Vegetatio vol. 38, 1: 29–48

GRADIENT STRUCTURE OF FOREST VEGETATION IN THE CENTRAL WASHINGTON CASCADES*

Roger del MORAL & Alan F. WATSON**

Department of Botany, University of Washington, Seattle, Washington 98195, USA

Keywords:
Coniferous forest, Ordination, Polar ordination, Principal components analysis, Reciprocal averaging, Vegetation pattern, Vegetation structure

Introduction

The Alpine Lakes region of Washington occupies over 400,000 ha of forest and alpine vegetation in the Cascades between Stevens Pass and Snoqualmie Pass. We proposed a vegetation classification of forest vegetation on granite-derived substrates in this region (del Moral et al. 1976). The purposes of this paper are to investigate gradient characteristics of this vegetation, to compare the complexity of the vegetation in each region, and to assess the utility of several ordination methods.

A general description of the vegetation of the central Washington Cascades is provided by Franklin & Dyrness (1973), but there are few detailed studies of these coniferous forests that use gradient analysis methods. Fonda & Bliss (1969) used polar ordination to describe montane and subalpine forests in the Olympic Mountains. The major vegetation patterns were interpreted as responses to moisture and temperature gradients. Del Moral (1974) used principal components analysis to study environmental gradients on contrasting substrates in the eastern Cascades. Moisture and temperature gradients, predominated on both serpentine and non-serpentine soils. Del Moral (1973) also studied a small subalpine basin in the western Cascades using direct gradient analysis. Here, soil moisture, temperature, and snow accumulation were the major determinants in undisturbed vegetation. Long (1977) described diversity trends in a succession of lowland to montane *Pseudotsuga menziesii* forests in the west-central Washington Cascades slopes. He found that diversity (H) and richness began to stabilize within 80 to 100 years. Long & Turner (1975) came to a similar conclusion with respect to biomass in these stands. Del Moral & Long (1977) classified montane and subalpine forests in the west Cascades and found strong correlations between community types and gradients of moisture and maximum snow depth.

Zobel et al. (1976) were able to measure temperature and plant moisture stress in 18 reference stands of montane coniferous forests in the Oregon Cascades. They related these measures to an earlier study which interpreted the ordinations in terms of moisture and temperature.

Our earlier analysis of this vegetation revealed that alpha diversity (richness) increased markedly along a gradient from maritime to continental climate. The number of community types and the number of significant canonical axes in discriminant analyses also increased. These measures suggested that vegetation structure is less complex under the influence of the cool, equable climate of western Washington than under the warm, eratic climate of the eastern Cascades.

All these studies suggest that factors correlated with temperature and moisture are the primary habitat variables that control overall vegetation structure. In this paper, we investigate some gradient properties of the vegetation to document that conclusion.

---

* Nomenclature follows Hitchcock & Conquist (1973).

** Funds provided by the Graduate School Research Fund, University of Washington and by grants GB-20963 and GB-36810X to the Coniferous Forest Biome, U.S. I.B.P. This is contribution # 318 to the Coniferous Forest Biome. M.F. Denton, R.S. Fleming, A.R. Kruckeberg, and R.H. Whittaker each made significant suggestions. We thank R.S. Fleming, S.G. Fleming, C. Brewer, B.C. Cannon, K.E. Wade, K. Loughney, and J.E. Canfield for their assistance with field work and data analysis.

Methods

Study area

Three regions were selected for study. These are aligned along a precipitation gradient, which dominates the climatic features of western Washington. A topographic map of the study area is presented by del Moral et al. (1976). The western region consists of two units, centered at Lat. 47°35N′, Long. 121°28′W. Sample elevation ranges between 556 m and 1710 m. The central region is centered at Lat. 47°20′N, Long. 121°10′W. Sample elevation ranged from 730 m to 1775 m. The eastern region is centered at Lat. 47°30′N, Long. 120°47′W, with samples obtained between 610 m and 1920 m.

Precipitation in mountainous terrain is notoriously variable, locally unpredictable, and difficult to measure. No permanent meterological stations exist in the study area. The general precipitation pattern is one of pronounced winter snowfall increasing with elevation, but decreasing from west to east as a consequence of the rainshadow of the Cascade crest. Summer droughts are increasingly intense from west to east, but August and September are often wet. Usually, less than 10 % of the precipitation occurs during July, August, and September. Lowland annual precipitation varies from 1500 to 2500 mm in the west and from 600 to 1200 mm in the east (Franklin & Dyrness 1973), though these values are extrapolations.

All sample plots were located on soils derived from granitic parent rocks. In the western region, soils consist primarily of acid Haplorthods at low elevations and Cryorthods at higher elevations. To the east, low elevation soils are poorly developed Haplumbrets and immature soils. At higher elevations, Cryothods or Haplorthods with thin humus layers predominate.

Vegetation and habitat sampling

Details of sampling methods are found in del Moral et al. (1976) and follow those of Whittaker & Niering (1965). There were 80, 81, and 70 0.1 ha plots, respectively; these were distributed to sample the available variety of old growth forest vegetation. Within each plot, tree density was determined for each species and the basal area of each individual measured. Shrub and herb cover was obtained from the mean of 25 1–m^2 subplots spaced at 2 m intervals along a 50 m transect. The elevation, slope, aspect, and physiographic features of each plot were recorded. Solar radiation was calculated from these data using tables provided by Buffo & Fritschen (no date). Aspect, slope, and radiation were combined to produce a moisture-insolation index that ranges from 1 for the wettest sites to 9 for the driest sites. Five soils samples were obtained from the top 15 cm in each plot. Soil pH (1: 1 saturation paste) and soil organic fraction (loss on ignition) were determined from the composited samples.

Analytical methods

The analysis of large sets of ecological data presents several problems yet to be resolved completely (Austin 1976a). These problems include the presence of discontinuities and outliers, the nonlinearity of variables and their interdependence, and the large number of zero values ('naughty naughts', sensu Austin 1976a) resulting from even moderate beta diversity. Depending upon the purpose, these problems can be mitigated in several ways.

Austin (1976b) states that the exploration of large data sets may involve the overlapping goals of summarization, stratification of heterogeneity, and hypothesis generation. We wish to summarize several data sets by ordination methods in order to clarify their general trends and compare the separate ordinations. These summaries will result in the statement of several hypotheses concerning the nature of the environmental variables controlling species patterns.

Data Reduction and Transformation

Our initial studies used importance values of trees (relative density and relative basal area) and of shrubs and herbs (relative cover and relative frequency). We used both similarity projection ordination (del Moral 1976) and reciprocal averaging on all species in each data set without further data reduction. These analyses demonstrated marked differences between the regions but were affected strongly by high beta diversity. In order to make detailed comparisons between the regions, several additional analyses were performed. Each type of analysis has virtues and faults that have been summarized by Noy-Meir & Whittaker (1977).

The data for each region were divided into two groups consisting of samples from lower and higher elevations respectively. Ordinations were performed separately on tree data and on the shrub and herb data because the different strata cannot be expected to respond similarly (Whittaker 1960). For trees, ordinations were based on $\log_{10}$ importance values calculated from relative basal area and relative density. For shrubs and herbs $\log_{10}$ mean cover was used. All transformed data were standardized by species and stand. Logarithmic transformation reduces dominance effects and improves normality. Williams (1976) suggests logarithmic transformations for data to be treated by polar ordinations or when distance metrics are employed.

Rare species contain little ordination information but do contribute to distortion effects (van Groenewoud 1976). Therefore, species with a single occurrence in the tree ordinations and those with fewer than three occurrences in the herb ordinations were deleted. Where indicated, particular species were deleted from some of the ordinations. When a stand was thought to be responsible for large distortions, it was deleted and the analyses repeated.

Polar ordination (PO)

Gauch (1973a) reviewed the features of polar ordination and made recommendations to improve interpretation. A major advantage of polar ordination is that subjective selection of stands is possible. Such selection eliminates potential distortions that arises from the selection of aberrant stands and can lead to more easily interpreted results.

In each ordination, end stands were selected to represent a moisture gradient and a temperature gradient. Polar ordinations were also calculated by automatic procedures based on end stands resulting from principal components analysis (PCA) and reciprocal averaging (RA). Second automatic axes were selected from stands in the middle fifth of the first axis that had maximum dissimilarity. All polar ordinations employed the percentage distance between stands, a metric that produces the fewest distortions (Gauch 1973b).

Weighted average ordination (WA)

Weighted average ordinations can produce efficient ordinations if there is a single predominant gradient and if something is known of species distributions along the gradient (Whittaker 1960). We used the RA species ordination to assign a weight from 1 to 4 to each of the species. A single WA stand ordination was then calculated.

Principal components analysis (PCA)

There are several forms of principal components analysis that vary depending upon whether or not the data are centered and standardized prior to analysis. We analyzed all data by both centered PCA and centered + standardized PCA. Results were usually comparable, but the latter were more easily interpreted. Thus all PCA reported are centered and standardized. The method has been the subject of several recent ringing denunciations (Gauch et al. 1977, van Groenewoud 1976), yet it retains utility under certain conditions. Its major drawback is that distortions increase with beta diversity. The elemination of rare species and the reduction of ordination distance reduce these effects. Noy-Meir et al. (1975) discuss the effects of these procedures.

Reciprocal Averaging (RA).

Hill (1973, 1974) described a factor method that is less sensitive to beta diversity than is PCA and which appears to be the best general ordination method now available (Gauch et al. 1977). This method uses Chi-square as the implied distance measure. It is robust against sampling errors and discontinuities. However, the first axis tends to describe a coenocline while the second often results from quadratic distortions around this axes. Computational details are found in Guinochet (1973), Hill (1973, 1974) and Gauch et al. (1977).

Computation

All data reduction, transformation and ordination was accomplished using program ORDIFLEX (Gauch 1977).

Diversity

We calculated alpha diversity as number of vascular plant species per 0.1 ha plot. Gamma diversity is the total number of species in a region. Beta diversity is defined as the number of half changes encountered along a coenocline. This number was estimated for each set of data by determining the floristic coefficient of similarity between the four stands at each end of Axis I in reciprocal averaging. This coefficient is defined by $2W/(A + B)$, where A and B are the number of species in two samples and W is the number of shared species. Then $\beta = (\log a - \log z) / \log 2$, where a is similarity at zero intervals and z is the similarity of the extreme samples (Whittaker 1960).

Composite mosaic diagrams

Vegetation patterns in each of the three regions were synthesized to produce mosaic diagrams. Stands were first positioned using elevation and the moisture-insolation index. Ordinations were inspected and some stands were repositioned according to their relative positions in the moisture gradients. Stands were then identified as to community type (del Moral et al. 1976) and the diagram completed by drawing the approximate boundaries. A second axis was added to each graph to indicate relative moisture conditions among the three regions. This axis was derived from a polar ordination of all stands using only tree species. (This method probably overestimates the range of moisture conditions in the middle region.) The inferred axis is obtained from determining the range over which stands from each region are distributed on the moisture axis of the polar ordination.

Comparison of ordinations

In order to determine the degree to which different methods produced similar ordinations of a particular data set and the degree to which ordinations of the same stands based on tree and herb data were similar, we used Spearman's (nonparametric) rank correlation test (Nie et al. 1975).

Table 1. Diversity properties of each data set

REGION	DATA SET	DIVERSITY VALUES A	B	C
WEST	TREE, LOW	3.3	6	1.15
	TREE, HIGH	2.9	5	0.42
	HERB, LOW	13.4	42	1.10
	HERB, HIGH	7.8	34	0.71
CENTRAL	TREE, LOW	4.9	11	1.05
	TREE, HIGH	4.4	10	1.37
	HERB, LOW	15.9	61	1.12
	HERB, HIGH	12.5	55	0.89
EAST	TREE, LOW	4.1	10	2.72
	TREE, HIGH	4.1	10	2.11
	HERB, LOW	19.5	79	3.65
	HERB, HIGH	14.2	60	2.43

A is alpha diversity, the mean number of species per 0.1 ha plot

B is total regional richness, excluding species of limited occurrence

C is beta diversity in terms of species half changes along the first RA axis

Results and discussion

Ordinations

Table 1 presents several diversity characteristics of the 12 data sets. Beta diversity values indicate that herb species composition usually changes more rapidly than tree species composition along the same coenocline, thus confirming the observation that dominant species have broader habitat ranges than subordinate species (Whittaker 1960). Alpha, beta and gamma diversity are each greater in the east than in the west, particularly in the herb stratum. These differences are accentuated when rare species, which were excluded for these comparisons, are considered.

Table 2 presents comparisons between PCA and RA for each set of data. RA routinely accounts for as much, or more, variation in the same data as PCA.

