AN ABSTRACT OF THE THESIS OF

Janet L. Ohmann for the degree of Doctor of Philosophy in Forest Science presented on November 29, 1995. Title: Regional Gradient Analysis and Spatial Pattern of Woody Plant Communities in Oregon.

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Thomas A. Spies

Knowledge of regional-scale patterns of plant community structure and controlling factors is largely qualitative and based on numerous local studies. Data from a subsample of 10,000 field plots were used to quantify and map compositional gradients of woody plant communities across Oregon forests. Canonical correspondence analyses explained 9-14% of the total species variation at three geographic scales. Climate contributed most to total variance explained (44-58%), followed by geology (6-16%), disturbance (7-13%), and topography (4-8%). The dominant compositional gradient was associated with climate, from the lower elevation, moderate, maritime climate of the coast to the higher elevation, drier, continental climate of the interior. The second canonical axis followed a gradient from the warm, dry growing seasons of the interior valleys and eastern Cascades, to cooler, wetter mountainous areas. Only those parent materials that present extreme growing conditions, primarily ultramafic soils, were significant at the regional level. Ecological relationships differed substantially among subregions within the state. Except for topography, which contributed more to explained variation at finer geographic scales, ecological differences among subregions overshadowed effects of geographic extent. Topographic effects were stronger and beta diversity greater in eastern Oregon, where moisture is more limiting for plant growth, and weakest near the coast where climate is more favorable. The secondary importance of topography, disturbance, and substrate can be attributed to their influence on relative abundances of species within a local area, rather than on species presence or absence within broader regions. Community structure varied at a finer spatial scale in eastern than in western Oregon, and species turnover along gradients was greater for shrubs than trees. Amount of unexplained variation in the species data was high but not atypical of gradient analyses. Yet spatial structure in the species data that was uncorrelated with explanatory factors suggests potential to improve the canonical correspondence analysis models, particularly in eastern Oregon. Study findings have implications for considering biological diversity in regional conservation strategies, in planning for global climate change, and in the design of regional inventory and monitoring programs.

Regional Gradient Analysis and Spatial Pattern of Woody Plant Communities in Oregon

by

Janet L. Ohmann

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APPROVED:

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Janet L. Ohmann, Author

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INTRODUCTION

Identifying the factors underlying the distribution, abundance, and diversity of species in ecological communities is a central problem in community ecology. Ecologists now recognize that community structure is controlled by multiple physical and biological factors that operate across a range of scales. Historically, ecological research focused primarily on intracommunity patterns, especially on the role of competition and other species interactions in community structure, and regional factors were considered by biogeographers. Recently, however, there has been renewed interest in ecological research at broader spatial scales. Community structure is now viewed as a product not only of local physical conditions and interactions among species, but also of regional constraints such as climate and processes such as dispersal, speciation, and accidents of history (Brown 1984, Menge and Olson 1990, Neilson and Wullstein 1983, Ricklefs 1987, Ricklefs and Schluter 1993). This view is consistent with hierarchy theory, which predicts that phenomena at a given level are a function of processes and constraints operating at higher and lower organizational levels (Allen and Starr 1982, O'Neill et al. 1986). Many current problems in natural resource and environmental policy, such as global climate change and conservation of species diversity, also demand a regional to global perspective.

Plant community ecologists have devoted considerable effort to quantifying local- to landscape-scale variation in vegetation, where a landscape might be considered an area of hundreds to thousands of hectares. Vegetation often is well known locally, but factors controlling patterns of community composition differ among localities. There currently are not systematic regionalizations or studies for placing these differences within a broader context, because the study of regional-scale vegetation patterns is still in its infancy. Debates about what factors control vegetation pattern may be largely artificial if these factors vary within and among regions. Current knowledge about regional vegetation patterns is generally qualitative and descriptive, often based on the collective findings of disparate local studies (Franklin and Dymess 1973). Very few studies have used plot-level datasets to examine regional-scale variation in community structure. Indeed, the synthesis and collation of plant-community data in regional analysis has been cited as a major research need in plant community ecology (Franklin 1988, Franklin and Blinn 1988). In particular, gradient representation is only recently beginning to be used to study geographic variation in community structure; such methods offer opportunities to evaluate the importance of, and interactions between, historical, biological, and environmental factors (Peet 1978). The growing number of vegetation plots installed by ecology programs and regional forest inventories bring unprecedented opportunities to quantify and analyze regional vegetation patterns. Recent development of regional-scale climate and other ecosystem models, digital data layers, and geographic information systems (GIS) offer new means of developing explanatory variables relevant to vegetation pattern at broad geographic scales. Such efforts are now limited primarily by the development of appropriate analytical methods (Allen et al. 1991) and tools, and by the practical challenges of working with extremely large and complex datasets.

The purpose of my study was to quantify, describe, and map compositional gradients of woody plant communities in Oregon's forests and woodlands (fig. 1), relate them to regional environmental gradients, and provide the scientific basis for generating hypotheses for future research. The primary approach was gradient analysis of plot-level vegetation data. Study objectives were to: (1) Identify and quantify environmental factors associated with regional gradients in the composition of woody plant communities, and explore how these factors change among scales, locations, and taxonomic groups; and (2) characterize and map spatial patterns of compositional gradients and community types. Current knowledge and key hypotheses associated with these objectives are discussed below.

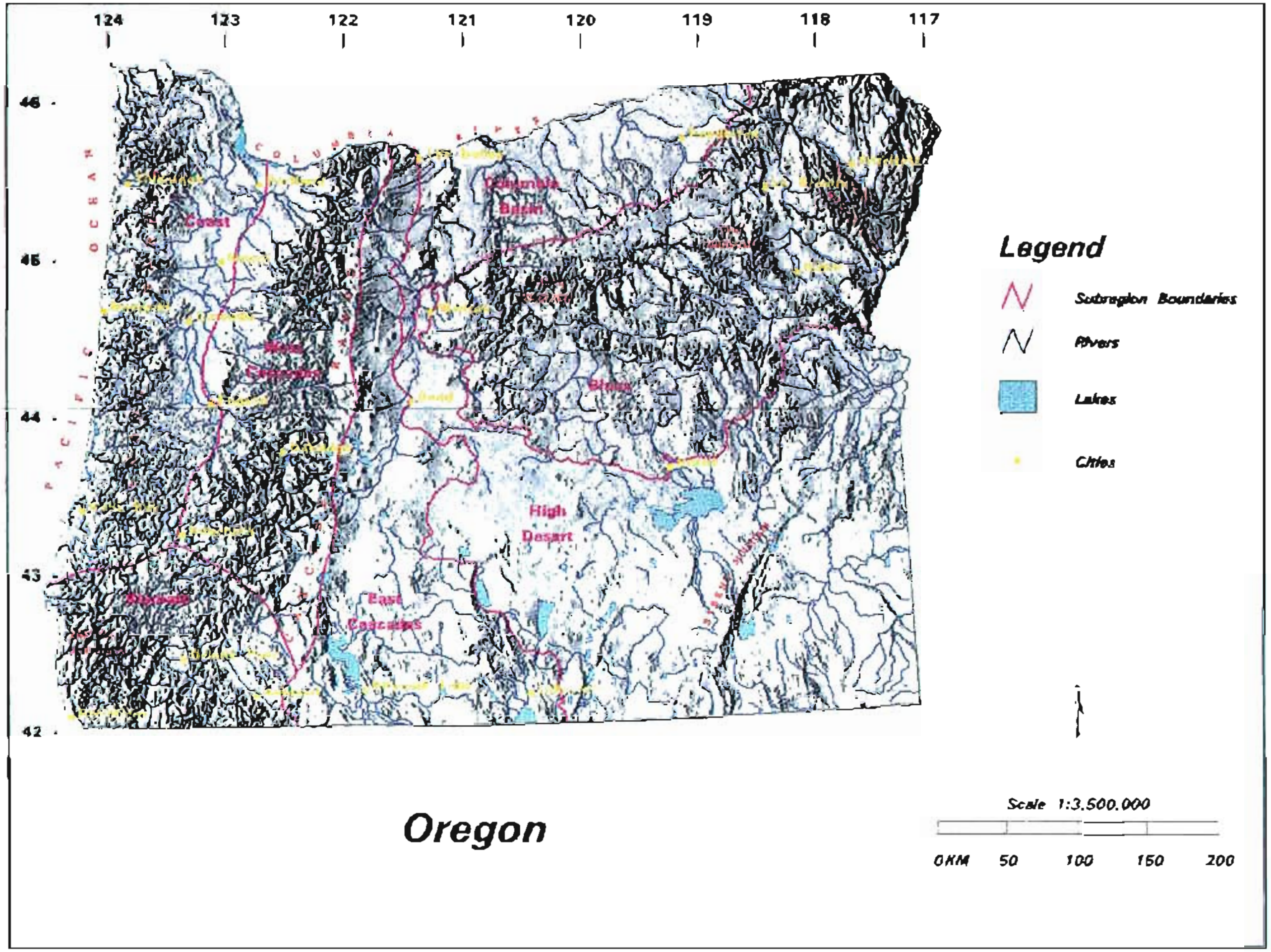


Figure 1. Map of Oregon showing major cities, rivers, and physiographic features, subregion boundaries, and latitude/longitude.

Current Knowledge of Regional Patterns in Forest Communities

Patterns of community composition, structure, and function, and the factors controlling them, are the product of ecological processes operating over a range of spatial and temporal scales. At a biogeographical scale, patterns of vegetation physiognomy and community composition are associated primarily with large-scale climate (Daubenmire 1978, Woodward 1987), which influences communities indirectly by modifying or regulating the importance of local-scale factors, and also directly by limiting populations (Menge and Olson 1990). Indeed, plant response to climate is crucial to a plant's presence at all spatial scales (Woodward 1987). Historical (e.g., evolution) and population processes operating at regional to landscape scales influence which taxa are available to occupy a particular site.

Local variations in community structure are influenced by biotic interactions; by the selection of specific life history, physiognomic, and physiological traits by weather cycles (Neilson 1987, Neilson et al. 1992); and by disturbance events that are stochastic and highly variable over time and space. Within a local area, the range of climatic conditions is much less and most sites fall within species' physiological tolerances, and so shifts in species relative abundances are associated with local variations in topography, microclimate, and substrate (Neilson 1987, Neilson et al. 1992). These local shifts are muted in favorable climates and more pronounced where climate is more stressful (Neilson and Wullstein 1983). Response to environment--biotic and abiotic--is known to vary among vegetation strata as well (Daubenmire 1989, Whittaker 1960). Trees are more faithful indicators of the regional environment, particularly climate, than are understory plants (Daubenmire 1989, Whittaker 1960), owing to their taller stature and longer lifespans. Understory shrubs and herbs are more sensitive to fine-scale variation in environment, disturbance, and competition, and respond to conditions imposed by the overstory canopy as well as to the surrounding micro- and macro-climate.

In summary, a predictive framework of community structure across a broad region would thus be hierarchical, with simpler local-scale models nested within more complex, larger-scale models (Menge and Olson 1990). The fine-scale models would be tailored to a location's particular biota, physical environment, and history. However, the scientific and quantitative basis for such a model is lacking. Regional-scale patterns of species composition and controlling factors in forest communities still are understood only generally. In particular, the contributions of large-scale and local-scale processes to variation in community composition are poorly understood (Menge and Olson 1990, Ricklefs 1987), as are the relative contributions of physical environment, biotic factors, and the role of disturbance and successional processes. The few quantitative studies of patterns of forest community composition in the western United States have been limited to older, natural forests, to incomplete segments of regional environmental gradients, or to certain community types (Allen et al. 1991; Allen and Peet 1990; Daubenmire and Daubenmire 1968; del Moral and Fleming 1979; del Moral and Watson 1978; Dyrness et al. 1974; Fonda and Bliss 1969; Minore 1972; Peet 1978, 1981; Riegel et al. 1992; Spies 1991; Spies and Franklin 1991; Whittaker 1960; Whittaker and Niering 1965; Zobel et al. 1976), and almost all have been conducted at the landscape scale.

