K. Klinka, Faculty of Forestry, University of British Columbia, Vancouver, B.C., Canada V6T 1W5

J. Pojar, B.C. Forest Service, Prince Rupert Region, Bag 5000, Smithers, B.C., Canada V0J 2N0

and

D. V. Meidinger, B.C. Forest Service, Research Branch, 31 Bastion Square, Victoria, B.C., Canada V8W 3E7

Revision of Biogeoclimatic Units of Coastal British Columbia

Abstract

Tabular and multivariate analyses using subsets of 1299 samples of alpine, subalpine, montane, and submontane, zonal, climax vegetation resulted in a revision and refinement of the biogeoclimatic units for coastal British Columbia originally proposed by Krajina and modified by subsequent workers. The revision conserved the existing four biogeoclimatic zones (Coastal Douglas-fir, Coastal Western Hemlock, Mountain Hemlock, and Alpine Tundra) but increased the number of subzones from two to ten in the Coastal Western Hemlock zone, from two to four in the Mountain Hemlock zone and reduced the number of subzones from two to one in the Coastal Douglas-fir zone. Diagnostic tables, climatic summaries, and ordination results are presented to show relationships among the zones and subzones. Climatic data suggest that the four zones, each characterized by a unique Koppen's climatic type, represent major segments of the regional temperature gradient, while subzones reflect division of this gradient according to continentality, precipitation, and temperature.

Introduction

Biogeoclimatic ecosystem classification (BEC), recently reviewed by Pojar *et al.* (1987), is used both as a research and forest management tool in British Columbia. This paper focuses on zonal classification of the BEC system, at which ecosystems are organized into biogeoclimatic subzones and zones according to similarities in regional climate.

Many ecological classifications have organized ecosystems according to regional climate. Some classifications are based on the results of climatic analysis (e.g., Rauscher 1984, van Groenewoud 1984, Denton and Barnes 1988) while others have adopted the zonal or climatic climax concept to delineate regional climates (e.g., Krajina 1965, Daubenmire 1968, Damman 1979, Bailey 1988). In the latter approach, vegetation is used as a surrogate for climate. The BEC system uses the zonal concept and the vegetation of zonal climax ecosystems to frame biogeoclimatic subzones—classes of ecosystems each presumed to be influenced by roughly the same climate. Zonal ecosystems are those in which the integrated influence of climate on vegetation, soil, and other ecosystem components is most strongly expressed. Climate influences ecosystems most strongly if its effects are modified as little as possible by disturbance, local topography, and physical and chemical properties of the soil. Zonal climax ecosystems must feature (i) intermediate topographic and edaphic conditions in relation to the existing extremes and (ii) the near-climax or climax stage of vegetation development (*op. cit.*).

The original zonal classification for coastal British Columbia, developed by Krajina (1959, 1965, 1969, 1972) was based mostly on dissertation data from the south coast (McMinn 1957, Mueller-Dombois 1959, Archer 1963, Orloci 1964, Cordes 1972, Brooke *et al.* 1970, Kojima 1971). From 1975 to 1985, further sampling was carried out throughout the coast by the Ecological Program Staff of the British Columbia Forest Service, from low to high elevations and across the range of climates (Figure 1). The new data indicated that the original biogeoclimatic subzones were too general (see Table 1) and that the subsequent modifications were local and inconsistent revisions of the zonal classification (e.g., Packee 1974; Klinka *et al.* 1979, 1984).

In the western United States, ecological zones of habitat type classification (Pfister and Arno 1980; Franklin *et al.* 1988) or vegetation zones of plant community classification (Franklin and Dyrness 1973) occupy a similar place in the classification hierarchy as biogeoclimatic zones do in the BEC system (see Ferguson *et al.* 1989). However, the resultant zones are not the same in coastal British Columbia and Alaska-Washington-Oregon.

The aim of this study is to present the result of a refined zonal classification which combines and

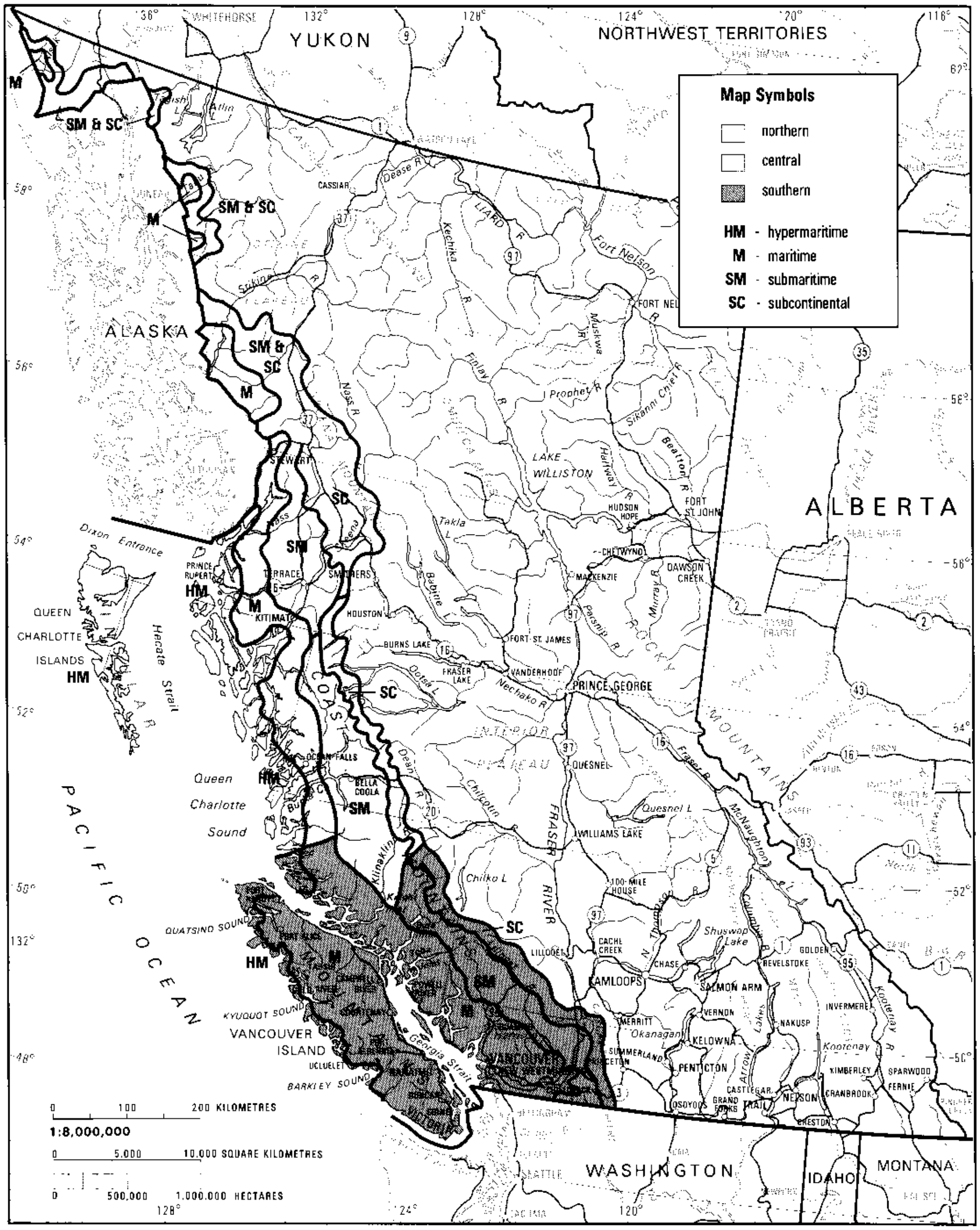

Figure 1. Outline of four continentality strata (hypermaritime, maritime, submaritime, and subcontinental) and three latitudinal strata (north, central, and south) as applied in zonal classification in coastal British Columbia.