Tables 3 to 14 and Figures 1 to 12 provide, for each data set, a stand table derived from the most effective single axis and a two-dimensional plot of stands in the most effective ordination. In each figure, letters marking stand position refer to community types described in Appendix I. Limited environmental data are provided for each stand in Appendix II. Distributions of species with known

Table 2. Distribution of variance determined by Principal Components Analysis and Reciprocal Averaging for each data set.

REGION	DATA SET	N	PCA I	II	III	SUM	RA I	II	III	SUM
WEST	TREE, LOW	6	36.9	28.3	16.1	81.3	43.3	21.6	17.0	81.9
	TREE, HIGH	5	37.5	34.1	20.5	92.1	42.4	32.1	23.0	97.5
	HERB, LOW	42	15.0	11.1	10.1	36.2	13.6	11.5	10.5	35.8
	HERB, HIGH	34	19.7	10.6	9.9	40.2	18.4	12.8	9.7	40.8
CENTRAL	TREE, LOW	11	23.9	19.8	15.5	59.2	25.9	18.5	14.6	59.0
	TREE, HIGH	10	28.1	20.3	16.4	64.8	30.0	24.7	12.8	67.3
	HERB, LOW	61	11.0	8.4	7.5	26.9	11.7	9.8	8.6	30.2
	HERB, HIGH	55	15.4	9.4	7.8	32.6	12.9	11.2	8.6	32.0
EAST	TREE, LOW	10	34.5	17.2	13.1	64.8	34.3	15.7	14.6	67.6
	TREE, HIGH	10	21.1	18.8	12.2	52.1	23.3	20.7	15.5	59.5
	HERB, LOW	79	13.5	9.2	7.0	29.7	14.5	9.1	8.5	29.1
	HERB, HIGH	60	12.8	11.9	7.4	32.1	15.8	11.6	8.2	35.6

TABLE 3. Weighted average ordination of low elevation stands by tree species in the West. Values are deciles based on matrix maximum. Stand characteristics described in Appendix II.

SPECIES	LOW ELEVATION STANDS
	2233333313210222043212213010012111010300 9174261570235350409654793388968041722861
Pseudotsuga menziesii	774444 3 4 542342 33
Thuja plicata	4 4432624 5 32 31+ 3 +
Tsuga heterophylla	584343547643544527888887744366665432 1
Abies amabilis	+ 234544345663364677777783537666644448575
Chamaecyparis nootkatensis	2322 3234 2
Tsuga mertensiana	22 2 1 1 223 4436679
	ACAAACBABABCFCCCFCCCCCCCCCCGCCCGCBHCDEFE

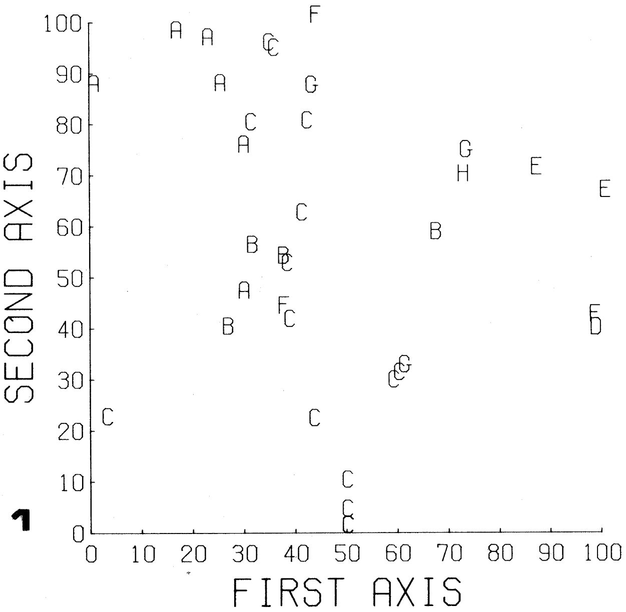

Fig. 1. PO-RA ordination of lowelevation western stands using tree species.

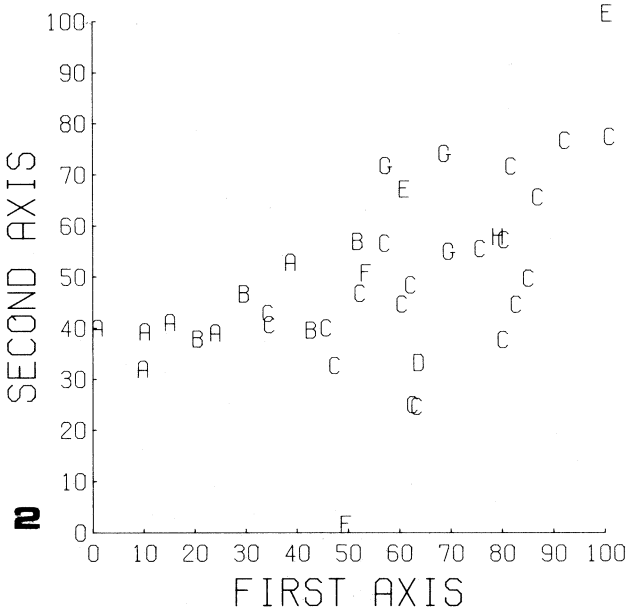

Fig. 2. PO of low elevation western stands using herb species.

environmental relationships and the stand environment data were used to interpret the ordinations.

Trees of the lowland western region fit into an essentially unidimensional coenocline (Table 3, Fig. 1). *Pseudotsuga menziesii* indicates warm, dry, lowland habitats, while *Chamaecyparis* and *Tsuga mertensiana* dominate subalpine sites. *Abies amabilis* and *T. heterophylla* occur throughout the coenocline, but dominance shifts towards *A. amabilis* in response to increasingly deep snow pack at higher elevation (Long 1976). The herbs were analyzed following deletion of stand 6, which proved to be an outlier (Table 4, Fig. 2). This analysis also suggests a unidimensional gradient. Species ordination reflects a gradient from higher, mesic sites to lower, drier sites.

TABLE 4. Reciprocal average ordination of low elevation stands by shrub and herb species in the West. Values are deciles based on species maxima. Species with fewer than five occurrences are deleted from this table.

SPECIES	LOW ELEVATION STANDS
	33132312413303132232102221110012201000[a] 217710990158944328666247085259335304718
Achlys triphylla	9144+5 3 6 +
Viola glabella	94 7 9 2 62
Polysticum munitum	4243965+ 65
Oplopanax horridum	9679 5 95593
Tiarella trifoliata	832778557394322+
Athyrium filix-femina	99 6 48 15 9
Gymnocarpium dryopteris	36744++9+89+14+
Streptopus amplexicaulis	2 + 93 6 +
Cornus canadensis	62644636122142 79 25 4 +
Rubus spectabilis	4 2 64194 1 7
Blechnum spicant	16939554161652669 6 6 + 4 6 6
Linnaea borealis	45 5+2+9 2 +7 1586 7 2 +
Trillium ovatum	2 37+5+3 13+2 12 13 9
Smilacina stellata	4 31 4 21 7+3153 241 9
Listera caurina	12+++151 1 2+ +19 + + 2
Maianthemum dilatatum	+ 1+ 4 + 9+ 6 +
Chimaphila umbellata	3 1 5 9 24+
Vaccinium ovalifolium	1+1+1111++++ 3+12251 9 132 2++22 + +
Vaccinium alaskense	11111+112111112424222119478 24234 +1
Rubus pedatus	1 + 1 12311 32+9 3142 1 34 4 3
Chimaphilla menziesii	1++ +4++ 12 + 9 1 2 119
Clintonia uniflora	+11+ 1111+1++++12 1211 2+ 191 + 2 3 3
Acer circinatum	+ 11+1+1 + 1 34 1 3 1 + 2 9
Corallorhiza mertensiana	1 1 + 1+2+9412 16124+ 92574 21
Menziesia ferruginea	+ + 1 1121++ 2 +3 1 49 3644 29
Pyrola secunda	+++1 + 1 + + + 5+ 714 3 9224+5+ 2 5
Sorbus sitchensis	+ ++ 4+ 9 1
Rubus lasiococcus	2 2 + 5 8 2 1 8 9
Vaccinium membranaceum	+ + 1 4 2223 6 469
Pachistima myrsinites	+ 9 457
	ABBACACACBAECACCBCCCCDCCCCCGFCCCCCGFHEG

[a] Plot 6 was deleted from this ordination

Trees of the upper western region demonstrate a single gradient correlated with elevation and manifested in the species by a shift from *Tsuga heterophylla* to *T. mertensiana* (Table 5, Fig. 3). The corresponding herb ordination reflects a more varied response (Table 6, Fig. 4). Species indicate a gradient from low elevation, mesic forests (*Gaultheria ovatifolia, Viola glabella*) through high elevation mesic sites (*Rhododendron albiflorum*) to open subal-

TABLE 5. Reciprocal average ordination of high elevation stands by tree species in the West. Values are deciles based on matrix maximum. Stand characteristics described in Appendix II.

SPECIES	HIGH ELEVATION STANDS
	0010112001313110321433323012132222320302 5751369822719044289061058377853026416394
Tsuga heterophylla	75545444442221+
Abies amabilis	7558667556574996887577755757645454747674
Chamaecyparis nootkatensis	4 2 2 1423 4 15 45 4 253435 5 1
Tsuga mertensiana	4 443353334465776577755858756666867955
	HGGGGCGGFGGGEGDCHHHEHFGHEFHHFHHFFHHFHFGF

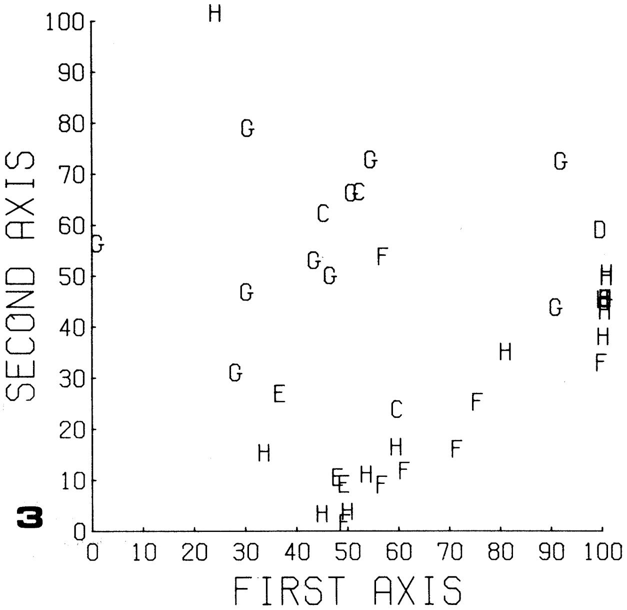

Fig. 3. RA ordination of high elevation western stands using tree species.

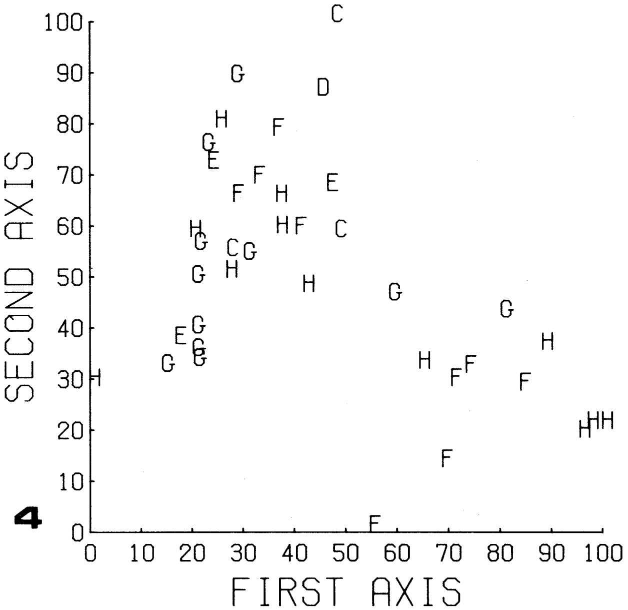

Fig. 4. PO-RA ordination of high elevation western stands using herb species.

pine habitats (*Phyllodoce empetriformis*, *Cassiope mertensiana*).

Trees of the lower central region reflect increased habitat complexity and greater coenocline complexity. Moisture and temperature gradients are identified in the first and second axes of Fig. 5, respectively and the RA ordination (Table 7) is demonstrably curved. Species patterns indicate a gradient from low elevation mesophytes (*Abies grandis*, *Thuja plicata*) through broadly distributed species (*A. amabilis*) to species of cold or exposed sites (*A. lasiocarpa*), to those of cold, moist sites (*Tsuga mertensiana*). The associated herb ordination confirms two directions of variation (Fig. 6). The species distributions from WA (Table 8) indicate that habitat differentiation is not great among the herbs. The widely distributed dominants (*Vaccinium membranaceum*, *Pyrola secunda*, and *Pachistima myrsinites*) are species of mesic, closed forests.