In the Pacific Northwest, much of the research in plant community ecology has involved classification of potential natural vegetation, rather than ordination or gradient analysis. A substantial body of work exists for defining plant associations and habitat types for forested areas in the Pacific Northwest (Wellner 1989), but results have been published only in non-peer-reviewed reports. In Oregon and Washington, the Regional Ecology Program of the Pacific Northwest Region, USDA Forest Service, has developed plant associations for some National Forest lands, using the general approach of Daubenmire (1952, 1989). However, classifications have been developed with the primary purpose of guiding forest management activities, and the relative placement of forest series and associations along environmental gradients has only been inferred or hypothesized (e.g., see Topik et al. 1988, p. 4). Regionally, there are large gaps in coverage of site classification efforts, most notably for nonfederal lands, reserved areas, less productive forest lands, and early- to mid-successional forests, and results have not been synthesized regionally.

In the only regional-scale account of natural vegetation of Oregon and Washington, Franklin and Dyrness (1973) also employed a classification approach. They organized their material, with some modifications, around vegetation zones that were defined and mapped *a priori* based on judgement of the authors (T. Dyrness, pers. comm.). Franklin and Dyrness' (1973) work was descriptive and based on scattered information in published articles, theses, and personal data files, rather than on any systematic sampling of vegetation, and vegetation was related to environmental factors only qualitatively. Very few quantitative studies based on gradient analysis of plot-level data have been conducted at the regional scale in the western U.S. (but see Allen et al. 1991) or elsewhere (but see Denton and Barnes 1987; Roberts and Wuest, submitted).

Studies that have explicitly addressed environmental factors associated with patterns of forest vegetation in the Pacific Northwest (Daubenmire and Daubenmire 1968, del Moral and Fleming 1979, del Moral and Watson 1978, Dyrness et al. 1974, Fonda and Bliss 1969, Minore 1972, Riegel et al. 1992, Spies 1991, Spies and Franklin 1991, Whittaker 1960, Whittaker and Niering 1965, Zobel et al. 1976, and others) and in other mountainous regions of the western United States (Allen et al. 1991; Allen and Peet 1990; Peet 1978, 1981), have consistently demonstrated the primary importance of temperature and moisture. For the central western Cascades of Oregon, Dyrness et al. (1974) hypothesized and Zobel et al. (1976) later found that temperature differentiated major vegetation zones, and moisture distinguished communities within the warmer zones, with some minor exceptions associated with soil nutrient availability. Zobel et al. (1976) hypothesized that moisture stress might play an important role in differentiating vegetation zones occurring between their study area and the Willamette Valley. Riegel et al. (1992) later concluded that precipitation was the key environmental factor governing distribution and composition of community types in the foothill oak (Quercus spp.) woodlands of southwest Oregon. Topographic position did not effectively differentiate vegetation types in the west-central Oregon Cascades (Zobel et al. 1976). Aspect-elevation compensation (i.e., reversal of the aspect occupied by a forest type with increasing elevation) has been documented in many mountain systems, but was not observed by Zobel et al. (1976).

In a study of Pseudotsuga menziesii-dominated forests over 40 yr old in western Oregon and Washington, regional patterns in community structure and composition were stronger than within-province differences (Spies and Franklin 1991, Spies 1991). Moisture was the most important factor explaining within-province variation: moist sites had higher basal area of shade-tolerant tree species and lower abundances of sub-canopy trees and evergreen shrubs. The authors surmised that regional compositional differences were attributable to climate, site productivity, and disturbance history, particularly fire. Species more often responded in terms of their relative abundance than in their occurrence among stand age-classes (Spies 1991).

In summary, both ordination and site classification efforts in the Pacific Northwest have demonstrated or inferred the primary importance of temperature and moisture. Current thinking about vegetation-environment relations at the regional level in the Pacific Northwest was synthesized by Franklin and Dyrness (1973, p. 50) (fig. 2) using ecological indexes described by Emmingham (1982). This diagram (fig. 2) can be considered a hypothesis for the regional distribution of major forest zones within an environmental field defined by the primary controls of temperature and moisture.

Soil chemistry has been shown to be associated with vegetation patterns in the Klamath Mountains and redwood regions (Whittaker 1960, Waring and Major 1964, Waring 1969), and in the pumice region of central Oregon (Volland 1985). But studies in several western mountain systems have shown that soil differences usually are important only at a secondary level (Whittaker and Niering 1965, Daubenmire and Daubenmire 1968, Fonda and Bliss 1969, Minore 1972, Zobel et al. 1976). At higher elevations, snow plays an important role through mechanical and microclimatic effects and by influencing seasonal water availability (Arno and Hammerly 1984).

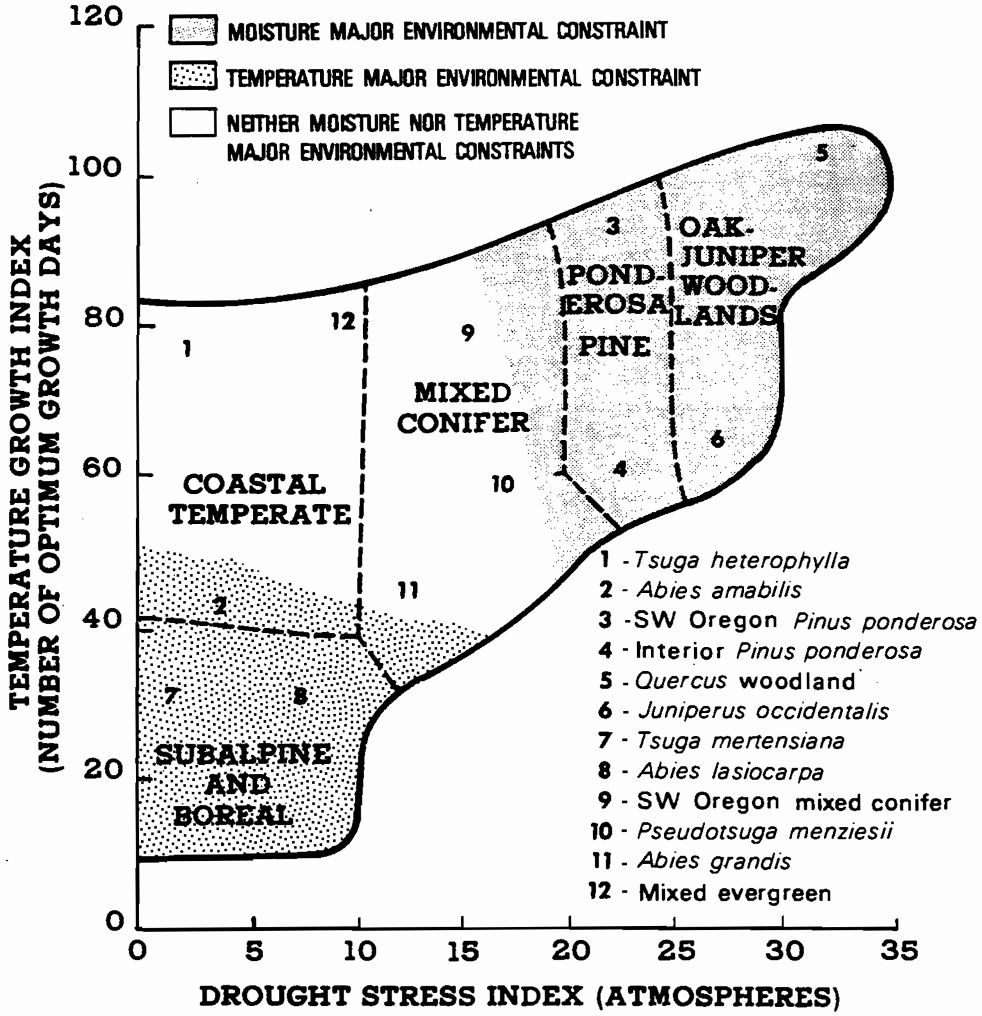


Figure 2. Tentative distribution of some of the major forest zones within an environmental field based on moisture and temperature indices (Emmingham 1982) (adapted from Franklin and Dyrness 1973, p. 50).

The interactions between disturbance and successional processes with other environmental and historical factors in regional vegetation patterns has not been addressed in any systematic way. Plant community studies have concentrated nearly exclusively on mature to old-growth stands originating after natural disturbances. In general, disturbances associated with forest management practices tend to be less variable in both time and space, and have a simplifying effect on stand and landscape structure (Hansen et al. 1991). However, no systematic studies have quantified disturbance effects across regional environmental gradients.

Research Objectives and Hypotheses

Ecological principles and findings from vegetation studies in the Pacific Northwest suggest several hypotheses related to the objectives of my study. Because of the exploratory and descriptive nature of my study, these hypotheses are stated in general terms rather than as formal, null hypotheses. Ordination methods by nature are suited for reducing a complex, multidimensional dataset into relatively few, interpretable dimensions (Gauch 1982), but present problems for formal hypothesis testing. Whereas recent software provides options for testing of hypotheses based on Monte Carlo simulations, these methods have limitations, and in practice most ordination studies continue to be exploratory.

Objective (1): Identify and quantify environmental factors that contribute most to explaining variation across regional gradients in the composition of woody plant communities, and explore how these factors change with scale, location, and taxonomic group.

* Temperature and moisture, as expressed in macroclimate, are the primary factors controlling regional patterns of community composition. Temperature

(including the complex-gradient of elevation) is most important in differentiating forest zones.

* Macroclimate contributes more to explained variation at larger geographic scales than at smaller scales.

* Local factors (microclimate, topography, and site disturbance history) are secondary to climate at the regional level, but contribute more to explained variation at smaller scales. These factors influence shifts in relative abundances of species found within a locale but do not explain species presence or absence within the broader region.

* Substrate (geologic parent material and soils) is a secondary control on community composition at broad (regional) spatial scales, but may assume local importance.

* Moisture assumes greater importance in eastern Oregon and at lower elevations in western Oregon, where climate is drier.

* The influence of microclimate, topography, and substrate on community composition is stronger in eastern Oregon and to a lesser extent the Klamath subregion, where climate is more stressful, particularly because of moisture limitations. Effects are most muted nearest the coast and in northwest Oregon, where climate generally is more benign.

* Tree growth forms and species more faithfully reflect regional gradients than do shrubs. Understory shrub response is more complex, as the greater number of species represent greater variability in ecologic and physiologic traits, species ranges are smaller, and turnover along environmental gradients is more rapid. Smaller stature means shrubs respond to the structure, composition, and

processes of the tree overstory in addition to coarser-scale environmental signals, and to finer-scale variation in soils, litter depth, canopy gaps.

- Community types at one level in a classification of field plot data are analogous to the series level in site classification and to the forest zones of Franklin and Dyrness (1973), which are defined by a single tree species present at climax, despite analyzing existing rather than potential natural vegetation. This is because disturbance causes shifts in the relative abundances of species found on a site, but it is species presence or absence that is most important in regional-scale classifications.

Objective (2): Characterize and map spatial patterns of compositional gradients.

- Rate-of-change in community composition varies geographically and is not constant. Steeper gradients (sharper ecotones) alternate with areas of relatively little change.

- Ecotones in community composition coincide with steep environmental gradients, and are associated with physiographic features such as the Cascade Mountains and with zones of rapid transition in climate (e.g., between the Cascade and Siskiyou Mountains in southwest Oregon).

