedge subcommunity by deterring heath species such as Phyllodoce empetriformis and Cassiope mertensiana from invading since they are accustomed to soils that possess sufficient organic accumulation but are of a slightly more acidic nature (Brooke et al. 1970). Though water does not stand over the sedge area, the water table is generally high (Brink 1959, 1964) possibly because of longer snow persistence (Brooke et al. 1970), ground and above ground water flow during snow melt, and possible ground water influence from Mimulus Lake. A high water table may also deter P. empetriformis and C. mertensiana from invading the sedge area (Brooke et al. 1970).

Brink (1959) reported forb meadow soils as having higher pH as opposed to those soils found in a sedge-Caltha meadow. This conflicts with the findings in the Mimulus Lake wet meadow area and perhaps suggests a need to study more intensively the community structure of smaller area. This may be not only more informative but better recognize that broad descriptions of extremely variable habitats may obscure important issues of ecological complexity. Soil properties are a function of regional climate, topography, biota, and parent materials (Jenny 1941). These factors may contribute to pH variability in Garibaldi Park.

Community pattern has long been recognized as a function of snow distribution and duration (Billings and Bliss 1959; Holway and Ward 1963; Bell and Bliss 1979; Isard 1986; Evans and Fonda 1990).

Snowmelt as influenced by EL in the wet meadow may have a profound influence on the three encountered subcommunity types. The most snow usually accumulates in Carex nigricans dominated basins and remains there until late July to early August (Evans and Fonda 1990; Kuramoto and Bliss 1970; Hrapko and La Roi 1978; Selby and Pitt 1984). On better drained areas, heath communities typical of the heath subcommunity in the Mimulus Lake area are usually released earlier from snow in early June to early July. At steeper, more exposed and well drained forb meadow type areas, snow has disappeared between late May to early June (Douglas and Bliss 1977). Since EL has a profound effect in the wet meadow community, a snow melt gradient as influenced by EL may ultimately be a major determinant of community pattern by influencing a plant's growing season (Kuramoto and Bliss 1970).

Employment of different quadrat sizes as well as CCorA to select among nine possible subcommunity schemes per MVCA reveal different aspects of vegetation structure. At aggl the meadow study site is generally divided into the aforementioned three zones. Much variability is evident, however, with the subdivision of the upper meadow into two subcommunities (Figures 10a and 11a). A transition belt can barely be observed suggesting gradual vegetation change along a pronounced EL gradient. The lower meadow is predominately a monospecific stand of Carex nigricans. The interspersions of less abundant species such as Caltha biflora is clearly evident with the division of the lower into two

subcommunities. Not only are upper, middle, and lower meadow areas more clearly defined as simply three subcommunities at agg4, agg6a, and agg9, but the distinctiveness of all three subcommunities is also evident at progressively coarser scales. Ellipses representing subcommunities 1 (upper) and 3 (lower) become progressively smaller from agg4, agg6a, to agg9 (Figures 11b, c, and d). Thus, within-assemblage variability consistently decreases in subcommunities 1 and 3 from agg4, 6a, to agg9 which may mean that their distinctiveness becomes progressively more defined. Conversely, an ellipse representative of subcommunity 2 appears to grow larger. That is, within-assemblage variability consistently increases in subcommunity 2 from agg4, 6a, to agg9 emphasizing its presence as a transition belt. This is clearly illustrated in Figure 10b where subcommunity 2 is distinct but is mostly confined to one side of the grid. In Figures 10c and d, a transition belt has phased into view providing a clearer picture than agg1 and agg4 (Figures 10a and b). Figure 13 reaffirms improved perception of community structure as one moves from agg4, 6a, to agg9. Overall within-assemblage variability progressively decreases and variability between groups increases.