Trees of the upper central region are separated with little distortion by PCA (Fig. 7) while the RA ordination (Table 9) provides the best distribution of species. Species patterns reflect a temperature gradient ranging from *Abies grandis* and *Pseudotsuga menziesii* to *Chamaecyparis nootkatensis* and *Pinus albicaulis*, two timberline species.

TABLE 6. Weighted average ordination of high elevation stands by shrubs and herb species in the West. Values are deciles based on species maxima. Species with fewer than five occurrences are deleted from this table.

SPECIES	HIGH ELEVATION STANDS
	300010311102411000323213212230323323221 964567705219013389558692773802614123408
Corallorhiza mertensiana	5 9 +1+
Gaultheria ovatifolia	+ 1 1+ 8 9 2++ + 2 + 1 1
Viola glabella	1+1 9 + 1 +
Tiarella trifoliata	991 4 2
Vaccinium alaskaense	1 4394524 3+ + 2221+ ++ +
Rubus spectabilis	592 81
Gymnocarpium dryopteris	59+ 2 2
Rubus lasiococcus	82 + 3 9 4 71 8 7 +9
Clintonia uniflora	3246 1 5 49 585628
Blechnum spicant	4+9 + 7 +
Pyrola secunda	23515+1 49 2 3 5
Rubus pedatus	53 52 7 3 7 59 3 +
Smilacina stellata	+ 59 + 1 8
Vaccinium membranaceum	14 6 788 777398 8646266866666 63522+++
Menziesia ferruginea	1++ 41+13+ 431122542 2983662 3224
Sorbus sitchensis	1 9 2 + 3++ +++ 2
Xerophyllum tenax	2 9 99 3
Rhododendron albiflorum	25496 +68 4 4 25+
Vaccinium ovalifolium	6 1 319554432555
Phyllodoce empetriformis	1+22 12+ 4 324449554
Cassiope mertensiana	1 ++ ++ 2 +64569988
	EHCHCGGGCGGGEGGFGGHHEHHHHHHGFHFHFFFFFF

TABLE 7. Reciprocal average ordination of low elevation stands by tree species in the Center. Values are deciles based on matrix maximum. Stand characteristics described in Appendix II.

SPECIES	LOW ELEVATION STANDS
	1122224213231232130312233220101000003033 6767980189519452549030362241120453877683
Abies grandis	3234 12 12 1
Thuja plicata	122 32+11 1 +
Tsuga heterophylla	42 1221235 13+12 31111 +2 + 1
Pinus contorta	2 1 3
Pseudotsuga menziesii	13422222 2232119 32323214342432222222
Abies amabilis	+1 11 223 +3111 323+2 2 22+4+22222+12 3
Pinus monticola	+ 11 211 + 1 ++1 1 + 21 11
Picea engelmannii	1 + 1 +1211 + 1 +
Abies lasiocarpa	+ 12 1+1 2222122 31+21+2213
Chamaecyparis nootkatensis	+ 2++ 1 +++ 11 12+1311111
Tsuga mertensiana	+ + 2 + 2 + 1+11 1123
	GACCACGBAGBCBBHBBGCACBDHIBBCGCCCDCCCHEDF

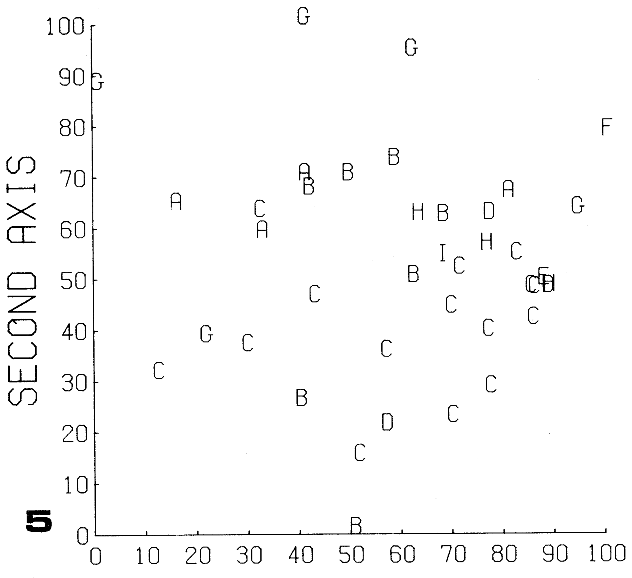

Fig. 5. PO-RA ordination of low elevation central stands using tree species.

TABLE 8. Weighted average ordination of low elevation stands by shrubs and herbs in the Center. Values are deciles based on species maxima. Species with fewer than five occurrences are deleted from this table.

SPECIES	LOW ELEVATION STANDS 332330322224023112321100112330001101120 3 2375679538403642307115894621845290187960
Rhododendron albiflorum	7+ 9 1 2
Menziesia ferruginea	97 9 6 5 38 3 3
Gaultheria ovatifolia	99664 +7 13 2 435 27 2
Amelanchier alnifolia	42 9 2+ + + 4
Oplopanax horridum	9 3 2 + + +7
Chimaphila menziesii	9 + 1 1 8 +
Linnaea borealis	75 9859 5 833 4 24 3 ++
Sorbus sitchensis	174+6+ 1 + +9 + 14+1 3 26
Vaccinium membranaceum	7569489464358536434473466533545336 2 +++
Chimaphila umbellata	98 4 3 32 683 7 2 761 +7
Taxus brevifolia	44 6 26 9 5 52
Spirea betulifolia	+ 2 7 9+2 ++ + 3 1 +
Pyrola asarifolia	99 + 5 9 +
Berberis repens	2 9373 3 4 5+ 214
Pachistima myrsinites	1432724 53 9829632 23 9 2635222++46+ 3
Goodyera oblongifolia	+ 1 + 9212+1 1 +1+ +11+3 + +1
Pyrola secunda	3 3 +133 139 +111138 4514++3431352 +
Pteridium aquilinum	13 1+1 +15 4 96 + 1+ 3 2 2
Hieracium albiflorum	+ 1 + 1 9 22 + 11 +12 + + 3
Streptopus roseus	5 6 9 5 4 8 2 2
Clintonia uniflora	3 4 35 3 +2349353 73214623 43322
Achlys triphylla	1+ + 6 189 7 7467 9 29
Rosa woodsii	1+47 15+4+6 + 2 443 46+2932
Tiarella trifoliata	4 1 3 5 + 1296
Rubus lasiococcus	+ + + 4 +34 +34+22414691+ 5546174++116
Antennaria racemosa	6 1 1 9 1 +
Smilacina stellata	+7 5+ 13 5 4 31 + 143675 +9
Trillium ovatum	1 2 1++32+946+ 32159443+35468
Listera caurina	5+ 41 89 3 4
Viola glabella	+ + 1 +23 3 + 373 + 643 3 +9
Arenaria lateriflora	2 9+ 53
Osmorhiza chilensis	1 1 9 154+ 1
Acer circinatum	+1 3 3 5 364+ 6 5 879 8
Disporum hookeri	2 3 + 4 291
Poa reflexa	51 1 9 9 14+ 44
Thalictrum occidentalis	3 +9 + 3+
Rubus parviflorus	+ + + 539
Alnus sinuata	+ + 1 3 ++ ++ + 9
Rubus ursinus	1 1 + + 2 + 9
Trientalis latifolia	+ + + 2 ++ + 17 9
Galium aparine	2 +13269
	IFCHHCGBDCBGCCGCCBHBGBCCCGBCDCDCBCCAAAEA

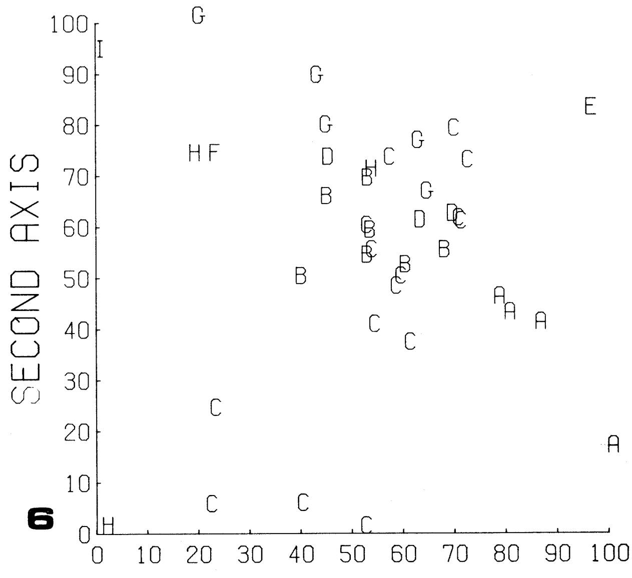

Fig. 6. RA ordination of low elevation central stands using herb species.

The herbs were analyzed after stands 5 and 36 were deleted. The factor methods remained distorted, but PO-RA resolved the stands into moisture and temperature axes (Fig. 8). Species patterns in WA (Table 10) indicated a pronounced gradient from hot, dry sites (*Arctostaphylos nevadensis* and *Penstemon fruticosus*) to cool, moist sites (*Rhododendron albiflorum* and *Alnus sinuata*).

Trees of the lower eastern region indicate a complex coenocline (Fig. 9). Species distributions in WA (Table 11) range from *Pinus ponderosa* and *Pseudotsuga menziesii* in xeric sites, through *Abies grandis* and *Thuja plicata* in mesic sites, to cooler, mesic sites dominated by *Abies amabilis*. Ordination by herb data confirms the essential features suggested by tree ordination. Fig. 10 suggests a combined temperature-moisture gradient and a moisture

TABLE 9. Reciprocal average ordination of high elevation stands by tree species in the Center. Values are deciles based on matrix maximum. Stand characteristics are described in Appendix II.

SPECIES	HIGH ELEVATION STANDS 004400313200022122313330023222123121311311 451061938032829963700517982174536424186 57
Abies grandis	62 +
Pseudotsuga menziesii	865545 434232213
Tsuga heterophylla	55 8 3+
Pinus monticola	4 42 3 232112 22
Abies lasiocarpa	22 55 334654+4327949584553254 3 5
Picea engelmannii	1 2 + 2 +2 2 1 3 121 4 3
Abies amabilis	66 2955 334436444615+613524735559295776
Tsuga mertensiana	421321333343333+57334354535766+554
Chamaecyparis nootkatensis	1 24+1 +24 33 327 233313243 312544
Pinus albicaulis	1 3 1
	CCHHCEHHHEEEHFFHHFIJHFFHJIFDIHFFHFHJHHIHH

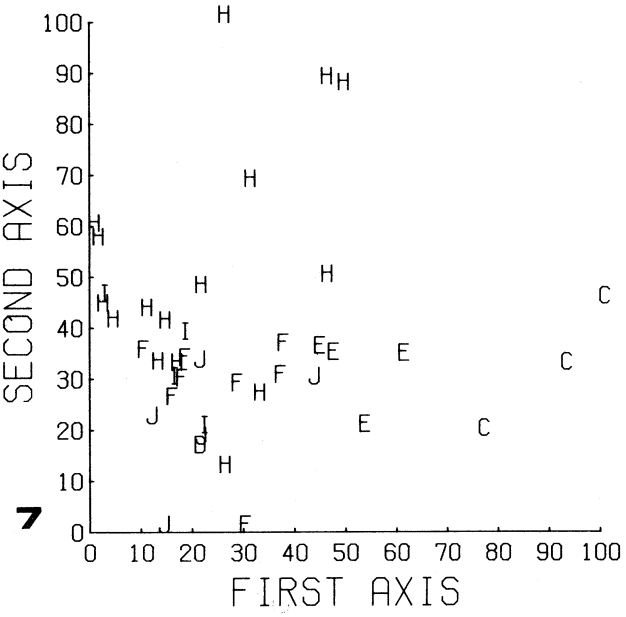

Fig. 7. PCA ordination of high elevation stands using tree species.

TABLE 10. Weighted average ordination of high elevation center stands using shrubs and herb species. Values are deciles by species maxima; species with fewer than five occurrences are not shown. Stands 5 and 36 were deleted from the ordination.