METHODS

Study Area

My study was limited to forested lands, including both closed forest and open woodlands. This was because of availability of ground plot data for forest lands, generally defined by the data sources as areas with at least 10% canopy cover of trees. The vegetation dataset encompassed 30 families, 71 genera, and 181 species (Table 1). I divided the forested area into five geographic subregions for analytical and descriptive purposes (fig. 1). Subregions were delineated based primarily on physiographic features, and were similar to the physiographic provinces of Franklin and Dyrness (1973, p. 6), except I divided the Willamette Valley longitudinally and did not recognize it as a separate province. In addition, I split the Cascades into western and eastern subregions along the length of the crest. Boundary placement was in many respects arbitrary, but the subregions broadly stratified Oregon into relatively homogenous areas. Several analyses were conducted at the half-state level as well: western Oregon included the Coast, western Cascades, and Klamath subregions, and eastern Oregon included the eastern Cascades and Blue Mountains subregions.

Physiography, Geology, and Soils

Patterns of physiography, geology, and soils in Oregon are varied and complex. The region is characterized by the north-south oriented Cascade and Coastal Ranges, as well as the Siskiyou Mountains in southwest Oregon and the Blue-Ochoco-Strawberry-Wallowa complex of mountains in the Blue Mountains subregion of eastern Oregon (fig. 1). The Cascade Range is the major topographic and climatic divide in the region, which is bisected at the northern Oregon boundary

Table 1. Codes (from Garrison et al. 1976), growth habits, constancies (numbers of 2,443 plots), and scientific names of species in this study. Plant names are from Hitchcock and Cronquist (1973) and Hickman (1993). Growth habit 10=tree, 20=tall shrub, 30=low shrub. Some taxa were recorded to genus only.

Code	Growth Form	Con-stancy	Scientific Name
ABAM	10	120	*Abies amabilis* (Dougl.) Forbes
ABGRC	10	734	*Abies grandis* (Dougl.) Forbes or *A. concolor* (Gord. & Glend.) Lindl.
ABLA2	10	96	*Abies lasiocarpa* (Hook.) Nutt.
ABMAS	10	59	*Abies magnifica* var. *shastensis* Lemmon
ABPR	10	56	*Abies procera* Rehder
ACCI	20	507	*Acer circinatum* Pursh
ACGL	20	100	*Acer glabrum* Torr.
ACMA	10	312	*Acer macrophyllum* Pursh
ALIN	20	1	*Alnus incana* (L.) Moench
ALRH	10	2	*Alnus rhombifolia* Nutt.
ALRU	10	318	*Alnus rubra* Bong.
ALSI	20	14	*Alnus sinuata* (Regel) Rydb.
AMAL	20	327	*Amelanchier alnifolia* Nutt.
AMPA	20	16	*Amelanchier pallida* E. Greene
ARME	10	214	*Arbutus menziesii* Pursh.
ARCI	20	2	*Arctostaphylos xcinerea* Howell
ARCO3	20	23	*Arctostaphylos columbiana* Piper
ARNE	30	87	*Arctostaphylos nevadensis* Gray
ARPA	20	155	*Arctostaphylos patula* Greene
ARUV	30	36	*Arctostaphylos uva-ursi* (L.) Spreng.
ARVI	20	31	*Arctostaphylos viscida* C. Parry
ARAR	30	23	*Artemisia arbuscula* Nutt.
ARCA	30	1	*Artemisia cana* Pursh
ARRI	30	12	*Artemisia rigida* (Nutt.) Gray
ARSP	30	1	*Artemisia spinescens* Eat.
ARTR	20	122	*Artemisia tridentata* Nutt.
BAPI	30	9	*Baccharis pilularis* DC.
BEAQ	20	65	*Berberis aquifolium* Pursh
BENE	30	653	*Berberis nervosa* Pursh
BEPI	30	48	*Berberis piperiana* (Abrams) McMinn
BEPU	30	4	*Berberis pumila* E. Greene
BERE	30	280	*Berberis repens* Lindl.
BEOC	10	7	*Betula occidentalis* Hook.
CADE3	10	227	*Calocedrus decurrens* (Torr.) Florin.
CHCH2	10	263	*Castanopsis chrysophylla* (Dougl.) DC.
CECU	20	14	*Ceanothus cuneatus* (Hook.) T. & G.
CEIN	20	33	*Ceanothus integerrimus* H. & A.
CEANO	20	4	*Ceanothus* spp. L.
CEPR	30	68	*Ceanothus prostratus* Benth.
CEPU	30	3	*Ceanothus pumilus* Greene
CESA	20	8	*Ceanothus sanguineus* Pursh
CETH	20	15	*Ceanothus thyrsiflorus* Eschsch.
CEVE	20	141	*Ceanothus velutinus* Dougl.
CELE	10	118	*Cercocarpus ledifolius* Nutt.
CEMO	10	9	*Cercocarpus montanus* Raf.
CHLA	10	54	*Chamaecyparis lawsoniana* A. Murray
CHNO	10	4	*Chamaecyparis nootkatensis* (D. Don) Spach
CHME	30	205	*Chimaphila menziesii* (R. Br.) Spreng.
CHUM	30	432	*Chimaphila umbellata* (L.) Bart.
CHNA	30	39	*Chrysothamnus nauseosus* (Pall.) Britt.
CHVI	30	47	*Chrysothamnus viscidiflorus* (Hook.) Nutt.
CLCO	30	3	*Clematis columbiana* (Nutt.) T. & G.

Table 1 (continued).

Code	Growth Form	Con-stancy	Scientific Name
COCA	30	2	*Cornus canadensis* L.
CONU	10	167	*Cornus nuttallii* Aud.
COST	20	12	*Cornus stolonifera* Michx.
COCOC	20	367	*Corylus cornuta* var. *cornuta* (DC.) Sharp
CRDO	20	10	*Crataegus douglasii* Lindl.
CRATA	20	5	*Crataegus* spp. L.
CUBA	10	1	*Cupressus bakeri*
CYSC	20	13	*Cytisus scoparius* (L.) Link
FRLA2	10	36	*Fraxinus latifolia* Benth.
GABU	20	10	*Garrya buxifolia* A. Gray
GAFR	20	3	*Garrya fremontii* Torr.
GAHU	30	1	*Gaultheria humifusa* (Grah.) Rydb.
GAOV	30	26	*Gaultheria ovatifolia* Gray
GASH	30	523	*Gaultheria shallon* Pursh
HABL	30	79	*Haplopappus bloomeri* Gray
HODI	20	405	*Holodiscus discolor* (Pursh) Maxim.
ILEX	20	2	*Ilex* spp. L.
JUCO4	30	11	*Juniperus communis* L.
JUOC	10	261	*Juniperus occidentalis* Hook.
JUSC	10	2	*Juniperus scopulorum* Sarg.
LAOC	10	179	*Larix occidentalis* Nutt.
LEGL	30	3	*Ledum glandulosum* Nutt.
LEDA	30	2	*Leucothoe davisiae* Torrey
LIDE3	10	136	*Lithocarpus densiflorus* (Hook. & Arn.) Rehder
LOCI	30	40	*Lonicera ciliosa* (Pursh) DC.
LOCO	30	2	*Lonicera conjugialis* Kell.
LOHI	30	98	*Lonicera hispidula* (Lindl.) Dougl.
LOIN	20	20	*Lonicera involucrata* (Rich.) Banks
LONIC	30	5	*Lonicera* spp. L.
LOUT2	20	71	*Lonicera utahensis* Wats.
MEFE	20	51	*Menziesia ferruginea* Smith
MYCA	20	15	*Myrica californica* Cham.
OECE	20	23	*Oemleria cerasiformis* (H.&A.) Landon
OPHO	20	44	*Oplopanax horridum* (Smith) Miq.
PAMY	30	206	*Paxistima myrsinites* (Pursh) Raf.
PERA3	20	1	*Peraphyllum ramosissimum* Nutt.
PHLE2	20	24	*Philadelphus lewisii* Pursh.
PHEM	30	4	*Phyllodoce empetriformis* (Sw.) D. Don
PHCA3	20	10	*Physocarpus capitatus* (Pursh) Kuntze
PHMA	20	73	*Physocarpus malvaceus* (Greene) Kuntze
PIBR	10	2	*Picea breweriana* S. Watson
PIEN	10	133	*Picea engelmannii* Parry
PISI	10	95	*Picea sitchensis* (Bong.) Carr.
PIAL	10	23	*Pinus albicaulis* Engelm.
PIAT	10	13	*Pinus attenuata* Lemmon
PICO	10	358	*Pinus contorta* Dougl.
PICOC	10	23	*Pinus contorta* Dougl. var. contorta
PIFL	10	1	*Pinus flexilis* James
PIJE	10	19	*Pinus jefferyi* Grev. & Balf.
PILA	10	133	*Pinus lambertiana* Dougl.
PIMO	10	111	*Pinus monticola* Dougl.
PIPO	10	845	*Pinus ponderosa* Dougl.
POTR	10	23	*Populus tremuloides* Michx.
POTR2	10	7	*Populus trichocarpa* T. & G.
PREM	10	56	*Prunus emarginata* (Dougl.) Walp.

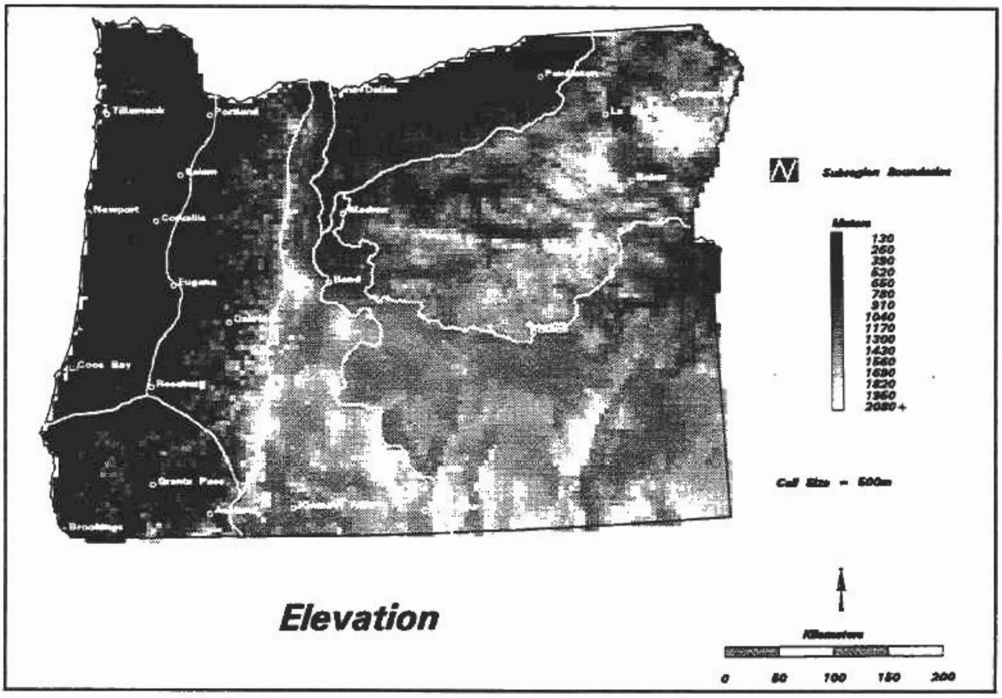
Table 1 (continued).