TABLE 1. Biogeoclimatic zones and subzones of coastal British Columbia, and correspondence between biogeoclimatic zones and the ecological zones of habitat type classification.

Revised units Zone Subzone	Krajina (1969) Zone Subzone	Corresponding ecological zones of habitat type classification to biogeoclimatic zones
Coastal Douglas-fir (CDF)	**Coastal Douglas-fir** (CDF)	*Abies grandis*
Moist Maritime CDF (CDFmm[1])	Drier CDF (CDFa)	*Pseudotsuga menziesii*
		Quercus garryana
		Thuja plicata[2]
Coastal Western Hemlock (CWH)	**Coastal Western Hemlock** (CWH)	*Abies amabilis*[2]
Wet Hypermaritime CWH (CWHwh)	Wetter CWH (CWHb)	*Chamaecyparis nootkatensis*[2]
Very Wet Hypermaritime CWH (CWHvh)	Wetter CWH (CWHb)	*Picea sitchensis*
		Thuja plicata
Very Dry Maritime CWH (CWHxm)	Wetter CDF (CDFb), Drier CWH (CWHa)[2]	*Tsuga heterophylla*[2]
Dry Maritime CWH (CWHdm)	Drier CWH (CWHa)[2]	
Moist Maritime CWH (CWHmm)	Wetter CWH (CWHb)	
Wet Maritime CWH (CWHwm)	Wetter CWH (CWHb)	
Very Wet Maritime CWH (CWHvm)	Wetter CWH (CWHb)	
Dry Submaritime CWH (CWHds)	Drier CWH (CWHa)	
Moist Submaritime CWH (CWHms)	Wetter CWH (CWHb)	
Wet Submaritime CWH (CWHws)	Wetter CWH (CWHb)	
Mountain Hemlock (MH)	**Mountain Hemlock** (MH)	*Abies amabilis*[2]
Parkland Hypermaritime MH (MHph)	Parkland MH (MHb)	*Abies lasiocarpa*[2]
Forested Hypermearitime MH (MHfh)	Forest MH (MHa)	*Chamaecyparis nootkatensis*[2]
		Tsuga mertensiana
Parkland Maritime MH (MHpm)	Parkland MH (MHb)	
Forested Maritime MH (MHfh)	Forest MH (MHa)	
Alpine Tundra (AT)	**Alpine Tundra** (AT)	
Maritime AT (ATm)	Coastal AT (ATa)	

[1] The lowercase symbols used for subzones designate precipitation (x—very dry, d—dry, m—moist, w—wet, v—very wet), continentality (h—hypermaritime, m—maritime, s—submaritime), and physiognomy (p—parkland, f—forested).

[2] in part.

analyzes all the coastal zonal vegetation data available to date. The tabular method was used to classify zonal climax ecosystems and multivariate methods were used to analyze floristic relationships. The results include diagnostic vegetation and selected climatic characteristics of biogeoclimatic zones and subzones and an evaluation of floristic relationships.

Materials and Methods

The complete data set included 1299 sample plots selected, from over 5000 plots using the topographic and edaphic criteria given in Pojar *et al.* (1987, p. 127), to represent zonal, late-seral ecosystems (usually mature forests older than 200 years). The data were obtained from dissertations (McMinn 1957; Orloci 1961, 1964; Archer 1963; Brooke *et al.* 1970; Kojima 1971; Cordes 1972; Roemer 1972; Klinka 1976; Beese 1981; Roy 1984; Kabzems 1985), research reports (Lewis 1982, 1985), and from unpublished survey results on file with the B.C. Forest Service.

We have used the same methods of sampling and vegetation description as outlined in Brooke *et al.* (1970). At each 0.04 ha plot, chosen to represent a relatively uniform community, all plant species present in the tree, shrub, herb, and moss strata were identified and their cover was estimated using the Domin-Krajina scale of species significance (Mueller-Dombois and Ellenberg 1974). In addition, the environment of each sample plot was described, with emphasis on site features which could be feasibly measured (Brooke *et al.* 1970). In this paper, nomenclature for vascular plants follows Taylor and MacBryde (1977); for bryophytes Ireland *et al.* (1987) and Stotler and Crandall-Stotler (1977); and for lichens Hale and Culberson (1970).

The vegetation classification followed the methods described by Pojar *et al.* (1987). Reciprocal averaging (Gauch 1977) was used to group floristically similar sample plots. The Braun-Blanquet tabular method was used to identify diagnostic combinations of species (including differential[1] and dominant-differential[2] species) that were exclusive[3] for each group of plots (Pojar *et al.* 1987).

Distinguished zonal, climatic climax plant associations were used to define biogeoclimatic subzones, and the distribution of these associations on zonal sites delineated the geographical extent of the subzones. Floristically similar subzones were grouped into zones. Each zone was defined by a plant order circumscribing all zonal plant associations in that zone. Nomenclature of zones followed Krajina (1965 *et seq.*); subzones were named by adding two or three adjectives indicative of regional climate or vegetation physiognomy (see Table 1).

To examine floristic relationships among the biogeoclimatic zones and subzones, the vegetation data were submitted to principal components analyses (PCAs). PCA, using a reduced number of plots and mid-point percent cover of diagnostic species (see footnote 3 in Table 2), was performed on a correlation matrix (Noy-Meir and Whittaker 1977). The plot reduction, due to our concern of over large variation in sample size, was done randomly to a maximum of 50 plots per biogeoclimatic subzone (zonal plant association). Thus from a total number of 1299 only 633 plots were submitted to PCA. The selective species reduction to diagnostic species (Tables 2 and 4) were shown by Klinka *et al.* (1985) and Courtin *et al.* (1989) to account for the greatest variability in vegetation data.

Overall eigenstructure and significance of axes extracted by PCA were evaluated by tests of variable independence and equicorrelation (Morrison 1976). Relationships between the principal components and vegetation was examined by correlating component scores with individual species values ['component correlation,' Pimentel (1979)]. To avoid cluttering the PCA ordination with a large number of plots, zones and subzones were represented by centroids and 95% confidence ellipses of the first two PCA axis scores (Owen and Chmielewski 1985). Location, orientation, and overlap of confidence ellipses in the two-dimensional space were used to assess affinities among and variability within zones and subzones.

Climate is used in zonal classification only as an accessory characteristic. Each recognized biogeoclimatic unit was climatically characterized, using selected climatic parameters (Trewartha 1968), to assure its ecological significance, i.e., to show correspondence between zonal climax ecosystems and climate. Climatic data were obtained from short- and long-term stations operated by the Atmospheric Environmental Service, Environment Canada (Anonymous 1982), and short-term stations in the network of the Waste Management Branch, B.C. Ministry of Environment. Due to the poor representation of montane, subalpine, and alpine climates, predictions were made for areas outside the networks using isorhythmic maps compiled by the Waste Management Branch or parameter-elevation relationships. The latter involved extrapolating climatic data from selected base stations to predict values at certain elevations where climatic stations are non-existent, as in alpine and some montane and subalpine areas.