SPECIES	HIGH ELEVATION STANDS 0000032130033302231313122212412121412 13 21364400387479915831401964280677381925 2
Arctostaphylos nevadensis	95932 5
Penstemon fruticosus	34951
Pachistima myrsinites	9972412 5 2 ++ + + +++1
Vaccinium scoparium	4 49 + +
Polemonium pulcherrimum	1+ 95 1
Erythronium grandiflora	4 9 41 2 +
Poa reflexa	529 4 4 1+ +
Senecio integerrimus	4 1 934 3 1
Lupinus polyphyllus	936 52+8323 2
Hieracium albiflorum	9446+3 84 73 +
Gaultheria ovatifolia	9 1 1 1 3
Arenaria lateriflora	+ 9 81+ 7 +
Aster foliaceus	+ 9 7 1+ 1 8
Luzula hitchcockii	1 2 52 9 + 3
Viola glabella	2219 343+ 23 3 1 + 2 + 2 1+1 231
Carex spectabilis	+294 1 + +
Sorbus sitchensis	199122 33 3832++34+9 346 1 +++
Pedicularis contorta	99 314 1 +
Pedicularis bracteosa	+3 25+ 1 91 7 + + 2 + +
Ligusticum grayi	3 1 9 5 4 +
Osmorhiza chilensis	36 1 9+
Arnica cordifolia	+ 6 +6 931535 144 3 25+ + 6
Vaccinium membranaceum	756122333224892363967874666554555444433
Rubus lasiococcus	231+1541319598435 5+53486 5444822 2568
Valeriana sitchensis	+ +2 3 9 + + 3+ +++1 7+
Pyrola secunda	1 2+ 3 + 61+2 6+9+ 2+ 15 +15+ 3+1
Clintonia uniflora	2 3 73 8186961
Smilacina stellata	+ 4 5 36 9
Listera caurina	1 89 1++ 6
Trillium ovatum	+ 1 3 948+65
Rhododendron albiflorum	2 + +1255675695 566786347667
Streptopus roseus	41+ 2 + 71 912
Alnus sinuata	3 + +6+9
Tiarella trifoliata	73 911
Phyllodoce empetriformis	+ + 6 5 9 8
	EEECCJEJJJHFIHJDFHHFHHHFHFHIHHIHFHHHFHF

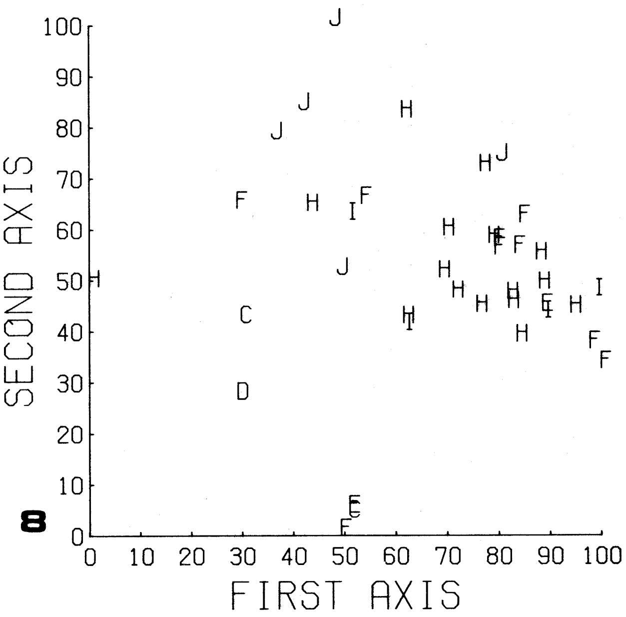

Fig. 8. PO-RA ordination of high elevation central stands using herb species.

gradient in the two axes, an interpretation confirmed by species distributions in WA (Table 12). The coenocline moves from hot, dry sites (*Arctostaphylos*, *Agropyron*) through warm, mesic sites (*Lupinus*, *Spiraea*, *Chimaphila*) to moist, cooler sites (*Linnaea*, *Trillium*, *Viola*, *Dodecatheon*).

Trees of the upper eastern region reveal distinct temperature and moisture gradients (Fig. 11). Species patterns confirm this interpretation. RA-I (Table 13) indicates species patterns ranging from *Pinus ponderosa* in the warmest, driest sites to *Larix yallii* in the coldest, moist timberline sites. Ordination of the herb data reflects the high beta diversity by the characteristic hump (Fig. 12). Table 14 provides the WA ordination and is essentially a moisture gradient. The xerophytes *Arctostaphylos*, *Ceanothus*, and *Achillea* occur first, followed by closed-forest mesophytes

TABLE 11. Weighted average ordination of low elevation stands by tree species in the East. Values are deciles based on matrix maximum. Stand characteristics are described in Appendix II.

SPECIES	LOW ELEVATION STANDS 2223333000201012313110210022111102 2 5781234234962536065109457803897411 2
Pinus ponderosa	7778777675444443 4 1 2
Pseudotsuga menziesii	887687786765544672943332 2+263 1214
Populus trichocarpa	5 2 3 3 2
Abies grandis	+1245565335 65242434 324+3
Thuja plicata	1 46433543+ 7243 3
Abies lasiocarpa	+ ++ + 1 11 3122 4
Pinus monticola	+ 1 5 1 321 1 2
Tsuga heterophylla	4 +2 41 3
Abies amabilis	+ 22
Picea engelmannii	+ 1 +1 13135112233+
	FFFFFFFEFEEDDDDEEDDDCABAAACGGADBGGB

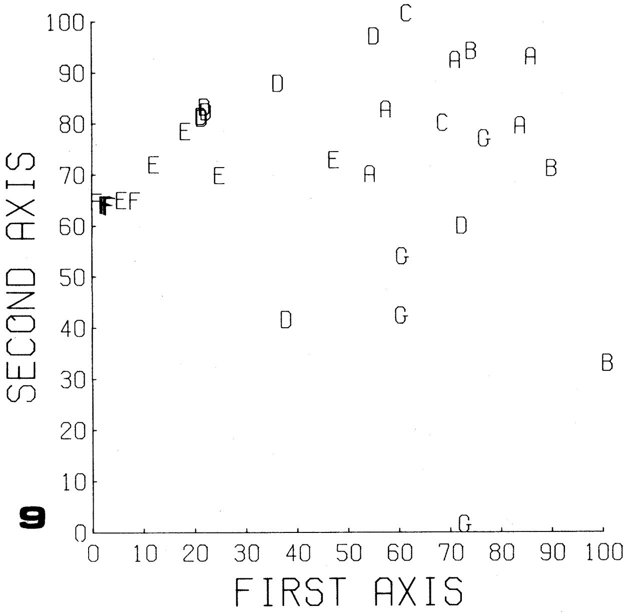

Fig. 9. RA ordination of low elevation eastern stands using tree species.

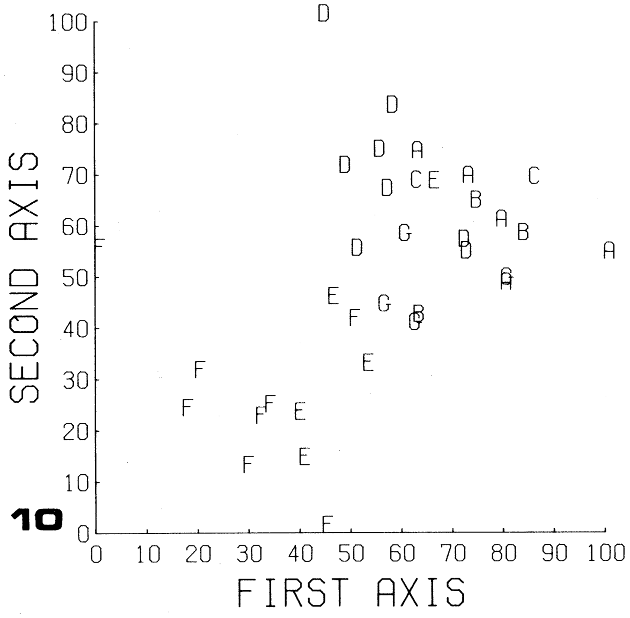

Fig. 10. PO-RA ordination of low elevation eastern stands using herb species.

TABLE 12. Weighted average ordination of low elevation east stands using shrubs and herb species. Values are deciles by species maxima; species with fewer than five occurrences are not shown.

SPECIES	LOW ELEVATION STANDS 32333222200030111011212112200302011 45321769823456832565113704291080749
Arctostaphylos nevadensis	9 +++ +
Eriogonum compositum	892 6 +
Collinsia grandiflora	39113 1
Agropyron spicatum	7349222
Balsamorhiza sagittata	9+9 3 +
Hydrophyllum fendleri	4 19 + 22
Achillea millefolium	698974 5 + +1+
Prunus emarginata	9 13 5 1 + +
Poa sp.	13+319 1 1
Carex geyeri	3899528873+1 3
Aster foliaceus	6 24 4+93 +1 + 4
Berberis aquifolium	9 227 + + 2
Ceanothus velutinus	81 49 58951 1
Hieracium albiflorum	4 98 +7 253757+
Amelanchier alnifolia	5 93 1 8 2 ++
Epilobium angustifolium	3 9312 11 12+
Lupinus polyphyllus	+ 9 85 565+2 +
Apocynum androsaemifolium	1 6 9 1 4 551 4
Poa reflexa	79 2 6 1 +
Antennaria racemosa	659 9 5
Acer glabrum	96+ 51 1++++ 9 9 1+22 +
Bromus carinatus	9 687 82 1 1
Chimaphila umbellata	7 +439 23 23+41 4 2 2 ++
Spiraea betulifolia	+ 1559346456 4 12 1 +
Pachistima myrsinites	+1+ 23741123 +212436493362+5+3+2+
Arenaria lateriflora	+ 5 49 989+7+ 1 6 33
Symphoricarpos albus	42 6 35 1 1 7 9
Salix scouleriana	245 +2++ 49 + 22
Arnica latifolia	11 4 9 13 3
Streptopus amplexifolius	9 + + 13 512+
Pteridium aquilinum	77366559 + 3+3 1 2 +
Rosa woodsii	343 ++5334+33932+ 22 2 13
Sorbus sitchensis	1+ 4 + + 9 +
Arnica cordifolia	1 + + +9+ 2 +
Berberis repens	32 334 924188+2 26 4+112
Rubus parviflorus	+ +8 487935+288 54 2641
Goodyera oblongifolia	1 821 9 65 827 2 265 2
Castilleja miniata	++ + 2 4 9
Listera cordata	96 281 64
Vaccinium membranaceum	2 3 +8 55 +9 1 + 1
Pyrola secunda	112 17+1219434 29+712+462
Disporum hookeri	+ 13 2 9 61 2
Galium aparine	+ 5 2 3 2 9353+
Osmorhiza chilensis	+ 1 25 1+ 29 9+ 4
Alnus sinuata	+15 9 ++
Adenocaulon bicolor	+ 2++ 7 25 9 9+1+
Trillium ovatum	55194 5292321
Trientalis latifolia	1 3 16 +4 9 3+1
Linnaea borealis	1 4 8 9+ 8 8 576
Clintonia uniflora	3 5 4 6324 63529
Smilacina stellata	2 + 2 +3 62 19527
Ribes lacustre	46+ 53 47+96
Viola glabella	1 12 14866359
Dodecatheon dentata	3 1 ++98
	FFFFFFEEFEFEDDGDDDDAGDGDCBBABEACABA

TABLE 13. Reciprocal average ordination of high elevation east stands using tree species. Values are deciles by matrix maximum. Stand characteristics described in Appendix II.

SPECIES	HIGH ELEVATION STANDS 113102330300100021123031012222122 12 0223293144654839776557051804831 6192
Pinus ponderosa	+ 2
Pseudotsuga menziesii	99344342221122211111+
Pinus contorta	2 2 312 + ++ 1
Pinus monticola	1 2 1 + 1 1 + 1 1
Pinus albicaulis	+ 2113 1 1 3 4 5 1 + + 1
Picea engelmannii	22+ 1 2213323122 3 2552323 211
Abies lasiocarpa	1 4323242222312 21424244322151125
Abies amabilis	+ +1+1 212 + 2 + 234423
Tsuga mertensiana	+ + 2+1 + 2++ 232+
Larix lyallii	24
	EEEEDNENGNGGGGGGLKHHNHNIMJJHIIMIKLJ

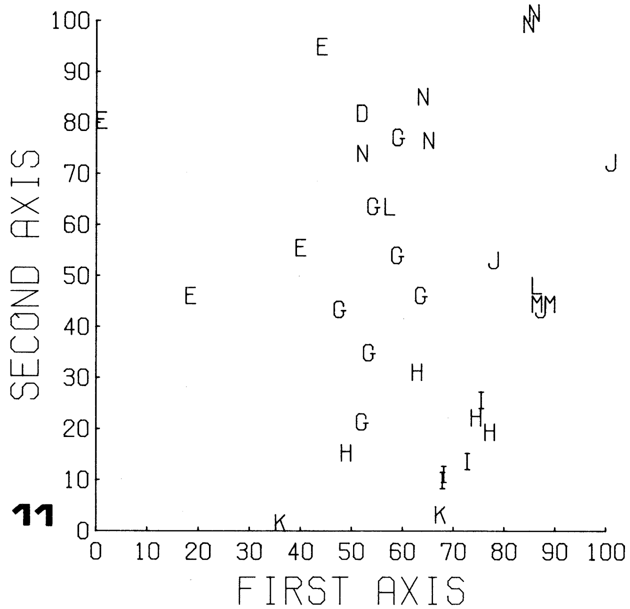

Fig. 11. PO-RA ordination of high elevation eastern stands using tree species.