Code	Growth Form	Constancy	Scientific Name
PRUNU	20	36	*Prunus* spp. L.
PRVI	20	22	*Prunus virginiana* L.
PSME	10	1526	*Pseudotsuga menziesii* (Mirbel) Franco.
PUTR	20	316	*Purshia tridentata* (Pursh) DC.
PYRUS	20	6	*Pyrus fusca* Raf.
QUCH	10	71	*Quercus chrysolepis* Liebm.
QUGA	10	119	*Quercus garryana* Dougl.
QUKE	10	67	*Quercus kelloggii* Newberry
QUSA	20	15	*Quercus sadleriana* R. Br. Campst.
QUVA	20	22	*Quercus vaccinifolia* Kellogg
RHCA	20	14	*Rhamnus californica* Eschsch.
RHPU	10	123	*Rhamnus purshiana* DC.
RHAL	20	1	*Rhododendron albiflorum* Hook.
RHMA	20	242	*Rhododendron macrophyllum* G. Don
RHOC	20	5	*Rhododendron occidentale* (T. & G.) Gray
RHDI	20	213	*Rhus diversiloba* T. & G.
RHGL	20	2	*Rhus glabra* L.
RIBI	20	13	*Ribes binominatum* A.A. Heller
RIBR	20	8	*Ribes bracteosum* Douglas
RICE	20	168	*Ribes cereum* Dougl.
RICR	20	3	*Ribes cruentum* Greene
RIBES	20	48	*Ribes* spp. L.
RILA	20	71	*Ribes lacustre* (Pers.) Poir.
RILO	20	12	*Ribes lobbii* Gray
RIME	20	2	*Ribes menziesii* Pursh
RIMO	20	5	*Ribes montigenum* McClatchie
RINI	20	2	*Ribes niveum* Lindl.
RISA	20	10	*Ribes anguineum* Pursh
RIVE	20	5	*Ribes velutinum* Greene
RIVI	20	62	*Ribes viscosissimum* Pursh
RIWA	20	1	*Ribes watsonianum* Koehne
ROPS	10	2	*Robinia pseudo-acacia* L.
ROEG	20	10	*Rosa eglanteria* L.
ROGY	20	626	*Rosa gymnocarpa* Nutt.
ROSA	20	41	*Rosa* spp. L.
RONU	20	3	*Rosa nutkana* Presl
ROWO	20	6	*Rosa woodsii* Lindl.
RUDI	30	39	*Rubus discolor* Weihe & Nees
RUID	20	1	*Rubus idaeus* L.
RUBUS	20	12	*Rubus* spp. L.
RULA2	20	11	*Rubus laciniatus* Willd.
RULA	30	76	*Rubus lasiococcus* Gray
RULE	20	34	*Rubus leucodermis* Dougl.
RUNI	30	50	*Rubus nivalis* Dougl.
RUPA	20	205	*Rubus parviflorus* Nutt.
RUPE	30	5	*Rubus pedatus* J. E. Smith
RUSP	20	232	*Rubus spectabilis* Pursh
RUUR	30	501	*Rubus ursinus* Cham. & Schlecht.
SAGE	20	5	*Salix geyeriana* Anderss.
SAHO	20	5	*Salix hookeriana* Barratt
SALIX	20	83	*Salix* spp. L.
SAPH	20	9	*Salix phylicifolia* L. var. monica (Bebb) Jepson
SASC	10	47	*Salix scouleriana* Barratt
SACE	20	9	*Sambucus cerulea* Raf.
SAMBU	20	2	*Sambucus* spp. L.

Table 1 (continued).

Code	Growth Form	Con-stancy	Scientific Name
SARA	20	85	*Sambucus racemosa* L.
SESE2	10	4	*Sequoia sempervirens* (D. Don) Endl.
SHCA	20	11	*Shepherdia canadensis* (L.) Nutt.
SOSC2	20	13	*Sorbus scopulina* Greene
SOSI	20	20	*Sorbus sitchensis* Roemer
SPBE	20	186	*Spiraea betulifolia* Pall.
SPDE	20	4	*Spiraea densiflora* Nutt.
SPDO	20	12	*Spiraea douglasii* Hook.
SYAL	20	398	*Symphoricarpos albus* (L.) Blake
SYMPH	20	90	*Symphoricarpos* Duhamel
SYMO	20	268	*Symphoricarpos mollis* Nutt.
SYOR	20	29	*Symphoricarpos oreophilus* Gray
TABR	10	160	*Taxus brevifolia* Nutt.
TECA	20	2	*Tetradymia canescens* DC.
THPL	10	230	*Thuja plicata* Donn.
TSHE	10	538	*Tsuga heterophylla* (Raf.) Sarg.
TSME	10	87	*Tsuga mertensiana* (Bong.) Carr.
UMCA	10	59	*Umbellularia californica* (Hook. & Arn.) Nutt.
VAAL	20	42	*Vaccinium alaskaense* Howell
VACA	30	7	*Vaccinium caespitosum* Michx.
VACCI	20	4	*Vaccinium* spp. L.
VAME	20	296	*Vaccinium membranaceum* Dougl.
VAMY	30	1	*Vaccinium myrtillus* L.
VAOC2	20	5	*Vaccinium occidentale* Gray
VAOV	20	43	*Vaccinium ovalifolium* Smith
VAOV2	20	154	*Vaccinium ovatum* Pursh
VAPA	20	489	*Vaccinium parvifolium* Smith
VASC	30	124	*Vaccinium scoparium* Leiberg
VAUL	20	2	*Vaccinium uliginosum* L.
WHMO	30	201	*Whipplea modesta* Torr.

by the Columbia River. Elevations in Oregon range from sea level to over 4,450 m (Franklin and Dyrness 1973), although the highest stand sampled in my study was 2,621 m (fig. 3.a.). Geological formations date from the Paleozoic (over 400 million yr old) to Recent (Walker and McLeod 1991) (fig. 4). Vulcanism has shaped much of the landscape, but sedimentary and metamorphic rocks are plentiful, and deposition of parent materials by alluvial, colluvial, or eolian processes is common (Walker and McLeod 1991) (Tables 2-3, fig. 4). Forest soils are tremendously variable, reflecting the diverse parent materials and topography. Soil types are primarily inceptisols, spodosols, and ultisols. The great relief in extensive mountainous areas perpetuates many soils in a state of profile immaturity. Soils on steep slopes are constantly influenced by soil creep or landslides, often severely a.



b.

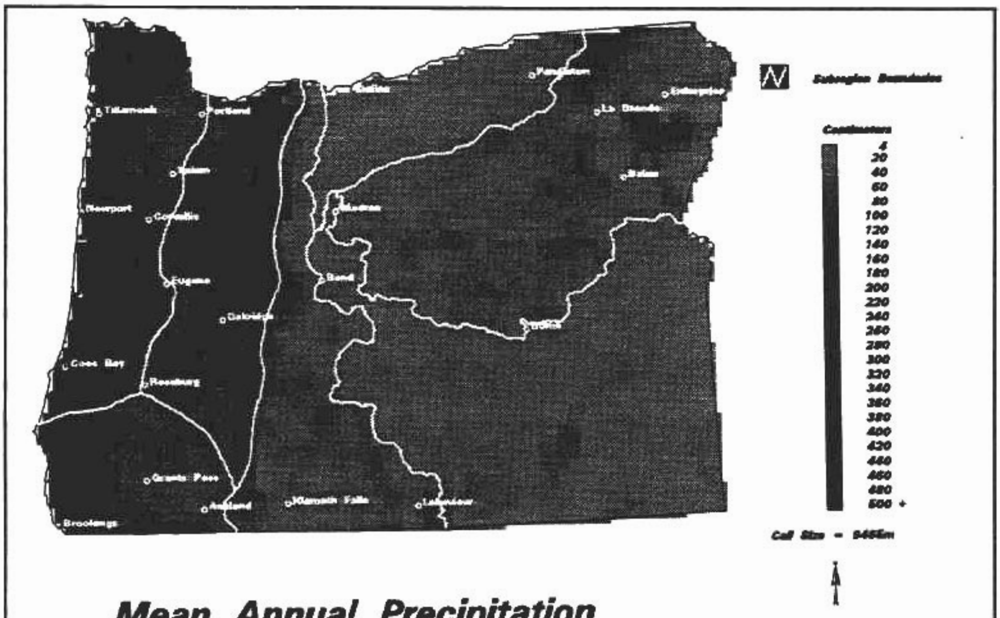
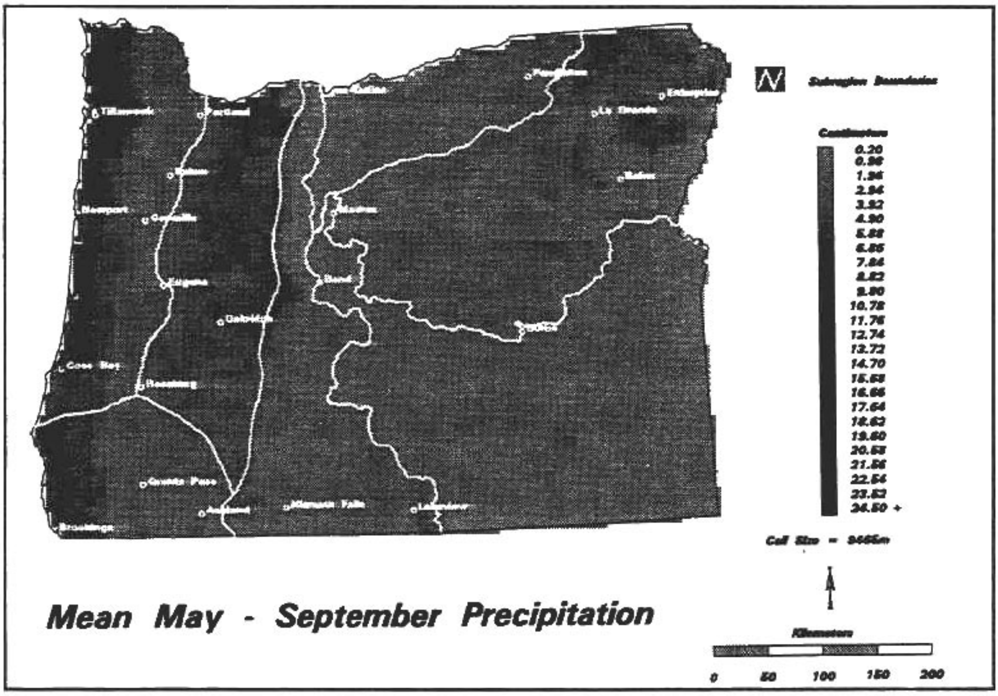
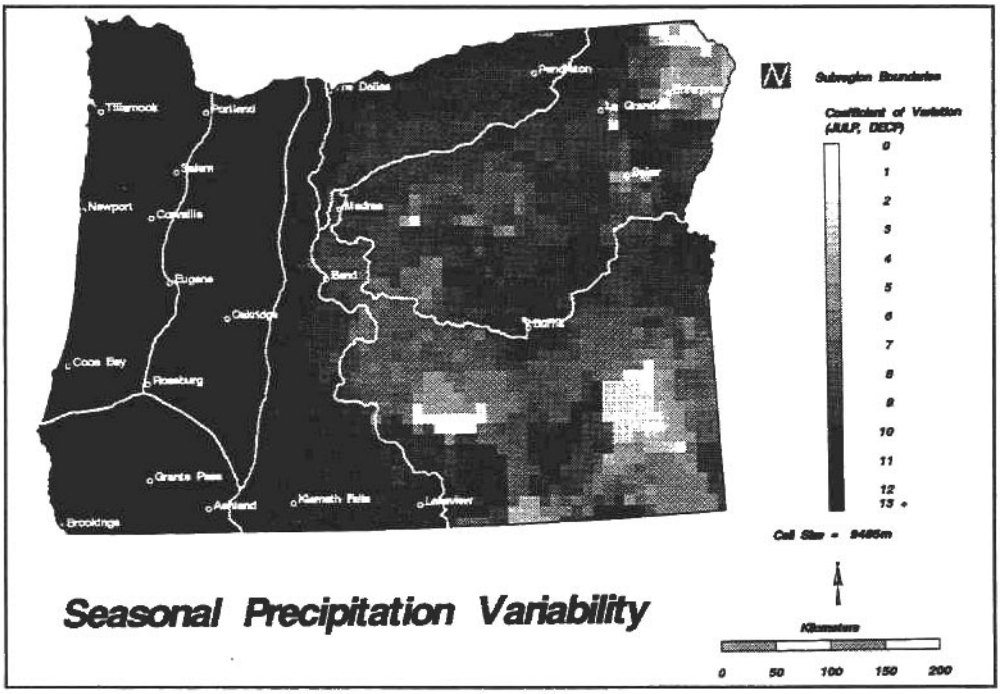


Figure 3. Maps of selected explanatory variables. a. Elevation (m); b. Mean annual precipitation (mm); c. Mean growing-season (May-September) precipitation (mm); d. Seasonal variability in precipitation (coefficient of variation of wettest and driest months (usually December and July), mm); e. Percent of mean annual precipitation that falls in June-August; f. Mean monthly temperature (°C) during the growing-season (May-September); g. Seasonal variability in temperature (coefficient of variation of mean monthly temperature (°C rescaled to a 0-255 scale) of the coldest and warmest months (usually December and August). Precipitation and temperature maps are based on Daly et al. (1994) and Marks (1990).



c.