Results and Discussion

Biogeoclimatic Zones

When compared to Krajina (1959), the revision conserved all four coastal zones (Table 1), which are well segregated floristically (Table 2). The CDF and CWH zones are differentiated from other zones by the presence of *Thuja plicata* and *Vaccinium parvifolium. Abies grandis, Holodiscus discolor, Mahonia nervosa, Rosa gymnocarpa, Rubus ursinus,* and *Trientalis latifolia* are the prominent differential species for the CDF zone, *Tsuga heterophylla* for the CWH zone, *Tsuga mertensiana* for the MH zone, and *Cassiope mertensiana, Phyllodoce empetriformis,* and *Luetkea pectinata* for the AT zone.

Series in habitat type classification represent aggregations of plant associations, which in practice in the western United States represent groupings of plant associations with the same dominant climax tree species (Pfister and Arno 1980, Franklin *et al.* 1988). A 'habitat type' zone is the land area where a single series is dominant under stable or climax conditions (Franklin *et al.* 1988, p. 30); i.e., the land area with the same dominant climax tree species. According to this system, zones recognized in the coastal forests of western North America include the *Pseudotsuga menziesii, Tsuga heterophylla, Thuja plicata, Picea sitchensis, Abies amabilis, Abies lasiocarpa, Chamaecyparis nootkatensis,* and *Tsuga mertensiana* zones. These

TABLE 2. Diagnostic combinations of species for zones of coastal British Columbia.

Column identification		CDF		CWH		MH		AT	
Number of plots		83		1009		187		20	
Biogeoclimatic zone and species	Diagnostic value[1]	Presence class[2] and mean species significance[3]							
CDF and CWH zones									
Thuja plicata	(d)	IV	5	IV	5	I	1		
Vaccinium parvifolium	(d)	IV	2	IV	3	II	1		
Coastal Douglas-fir (CDF) zone and Moist Maritime CDF (CDFmm) subzone									
Abies grandis	(d)	IV	5	I	+				
Acer macrophyllum	(d)	III	3	I	+				
Achlys triphylla	(d)	III	3	I	1	I	+		
Cornus nuttallii	(d)	III	3	I	+				
Festuca subulata	(d)	IV	1	I	+				
Gaultheria shallon	(d,cd)	V	6	II	5	I	+		
Holodiscus discolor	(d)	IV	5	I	+				
Lonicera ciliosa	(d)	IV	1	I	+				
Mahonia nervosa	(d,cd)	V	7	I	2				
Polystichum munitum	(d)	IV	2	II	1	I	+		
Pseudotsuga menziesii	(d,cd)	V	8	III	5	I	+		
Pteridium aquilinum	(d)	IV	3	I	1	I	+		
Rosa gymnocarpa	(d,c)	V	2	I	+				
Rubus ursinus	(d,c)	V	3	I	+				
Kindbergia oregana	(d,cd)	V	6	II	3	I	+		
Symphoricarpos albus	(d)	III	2	I	+				
Symphoricarpos hesperius	(d)	III	4	I	+				
Trientalis latifolia	(d,c)	V	3	I	+				
Coastal Western Hemlock (CWH) zone									
Hylocomium splendens	(d,cd)	III	4	V	5	III	3		
Tsuga heterophylla	(d,cd)	I	2	V	7	III	4		
Mountain Hemlock (MH) zone									
Coptis aspleniifolia	(d)			I	+	III	1		
Rubus pedatus	(d)			II	2	IV	2		
Tsuga mertensiana	(d,cd)			I	2	V	6	II	2
Vaccinium ovalifolium	(d)			II	3	IV	3		
Alpine Tundra (AT) zone and Maritime AT (ATm) subzone									
Barbilophozia floerkei	(d)			I	+	I	1	III	4
Cassiope mertensiana	(d,cd)					II	3	V	7
Luetkea pectinata	(d)					II	2	IV	3
Lycopodium sitchense	(d)					I	+	III	3
Phyllodoce empetriformis	(d,cd)			I	+	II	4	V	7
Rhacomitrium heterostichum	(d)			I	+	I	+	III	3
Vahlodea atropurpurea	(d)					I	+	III	1

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[1] Species diagnostic values: d—differential, dd—dominant differential, cd—constant dominant, c—constant (Pojar *et al.* 1987).

[2] Presence classes as percent of frequency: I = 1-20, II = 21-40, III = 41-60, IV = 61-80, V = 81-100.

[3] Species significance class midpoint percent cover and range: + = 0.2 (0.1-0.3), 1 = 0.7 (0.4-1.0), 2 = 1.6 (1.1-2.1), 3 = 3.6 (2.2-5.0), 4 = 7.5 (5.1-10.0), 5 = 15.0 (10.1-20.0), 6 = 26.5 (20.1-33.0), 7 = 41.5 (33.1-50.0), 8 = 60.0 (50.1-70.0), 9 = 85.0 (70.1-100).

zones correspond only roughly to biogeoclimatic zones (Table 1), which represent land areas on which climatic climax vegetation (vegetation of zonal sites) is closely related—but does not necessarily have the same dominant climax tree species.

The first two PCA axes accounted for 41% of the total variance, and all 28 diagnostic species (Table 2) were found to be significantly correlated with the first, or second, or both PCA axes. The species diagnostic for the CDF zone were most strongly and positively correlated with the first axis, whereas the species diagnostic for the AT were most strongly and positively correlated with the second axis. The species diagnostic for the MH and CWH zones were most strongly and negatively correlated with the first and second axis, respectively.

The 95% confidence ellipses obtained from the PCA ordination of 633 sample plots showed that the CDF zone was almost completely separated from the CWH, MH, and AT zones along the first PCA axis; along the second PCA axis the AT zone was almost completely separated from the MH and CWH zones but the MH and CWH zones overlapped (Figure 2). Considering the joint distribution of species and zones (Table 2) and climatic characteristics (Table 3), the first PCA axis represents a precipitation gradient (by isolating the driest CDF zone), and the second PCA axis a temperature gradient. These results can be interpreted as