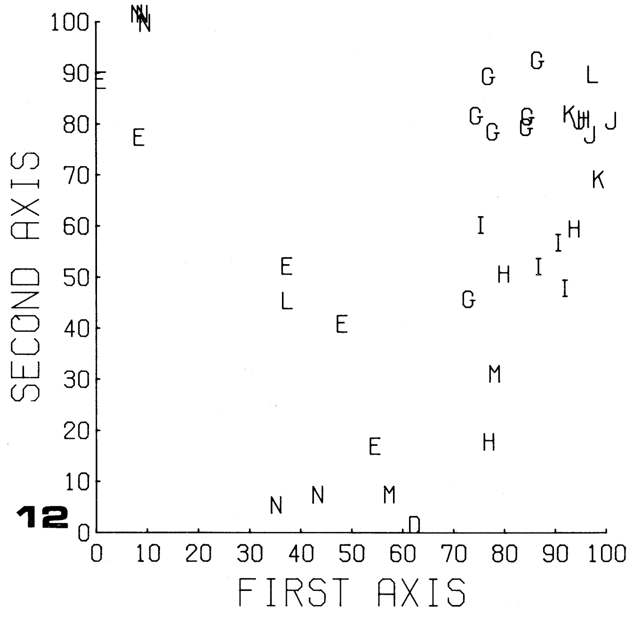

Fig. 12. RA ordination of high elevation eastern stands using herb species.

TABLE 14. Weighted average ordination of high elevation east stands using shrubs and herb species. Values are deciles by species maxima; species with fewer than five occurrences are not shown.

```
SPECIES                           HIGH ELEVATION STANDS
                             33333122131001100020001220222121121
                             23450097312124584953751866304718629

Castilleja miniata            +389+
Arctostaphylos nevadensis    2+897  1
Ceanothus velutinus          79211 4+2+
Achillea millefolium         78 38 49
Carex geyeri                 933155+3 +      1  +
Sorbus sitchensis            491+1   14+  1
Lomatium brandegei            2924  8        5  1   +
Epilobium angustifolium         3 9124391 +3
Angelica arguta                    +9 9 1      2   3+
Pachistima myrsinites        368988135224145839+5351 14 2 1 11
Ribes viscosissimum                 96 9 214   +
Thalictrum occidentale             7+496282 2  2   1   +
Aster foliaceus                  2  792567     83
Salix scouleriana                 7 46 34  9 +      3
Rubus parviflorus                  95 9386 1  +4 4 5 2
Trillium ovatum                    +  3 93    +   +
Ribes lacustre                    79  651+2+     6 416
Smilacina racemosa                   499+4          6
Berberis nervosa                     7  93     21   +
Bromus carinatus                  4 2   +3     9    +
Rosa woodsii                            9 1  3 +       +
Lupinus polyphyllus                 9        +     5+    6
Galium aparine                        12 9     1 7 1+
Chimaphila umbellata             1   4 ++ 4 93  ++6
Clintonia uniflora                 3  4 7792   5     6 7  +
Hieracium albiflorum            1 1 1     2  1  9
Smilacina stellata                      387    7   ++  9
Goodyera oblongifolia                1  2+  639+61+   1      1
Osmorhiza chilensis                 3  1 52   29 4 43+ 2 9
Alnus sinuata                          5+      222 +629   4
Pyrola secunda                    +  4 1++4+7+8+129+ 212337+47
Viola glabella                        1+192    7 2 22+ 8 4 72
Vaccinium scoparium                         27        9   +    2
Tiarella trifoliata                       2    9 7 8+5 9 1  4
Menziesia ferruginea                   1  4  ++    79   5
Rubus lasiococcus                         55   2   +44 4 9+7 +
Arnica cordata               ++   + + +  1 +81313 1+2  336 6679
Vaccinium membranaceum                   +133 3+3131+1 132721319
Valeriana sitchensis                            4   +55 5 9 7  1
Rhododendron albiflorum                   2    423+33427 +3559
Senecio triangularis                            2 +9+  +  54

                             EENNNENLENEMDGIGGGHGHGMIIGIJHKKJHJL
```

such as *Pachistima*, *Chimaphila*, and *Goodyera*, and species of wetter, cold forests including *Valeriana*, *Rhododendron*, and *Senecio*.

Mosaic diagrams

The ordination studies may best be summarized by means of mosaic diagrams for each of the three regions. These diagrams are based on topographic position, elevation, and the ordination results, which were used to revise stand positions and to rectify anomalous situations. The diagrams are drawn to reflect the classification of del Moral et al. (1976), which is summarized in Appendix I. The first horizontal axis is scaled by the inferred moisture-insolation gradient. The second horizontal axis is scaled to reflect the estimated proportion of the overall gradient represented. This determination is based on a similarity projection analysis of all stands using only tree species distributions (del Moral 1976). Western stands are found only along the first 40 % of the gradient, central stands occur between 10 and 80 % and eastern stands occur from 10 to 100 % of the total distance.

The three diagrams (Figs. 13, 14, 15) indicate that community types occupy diminishing portions of the landscape from west to east. Community boundaries generally run diagonally from lower wetter positions to higher drier sites, suggestive of the mitigating effects of elevation on drought. The number of recognizable community types also increases from west to east and, at any given elevation, there will be more rapid species turnover along a moisture gradient in the east than in the west. Thus, there are three or four community types at a given elevation in the east and only two or sometimes three in the west. The forests of the west are all closed-canopy until the highest elevations are reached. The same is true of the central region, though there, the riparian element is more distinct than in the west. In the east, low elevation forests may be quite open and dry, providing a substantial contrast to riparian and protected stands at the same elevation with respect to both the moisture and the light environments. These differences are partially responsible for the greater beta diversity of the eastern forest understory species.

The sequence of vegetation types is similar in each region even though there are few directly comparable types. In the west, the driest subalpine forests are dominated by *Tsuga mertensiana* (Type F) and occur in exposed sites. Such forests are displaced into more mesic sites in the central area (I), where they are fairly extensive. In the east (K), they are confined to the most favorable, protected sites, where *Larix lyallii* also occurs.

Stands dominated by *Abies amabilis* and *Clintonia uniflora* occur in mid-elevation, mesic sites in both west (G) and central (G) sites, though *A. amabilis* is more widely distributed in the west. In the east, *A. amabilis* is displaced to higher elevations and more mesic sites (I, J) by *A. lasiocarpa* and *Picea engelmannii.*

Stands dominated by *Abies asiocarpa* and by *Pseudotsuga menziesii* increase in cover from west to east. While mesic site community types often shrink in distribution.

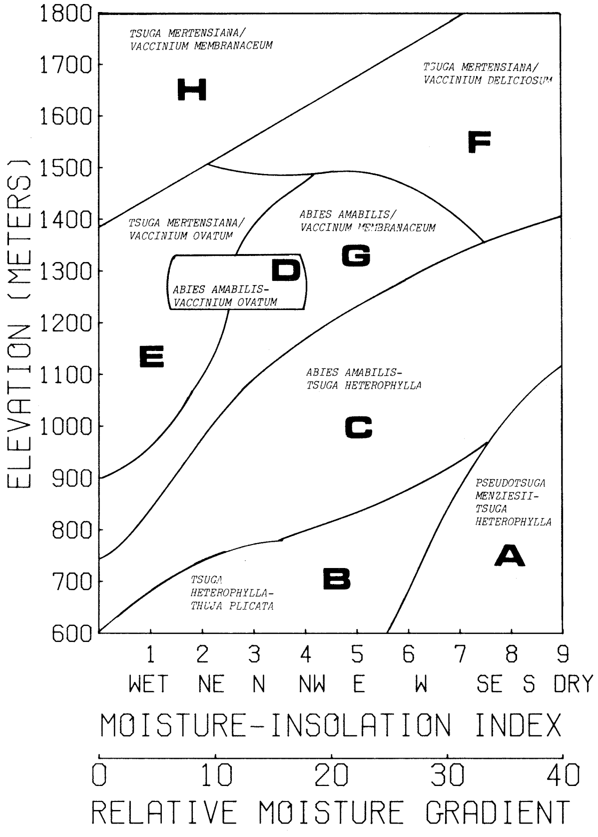

Fig. 13. Mosaic diagram of Western region.

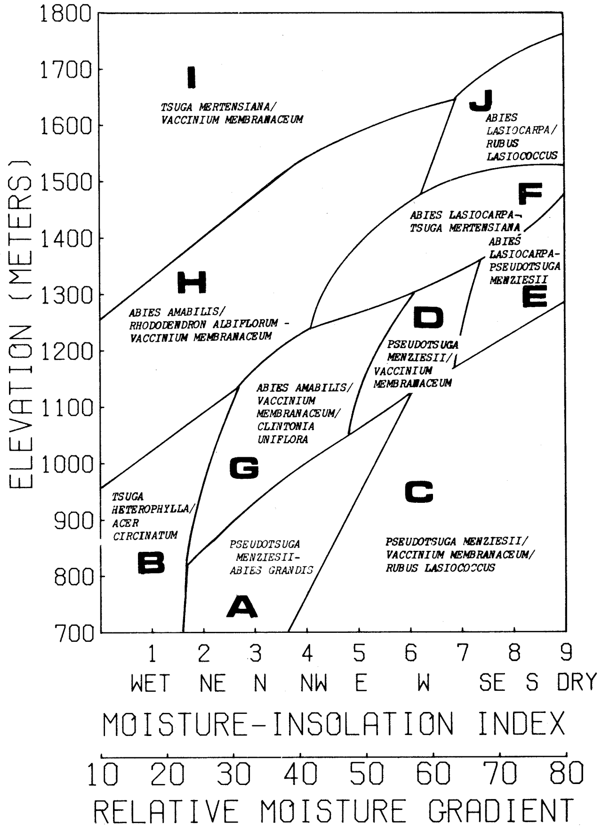

Fig. 14. Mosaic diagram of Central region.

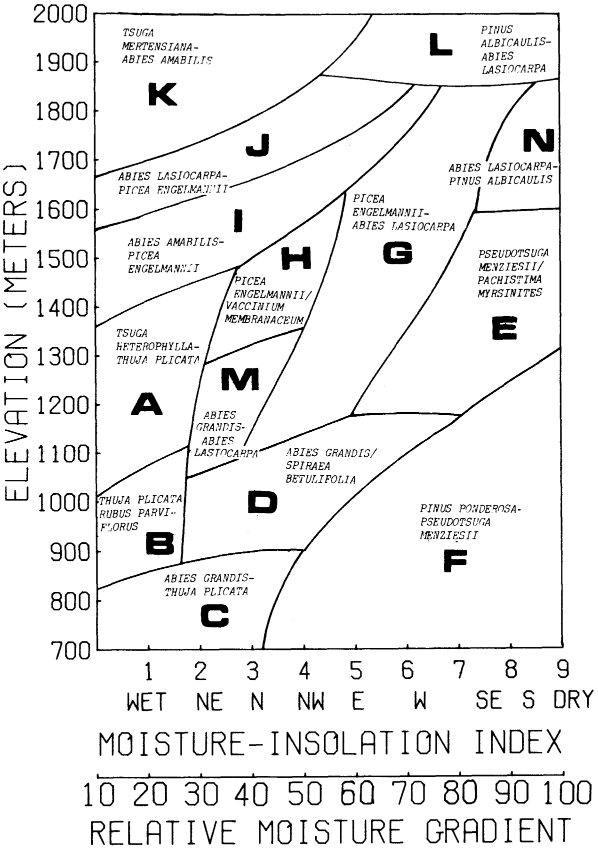

Fig. 15. Mosaic diagram of Eastern region.

Additional community types, dominated by *Pinus albicaulis*, *Abies grandis*, or *Pinus ponderosa* are encountered in the central and eastern regions. These general patterns emphasize the increasing aridity of forest stands in the eastern study regions.

Comparisons of ordinations to classifications

The ordinations presented in Fig. 1 and 2 (west, low elevation) were compared to the community classification and in both cases, the interpretation of the gradients was confirmed by the classification. The tree Axis I runs from *Pseudotsuga menziesii-Tsuga heterophylla* (type A) to *Tsuga mertensiana-Abies amabilis* (type E) found in higher, moist sites and was considered to be a composite moisture-temperature gradient. The second axis was considered to be a temperature gradient, and this is generally confirmed, since it runs from the lower elevation *Abies amabilis-Tsuga heterophylla* stands (type C) to high elevation *T. mertensiana* stands (Type F). However, this gradient is less well defined and does not appear to run between habitat extremes. Axis I of the herb stand analysis indicated a composite gradient which is confirmed by the community analysis. This first axis is bounded by types A and E which are the most extreme of the lower samples. The second axis, an inferred temperature axis is not well correlated. This gradient is similar to the first. This analysis suggests that the low elevation stands are arrayed in an essentially one-dimensional gradient defined by temperature and its correlates.