Mean May - September Precipitation

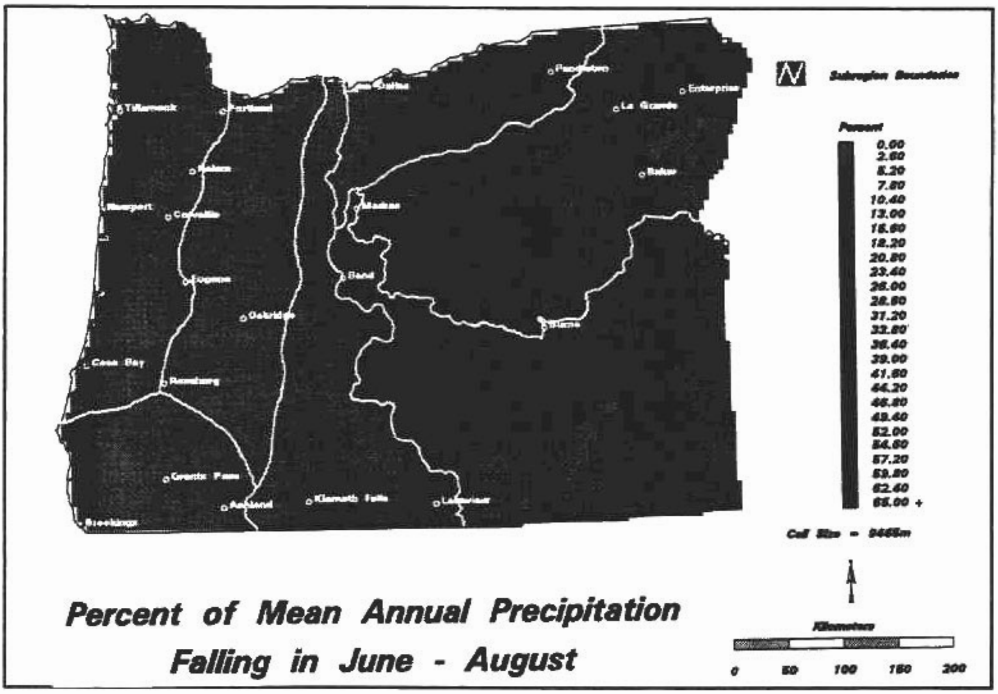


d.

Seasonal Precipitation Variability

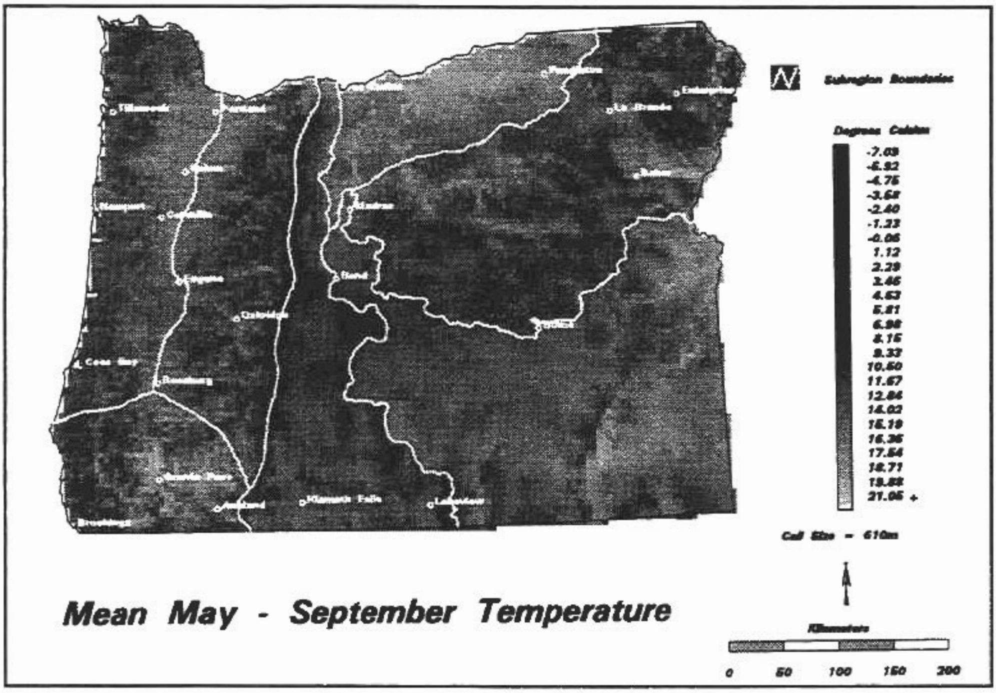
Figure 3 (continued).

e.



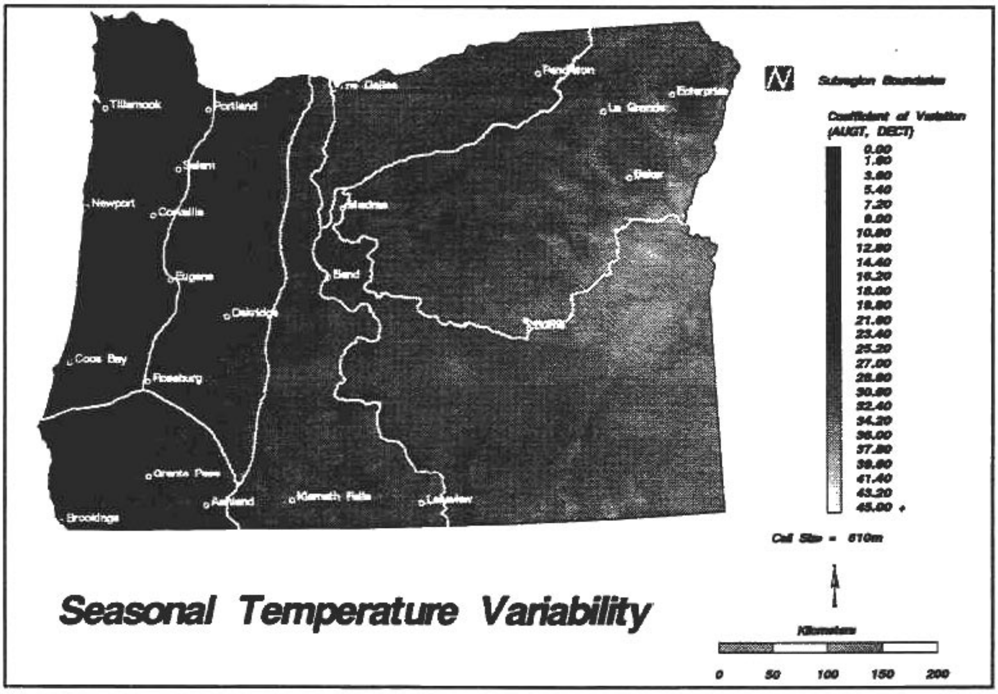
Percent of Mean Annual Precipitation Falling in June - August

f.



Mean May - September Temperature

Figure 3 (continued).



g.

Figure 3 (continued).

limiting profile development. Consequently, many mountains soils lack genetic horizons except for a thin A. In these areas parent rock has a major effect on soil properties. Volcanic activity along the crest of the Cascade Range during the Pleistocene and Recent times has extensively influenced regional soils. Large tracts at higher elevations in the Cascades and in central Oregon are mantled with deposits of pumice and volcanic ash which, because of their youth, generally exhibit little genetic development (Franklin 1988, Franklin and Dyrness 1973).

Climate

The Oregon climate is basically mild with dry summers. Variation within the region is influenced by the interplay among westerly winds of maritime airmasses, northeasterly winds of continental airmasses, and the blocking effects of mountain ranges, which primarily trend north-south (Franklin and Dyrness 1973).

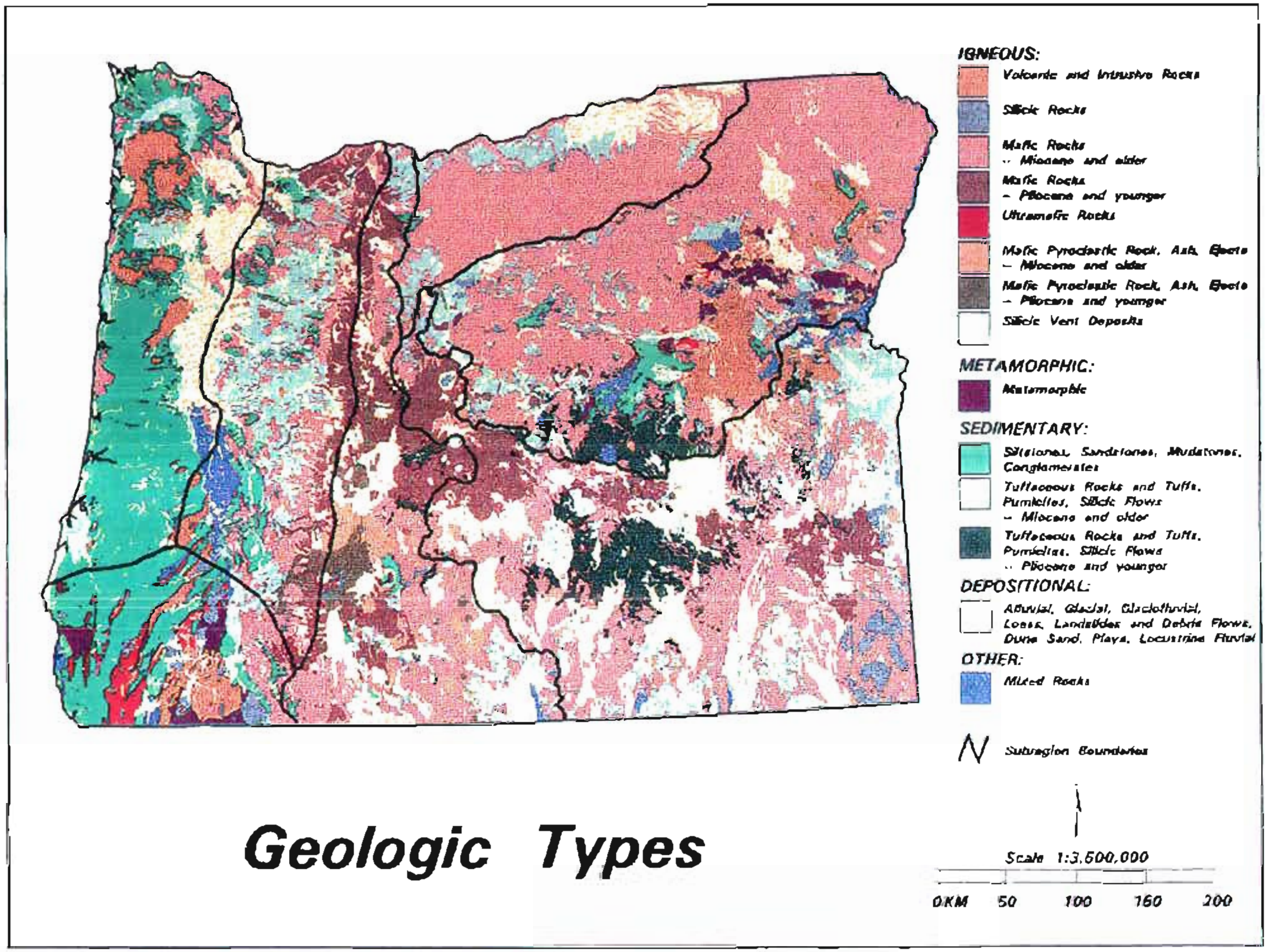


Figure 4. Geologic types of Oregon.