CHAPTER 4: SYNTHESIS

4.1 Quadrat Shape and Orientation

Though it has long been the custom to employ square quadrats during field sampling, there exists strong support for the use of rectangular sampling units. Variance per unit area has been found to be lower in rectangular plots than in square plots of the same area (Clapham 1932; Kalamkar 1932; Justesen 1932). The results of this thesis may conform with those who have found this to be true when the rectangular sampling unit is positioned at right angles to the observed vegetational or soil banding (Clapham 1932; Bormann 1953). During field sampling, a rectangular quadrat oriented in this fashion is more likely to include more (species) variability, ultimately reducing heterogeneity between sampling units (Kalamkar 1932; Greig-Smith 1983). In both the marsh and meadow systems, the use of rectangular quadrats oriented at right angles to the observed bands of vegetation (agg6b) facilitated the recognition of subcommunities. That is, overall (standardized) within-assemblage variability was least and between-assemblage variability was greatest at agg6b (10 X 5 m) (Figures 9 and 13). Interestingly, at agg6b in both marsh and meadow systems, redundancy estimates were highest at the dendrogram level yielding eight groups (C8) (Tables II and VIII). Since vegetation heterogeneity between 10 X 5 m quadrats (agg6b) is presumed to be less than at other scales, relatively fewer differences between sampling units exist at agg6b. Fewer, yet better defined, differences between quadrats at agg6b

may be unique to only a few cases. Since the clustering algorithm may have used these distinctive differences as criteria to segregate quadrats into groups and only a few quadrats share these differences per group, more groups are formed. An example of the preceeding explanation is illustrated in Appendix B. Three subcommunities can be easily observed in the vegetation data matrix at agg6a in the subalpine meadow. However, at agg6b it is considerably more difficult to observe three or eight subcommunities. This may illustrate less heterogeneity between sampling units at agg6b as opposed to agg6a. Differences in species composition and abundance at agg6b, appear to be fewer than at agg6a, but those that do exist are much more noticeable. In particular, Cassiope mertensiana is most abundant within subcommunity 2 at agg6a; however, at agg6b, C. mertensiana tends to vary more erratically. Since quadrat 12 in agg6b is the only sampling unit where C. mertensiana was given an aerial coverage class of 4, this could have influenced the clustering algorithm in defining case 12 as a unique subcommunity. Another example is Lupinus latifolius where it tends to be most abundant in subcommunity 1, at agg6a. At agg6b, abundance of L. latifolius tends to be more variable between subcommunities; specifically, it is most abundant in subcommunity 3. These and other subtle differences may explain why eight subcommunities were defined in both the marsh and meadow at agg6b. Fewer, yet more distinctive differences between quadrats ultimately contribute to maximizing between and minimizing within-subcommunity variability estimates at

agg6b compared to other scales.

4.2 Noisy Data and Redundancy Estimates

The restrictions of a finite number of samples and the use of various measurement scales to estimate species abundances have been recognized by Gauch (1982) as sources of noise in vegetation data. Furthermore, the chance distribution and establishment of individual plants, faunal activity, disturbance (Gauch 1982), and mixed and largely unpredictable species' responses to many environmental gradients (Austin 1980) are other possible causes of noisy data. In this study, dendrogram levels were used at each scale to describe community structure. Redundancy estimates for each scale in both meadow and marsh systems have been shown to be quite low (6-47%). Much variation in the vegetation data sets was left unexplained and may be attributed to noise. There are two major setbacks that warrant concern. First, the clustering algorithm attempts to agglomerate samples that contain a mixture of interpretable variation and noise. Some of the noise may have been interpretable had either a different quadrat size or shape or sampling strategy been used to capture more information. The variation required to explain some of the noise may operate at different scales to those imposed by the observer. Noise, may be an indicator of a conflict between ecological complexity and imposed anthropocentric scales used to (insufficiently) assess variation. Second, the clustering algorithm is forcing variation

to be segregated into somewhat artificial groupings. Natural zones may correspond to those dictated by the method or they may not. Given these considerations, it is not surprising that each dendrogram level was only able to explain a small percentage of the total variation.