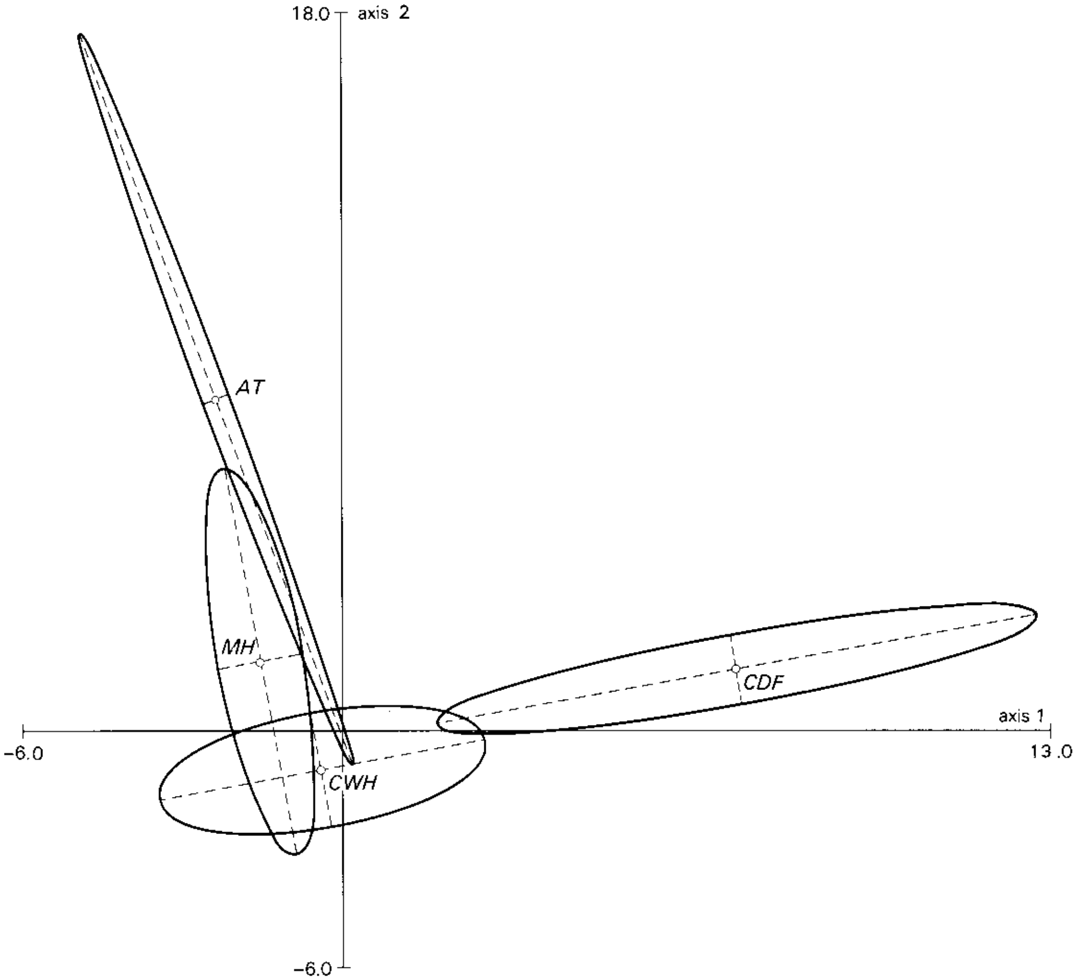

Figure 2. Ordination of plots along the first two axes of PCA on diagnostic species showing centroids and 95% confidence ellipses for the AT, MH, CDF, and CWH zones.

TABLE 3. Means and standard deviations (in parentheses) of selected climatic characteristics for AT, MH, CDF, and CWH zones.

Climatic characteristic	CDF	CWH	MH[1]	AT[1]
Number of stations for precipitation data	112	169	47	7
Mean annual precipitation (mm)	1233 (368)	2228 (713)	2620 (578)	2706 (555)
Mean precipitation April-Sept. (mm)	289 (98)	611 (227)	632 (114)	647 (65)
Mean ppt. of the driest summer month (mm)	30 (12)	63 (24)	62 (13)	70 (8)
Mean ppt. of the wettest winter month (mm)	210 (64)	350 (108)	414 (107)	434 (110)
Number of stations for temperature data	73	11	47	17
Mean annual temperature (°C)	9.6 (0.5)	7.9 (1.6)	3.0 (1.1)	0.3 (0.9)
Mean temperature of the warmest month (°C)	17.0 (0.8)	15.6 (1.7)	11.1 (1.1)	9.2 (0.8)
Mean temperature of the coldest month (°C)	2.3 (1.0)	0.2 (3.0)	−5.1 (1.7)	−8.9 (2.7)
Number of months with mean temperature > 10°C	5.5 (0.5)	4.7 (0.8)	1.7 (0.9)	0.1 (0.4)
Index of continentality[2]	12 (3)	13 (7)	16 (3)	20 (7)

[1] All values given for the AT and MH zones were extrapolated from selected base stations in the CWH zone.

[2] Index of continentality = $[1.7(\text{mean } T_{JULY} - \text{mean } T_{JAN})/\sin c_{DEGREES\ LATITUDE}] - 20.4$, where T—temperature (°C) (after Rose and Grant 1976).

demonstrating that the CDF zone is a discrete regional ecosystem, while the AT, MH, and CWH zones represent floristically-defined segments of an altitudinal climatic gradient.

In the Pacific Northwest, the same gradients have been interpreted or identified as the primary environmental gradients underlying the variation in zonal vegetation (e.g., Franklin and Dyrness 1973, Dyrness *et al.* 1974, Zobel *et al.* 1976, del Moral and Watson 1978, Agee and Kertis 1987). Temperature appears to be more important in separating between vegetation zones, whereas moisture tends to be more useful in differentiating within submontane and montane zones (Zobel *et al.* 1976). The array of zonal climax plant associations in the two-factor ordination in Figure 2 generally corresponds to the ordinations presented by Zobel *et al.* (1976, Figure 7) and Agee and Kertis (1987, Figure 2).

From the suite of available climatic characteristics, we choose to emphasize the differences in temperature and precipitation, with temperature-related variables appearing to best summarize the differences among the zones (Table 3). Precipitation-related variables segregated the CDF zone from the CWH zone—the former associated with a dry cool mesothermal (Csb) climate, the latter with a wet cool mesothermal (Cfb) climate (Trewartha 1968). At approximately 10°C, mean annual range of temperature (i.e., the mean temperature of the warmest month minus that of the coldest month) in the CDF and CWH zones is the smallest for regional climates in Canada (Schaefer 1978). Mean annual temperatures in the CDF zone are among the highest in Canada, and heavy precipitation makes the CWH and MH zones and Maritime AT subzone by far the wettest part of Canada.

The CDF, CWH, MH, and AT zones manifest abrupt vegetation changes that occur in response to abrupt climatic changes in coastal mountains. At elevations above approximately 1500 m, scattered clumps of trees give way to krummholz, low shrub, and heath (dwarf evergreen shrub) communities under the influence of alpine tundra (ET) climate. Below 1500 m and above approximately 1000 m and with decreasing elevation, scattered clumps of trees merge with more continuous forest under the influence of maritime subalpine boreal (Dfc) climate with deep snow cover. Heavy snowpacks insulate MH soils from frost. The MH zone is the core distributional area of *Tsuga mertensiana*. Snow depth in the AT zone is generally less than in the MH zone. Lower temperatures, however, retard the melting rate of snow in alpine ecosystems so that snow duration critically influences alpine vegetation. When the subalpine climate becomes more continental and soils freeze before deep snow accumulates, *Tsuga mertensiana* and *Abies amabilis* are replaced by *Picea engelmannii* and *Abies lasiocarpa*, and the MH zone is replaced by the Engelmann Spruce–Subalpine Fir (ESSF) zone.

Snow depth and duration have less influence on the vegetation at elevations below approximately 1000 m (Brooke *et al.* 1970). These lower elevations feature a wet cool mesothermal (Cfb) climate which coincides with the core distributional area of coastal *Pseudotsuga menziesii*, *Thuja plicata*, and *Tsuga heterophylla*. *Tsuga heterophylla* is nearly absent in the CDF zone, with the mean precipitation of the driest month of summer ≤30 mm, whereas in the CWH zone, with a mean precipitation of the driest month of summer >30 mm, this shade-tolerant species has the potential to dominate the tree stratum on zonal sites. Inland from the core distributional area of *Tsuga heterophylla*, with increasing continentality and decreasing temperature and/or precipitation, the CWH zone is replaced by interior or continental biogeoclimatic zones east of the Coast-Cascade Mountains.

Coastal Douglas-fir Subzone

We have retained only one subzone–the Moist Maritime CDF (CDFmm) subzone (formerly the Drier CDF subzone)–within the CDF zone and amalgamated the former Wetter CDF subzone and the Vancouver Island portion of the former Drier CWH subzone into a Very Dry Maritime CWH (CWHxm) subzone (Table 1). A comparison of these latter two units showed high floristic similarities (exemplified by widespread occurrence of *Rhytidiadelphus loreus* and *Tsuga heterophylla*) and climatic similarities (a relatively uniform, wet cool mesothermal climate) (see Table 4); the original Drier CDF subzone, however, has distinct zonal vegetation (Table 2), and a dry cool mesothermal climate (Table 3). The diagnosis of the CDFmm subzone is based on 82 samples from the Saanich Peninsula (Roemer 1972), which

TABLE 4. Means and standard deviations (in parentheses) of selected climatic characteristics for CWH subzones[1].