Table 2.--Descriptive statistics of explanatory variables for Oregon, western Oregon, and eastern Oregon.

Var. No.	Variable[a]	Oregon (N=2443)		Western Oregon (N=1233)		Eastern Oregon (N=1210)	
		MEAN and CV (%)					
1	ASPECT	1.03	67	1.10	63	0.96	71
2	SLOPE	26.16	84	33.34	68	18.85	98
3	SOLAR	6.84	17	6.60	19	7.09	14
4	AGE	140.44	79	138.74	97	142.17	56
6	TREOCOV	54.05	58	69.28	44	38.52	64
7	ELEV	1048.74	55	627.70	72	1477.78	22
8	ANNPRE	6.91	10	7.44	5	6.37	6
9	WTRPRE	6.49	12	7.11	5	5.85	8
10	SMRPRE	5.24	9	5.48	7	4.98	7
11	CVPRE	110.83	17	125.30	4	99.09	18
12	CONTPRE	9.82	51	6.03	24	13.68	32
13	SMRTSMRP	2.45	22	2.42	22	2.48	22
14	ANNTMP	6.71	43	8.41	28	4.97	45
15	MAXTMP	30.10	18	34.08	12	26.04	12
16	MINTMP	-28.27	26	-22.31	21	-34.35	10
17	WTRTMP	0.76	480	3.41	79	-1.93	120
18	SMRTMP	12.70	19	13.46	18	11.94	19
19	CVTMP	26.08	24	20.92	18	31.34	9
		PERCENT OF PLOTS					
5	CLEARCUT	15		27		4	
20	VOLC	7		9		6	
21	SILR	3		3		2	
22	MAFO	34		17		52	
23	MAFY	7		6		8	
24	UMAF	1		2		1	
25	PYRO	1		<1		3	
26	PYRY	2		1		4	
27	SILV	1		1		2	
28	META	3		3		2	
29	SEDR	18		34		2	
30	TUFO	11		15		6	
31	TUFY	2		0		3	
32	DEPO	7		8		7	

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[a] Variables are defined in Table 5.

Table 3.--Descriptive statistics of explanatory variables by subregion.

Var. No.	Variable[a]	Coast (N=461)		Western Cascades (N=465)		Klamath (N=307)		Eastern Cascades (N=479)		Blue Mountains (N=731)	
		MEAN and CV (%)									
1	ASPECT	0.95	71	0.88	80	1.08	61	1.14	60	1.08	66
2	SLOPE	32.78	74	30.81	70	38.00	54	12.03	115	23.31	84
3	SOLAR	6.37	18	6.82	17	6.63	21	7.35	10	6.92	16
4	AGE	66.57	90	184.72	84	177.45	78	130.67	68	149.70	48
6	TREOCOV	67.55	46	73.44	39	65.59	46	33.43	62	41.85	63
7	ELEV	266.16	63	886.97	49	777.89	52	1489.28	22	1470.24	22
8	ANNPRE	7.54	5	7.44	4	7.29	7	6.33	6	6.39	6
9	WTRPRE	7.21	5	7.08	4	7.00	8	5.92	7	5.81	9
10	SMRPRE	5.54	7	5.62	5	5.19	8	4.72	7	5.15	6
11	CVPRE	124.32	5	123.54	3	129.42	3	108.24	12	88.13	16
12	CONTPRE	5.72	20	7.10	13	4.85	26	10.83	30	15.55	26
13	SMRTSMRP	2.54	16	2.32	21	2.63	27	2.60	20	2.30	22
14	ANNTMP	9.47	15	7.37	35	8.40	30	5.45	35	4.65	50
15	MAXTMP	37.33	5	31.87	14	32.55	11	25.83	13	26.18	12
16	MINTMP	-20.62	20	-24.98	17	-20.82	20	-32.70	11	-35.42	8
17	WTRTMP	5.01	31	1.81	149	3.44	77	-1.07	178	-2.50	95
18	SMRTMP	13.94	11	12.99	20	13.45	22	12.16	17	11.79	20
19	CVTMP	18.58	16	23.48	8	20.55	22	29.06	7	32.84	7
		PERCENT OF PLOTS									
5	CLEARCUT	44		17		13		4		3	
20	VOLC	15		3		9		0		10	
21	SILR	0		<1		12		3		2	
22	MAFO	11		28		8		33		65	
23	MAFY	0		14		1		21		<1	
24	UMAF	0		0		9		0		1	
25	PYRO	0		1		0		6		<1	
26	PYRY	0		2		0		9		<1	
27	SILV	0		2		0		4		<1	
28	META	0		0		12		0		4	
29	SEDR	54		8		40		1		3	
30	TUFO	9		29		3		10		4	
31	TUFY	0		0		0		1		5	
32	DEPO	9		11		2		12		4	

[a] Variables are defined in Table 5.

Western Oregon, defined as the area west of the Cascades crest, has a maritime climate, characterized by mild temperatures with prolonged cloudy periods, muted extremes in temperature, and narrow seasonal and diurnal fluctuations (typically 6°-10°) (Franklin and Dyrness 1973) (figs. 3.f.-g.); mild, wet winters and cool, relatively dry summers (figs. 3.c.-f.) and a long frost-free season; and heavy precipitation (fig. 3.b.), most of which falls as rain between October 1 and March 31 (Tables 2-3). Mean annual precipitation for plots in western Oregon ranged from 466-4,797 mm. Most precipitation results from cyclonic storms that approach from the Pacific Ocean on the dominant westerlies. Storm tracks shift to the north during summer, and high-pressure systems bring fair, dry weather for extended periods. To varying degrees, coastal mountains block maritime airmasses from the Willamette Valley and interior valleys of southwest Oregon, where climates are less muted (fig. 3.g.) and precipitation declines markedly in the resultant rain shadows (fig. 3.b.). Orographic effects of mountain ranges produce local increases in precipitation and in the proportion of precipitation that falls as snow (Franklin 1988) (fig. 3.b.). There also is a general latitudinal increase in precipitation and decrease in temperature from south to north, so the interior valleys of southwest Oregon have the hottest (fig. 3.f.) and driest (figs. 3.b.-c.) climate in western Oregon (Franklin and Dyrness 1973).

Eastern Oregon contains characteristics of both maritime and continental climates. Temperatures are milder than those in the Great Plains since the Rocky Mountains buffer the full brunt of the continental airmasses (Franklin and Dyrness 1973). However, temperatures fluctuate more widely than west of the Cascades over the year (Tables 2-3, fig. 3.g.), and diurnal fluctuations of 10°-16°C are typical (Franklin and Dyrness 1973). Temperatures are more extreme, winters are colder, summers are hotter (fig. 3.f.), and frost-free seasons are shorter (Tables 2-3). Precipitation is still primarily cyclonic in origin but is considerably less than to the west since the areas lies in the rainshadow of the Cascade Range (Tables 2-3, fig. 3.b.). Mean annual precipitation for plots in eastern Oregon ranged from 177-3,450 mm. Precipitation is less seasonal than in western Oregon (figs. 3.d.-e.), but summers are very dry (fig. 3.c.) (Tables 2-3). A high proportion of annual precipitation falls as snow, which is relatively uncommon in the coastal areas.

Vegetation

Forests dominate the landscapes west of the Cascade Range and the mountain slopes to the east, covering 11 million ha (46%) of the total land area (Powell et al. 1993) and limited largely to the five subregions delineated for my study (fig. 1).

About 60% of the timberland is in public ownership, 23% is owned by timber industry, and 17% by nonindustrial private landowners (Powell et al. 1993) (fig. 5).

With few exceptions, coniferous tree species dominate Oregon's forest communities. The absence of major hardwood dominants is unique among temperate zone forests of the world (Franklin 1988, Franklin and Dyrness 1973, Waring and Franklin 1979). Outside of the mixed-evergreen zone of southwest Oregon, where several evergreen hardwood trees codominate (e.g., Lithocarpus densiflorus), hardwoods tend to occupy harsh sites (e.g., Quercus spp.) or specialized habitats (e.g., Populus trichocarpa), or serve as pioneers (e.g., Alnus rubra). Conifer domination probably can be attributed to climatic events over geologic time (Daubenmire 1978, Kuchler 1964) as well as to prevailing climate. Conditions during the Pleistocene were important in selecting a coniferous-dominated forest from the mixed Arcto-Tertiary forests of the Miocene. The present climate of wet, mild winters and relatively dry summers favors evergreen growth forms and needle-leaved conifers by permitting extensive photosynthesis outside of the growing-season and reducing net photosynthesis during the summer months (Waring and Franklin 1979). In addition, conifers have low respiration rates at low temperatures, increasing the total daily net photosynthesis, net photosynthesis rates reach maxima at about one-third full sunlight, and stomatal opening occurs at much lower light intensities. The result is net carbon uptake even in the lower canopy and on cloudy days, which are characteristic of the coastal Pacific Northwest (Lassoie et al. 1985).