4.3 Hierarchical Perspective: An Assessment

Employment of different observation scales (quadrat sizes) in both marsh and subalpine meadow, suggests that the scale at which observations are made will undoubtedly affect our perception of vegetation-environment relationships as well as community structure. In this study, correlations among environmental variables and species axes generally tended to become stronger at progressively coarser scales. Correlations that were regarded as weak (unimportant) at a fine scale usually became more noticeable as larger quadrat sizes were used. Subcommunity-pH relations in both marsh and subalpine meadow may serve as an example where a weak agg1 correlation became stronger at agg4. However, a strong agg4 correlation weakened at agg9 in the tidal marsh, recognizing exceptions to this generalization. In the marsh and subalpine/alpine literature, researchers have recognized the interaction of many factors in determining pattern, and many have assessed the importance of measured environmental variables. Moreover, different factors have been attributed as having a major influence on vegetation pattern in marsh and meadow systems. One

of the reasons for this may be that each study site is unique. However, most of these studies have used only one quadrat size and shape. Changing the scale and reference point in this study demonstrated that the strength of vegetation-environment correlations is a function of scale. The 'importance' of environmental factors, estimated by their correlation with vegetation pattern, may be dependent on the scale at which the data were analyzed. An hierarchical approach warns one to be cautious when 'ranking' the importance of environmental variables. Community structure has been demonstrated also to be a function of scale. An hierarchical perspective reinforces the notion that the criteria used for defining a community or subcommunity are entirely man-selected and may or may not correspond to undefinable natural zones in the field.

In summary, multivariate statistical techniques and other tools have been used to filter out noise in the hope of isolating interpretable variation. Benefits of comparing differently scaled analyses are fourfold: 1) certain vegetation-environment relationships are clarified by appearing progressively stronger at coarser scales, 2) at coarser scales, new relationships may be uncovered and established relationships at finer scales may phase out of view, 3) interpretation of community structure may change as a function of scale, and 4) confidence is added to the observers overall interpretation of ecological complexity. Given that ecological reality has been described as "loosely ordered,

complexly patterned, multiply determined" (Whittaker 1952), an hierarchical perspective can contribute significantly to an ecologist's existing arsenal of statistical techniques and observation skills.

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APPENDIX A

The following is a list of encountered plant species and their respective codes in the tidal marsh and wet meadow. A list of encountered bryophytes in the meadow is also included. Nomenclature follows Hitchcock and Cronquist (1973) for vascular plants and Ireland et al. (1987) and Stotler and Stotler (1977) for bryophytes.

Tidal Marsh

Encountered Plant Species

Code

<u>Carex lynqbyei</u> Hornem.	CARLYN
<u>Potentilla pacifica</u> Howell	POTPAC
<u>Triglochin maritimum</u> L.	TRIMAR
<u>Agrostis alba</u> L.	AGRALB
<u>Sium suave</u> Walt.	SIUSUA
<u>Stellaria humifusa</u> Rottb.	STEHUM
<u>Deschampsia cespitosa</u> (L.) Beauv.	DESCES
<u>Ranunculus cymbalaria</u> Pursh	RANCYM
<u>Juncus balticus</u> Willd.	JUNBAL
<u>Hordeum brachyantherum</u> Nevski	HORBRA
<u>Atriplex patula</u> L.	ATRPAT
<u>Aster eatonii</u> (Gray) Howell	ASTEAT
<u>Lathyrus palustris</u> L.	LATPAL
<u>Elymus</u> sp.	ELYMSP
<u>Scirpus maritimus</u> L.	SCIMAR
<u>Trifolium wormskjoldii</u> Lehm.	TRIWOR
<u>Sonchus arvensis</u> L.	SONARV
<u>Plantago maritima</u> L.	PLAMAR
<u>Conioselinum pacificum</u> (Wats.) Coult and Rose	CONPAC

Wet Meadow

Encountered Plant Species

<u>Carex nigricans</u> Retz.	CARNIG
<u>Carex spectabilis</u> Dewey	CARSPE
<u>Erigeron peregrinus</u> (Pursh) Greene	ERIPER
<u>Caltha biflora</u> D.C.	CALBIF
<u>Epilobium anagallidifolium</u> L.	EPIANA
<u>Juncus</u> sp.	JUNCSP
<u>Luetkea pectinata</u> (Pursh) Kuntze.	LUEPEC
<u>Valeriana sitchensis</u> Bong.	VALSIT
<u>Leptarrhena pyrolifolia</u> (D. Don) R.Br.	LEPPYR
<u>Cassiope mertensiana</u> (Bong.) G. Don	CASMER
<u>Poa cusickii</u> Vasey	POACUS
<u>Hieracium gracile</u> Hook.	HIEGRA
<u>Lupinus latifolius</u> Agardh	LUPLAT
<u>Agrostis thurbergiana</u> Hitchc	AGRTHU
<u>Phyllodoce empetriformis</u> (Sw.) D. Don	PHYEMP
<u>Veronica wormskjoldii</u> Roem. and Schult.	VERWOR