Characteristic	CWHwh	CWHvh	CWHxm	CWHdm	CWHmm	CWHwm	CWHvm	CWHds	CWHms	CWHws
Number of stations for precipitation data	5	28	81	53	13	6	34	9	5	4
Mean annual precipitation (mm)	1349 (146)	2951 (657)	1505 (385)	1827 (326)	2349 (453)	2124 (342)	2787 (680)	1627 (367)	1683 (312)	1449 (410)
Mean precipitation April-Sept. (mm)	433 (61)	890 (193)	363 (96)	498 (89)	470 (50)	780 (242)	752 (200)	419 (109)	423 (90)	412 (148)
Mean ppt. of the driest summer month (mm)	54 (10)	96 (22)	39 (13)	53 (10)	45 (5)	86 (29)	75 (21)	45 (11)	40 (4)	45 (18)
Mean ppt. of the wettest winter month (mm)	204 (21)	431 (113)	251 (70)	292 (55)	400 (75)	362 (44)	436 (103)	259 (54)	262 (48)	244 (64)
Number of stations for temperature data	5	21	54	53	13	6	21	7	3	4
Mean annual temperature (°C)	7.6 (0.2)	8.2 (0.9)	9.3 (0.6)	9.8 (0.4)	5.7 (0.9)	5.5 (0.3)	8.2 (1.1)	7.8 (1.2)	5.9 (0.8)	5.5 (0.8)
Mean temperature of the warmest month (°C)	14.6 (0.3)	13.9 (0.8)	17.0 (0.8)	17.6 (0.5)	14.1 (1.0)	14.1 (0.8)	16.0 (1.1)	17.4 (1.4)	15.1 (0.8)	15.5 (1.0)
Mean temperature of the coldest month (°C)	1.3 (0.6)	3.0 (1.4)	1.8 (0.9)	1.9 (0.7)	−2.2 (1.1)	−4.2 (1.3)	0.3 (2.7)	−3.0 (2.3)	−4.2 (0.8)	−6.0 (0.6)
Number of months with mean temp. >10°C	4.0 (0.0)	4.4 (0.7)	5.4 (0.5)	5.7 (0.4)	3.9 (0.5)	3.8 (0.4)	4.9 (0.6)	5.0 (0.6)	4.3 (0.6)	4.2 (0.5)
Index of continentality	6 (2)	3 (2)	14 (3)	15 (2)	16 (2)	17 (4)	14 (6)	24 (7)	23 (0)	24 (3)

[1] Symbols for CWH subzones are defined in Table 1.

form the zonal *Pseudotsuga-Mahonia* plant association.

This revision restricts the CDF zone to the driest part of Vancouver Island, the Gulf Islands, and the southern mainland coast, in the rain shadow of the Olympic and Vancouver Island Mountains; i.e., to the area where coastal Douglas-fir is a moderately shade-tolerant tree and has the potential to dominate the tree stratum on zonal sites. This area extends south through Washington (in the Puget Sound rain shadow of the Olympic Mountains) and Oregon (Willamette Valley and Umpqua and Rogue Valleys) (Franklin and Dyrness 1973). If our sampling, classification, and analysis included the entire area influenced by a dry cool mesothermal climate, more CDF subzones would likely be recognized in response to floristic and climatic variations along a latitudinal gradient.

Coastal Western Hemlock Subzones

Our initial tabular analysis of CWH subzones failed to differentiate each zonal plant association (subzone) from the others, except at the climatic extremes of the data set. The analysis suggested that the differentiation could be more successful and clearer vegetation-climate relationships could be shown if subzones were subset into more inclusive groups. Therefore, we interpolated two categories between subzone and zone categories.

The two intercalary categories helped differentiate ten zonal plant associations, each delineating a subzone (tabular data available from the authors on request). All these associations belong to the *Tsuga heterophylla-Rhytidiadelphus loreus* plant order. The ten proposed CWH subzones [compared to the former drier and wetter subzones (Krajina 1965)] resulted from a combination of the three continentality strata (hypermaritime, maritime, and submaritime strata or subzones) and five relative precipitation strata [very dry, dry (drier stratum or subzones) and moist, wet, and very wet (wetter stratum or subzones)]. The first (more-inclusive) intercalary category related subzones to the three continentality strata, and the second (less-inclusive) category related subzones to two general precipitation strata (drier and wetter).

This large increase in the number of proposed CWH subzones can be explained by the large increase in the data base. The former drier and wetter subzones were based on data obtained only from the southern maritime portion of the CWH zone. We now have a fairly complete sampling over the broad range of floristic and climatic variation included in the CWH, our largest coastal zone.

Maritime subzones that represent the central concept of the CWH zone are without diagnostic species, which is permissible for one unit in relation to other units of the same rank and circumscription (Pojar *et al.* 1987). *Blechnum spicant, Coptis aspleniifolia, Listera cordata, Rhizomnium glabrescens, Picea sitchensis,* and *Scapania bolanderi* are diagnostic species for hypermaritime subzones; *Clintonia uniflora, Orthilia secunda,* and *Pleurozium schreberi* are diagnostic species for submaritime subzones.

Within each continentality stratum, a diagnostic combination of species was identified for each precipitation stratum. For example, within the maritime and submaritime strata, the wetter (moist to wet or very wet) subzones are segregated from the drier (very dry to dry) subzones by a prominent presence of *Abies amabilis, Cornus canadensis, Vaccinium alaskaense,* and *V. ovalifolium. Pseudotsuga menziesii* is the only diagnostic species common to the drier subzones. With the exception of *Gaultheria shallon,* differences between the Wet and Very Wet Hypermaritime CWH subzone are not strong (essentially showing trends in significance of diagnostic species); similar differences are apparent for wetter submaritime subzones (tabular data available from the authors on request).

The first two PCA axes accounted for 28% of the total variance, and all 43 diagnostic species were significantly correlated with the first, the second, or both PCA axes. The species diagnostic for the drier subzones were negatively correlated with the first axis, whereas the species diagnostic for the wetter subzones were postively correlated. This suggests that the greatest proportion of variance in species significance coincides with precipitation, and that the CWH subzones are primarily separated by precipitation (Dyrness *et al.* 1974, Zobel *et al.* 1976). The second axis appeared to be related to a temperature (continentality) gradient.