The mesic temperate coniferous forests of northwestern Oregon contain the greatest biomass accumulation and some of the highest productivity levels of any forests in the world (Franklin 1988). The mild environment is extremely favorable to forest development. Many of the dominant tree species (e.g., Pseudotsuga menziesii, Tsuga heterophylla, and Thuja plicata) are endemic to the Pacific Northwest, and many others find their center of distribution and attain maximum development here. Moving southward where the climate becomes warmer and drier, California species (e.g., Pinus lambertiana, Calocedrus decurrens, and

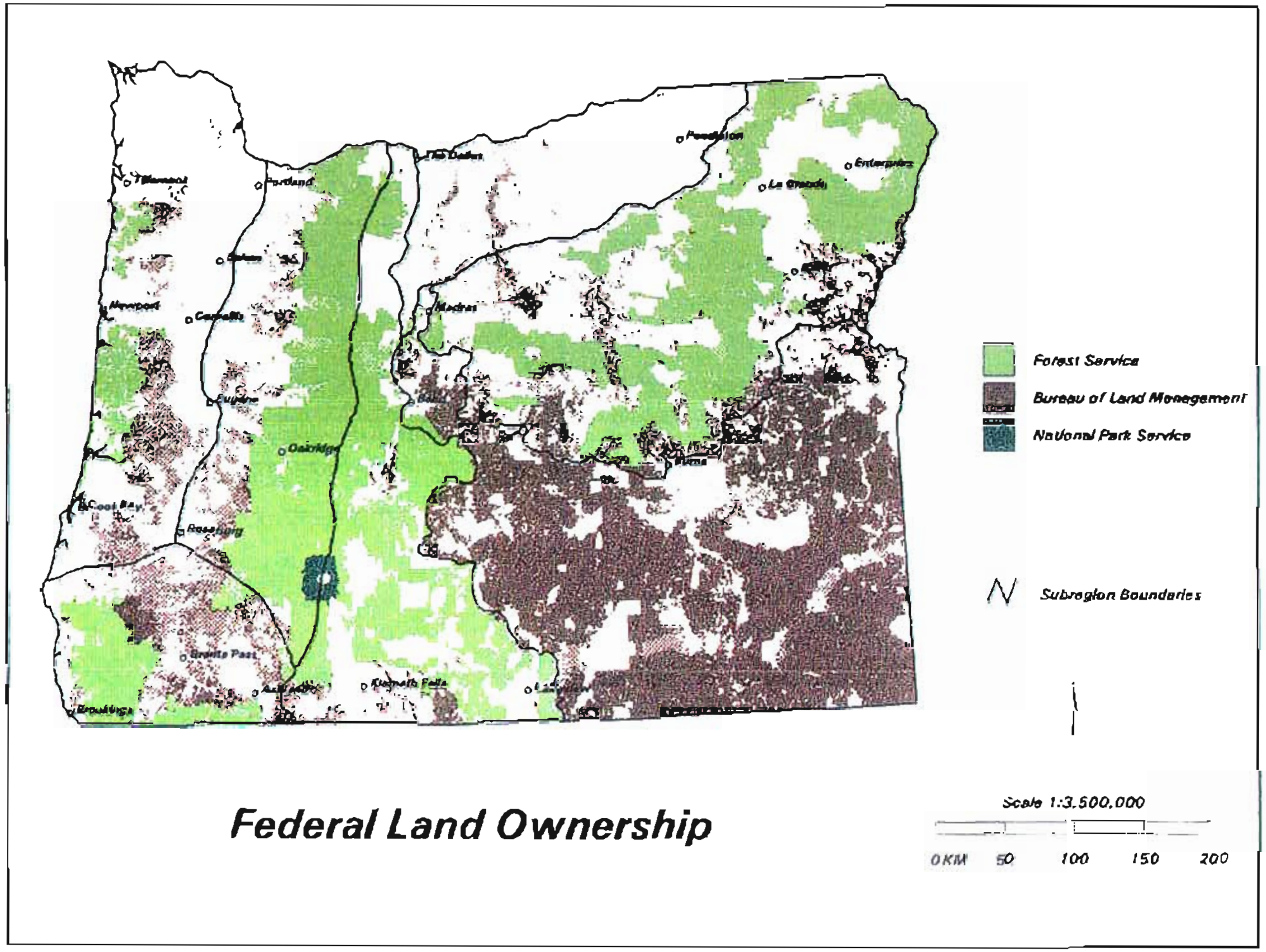


Figure 5. Federal land ownerships in Oregon.

Lithocarpus densiflorus) are added to the flora and give the forest region of interior southwest Oregon much of its character. The forest zones of this region represent northern extensions of the mixed-conifer forest of the Sierra Nevada and the mixed sclerophyll forest of the California Coast Ranges. In the interior forests of eastern Oregon, Pacific coastal elements mix with Rocky Mountain elements. Pinus ponderosa characterizes forests at lower elevations, and Abies lasiocarpa those at higher elevations. Franklin and Dyrness (1973) provided detailed descriptions of patterns of community composition across Oregon.

Disturbance and Landscape Patterns

Disturbance regimes and resulting landscape pattern and stand structure vary tremendously across Oregon's physiographic provinces and land ownerships. Most remaining old growth, which is concentrated on federal lands and at higher elevations (Bolsinger and Waddell 1993), originated after catastrophic wildfires of varying size (Agee 1993). This domination of natural disturbance regimes by infrequent, catastrophic events contrasts with a pattern of frequent, noncatastrophic fires that dominate many other forested regions of western North America, including California and the Rocky Mountains (Franklin 1988). Periodic, low-intensity underburns were common in places (Teensma 1987, Morrison and Swanson 1990). Prior to suppression of fire following Euro-American settlement, natural fire return intervals in Oregon ranged from 15 yr in drier eastside pine forests, to 400 yr in moist, coastal forests, to 800 yr in subalpine forests (Agee 1993). Fires set by Native Americans also were important in many parts of Oregon (Agee 1993). Windstorms, pathogens, and other disturbance agents also have influenced forest development.

Within the last 100 years, pre-Euro-American disturbance regimes largely have been supplanted by timber harvest and management and wildfire suppression, as well as by livestock grazing and urbanization. Management activities generally are more frequent and intense and less variable in size and intensity than natural disturbances (Hansen et al. 1991). Intensive management of forest plantations in most of the Coast and western Cascades subregions has included some or all of the following: clearcutting of all trees and most snags; site preparation using prescribed fire or herbicides to control competing vegetation; replanting with a single species (usually Pseudotsuga menziesii); periodic thinning to maintain vigorous, evenly spaced crop trees; and harvesting at 40-to 100-year intervals (Hansen et al. 1991). In the drier climates of southwest and eastern Oregon forests, uneven-aged management is commonly practiced, where stands are harvested by removing selected trees rather than by clearcutting.

Forest management objectives and practices have varied among land ownerships over time. On federal lands (fig. 5), logging of old-growth forest began after World War II and accelerated in the 1970s. In eastern Oregon, silvicultural practices before the 1960s were usually selective or for salvage. Harvest accelerated and the first clearcuts were performed during the 1970s. At the landscape level, clearcut harvest units on federal lands generally have been staggered in space and harvested at a constant rate, thus maintaining a uniform mosaic of stand sizes and ages (Franklin and Forman 1987). However, almost all of the vegetation plots in my study on federal lands were established in older, natural stands. Some selective logging had occurred on some sites, particularly in the eastern Cascades subregion (W. Hopkins, pers. comm.). In contrast, virtually all forest lands in private and state ownership, and almost all vegetation plots in my study on nonfederal lands, have been harvested in some manner (figs. 5-6). Logging of the most accessible and productive lands in private ownership began in the mid-1800s, and some of these areas are now in their third rotation. By the1980s, 64% of nonfederal timberlands in western Oregon and 13% in eastern Oregon had been clearcut at least once. An additional 28% of plots in western Oregon and 74% in eastern Oregon had been partially harvested. As a result, almost all (97%) of the nonfederal timberland is in an early- (16%) or mid-successional (81%) stage; only 3% is late-successional (fig. 6) (Inventory and

Economics Program, Pacific Northwest Research Station, Portland, OR, unpubl. data).

Despite the recent domination of disturbance regimes by timber management, quantitative evidence on how this has influenced broad-scale patterns of plant community composition is scant (but see Bailey et al. in prep., Bolsinger et al. in press, Halpern and Spies 1995, Ohmann and Bolsinger 1991). In eastern Oregon, fire suppression for over 50 years has allowed ingrowth of fire seral and late-successional tree species to overstock forest stands. Selective harvests and overstory removals deemed necessary for sanitation and rejuvenation, or simply aimed at harvesting the largest and most valuable trees, have resulted in the conversion of large areas of parklike forests of Pinus ponderosa to greater dominance by firs (Johnson et al. 1994). In the 1980s, shifts in forest composition from the combined effects of fire exclusion and drought have led to high tree mortality rates from drought, insects, and diseases (Johnson et al. 1994).

Disturbance from grazing along with fire suppression, fuelwood harvesting, and the introduction of non-native plant species have altered the composition of forest and woodlands, especially in areas in close proximity to population centers in the interior valleys of western Oregon (Franklin and Dyrness 1973, Riegel et al. 1992). These forests have been highly fragmented by clearing for agriculture (especially in bottomland stands), roads, and buildings. In recent decades (1961-1986), timberland area on nonfederal lands in western Oregon has declined by about 0.2% per year (MacLean 1990). Most (60%) of the loss was caused by conversion to agricultural or urban land uses--almost all on nonindustrial private ownerships--and 40% was the result of road building or widening associated with timber harvest (MacLean 1990). Urban development continues to spread into areas of predominantly agriculture or timberland land-uses: area of urban and low-density urban land-uses increased by 13% in western Oregon between 1971-74 and 1982 (Gedney and Hiserote 1989).

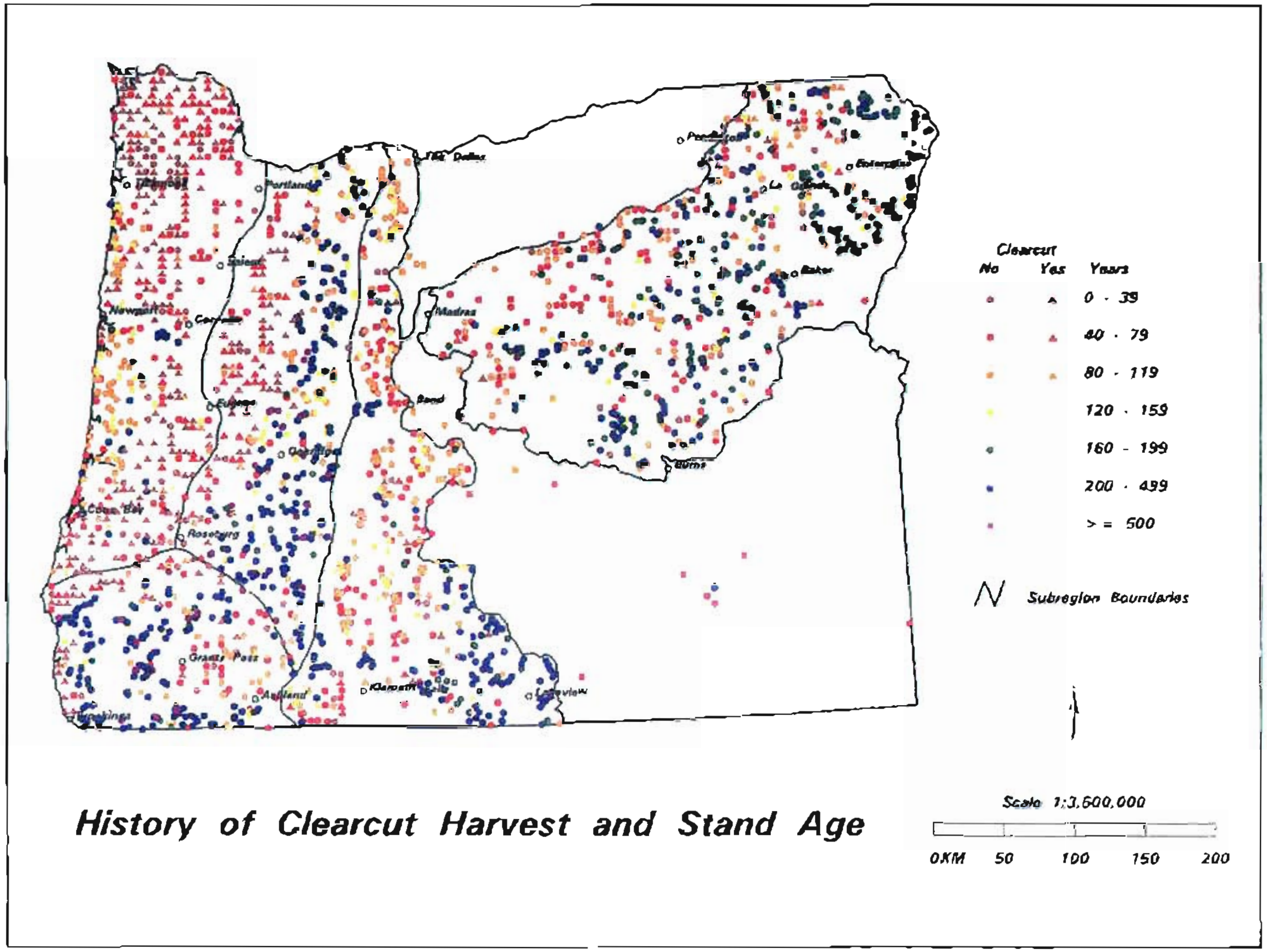


Figure 6. Stand age and history of clearcutting on field plots.