The ordinations of high elevation western stands (Fig. 3 and 4) were compared to the mosaic diagrams. The tree ordination suggests a temperature gradient and is consistent with the mosaic diagram. The second axis cannot be interpreted either on the basis of stand habitat characteristics or on the basis of community designations. Mesic and xeric stands are found close together and floristic contrasts are not marked; no interpretation is attempted. This result occurs because types F and H are distinguished primarily on the basis of understory species and all contain *Abies amabilis* and *Tsuga mertensiana*.

The first herb ordination axis also is interpreted as a temperature gradient. This is confirmed when it is realized that type H stands, which occur at both ends of this gradient, indeed span the elevational range of the upper western region (Fig. 13). The second axis may reflect a weak moisture gradient, running from a mesic type C stand to several dry, exposed subalpine stands of type F. However, there is a great deal of variability and the second gradient is not well established.

The lower elevation middle ordinations are shown in Fig. 5 and 6. The first axis is a temperature gradient with some confounding moisture effect. End stands from the lower portion of these figures are from the lower elevation communities, though they have a range of moisture conditions (Fig. 14). The higher end points are from the higher end of the low elevation data, that is, from the middle of Fig. 14. The second axis trends from drier to wetter types which confirms the gradient analysis. The dry end stand in the tree ordination is from the driest of type B stands, which otherwise reflect low elevation riparian conditions. This stand contains considerable quantities of *Pseudotsuga*, which dominates in types A and C and which reflects the drier sites of this region. The ordination reflects two correlated axes of variation.

The lower elevation ordination by herbs emphasizes different features from those of the tree ordination (Fig. 6). **The first axis is a combined gradient, but moisture predominates. Both I and H stands are in high elevation,** wet to moist sites, while type E and A stands form the other end region of this gradient and represent high and low elevation dry sites, respectively. Axis II is bounded by type C stands from low, dry sites and type G stands from high, mesic stands. The type B stand that was extreme in the tree ordination returns to an area close to the other B type stands. This combined gradient is dominated by temperature effects.

Both ordinations agree with the mosaic diagram. The herb ordination better recognizes the extreme positions of the high, moist type H and I stands that are more common in the high elevation stands. Type A stands are considered to be more xeric by virtue of herb vegetation than by tree vegetation. In other respects the graphs are similar.

Fig. 7 and 8 show the high elevation, central region ordinations. These figures are compared to the upper portion of the mosaic diagram (Fig. 14). The first axis of the tree ordination is a composite moisture-temperature coenocline that ranges from stands in high elevation, moist to mesic sites, which are found in samples of types H and I, to stands of type C from the lowest, driest sites of this set. Type C, dominated by *Pseudotsuga* is distributed primarily in the lower region. Axis II of the tree ordination is difficult to interpret on the basis of community types because type H occurs throughout most of the elevation range of this gradient.

The herb ordination (PO-RA) has an interpretation similar to that of the tree ordination. Type H occurs throughout Axis I, but analysis of the remaining stands indeed suggests a combined coenocline. Axis II is a temperature gradient. This ordination is not simply interpreted and indicates the importance of *Vaccinium membranaceum* in all stands.

The lower east region ordinations (Fig. 9 and 10) accurately reflect the mosaic diagram (Fig. 15). The tree ordination (RA) fails to separate type F stands well because these contain only *Pinus ponderosa* and *Pseudotsuga menziesii* in neraly equal proportions. Nevertheless, the first axis is a distinct moisture gradient bounded by the dry hot type F stands and the mesic, cool type B stands dominated by *Thuja plicata*. This confirms the previous interpretation based on habitat values and is consistent with the mosaic diagram. Axis II is a clear temperature gradient. It ranges from the upper elevation type G stands found in mesic sites to lower elevation type C stands confined to mesic and riparian sites. The distribution of other types is consistent with this ordination and with the mosaic diagram. The distinct hump noted with earlier ordinations using all eastern stands has disappeared completely.

The herb data (PO) present a similar picture, but here the two axes are more strongly correlated. Type F stands are extreme in both axes, while type A and B stands, higher elevation, riparian types, are extreme in the first axis. This distribution indicates a composite moisture-temperature gradient, as indicated by the habitat analysis. The second gradient may represent a moisture gradient, but fails to be bounded by extreme stands. This ordination is therefore less successfully related to the mosaic diagram than the tree ordination.

The high elevation east region ordination (Fig. 11 and 12) are comparable to the upper portion of the mosaic diagram (Fig. 15). The interpretation of the first tree axis (PO-RA) as a temperature gradient is confirmed by community analysis. The axis is bounded by low elevation type E stands and high elevation type J stands. Axis II is bound by the high elevation, moist stands (type K) and dry stands in either low (type E) or high (type N) conditions. The tree ordination is comparable to the mosaic diagram and is corroborated by analysis of habitat data.

The herb ordination (RA) was interpreted as a combined moisture-temperature gradient in Axis I and as a temperature gradient in Axis II. This ordination is curved and such interpretations are not clear from analysis of individual stands. The first gradient is bounded by types E and N, which represent dry sites, and by types J and K, which represent wet sites. Interpreted in this way, the axis appears to be a moisture gradient. Axes II is bounded by the low elevation, mesic type D and by high elevation xeric stands (type N) and higher elevation mesic stands (types G and L). Thus we see that, where beta diversity is high, the low alpha richness tree ordinations can provide a more readily interpretable result.

Species patterns

The contrasts between ordinations may also be investigated with reference to individual species. The degree to which a species occupies the range of habitats is a measure of its breadth of tolerance relative to the available environments within a region. Between regions, the range of available habitat types can differ greatly, as indeed we believe they do. However, simple calculations of relative distribution can be used to infer differences in the extent of habitat dimensions. For the present purposes, it is sufficient to examine the distributional patterns of only selected species to provide a comparison between the environmental gradients.

One simple estimate of environmental gradient breadth is this index, which expresses the degree to which species occupy the available habitats:

$$\sum_{i=1}^{s} n_i/SN$$

where S is the number of species, n_i is the number of occurrences of species i and N is the maximum number of occurrences. The index is bounded between $1/N$ and 1.0. The smaller the index, the more restricted is the typical species in the region and the longer is the implied environmental gradient. The rare species excluded from these calculations, were they to be included, would accentuate the differences because rare species are far more numerous in the eastern region.

This index ranges from 0.502 in the west to 0.354 in the east when low elevation tree species are considered. At high elevation, the index ranges from 0.475 to 0.414. In the low elevation herbaceous data, the index goes from 0.387 in the west to 0.247 in the east. At high elevations, the index drops from 0.416 in the west to 0.237 in the east. These values support the inferrence derived from similarity projection ordination that there is a greater range of habitat conditions in the east.

An inspection of the stand by species tables indicates that mesophytic species become increasingly constricted from west to east while xerophytic species expand. However, as seen above, the expansion does not match the constriction, so that there is an overall decline in mean habitat occupancy for many species and for most growth form groups (del Moral 1976). The results of these comparisons are listed in Table 15. Species such as *Abies amabilis*, *Thuja plicata*, *Tsuga heterophylla*, and *T. mertensiana*, which are dominants in the western Cascades, are substantially restricted in the east. This restriction is greater for the low elevation species *T. heterophylla* than it is for most of the high elevation species. In contrast, most of the species that expand from west to east are lacking in the west. These species are distributed primarily in the Rocky Mountains and the Great Basin region. *Pseudotsuga menziesii*, a moderately xerophytic species that occurs throughout our study, increases its distribution from west to east in both elevational ranges, but it is always more frequent in warmer, drier, low elevation sites.

Table 15. Summary of species with marked changes in habitat use patterns within the western, central, and eastern regions. A species must occur in at least two regions; infrequent species are omitted.

<u>SPECIES THAT DECLINE FROM WEST TO EAST</u>

Abies amabilis, Thuja plicata, Tsuga heterophylla, T. mertensiana; Acer circinatum; Athyrium filix-femina, Berberis aquifolium, Caltha biflora, Cassiope mertensiana, Clintonia uniflora, Cornus canadensis, Disporum hookeri, Gaultheria shallon, Gymnocarpium dryopteris, Listera caurina, L. cordata, Oplopanox horridum, Phyllodoce empetriformis, Polysticum munitum, Pterospora andromedea, Rubus spectabilis, Smilacina racemosa, Streptopus amplexifolius, Tiarella trifoliata, Vaccinium alaskense, V. deliciosum, V. ovalifolium, Veratrum viride, Viola glabella, and *V. orbiculata.*

<u>SPECIES THAT INCREASE FROM WEST TO EAST</u>

Abies grandis, A. lasiocarpa, Picea engelmannii, Pinus albicaulis, P. monticola, Pseudotsuga menziesii; Acer glabrum, Alnus sinuata, Ceanothus velutinus, Sorbus sitchensis; Achillea millefolium, Agropyron spicatum, Arctostaphylos nevadensis, Arnica cordifolia, Berberis nervosa, Carex geyeri, Chimaphila umbellata, Hieracium albiflorum, Pachistima myrsinites, Pteridium aquilinum, Pyrola secunda, Rosa woodsii, Rubus parviflorus, Spirea betulifolia, and *Trillium ovatum.*

Similar patterns are found in the herbs as one moves from west to east. Mesophytic species generally contract, xerophytic species expand their distributions. Ferns, several ericads, orchids, other saprophytes, and small evergreen species become increasingly restricted from west to east. Such species are adapted to acid soils with low light intensity (del Moral & Denton 1977). In contrast, composites, graminoids, roses, and tall deciduous shrubs expand. Such species are better adapted to drier, more open habitats.

The moisture gradient, for the reasons stated above, is inferred to be considerably longer in the east than in the west. The east receives only between 600 and 1200 mm precipitation annually compared to a range of from 1500 to 2500 mm precipitation annually in the west. Therefore, while the distributions of many species shift in each region, the shift is primarily a response to the climatic factors and does not reflect changes in environmental requirements from one population of a species to another.

Complexity of the ordinations

The complexity of ordinations bears on the question of the number of habitat variables to which the vegetation responds in each region. One indication of increased dimensionality from west to east is alpha diversity, which increases markedly along this transect in comparable habitats (del Moral 1976).

This impression may be checked by additional comparisons of the ordinations. Eigenstructure analysis is dependent upon the number of variables in the analysis. The higher the number of variables, the lower will be the first several eigenvalues. Therefore, except as they correlated with species richness, these analysis indicate differences in structure only as they differ in the earlier and more information-rich axes. Comparisons within Table 2 show that variances on the first three axes decrease from west to east.

A second way in which to assess the complexity of the data is to determine the number of gaps in species runs between samples as arranged along the first axes of comparable ordinations. This was done using the entire species matrix (rather than the edited versions shown in Tables 3 to 14) and employing only the RA ordinations. Only gaps of 2 or more stands were counted. The maximum possible number of gaps depends upon the number of species occurrences; a species with few or many occurrences will have fewer possible gaps of 2 or more than a species of moderate frequency. The maximum number was calculated for each species and summed over the matrix. The more complex the data, the larger should be the ratio of observed to maximum number of gaps. For the tree samples, the western ratios were 0.148 and 0.200; for the central trees, 0.216 and 0.279; and for the eastern trees, 0.285 and 0.285. For the herbs, the values are higher, but the trend is similar. In the west, 0.300 and 0.310; for the central herbs, 0.373 and 0.363; and for the east, 0.320 and 0.340. These data suggest reduced complexity in the western region. That greater coenocline complexity exists in the east is also demonstrated by the changes in the index of gradient occupancy described above.

Habitat complexity

It has already been suggested that the three regions differ in habitat complexity. Direct evidence for this assertion is limited. There is a greater range of soil pH in the east than in the west (Appendix II, del Moral et al. 1976), despite the decreasing average acidity. Soil characteristics that are determined by conifer dominants are much more uniform in the west than in the east because the distribution of individual trees is more uniform and because the alpha diversity of tree species is half that of the east. These two factors suggest that the soil is a mosaic of qualities including nutrient content and availability, organic content, litter thickness, and so on. The light environment is similarly complex in the east, owing to the range of canopy conditions, from nearly completely closed in the more mesic habitats to quite sparse in the higher or drier sites (del Moral et al. 1976). The mosaic light-temperature-moisture pattern within a habitat creates a greater range of opportunities for species survival in the east than in the west.

Data presented in Table 1 and discussed above emphasize, through indirect means, that this trend of increased habitat complexity is real. We emphasize that the gamut of moisture conditions in the east is greater than in the west (Fig. 13–15) because the maximum drought conditions become more severe along this transect.