<u>Senecio triangularis</u> Hook.	SENTRI
<u>Ranunculus eschscholtzii</u> Schlecht.	RANESC
<u>Castilleja parviflora</u> Bong.	CASPAR
<u>Poa leptocoma</u> Trin.	POALEP
<u>Anemone occidentalis</u> Wats.	ANEOCC
<u>Potentilla flabellifolia</u> Hook.	POTFLA
<u>Antennaria alpina</u> Gaertn.	ANTALP
<u>Cetraria subalpina</u> Imsh.	CETSUB
<u>Luzula parviflora</u> (Ehrh.) Desv.	LUZPAR
<u>Kalmia microphylla</u> (Hook.) Heller	KALMIC
<u>Equisetum arvense</u> L.	EQUARV
<u>Trisetum spicatum</u> (L.) Richter	TRISPI
<u>Lycopodium selago</u> L.	LYCSEL
<u>Phleum alpinum</u> L.	PHLALP
<u>Vaccinium deliciosum</u> Piper	VACDEL
<u>Petasites frigidus</u> (L.) Fries	PETFRI
<u>Sphagnum warnstorffii</u> Russ.	SPHWAR
<u>Abies lasiocarpa</u> (Hook.) Nutt.	ABILAS
<u>Erythronium grandiflorum</u> Pursh	ERYGRA
<u>Pedicularis bracteosa</u> Benth.	PEDBRA

Encountered Bryophytes

<u>Lescuraea radicata</u> (Mitt.) Moenk.
<u>Polytrichum piliferum</u> Hedw.
<u>Polytrichum sexangulare</u> Brid.
<u>Kiaeria blyttii</u> (Schimp.) Broth.
<u>Dichodontium olympicum</u> Ren. and Card.
<u>Racomitrium sudeticum</u> (Funk) B.S.G.
<u>Cladonia chlorophaea</u> (Floerke ex Somm.) Spreng.
<u>Aulacomnium palustre</u> (Hedw.) Schwaegr.
<u>Drepanocladus uncinatus</u> (Hedw.) Warnst
<u>Drepanocladus aduncus</u> (Hedw.) Warnst
<u>Desmatodon latifolius</u> (Hedw.) Brid.
<u>Pohlia</u> sp.
<u>Pohlia nutans</u> (Hedw.) Lindb.
<u>Lophozia floerkei</u> (Web. and Mohr) Schiffn.
<u>Nardia geoscyphus</u> (De Not.) Lindb.
<u>Bryum</u> sp.
<u>Philonotis fontana</u> (Hedw.) Brid.
<u>Cephalozia bicuspidata</u> (L.) Dum.
<u>Dicranum scoparium</u> Hedw.
<u>Brachythecium reflexum</u> (Starke ex Web. and Mohr) B.S.G.

APPENDIX B

Vegetation (species X quadrats) data matrices at agg6a and 6b in the subalpine meadow. Data matrices are divided into subcommunities 1-3 at agg6a and 1-8 at agg6b. Species names corresponding to the codes used below may be found in Appendix A. Cover scale values: - (absent), 1 (<5% aerial cover), 2 (6-25%), 3 (26-50%), 4 (51-75%), 5 (76-100%).