The PCA ordination of CWH sample plots was further examined by calculating 95% confidence ellipses for the three continentality and two precipitation strata and the subzones within each continentality stratum. The locations of the three continentality strata in the ordination indicated that the maritime subzones encompass most of the variation in the data set while the hypermaritime and submaritime subzones refer to specific regions within the total variation (Figure 3). Within the

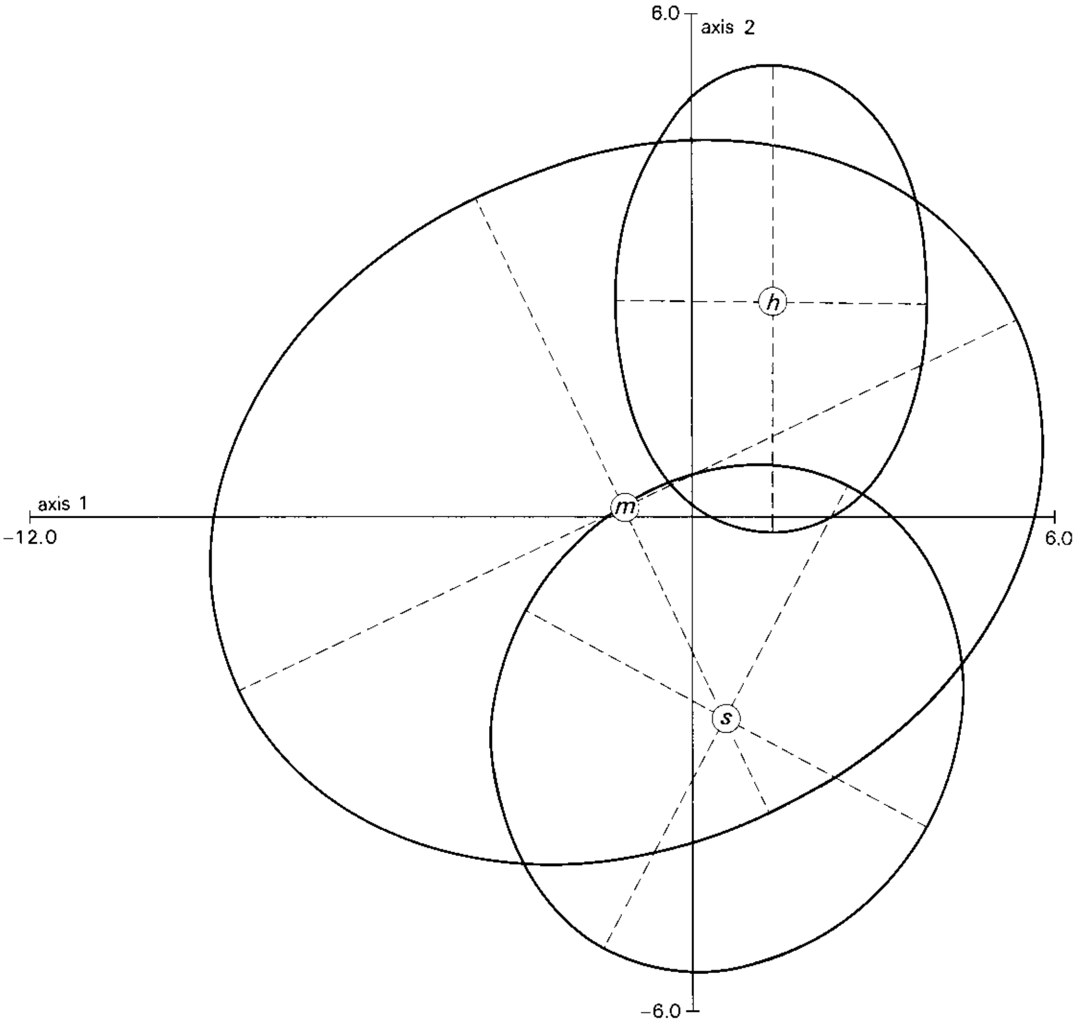

Figure 3. Ordination of plots along the first two axes of PCA on diagnostic species showing centroids and 95% confidence ellipses for the hypermaritime (h), maritime (m), and submaritime (s) CWH subzones.

hypermaritime stratum, the confidence ellipses for the wet and very wet subzones nearly completely overlapped. Within the maritime stratum the very dry, dry, and moist subzones were distinct from the wet and very wet subzones, which showed a nearly complete overlap (Figure 4). Within the submaritime stratum, all three subzones appeared to form distinct groups.

Climatic data compiled for continentality strata manifest decreasing precipitation (most apparent in the mean precipitation data of the wettest winter month), decreasing temperature of the coldest month, and increasing index of continentality along the longitudinal gradient (Table 4). Furthermore, marked differences between the drier and wetter precipitation strata in both precipitation and temperature related parameters are evident in the climatic summary.

There are pronounced differences in precipitation between the wet and the very wet hypermaritime subzones (Table 4). The former is located on the leeward side of the Queen Charlotte Islands, the latter occurs on the windward side of the Queen Charlotte Islands, the outer central mainland coast, and the outer west coast of Vancouver Island. In relative terms, the wet hypermaritime subzone is

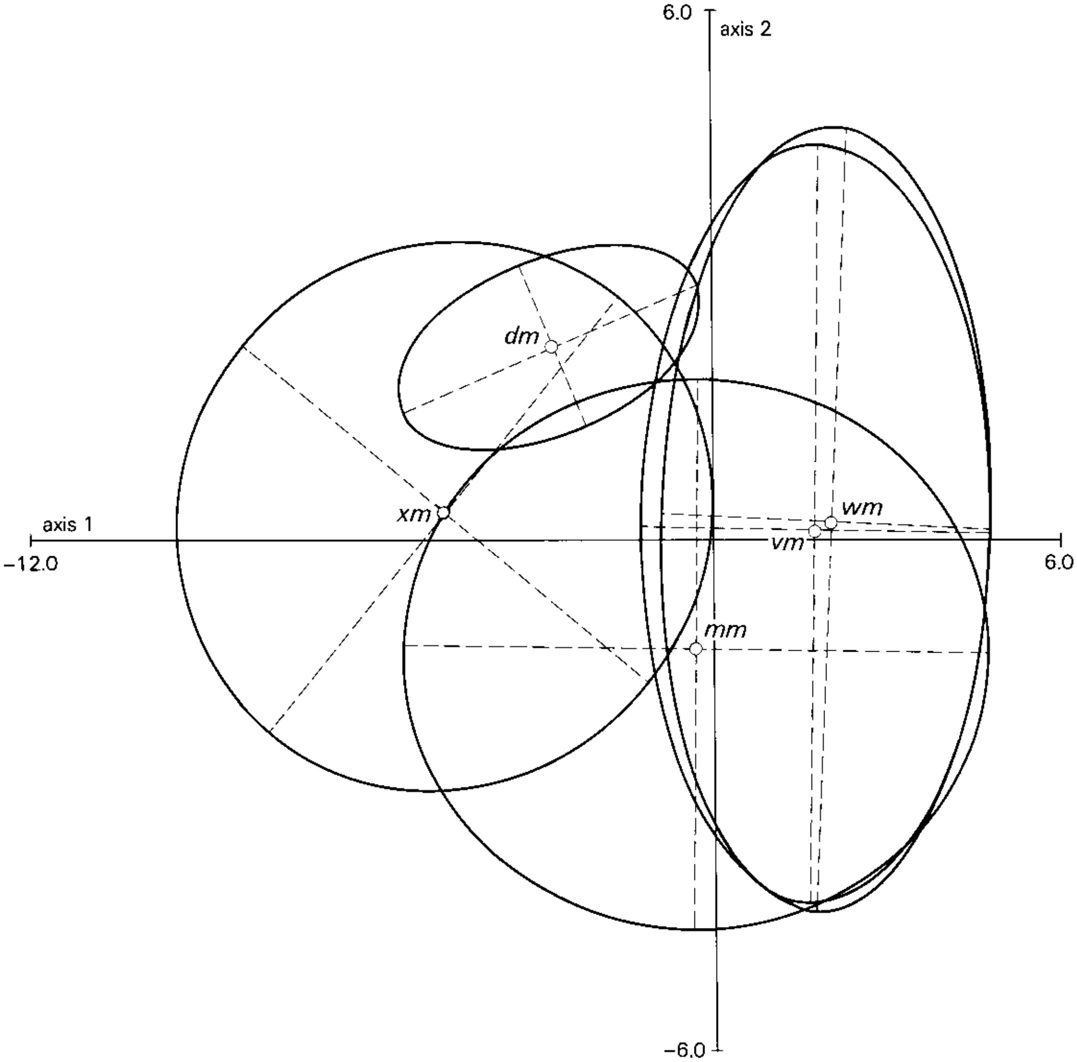

Figure 4. Ordination of plots along the first two axes of PCA on diagnostic species showing centroids and 95% confidence ellipses for the very dry maritime (xm), dry maritime (dm), moist maritime (mm), wet maritime (wm), and very wet maritime (vm) CWH subzones.

drier and cooler than the very wet hypermaritime subzone. Rainy and cloudy summer, wet fall, rainy winter with relatively low snowfall and ephemeral snowpack, and equable temperature are the characteristic climatic features of the hypermaritime subzones.