Comparison of tree with herb ordinations

The results demonstrate that, while the ordinations of the same stands based on different character sets gave similar environmental interpretations (and can usually be related to the mosaic diagrams), differences in the number of attributes and in beta diversity lead to different ordination results. Stand patterns were often quite different. This result suggests that the different types of species relate to environmental gradients in different ways. Spearman rank correlations between ordinations of stands using different data but the same ordination technique give fairly low correlations. In the west, low elevation RA-I results are correlated, $r = 0.47$; in the high elevation stands, PCA-I ($r = 0.79$) and RA-PO-I ($r = 0.45$) are correlated. In the central area, low elevation, only PCA-I ($r = -0.22$) is correlated, while in the high elevation, only RA-II ($r = 0.36$) is correlated. In the east, the correlations are higher. At low elevation, WA ($r = 0.82$), PCA-I ($r = -0.87$), and RA-I (-0.90) each show strong relationships between the strata. At high elevation, the relationships are weaker: WA ($r = -0.44$), PO ($r = 0.52$), RA-I ($r = -0.71$), RA-PO-I ($r = 0.47$), and PCA-I ($r = 0.25$) are all significant. (Negative coefficients reflect only arbitrary differences in axis direction in RA.)

The higher correlations in the east may be explained as follows. In the west and central regions, the environmental gradients to which the understory species respond are controlled largely by the canopy species. Thus, the understory must respond to both physical and biotic properties, and the correlation between strata may break down. In the drier east, both the strong gradient of canopy cover and the physical environment affect the understory species. Since the canopy itself responds to the physical environment, the understory responds in a similar way. That this is so is supported by the reduced correlation between ordinations in the higher elevations, where the canopy is often closed, and more like the situation in the western and central forests.

Richness trends

Patterns of species richness often reflect the severity of environmental conditions (del Moral 1972), though generalizations are best restricted to within-region comparisons over limited ranges of environments (Glenn-Lewin 1976, Peet 1978). In the west, the major trend is richness decreasing with elevation, but the trend is not smooth. At any elevation, riparian stands will have the highest richness, with essentially monotonic decline to lower richness in drier sites. At the lowest elevations, warm, dry sites in which light gaps exist have richness comparable to riparian sites; intermediate sites are less rich. Temperature, as it controls snow pack and the length of the growing season, is a major factor in the west. At any elevation, the poorest sites never have less than 50 % of the species number in the richest sites, whereas decrease in richness with elevation often exceeds a threefold change.

The situation in the central region is more complex. High elevation stands do not suffer the richness depletion to the extent that their western counterparts do. At lower elevations, the canopy opens slightly in the driest sites, resulting in some richness increase; therefore richness contrasts are not large along the moisture gradient at any elevation. Maximum values are in low, moist stands, minimum values in the closed, mesic subalpine forests. At the higher elevations, there is a rough Gaussian distribution of richness from the moist to xeric sites, with intermediate (mesic) sites having maximum values. Thus, in the central regions, values do not differ as markedly as they do in the west because compensatory mechanisms interact to maintain fairly high richness values.

In the east, there are pronounced species richness patterns along both temperature and moisture gradients. Maximum richness (over 40 species per plot) occurs in mid-elevation, riparian sites. Minimum richness occurs in the lowest, driest sites and in the coldest, wetter sites. There is a local maximum in mid-elevation, dry sites. This peak corresponds to the open-canopy forests that are not too dry. Wetter forests are too dark and more xeric forests too dry to support as many species. Thus in the east, at least three gradients, temperature, moisture, and light are recognized, with moisture probably the most significant.

Effectiveness of ordination techniques

It is instructive to rate each of the techniques on the 12 sets of data in terms of distortion, spread of stands, and species continuity in the first dimension. Each method was rated from excellent to poor on a 4 point scale, with these results: WA 13 excellent, 8 good, 1 fair; PO 12 excellent, 19 good, 5 fair; RA 12 excellent, 15 good, 8 fair, 1 poor; PCA 6 excellent, 17 good, 9 fair, 1 poor. (WA was not scored for distortion.)

If beta diversity is moderate to low, the number of species moderate and sampling error low, any of the methods give interpretable results without creating distortion. As beta becomes large, or alpha becomes either small or large, or sampling variability increases, RA or PO-RA becomes increasingly suitable. WA and PO are useful methods, but both require some information about the data to provide good ordinations. PCA often gives results comparable to RA, but with high beta becomes increasingly prone to distortion, despite the limited range of beta in this study. Automatic polar ordinations will fail in a second dimension if the data are skewed as a result of there being few species. These results agree with those of Gauch et al. (1977) and Gauch & Whittaker (1972).

WA, RA, and PO are similar, while PCA is inferior to RA in most instances. WA performance is best because it is based on the appropriate RA ordination. If the data are nearly unidimensional, this method is superior to the others, but where one gradient dominates another, the method remains useful. The PO is the best PO of any tried on the data. Not all PO ordinations were as successful. When compared to PCA, RA is superior in 16 cases and inferior in two, and equivalent in the remainder. Thus, even where beta diversity is low, RA provides better spread of stands, reduced distortion, and usually more compact species distributions than PCA. It is to be preferred to PCA as a general indirect ordination method and as a basis for selective refinements of the analysis.

Conclusions

Analysis of vegetation data by ordination may well proceed in this order, following decisions about standardization and data transformations: (1) A first general ordination by RA is undertaken, to determine the overall pattern of floristic variation, followed by automatic PO-RA. (2) Data may then be inspected for discontinuities, and decisions concerning the fate of rare species and outlier stands may be made. The data set may be divided into two or more homogenous sets if distortion is great or beta is large. (3) Subjective PO and WA, based on either RA results or external data may follow, along with an additional RA if the data set has been materially altered. (4) Other, more specialized analyses may be undertaken, depending upon the goal of the study.

In this study, we have found that different strata respond differently to environmental conditions, even though the ordinations result in similar environmental interpretations. This result is common to ordination studies. In this instance, the major effect results from the different influences of canopy species in the three regions. In the west, the canopy is more homogeneous than the east and represents a more constant condition. In the east, these conditions do not obtain. The strongest correlations between strata occurred in the east where both strata tested are more directly coupled to the physical environment. Additional division of the data by growth form is a tactic that may be useful for very detailed ordination analysis or for investigations in which the number of species is excessively large.

The major differences between the western and eastern regions result from differences in alpha, beta and gamma diversity. These result in a decline of ordination efficiency from west to east and reflect greater structural complexity of the eastern vegetation. The higher alpha and beta diversity of the eastern stands imply that the relative ecotope breadth of these species is narrower, even though species may occupy the same range of absolute conditions in each region.

The data presented in this paper suggest that vegetation is structured differently in the three regions as a consequence of response to the general climatic gradient. Mesophytic species occupy a smaller fraction of available habitats in the east than in the west, while xerophytes occupy a larger fraction. Species richness increases from west to east, but the increase is variable among growth-forms. The following hypothesis is presented to account for these and the other noted differences.

The rainshadow created by the Cascade crest results in warmer summers, reduced snow pack and higher evapotranspiration during the growing season in eastern forests. Winters in these forests are colder with greater diurnal temperature fluctuation and lower humidity. Therefore, eastern forests have a greater probability of experiencing drought and when droughts occur they are more prolonged and severe than in the western forests. Increased drought frequency and severity imply that vegetation is more open due to competition between tree species for available moisture. Open habitats are more complex than those with continuous tree canopy and offer greater ranges of environmental conditions for undergrowth plants and tree seedlings. In the east there are more environmental dimensions to which species may respond than in the west, and therefore the average ecotope breadth among species will decline. While xeric habitats are more extensive in the east, others there are quite mesic. Thus, in the east there is a greater contrast of moisture conditions than in the west, and more diverse combinations of temperature and moisture. These considerations suggest that effective habitat gradients are longer, and the relative distributional range of mesophytic species is consequently reduced. In combination, these considerations suggest how greater species richness can be attained and also imply that diversity of growth-forms should be greater in the east than in the west.

Summary

Forest vegetation located in three areas of the central Washington Cascades, arrayed along a gradient of increasing continentality and decreasing rainfall, were compared using ordination methods. Within each region, lower and upper elevation sites were analyzed separately and for each set of sites, trees and ground story vegetation were analyzed independently. Principal components analysis, reciprocal averaging, weighted averaging, and polar ordination were applied to each set. The characteristics of the data determined which method gave the most readily interpretable results, but RA and WA usually best ordered the stands along a complex, combined coenocline, while PO often decomposed the gradient into moisture and temperature components. PCA was of little use, even with relatively low beta diversity.

Results are presented in the form of stand by species tables for each data set and the most appropriate two dimensional ordination. Both are correlated to the classification. A mosaic diagram for each region is synthesized from these analyses and habitat data. These diagrams indicate that community types occupy a smaller portion of the habitat as continentality increases.

The ordination results were in close agreement with our earlier classification of these stands. The maritime (west) region contains stands of low richness and with relatively little coenocline differentiation. In contrast, the continental (east) region has high alpha and beta diversity. Species in the west tend to occupy a broad portion of the available habitat range, while species in the east do not. The analyses reveal that ordinations by different strata may produce similar stand sequences if both strata are responding directly to the same factors, but that the correspondence degenerates where the understory responds primarily to the nature of the canopy dominant species.

Thus stand sequence correlations are highest in the lowland eastern region and lowest in the lowland western region.

This study demonstrates that none of these metric ordination methods is fool-proof and that none should be used exclusively or in isolation. RA and PO are demonstrated to be useful general methods; WA gave results similar to those of RA. PCA never produced uniquely superior results. Analyses with too few species and moderate beta diversity often produce distortions as pronounced as those with many species and high beta diversity.

Appendix I. Community classification in the three regions, from del Moral et al. (1976)

Western region

A. Pseudotsuga menziesii-Tsuga heterophylla/Vaccinium alaskaense/Linnaea borealis
B. Tsuga heterophylla-Thuja plicata/Vaccinium alaskaense/Blechnum spicant
C. Abies amabilis-Tsuga heterophylla/Vaccinium alaskaense
D. Abies amabilis/Vaccinium ovalifolium
E. Tsuga mertensiana-Abies amabilis/Vaccinium alaskaense-Menziesia ferruginea
F. Tsuga mertensiana-Abies amabilis/Vaccinium deliciosum-Phyllodoce empetriformis
G. Abies amabilis/Vaccinium membranaceum/Clintonia uniflora
H. Tsuga mertensiana-Abies amabilis/Vaccinium membranaceum-Menziesia ferruginea

Central region

A. Pseudotsuga menziesii-Abies grandis/Acer circinatum/Trientalis latifolia
B. Tsuga heterophylla/Acer circinatum-Vaccinium membranaceum/Linnaea borealis
C. Pseudotsuga menziesii/Vaccinium membranaceum-Pachistima myrsinites/Rubus lasiococcus
D. Pseudotsuga menziesii/Vaccinium membranaceum/Rubus lasiococcus
E. Abies lasiocarpa-Pseudotsuga menziesii/Vaccinium membranaceum/Arctostaphylos nevadensis
F. Abies lasiocarpa-Tsuga mertensiana/Vaccinium membranaceum-Rhododendron albiflorum
G. Abies amabilis/Vaccinium membranaceum/Clintonia uniflora
H. Abies amabilis/Vaccinium membranaceum-Rhododendron albiflorum/Rubus lasiococcus
I. Tsuga mertensiana/Vaccinium membranaceum/Phyllodoce empetriformis
J. Abies lasiocarpa/Vaccinium membranaceum/Rubus lasiococcus

Eastern region

A. Tsuga heterophylla-Thuja plicata/Cornus stolonifera/Clintonia uniflora
B. Thuja plicata/Rubus parviflorus/Clintonia uniflora/Equisetum arvense
C. Abies grandis-Thuja plicata/Acer glabrum/Rubus parviflorus
D. Abies grandis/Spiraea betulifolia-Pachistima myrsinites/Rubus parviflorus
E. Pseudotsuga menziesii/Pachistima myrsinites-Ceanothus velutinus/Carex geyeri
F. Pinus ponderosa-Pseudotsuga menziesii/Agropyron spicatum-Carex geyeri
G. Picea engelmannii-Abies lasiocarpa/Vaccinium membranaceum
H. Picea engelmannii/Vaccinium membranaceum/Rubus lasiococcus
I. Abies amabilis-Picea engelmannii/Rhododendron albiflorum/Arnica cordifolia
J. Abies lasiocarpa-Picea engelmanni/Rhododendron albiflorum/Arnica cordifolia
K. Tsuga mertensiana-Abies amabilis/Rhododendron albiflorum-Vaccinium membranaceum
L. Pinus albicaulis-Abies lasiocarpa/Arctostaphylos nevadensis-Pachistima myrsinites
M. * Abies grandis-A. lasiocarpa/Pachistima myrsinites/Rubus parviflorus
N. * Abies lasiocarpa-Pinus albicaulis/Pachistima myrsinites-Arctostaphylos nevadensis

* These groups split from Group G.