Agg6a

	1	2	3
	111111111111222222222233333333		
	12345678901347	2568901	234567890123456
CARSPE	22223222222321	111111-1	-----11111-11
LUPLAT	1231-2111121331	111113-	-----
VALSIT	12232132222121	1111-	-----
SENTRI	21-21-11-1-111	---11-1	-----
HIEGRA	-12-121111111111	111-11-1	-----
POACUS	111111--1111--	111--1	11111111-11--11-
JUNCSP	112121121112111	-2121212	-1111-1-----
VERWOR	1--1--11-111111	111111-	111-1-----1---
POTFLA	2--11-11-11--	-----	-----1-----
LUZPAR	-11111-11-----	1-----	-----
ANEOCC	---1--11-2111--	-1--1--	-----
ABILAS	---1-----1--	-----	-----
ERYGRA	----1-----	-----	-----
CASPAR	---1---1-1121-1	-1-1-111-	1-----
POALEP	---11-1112111-	-----	-----
RANESC	---11-11-1111-	-----	-----
TRISPI	-----1---11-1-	--1-1-	-----
PEDBRA	-----1-----	-----	-----
CARNIG	222333332332211	1111222343453443544554	
ERIPER	21121-111223221	222212122111-	-----1---
LUEPEC	112--21-2-11113	332232221111111-	-----1---
CASMER	1----1----11113	3222232111-	-----1-----
PETFRI	1-----	-----1-----	-----
PHLALP	1-----	-----1-----	-----
VACDEL	-----1-----	-----1-----	-----
LYCSEL	-----	-----1-----11-----	-----
KATMIC	-----	-----11111-1-----	-----
CETSUB	-1--11--1--1--1-	-21111-	1-----
PHYEMP	1-----	12232221111111-	1-----
CALBIF	1-----21112	212333231231121-	2-12
LEPPYR	1-----	-12112213212112-	-2--2
EPIANA	1111-1111111111	1-111212121121111-	2111
ANTALP	-----1-----	-----11-----1111111-	-----
AGRTHU	-----	-----1111121111-	1-1-1-1
EQUARV	-----	-----1-----1-----1-----1-----	1-1-1-1-1-1
SPHWAR	-----	-----	-----1-----

	1	2	3	4	5	6	7	8
	1	1	1	1	1	1	2	2
	12569	37814	40452	3687	9012	34825	67901	
SENTRI	22221	1	1	1	1	1	1	
VERWOR	11111	1	1	1	1	1	1	1
POTFLA	21111	1	1	1	1	1	1	1
CARSPE	23232	2	2	2	2	2	2	2
VALSIT	12222	2	2	2	2	2	2	2
PHLALP	11	1	1	1	1	1	1	1
ANEOCC	1121	1	1	1	1	1	1	1
ABILAS	1	1	1	1	1	1	1	1
POALEP	1111	1	1	1	1	1	1	1
RANESC	1111	1	1	1	1	1	1	1
HIEGRA	1111	1	1	1	1	1	1	1
JUNCSP	1111	2	2	2	2	2	2	2
LUZPAR	1111	1	1	1	1	1	1	1
ERYGRA	1111	1	1	1	1	1	1	1
LUPLAT	1111	1	1	1	1	1	1	1
TRISPI	1111	1	1	1	1	1	1	1
VACDEL	1111	1	1	1	1	1	1	1
PEDBRA	1111	1	1	1	1	1	1	1
CASMER	1111	1	1	1	1	1	1	1
POACUS	1111	1	1	1	1	1	1	1
LUEPEC	1111	1	1	1	1	1	1	1
ERIPER	2211	2	2	2	2	2	2	2
CALBIF	1111	1	1	1	1	1	1	1
PHYEMP	1111	1	1	1	1	1	1	1
CASPAR	1111	1	1	1	1	1	1	1
ANTALP	1111	1	1	1	1	1	1	1
KATMIC	1111	1	1	1	1	1	1	1
CETSUB	1111	1	1	1	1	1	1	1
LEPPYR	1111	1	1	1	1	1	1	1
EPIANA	1111	1	1	1	1	1	1	1
PETFRI	1111	1	1	1	1	1	1	1
LYCSEL	1111	1	1	1	1	1	1	1
AGRTHU	1111	1	1	1	1	1	1	1
EQUARV	1111	1	1	1	1	1	1	1
CARNIG	21323	3423	2311	1112	3224	5433	4544	5455
SPHWAR	1111	1	1	1	1	1	1	1