The very dry and dry maritime subzones are drier and warmer than the other maritime subzones (Table 4). The low growing-season precipitation of the moist maritime subzone (located on the windward side of Vancouver Island) and the cool winter temperature of the wet maritime subzone (located on the northern coastal mainland) segregate them from the very wet maritime subzone. Considering the mean temperature of the coldest month, the moist and the wet maritime subzones appear to have a wet cool temperate climate (Dfb) which is suggestive of an ecotone between the wet cool mesothermal and montane or subalpine boreal climates.

Submaritime subzones differed from each other mainly in temperature characteristics—the dry subzone being warmer than the moist and the wet subzones (Table 4). The wet submaritime subzone, located at higher latitudes, is the coolest in winter. All submaritime subzones also appear to have a wet cool temperate climate. Considering indices of continentality, the submaritime belt (see Figure 1) is likely dominated by a mild cool temperate climate.

As latitude increases, temperature decreases and the rain shadow of the Vancouver Island Ranges disappears—this is recognized in the presence of the 'cooler' wet maritime and wet submaritime subzones (Table 4) and the absence of drier subzones along the central and northern coast. Climatic changes along the longitudinal gradient are complicated by the presence of two successive large-scale mountain barriers aligned in a northwest to southeast direction—Queen Charlotte Island Mountains/Vancouver Island Ranges and Coast Mountains. When the air is forced up the west-facing slopes of these mountains, weather systems carried by prevailing westerly winds aloft drop considerable moisture; on the eastern slopes, the air descends and is heated by compression, causing the clouds to dissipate (Schaefer 1978). As a result, the windward slopes are always wetter and the leeward slopes are always drier and become more continental with increasing distance from the Pacific Ocean. Thus, drier subzones, with a prominent component of *Pseudotsuga menziesii*, are located at low elevations on the leeward side of coastal mountains (the very dry and dry maritime subzones in the rain shadow of the Olympic Mountains and Vancouver Island Ranges; and the dry submaritime subzone in the rain shadow of the Coast Mountains).

Wetter subzones, with a prominent component of *Picea sitchensis* or *Abies amabilis*, are located on the leeward side of the Queen Charlotte Mountains (the wet hypermaritime subzone) and Vancouver Island Ranges (the moist maritime subzone) and are drier and somewhat continental compared to their windward counterpart (Table 5).

Mountain Hemlock Subzones

By interpolating a category between the zone and subzone categories, it was possible to segregate four zonal plant associations corresponding to four subzones [compared to the former parkland and forested subzones (Krajina 1965)] (Tables 1 and 5). All four associations belong to the *Tsuga mertensiana* plant order. Relationships between subzones and continentality of a subalpine boreal climate were inferred from the continentality strata characterized for a cool mesothermal climate (CWH zone). This, however, cannot be confirmed without on-site climatic data (extrapolation of data from submontane stations was avoided).

Attempts to differentiate between maritime and submaritime subalpine strata showed primarily an increase in the presence and cover of *Abies lasiocarpa* and a decrease in *Chamaecyparis nootkatensis*. As a result, four proposed MH subzones were formed by a combination of merely two continentality strata (hypermaritime and maritime) and two physiognomic strata (parkland and forested) (Table 5). Minor floristic variations along the longitudinal gradient, presumably reflecting variations in continentality, were used to distinguish windward (more maritime) and leeward (less maritime) variants for each of the four subzones. It may be that in zonal climax vegetation the floristic contrast (and perhaps the climatic contrast) between maritime and submaritime strata diminishes with increasing altitude, or it may be that our present data base does not adequately represent the submaritime stratum of the MH zone. The recognition of additional subzones again reflects expanded sampling throughout the range of the zone. The former parkland and forested subzones were based on samples from the southern maritime portion of the MH zone.

The differentiation of MH subzones is not very strong, probably reflecting a low sampling intensity, especially in parkland subzones (Table 5). Hypermaritime subzones are distinguished by the nearly constant presence of *Blechnum spicant, Chamaecyparis nootkatensis, Coptis aspleniifolia, Hylocomium splendens, Picea sitchensis, Rhytidiadelphus loreus*, and *Tsuga heterophylla*—species that occur mainly within wet cool mesothermal climates. Maritime subzones, which represent the central concept of the MH zone, are differentiated by *Abies amabilis* and *Vaccinium membranaceum*, the latter species more typical of continental boreal climates.

In addition to the physiognomic differences (discontinuous versus continuous forest cover), diagnostic combinations of species for the parkland subzones include alpine elements, such as *Phyllodoce* spp. and *Cassiope* spp., while the intermediate presence of *Tsuga heterophylla* is characteristic for the lower portion of forested subzones (Table 5). The lack of differential species for the parkland hypermaritime subzone is attributed to inconsistencies in the nine samples collected on the Queen Charlotte Islands.

TABLE 5. Diagnostic combinations of species for subzones of the Mountain Hemlock (MH) zone.

Column identification Number of plots Biogeoclimatic zone and species	Diagnostic value	MHph 9		MHfh 31		MHpm 25		MHfm 122	
		Presence class and mean species significance							
Hypermaritime MH (MHh) subzones									
Blechnum spicant	(d)	IV	1	V	2			I	+
Chamaecyparis nootkatensis	(d)	IV	5	IV	6	II	2	II	3
Coptis aspleniifolia	(d,c)	IV	1	V	2			I	+
Cornus canadensis	(d)	III	2	IV	1			II	1
Hylocomium splendens	(d)	IV	4	V	4			II	2
Plagiothecium undulatum	(d)	III	1	IV	2			I	+
Rhytidiadelphus loreus	(d,cd)	V	5	V	6			III	3
Parkland Hypermaritime MH (MHph) subzone									
Cladina rangiferina	(d)	III	2			I	1	I	+
Phyllodoce empetriformis	(d)	III	5			V	5	I	1
Forested Hypermaritime MH (MHfh) subzone									
Calamagrostis nutkaensis	(d)	I	2	III	3				
Huperzia selago	(d)	I	+	IV	1			I	+
Listera caurina	(d)			III	1			I	+
Listera cordata	(d,c)	II	+	V	2	I	+	I	+
Menziesia ferruginea	(d)	I	+	III	2	I	+	IV	3
Mnium glabrescens	(d)	I	+	III	3			I	1
Moneses uniflora	(d)	I	+	III	1	I	+	I	+
Pellia neesiana	(d)	I	1	III	2				
Picea sitchensis	(d)	I	2	IV	4			I	+
Scapania bolanderi	(d,c)	II	3	V	4			I	+
Sphagnum girgensohnii	(d)	I	2	III	3			I	1
Streptopus roseus	(d)	II	+	IV	2	I	+	II	2
Tsuga heterophylla	(d,cd)	III	2	V	5	I	3	III	4
Vaccinium parvifolium	(d)	I	1	IV	2			I	+
Maritime MH (MHm) subzones									
Abies amabilis	(d,cd)	II	2	I	1	IV	4	V	6
Vaccinium membranaceum	(d)					V	5	IV	4
Parkland Maritime MH (MHpm) subzone									
Abies lasiocarpa	(d)			I	+	IV	4	II	3
Cassiope mertensiana	(d,cd)	II	2	I	2	V	5	I	+
Luetkea pectinata	(d)	II	2	I	+	IV	3	I	1
Phyllodoce empetriformis	(d,cd)	III	5			V	5	I	1
Vaccinium deliciosum	(d)	I	1			III	3	I	+
Forested Maritime MH (MHfm) subzone									
Menziesia ferruginea	(d)	I	+	III	2	I	+	IV	3
Rhytidiopsis robusta	(d,cd)	II	1	III	4	III	3	V	6
Rubus pedatus	(d,c)	IV	1	IV	2	III	1	V	4
Tsuga heterophylla	(d)	III	2	V	5	I	3	III	4
Vaccinium alaskaense	(d)	IV	3	III	4	I	2	IV	5