Appendix II. Summary of environmental data for each region

ENVIRONMENTAL DATA

Low Sequence number	Western region				Central region				Eastern region			
	A	B	C	D	A	B	C	D	A	B	C	D
1	1066	3	3.7	60.0	1109	7	5.9	11.7	1036	2	6.2	6.0
2	1036	2	4.0	65.0	1158	7	5.5	3.7	760	5	6.3	5.9
3	1143	8	4.5	10.2	1220	9	5.5	6.5	900	5	6.0	7.1
4	1045	8	4.1	62.0	1112	9	6.0	24.6	915	2	6.3	3.3
5	1036	9	3.6	70.0	1220	9	5.6	4.5	885	7	5.6	4.0
6	1012	2	5.0	7.5	1112	8	5.5	50.0	885	1	6.1	12.3
7	1066	8	3.8	70.0	1220	9	5.0	9.4	945	1	6.2	2.2
8	1098	3	4.1	47.1	1130	8	5.2	10.5	1040	1	6.1	2.8
9	1128	5	4.0	5.8	1130	8	6.0	5.0	610	1	7.0	4.4
10	991	3	3.8	65.0	1130	7	5.6	24.4	700	1	7.2	55.0
11	930	1	4.6	66.0	1160	8	4.2	34.2	760	1	5.7	6.9
12	1128	8	3.6	65.0	1155	8	5.5	8.7	825	5	6.3	4.4
13	869	7	4.8	9.3	1155	7	5.4	3.1	825	6	6.4	11.1
14	915	3	3.8	64.0	1085	8	5.1	8.8	1000	2	7.0	20.1
15	823	3	3.8	29.6	975	8	6.0	4.4	1035	4	7.2	51.0
16	960	5	3.7	70.2	853	1	4.0	35.5	1070	7	6.1	8.5
17	640	2	5.1	14.9	915	1	6.7	8.1	1175	6	5.2	3.4
18	915	7	4.0	60.0	945	1	6.4	6.7	1175	7	5.7	3.9

19	610	8	3.9	65.8	953	1	5.4	9.4	1175	1	6.2	12.1
20	884	4	4.0	31.4	960	2	5.1	9.7	1190	5	5.6	6.5
21	762	7	4.9	20.5	990	1	5.2	11.6	1295	4	6.1	6.2
22	762	3	4.0	19.4	940	1	4.3	9.0	1220	3	5.0	38.0
23	884	4	4.7	11.1	910	1	4.8	5.7	1190	4	6.0	3.4
24	853	2	3.6	72.2	885	1	4.5	11.1	1100	4	6.0	7.0
25	1021	2	4.6	13.8	823	1	5.6	10.1	1250	7	6.2	4.4
26	975	6	3.6	74.5	840	4	5.7	4.2	1295	9	6.2	5.4
27	1128	2	3.8	28.1	820	5	5.8	6.1	1160	7	6.6	2.5
28	1067	6	4.0	36.0	790	6	5.8	5.3	1100	7	6.6	4.2
29	655	6	5.0	13.9	760	7	6.1	6.1	1035	2	6.8	4.3
30	701	9	5.0	7.4	780	4	5.5	10.1	1020	1	6.9	3.6
31	549	1	5.5	10.1	1100	9	6.0	4.1	975	8	6.7	5.4
32	808	7	4.9	10.1	1205	2	4.8	5.5	915	8	6.5	14.3
33	549	1	4.8	13.0	1035	3	5.4	7.1	855	8	6.4	8.1
34	884	7	5.3	5.1	975	2	5.8	9.4	790	8	6.1	4.7
35	701	1	4.8	38.9	915	1	5.1	12.0	1280	7	6.0	6.0
36	945	6	4.5	9.9	920	3	4.6	3.0	—	–	—	—
37	610	2	3.9	25.0	915	4	4.2	3.0	—	–	—	—
38	1036	2	4.0	8.0	1100	6	5.1	7.8	—	–	—	—
39	610	6	4.1	14.5	1160	2	3.9	12.3	—	–	—	—
40	640	1	4.3	15.5	1080	4	4.8	13.0	—	–	—	—
High Sequence number												
1	1140	4	5.4	16.7	1280	8	5.6	8.3	1350	1	5.5	8.9
2	1265	8	4.0	36.2	1340	8	5.9	8.6	1310	7	6.7	12.4
3	1310	9	3.9	16.4	1400	8	5.2	7.2	1600	7	4.6	5.2
4	1320	7	4.3	14.8	1220	7	5.0	7.3	1590	5	5.3	5.4
5	1235	8	4.0	8.7	1340	7	5.2	8.3	1525	7	5.6	11.1
6	1145	1	4.5	60.0	1435	6	5.8	7.8	1475	7	5.4	4.3
7	1165	8	3.9	20.9	1450	5	4.9	8.8	1465	3	6.0	5.8
8	1205	5	4.2	70.0	1490	7	5.6	11.9	1385	5	6.0	5.4
9	1285	8	3.8	47.0	1585	5	4.9	11.0	1370	6	6.0	11.3
10	1145	4	4.3	18.5	1600	9	4.0	12.0	1465	8	6.7	4.7
11	1250	8	3.8	75.0	1540	5	4.1	6.0	1370	1	4.8	10.4
12	1250	6	3.9	67.2	1570	3	4.5	24.6	1370	7	5.9	31.0
13	1190	5	3.7	74.0	1450	8	3.6	40.0	1420	7	5.5	6.1
14	1255	3	3.4	75.0	1450	3	4.1	4.9	1385	5	5.8	4.0
15	1145	2	3.3	75.0	1310	9	4.0	10.6	1480	1	5.9	8.6
16	1235	2	3.7	60.8	1290	4	4.7	5.2	1540	6	5.8	9.2
17	1480	4	3.5	71.8	1295	6	4.5	22.2	1585	7	4.5	7.1
18	1465	2	4.2	19.8	1295	6	5.3	2.7	1540	2	5.5	6.0
19	1455	6	4.0	9.2	1265	6	4.6	7.3	1920	2	5.5	5.4
20	1480	4	3.9	20.0	1225	5	5.2	3.6	1615	2	5.8	4.5
21	1465	3	4.0	25.7	1270	5	5.3	4.9	1830	5	4.2	11.2
22	1450	1	3.9	28.3	1265	8	4.6	20.0	1615	2	5.6	7.1
23	1420	4	3.4	6.7	1310	5	5.1	11.6	1710	6	5.6	5.3
24	1400	6	4.1	5.2	1310	5	5.2	8.5	1555	2	5.4	9.7
25	1420	5	4.3	12.6	1360	8	5.1	10.3	1585	7	6.2	17.4
26	1370	3	3.9	72.5	1370	4	4.9	7.8	1540	5	5.7	15.6
27	1460	5	3.8	12.7	1480	8	4.6	20.3	1740	8	5.8	5.0
28	1495	5	4.0	5.0	1390	3	4.8	7.6	1465	2	6.0	6.0
29	1460	7	4.1	15.1	1435	9	4.3	9.4	1555	8	6.0	6.1
30	1540	3	4.2	9.0	1325	5	4.5	19.0	1755	8	6.0	6.0
31	1465	4	3.2	78.0	1350	9	4.8	14.4	1555	7	6.1	5.8
32	1555	2	4.3	6.5	1390	6	5.0	13.9	1615	8	6.0	—
33	1463	7	3.9	7.5	1465	8	4.6	21.3	1630	9	6.2	7.0
34	1670	3	4.5	11.5	1525	8	4.8	16.9	1720	8	6.2	6.3
35	1675	5	3.8	29.5	1585	8	5.3	12.2	1750	8	6.1	—
36	1690	5	3.8	17.6	1640	4	4.5	—	—	–	—	—
37	1310	8	3.8	13.8	1710	7	4.2	13.0	—	–	—	—
38	1355	1	4.0	8.0	1555	6	5.0	8.7	—	–	—	—
39	1160	2	4.0	30.9	1480	7	5.3	5.9	—	–	—	—
40	1220	6	4.2	15.5	1370	4	5.2	7.0	—	–	—	—
41	—	–	—	—	1250	2	4.7	7.4	—	–	—	—

A = elevation (m)
B = moisture-insolation index
C = soil pH
D = soil organic matter

References

Austin, M.P. 1976a. On non-linear species response models in ordination. Vegetatio 33: 33–41.

Austin, M.P. 1976b. Performance of four ordination techniques assuming three different non-linear species response models. Vegetatio 33: 43–49.

Buffo, J. & L.J. Fritschen. No date. Direct solar radiation on various slopes for 45 and 47.5 degrees north latitude. U.S.I.B.P. Coniferous Forest Biome, Ecosystem Analysis studies, Internal Report 51.

Fonda, R.W. & L.C. Bliss. 1969. Forest vegetation of the montane and subalpine zones, Olympic Mountains, Washington. Ecol. Monogr., 39: 271–301.

Franklin, J.F. & C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Pac. Northwest For. Range Exp. Sta. Gen. Tech. Rep. PNW-8, Portland, Oregon, 417 pp.

Gauch, H.G. 1973a. A quantitative evaluation of the Bray-Curtis ordination. Ecology 54: 829–836.

Gauch, H.G. 1973b. The relationship between sample similarity and ecological distance. Ecology, 54: 618–622.

Gauch, H.G. 1977. ORDIFLEX: a flexible computer program for four ordination techniques. Ecology and Systematics, Cornell University, Ithaca, New York. 123 pp.

Gauch, H.G., R.H. Whittaker & T. R. Wentwort. 1977. A comparative study of reciprocal averaging and other ordination techniques. J. Ecol. 65: 157–174.

Glenn-Lewin, D.C. 1976. Species diversity in North American temperate forests. Vegetatio 33: 153–162.

Groenewoud, H. van. 1976. Theoretical considerations of the covariation of plant species along ecological gradients with regard to multivariate analysis. J. Ecol. 64: 837–847.

Guinochet, M. 1973. Phytosociologie. Masson, Paris, VI + 228 pp.

Hill, M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol. 61: 237–249.

Hill, M.O. 1974. Correspondence analysis: a neglected multivariate method. J. Roy. Stat. Soc., Ser. C. 23: 340–354.

Hitchcock, C.L. & A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, 730 pp.

Long, J.N. 1976. Trends in plant species diversity associated with development in a series of Pseudotsuga menziesii/Gaultheria shallon stands. Northwest Sci. 51: 119–130.

Long, J.N. & J. Turner. 1975. Aboveground biomass of understory and overstory in an age sequence of four Douglas-fir stands. J. Appl. Ecol. 12: 179–188.

Moral, R. del. 1972. Diversity patterns in forest vegetation of the Wenatchee Mountains, Washington. Bull. Torrey Bot. Club 99: 57–64.

Moral, R. del. 1973. The vegetation of Findley Lake Basin. Amer. Midl. Natur. 89: 26–40.

Moral, R. del. 1974. Species patterns in the upper North Fork Teanaway River drainage, Wenatchee Mountains, Washington. Syesis 7: 13–30.

Moral, R. del. 1976. Wilderness in ecological research: an example from the Alpine Lakes. Pp. 173–194, in Terrestrial and Aquatic Ecological Studies of the Northwest, ed. R.A. Soltero, Eastern Washington State College Press, Cheney, Wash.

Moral, R. del & M. F. Denton. 1977. Analysis and classification of vegetation based on family composition. Vegetatio 34: 155–165.

Moral, R. del & J.N. Long. 1977. Classification of montane forest community types in the Cedar River drainage of western Washington, U.S.A. Can. J. For. Res. 7: 217–225.

Moral, R. del, A.F. Watson & R.S. Fleming. 1976. Vegetation structure in the Alpine Lakes region of Washington State: classification of vegetation on granitic rocks. Syesis 9: 291–316.

Nie, N.H., Hull, J.G. Jenkins, K. Steinbrenner & D.H. Bent. 1975. Statistical package for the social sciences, Second Edition. McGraw Hill Book Company, New York, 675 pp.

Noy-Meir, I., D. Walker & W. T. Williams. 1975. Data transformations in ecological ordination. II. On the meaning of data standardization. J. Ecol., 63: 779–800.

Noy-Meir, I. & R.H. Whittaker. 1977. Continuous multivariate methods in community analysis: some problems and developments. Vegetatio 33: 79–98.

Peet, R. 1978. Forest vegetation of the Colorado Front Range: patterns of species diversity. Vegetatio 37: 65–78.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30: 279–338.

Whittaker, R.H. & W.A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona. (II.) A gradient analysis of the south slope. Ecology 46: 429–452.

Williams, W.T. (ed.). 1976. Pattern analysis in agricultural science. CSIRO, Melbourne, 331 pp.

Zobel, D.B., A. McKee, G.M. Hawk, & C.T. Dyrness. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. Ecol. Monogr. 46: 135–156.

Accepted 29 March 1978