Diagnostic values, presence class, and mean species significance are defined in Table 2.

The first two PCA axes accounted for 45 percent of the total variance and all 24 diagnostic species (Table 5) were found to be significantly correlated with the first, the second, or both PCA axes. The species diagnostic for the hypermaritime subzones were correlated positively with the first axis, whereas the species diagnostic for the parkland and forested maritime subzones were correlated negatively. This suggests that the first axis reveals contrasts in continentality. The second axis appears to be related to a temperature gradient.

The PCA ordination of MH sample plots using 95% confidence ellipses for the four subzones complements the correlation pattern described for diagnostic species (Figure 5). The overlap of the confidence ellipses for the parkland and forested subzones indicates a gradual floristic change along an altitudinal gradient in the MH zone.

Scattered tree cover and persistent snowpack are the most obvious characteristics of parkland subzones. Trees grow largely on organic mounds that are free of snow for more than approximately

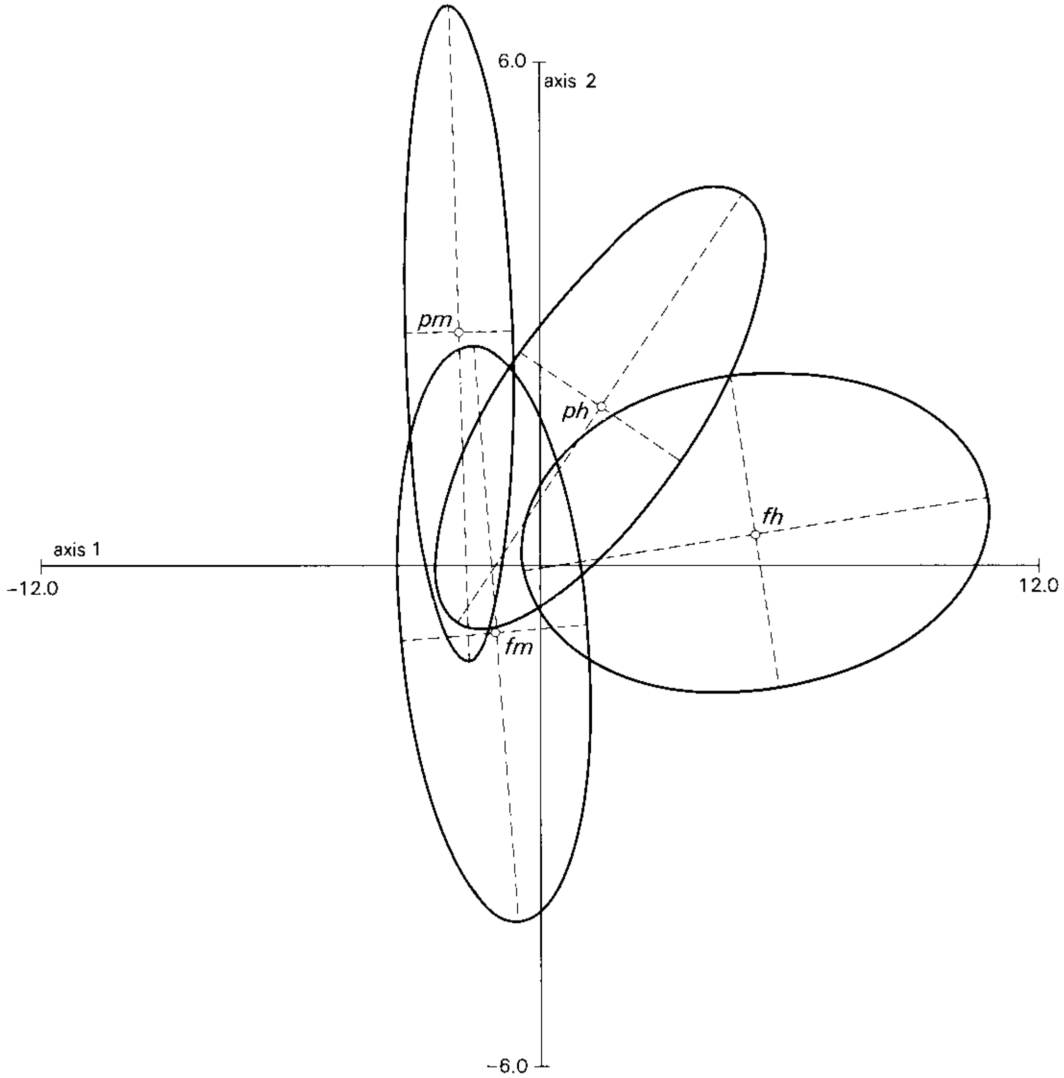

Figure 5. Ordination of plots along the first two axes of PCA on diagnostic species showing centroids and 95% confidence ellipses for the parkland, hypermaritime (ph), forested hypermaritime (fh), parkland maritime (pm), and forested maritime (fm) MH subzones.

three months. Heath, low shrub, graminoid, or forb communities influenced by more persistent snowpack cover much of the remaining area of parkland subzones. In contrast, forest cover is largely continuous in forested subzones and the climate is slightly warmer. Snow depth and duration are less than in the parkland subzones, resulting in a longer growing season and the establishment of complex forest communities (Brooke *et al.* 1970).

Alpine Tundra Subzone

There are insufficient data to differentiate the coastal portion of the AT zone beyond one subzone—the Maritime AT (ATm) subzone (Tables 1 and 2). This subzone is diagnosed by 40 samples that form the zonal *Cassiope-Phyllodoce* plant association (Archer 1963) in the southern portion of the Pacific Ranges. Field observations, however, indicate that the changes in zonal alpine communities along the longitudinal gradient parallel those described in this paper for zonal subalpine communities.

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Footnotes

1. Differential species are clearly associated with one or more than one unit in a hierarchy; presence class ≥III and at least two presence classes greater than in other units of the same category and circumscription.

2. Dominant-differential species do not meet the presence criteria above but show clear dominance in one or more than one unit in a hierarchy; presence class ≥III, mean species significance ≥5 and two or more significance classes greater than in other units of the same category and circumscription.

3. A unit is distinguished by an exclusive diagnostic combination of species that must include at least one differential or dominant-differential species; the unit that represents the central concept of a higher circumscribing unit can also be recognized without a diagnostic combination of species.

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