Paleoecology

Like most regions, the Oregon flora is polyphyletic. Species accumulated over geologic time from successive waves of species of differing ecological characteristics, which arrived from different directions and tended to concentrate in different habitats. Climate changes that allowed immigration from one direction are likely to have forced simultaneous emigration in the opposite direction, leaving behind relics of opposite affinity (Daubenmire 1978). In the Pacific Northwest, the Arcto-Tertiary geoflora was an important ancestral formation. This mixed hardwood-coniferous temperate forest was widespread during the warm period at the close of the Eocene. Cooling and the rise of mountain ranges during the Oligocene, Miocene, and Pliocene resulted in development of a more xerophytic flora. Most angiosperm tree species and genera became extinct and left their coniferous associates in control, including genera such as Abies, Chamaecyparis, Calocedrus, Picea, Pinus, Pseudotsuga, Sequoia, Thuja, and Tsuga. In addition, the Madro-Tertiary geoflora expanded northward and some elements were incorporated (Daubenmire 1978). By the early Pleistocene, about 1.5 million yr bp and before major glaciation, the flora of the Pacific Northwest was essentially established as it appears today (Waring and Franklin 1979).

More recently, pollen records indicate that lowlands of the Pacific Northwest supported tundra and taiga-like vegetation associated with glaciation about 17,000 bp, subalpine-type forests developed at 12,500 bp, a warmer and drier period occurred around 10,000-6,000 bp, and coniferous forests typical of today developed subsequently (Baker 1983, Brubaker 1991). In eastern Oregon, by 10,000 bp all sites now in steppe or ponderosa pine, and some in Douglas-fir mixed forest, supported grass and sagebrush. The first invading conifers colonized what had been glacier- or lake-covered terrain, flood tracts, or frozen ground in shrub-steppe vegetation during the last full glacial episode. By 4,000 bp the forest fringe had begun to advance and by between 2,500 and 1,000 bp fossil counterparts of modern forest were apparent at most sites (Johnson et al. 1994). Evidence suggests that western juniper (Juniperus occidentalis Hook.) woodlands were neither present nor regionally important in eastern Oregon until 4,000 to 7,000 bp (Johnson et al. 1994, Miller and Wigand 1994). A great increase in density and distribution of western juniper has occurred since the late 1800s, most frequently explained by climatic changes to warmer, wetter winters, reduced fire frequency, and grazing of domestic livestock following Euro-American settlement (Miller and Wigand 1994).

Vegetation Data

I obtained vegetation data collected on 10,000 field plots installed by the Regional Ecology Program of the Pacific Northwest Region, USDA Forest Service, on National Forest lands; the Inventory and Economics Program (I&E) of the Pacific Northwest Research Station, USDA Forest Service, on nonfederal lands; and the Forestry Intensive Research Program (FIR) of Oregon State University on Bureau of Land Management lands in southwest Oregon (Table 4; Appendix 1). I obtained the individual data files in DOS text (ASCII) format from the individual organizations. I then identified data elements for vegetation and environment that were common to all datasets, extracted those common data elements, and compiled the extracted data into a single relational database under consistent format and coding conventions.

The component datasets were collected under different objectives and sampling designs. The Regional Ecology and FIR plot locations were selected subjectively without preconceived bias (Mueller-Dombois and Ellenberg 1974), primarily in older, natural stands. The I&E inventory plots were established systematically, at intersections of a 5.5-km by 5.5-km grid. Plot sizes and configurations also varied among the component datasets and thus to some extent with geographic location and ownership (Table 4, Appendix 1).

Table 4.--Sources, sample sizes, and sample designs of vegetation data sets.

Data Source	Total N	Sub-sample N	Ownerships Sampled	Sample Design
Region 6 Ecology Program	7,542	1,482	National Forest	Plots generally selected subjectively without preconceived bias (Mueller-Dombois and Ellenberg 1974). Sampled mid- to late-successional stands. Plot size 378-1,350 m^2.
Inventory and Economics Program (I&E) inventory	1,474	849	Private and other public	Plots established at intersections of 5.5-km systematic grid. Sampled managed and natural stands of all ages. Plot size varied: variable-radius plot for trees (15, 20, 30, or 80 metric basal-area-factor) out to 4047-6750 m^2 fixed-radius plot; 91-908 m^2 fixed-radius plot for shrubs.
Forestry Intensive Research (FIR) study	983	112	Bureau of Land Management	Plots selected subjectively in mid- to late-successional stands in southwest Oregon. Plot size 500 m^2.

Vegetation measurements on all plots consisted of crown cover estimates for woody plant species. For analysis, I subsampled from the complete vegetation dataset in order to reduce the dataset to a manageable size; to even-out strong differences in sampling intensity among the individual datasets, which also generally coincided with major differences in land ownership, ecological conditions (e.g., elevation), and disturbance history; to introduce an element of randomness and reduce possible effects of bias in plot selection; and to reserve a portion of the dataset for future testing of hypotheses generated by exploratory analyses. To obtain an even geographic distribution of the subsample, I randomly selected ten plots from each 635-km^2 hexagon in the tesselation developed by White et al. (1992) for the Environmental Monitoring and Assessment Program of the U.S. Environmental Protection Agency. This resulted in a sampling intensity of about one plot per 6,400 ha.

Explanatory Variables

Data on the geographic location, physical environment, and disturbance history of each plot were compiled from a combination of field-recorded measures common to all datasets, and through overlay in a GIS with output from regional climate models and other mapped features (Table 5). See Appendix 2 for detailed information on compilation of climate data.

Field-Recorded Attributes

Field-recorded data were used for slope, aspect, elevation (fig. 3.a.), and stand age and history of clearcut timber harvesting (fig. 6) (Table 5). Aspect (degrees) was transformed using the cosine transformation (Beers et al. 1966), so that northeastern aspects have the highest values (2.0) and southwestern aspects the lowest (0.0). For the Ecology Program and FIR plots, stand age was usually the oldest of several trees on the plot, determined by increment boring. For I&E plots, age was based on all over- and mid-story trees on each plot, determined by increment boring or estimation. History of clearcutting was recorded on all inventory plots; plots in the other datasets were assumed to never have been clearcut.

Table 5.--Explanatory variables used in CCA. S = subset affiliation for variance partitioning analyses: L1 = topography, L2 = disturbance or biological, R1 = macroclimate, R2 = geology (nominal variables).

No.	Code	S	Variable Description
1	ASPECT	L1	Cosine transformation of aspect (degrees): ASPECT=COS(45-DEGREES)+1. Ranges from 0.0 (southwest aspect) to 2.0 (northeast aspect).
2	SLOPE	L1	Slope (percent).
3	SOLAR	L1	Total potential solar radiation, including direct and indirect (joules/$m^2/10^9$).
4	AGE	L2	Stand age (years).
5	CLEARCUT	L2	History of clearcut timber harvest (nominal variable).
6	TREOCOV	L2	Crown cover of all overstory trees (percent).
7	ELEV	R1	Elevation (m).
8	ANNPRE	R1	Mean annual precipitation (natural logarithm, cm).
9	WTRPRE	R1	Mean total amount of precipitation falling in the cool-season (November - March) (natural logarithm, cm).
10	SMRPRE	R1	Mean total mount of precipitation falling in the warm-season (May - September), an approximation of the growing-season (natural logarithm, cm).
11	CVPRE	R1	Coefficient of variation of mean monthly precipitation (cm) of the wettest and the driest months (usually December and July); a measure of seasonal variability and continentality.
12	CONTPRE	R1	Percent of mean annual precipitation that falls in summer (June - August); a measure of seasonal variability and continentality.
13	SMRTSMRP	R1	Moisture stress during the growing-season, computed as SMRTMP/SMRPRE.
14	ANNTMP	R1	Mean annual temperature (degrees C).
15	MAXTMP	R1	All-time maximum recorded temperature (degrees C).
16	MINTMP	R1	All-time minimum recorded temperature (degrees C).
17	WTRTMP	R1	Mean monthly temperature during the cool-season (November - March).
18	SMRTMP	R1	Mean monthly temperature during the warm-season, an approximation of the growing-season (May - September).
19	CVTMP	R1	Coefficient of variation of mean monthly temperature (degrees C, rescaled to a 0-258 scale) of the coldest and the warmest months (usually January and August); a measure of seasonal variability and continentality.
20	VOLC	R2	Igneous: volcanic and intrusive rocks.
21	SILR	R2	Igneous: silicic rocks (granite, diorite, rhyolite, and dacite).
22	MAFO	R2	Igneous: mafic rocks (basalt, basaltic andesite, andesite, gabbro)--miocene and older.
23	MAFY	R2	Igneous: mafic rocks (basalt, basaltic andesite, andesite, gabbro)--pliocene and younger.
24	UMAF	R2	Igneous: ultramafic rocks (serpentine).
25	PYRO	R2	Igneous: mafic pyroclastic rock, ash, ejecta, vent deposits--miocene and older.
26	PYRY	R2	Igneous: mafic pyroclastic rock, ash, ejecta, vent deposits--pliocene and younger.

Table 5 (continued).

No.	Code	S	Variable Description
27	SILV	R2	Igneous: silicic vent deposits.
28	META	R2	Metamorphic.
29	SEDR	R2	Sedimentary: siltstones, sandstones, mudstones, conglomerates.
30	TUFO	R2	Sedimentary: tuffaceous rocks and tuffs, pumicites, silicic flows--miocene and older.
31	TUFY	R2	Sedimentary: tuffaceous rocks and tuffs, pumicites, silicic flows--pliocene and younger.
32	DEPO	R2	Depositional: dune sand, alluvial, glacial, glaciofluvial, loess, landslide and debris flow, playa, lacustrine, fluvial.
33	X	S	Longitude (decimal degrees).
34	Y	S	Latitude (decimal degrees).
35	Y2	S	Y**2.
36	X3	S	X**3.
37	X2Y	S	X**2*Y.

Temperature

Fifteen air-temperature surfaces were generated using a model developed by Marks (1990): mean annual, all-time maximum, all-time minimum, and 12 mean monthlies. The model inputs temperature values, elevations, and geographic locations for weather stations, and topographic data from a digital elevation model (DEM). A DEM of 500-m resolution was used. The model systematically accounts for elevational differences in interpolating air temperature from the irregular network of weather stations to a uniform grid. Measured air temperatures are first converted to their sea-level equivalents, the sea-level temperatures are then interpolated across the entire DEM grid using a simple linear inverse-distance-squared algorithm (Isaaks and Srivastava 1989), and then the interpolated sea-level temperatures are re-converted to the appropriate air temperature for the DEM cell's elevation, assuming a constant lapse rate.

Temperature data were obtained from EarthInfo Inc. for National Weather Service weather stations, generally at low elevations in the western U.S., and from the Soil Conservation Service (SCS) for SNOTEL stations, generally in mountainous, high-elevation locations. Model input included data from 190 National Weather Service (NWS) stations and 68 SNOTEL stations in Oregon. All available SNOTEL data since October 1981 were obtained, but many stations recorded data only since 1989. The NWS data were extracted for January 1981 through December 1992. All-time maximum and minimum temperatures were based on each station's entire recorded history. Multi-year mean monthly temperatures were computed across all years with recorded mean monthly temperatures. Mean annual temperature was computed as a mean of the twelve mean monthly temperatures.

Temperature surfaces were converted to ArcInfo GRID format, and values from each temperature grid were assigned to plot locations using the ArcInfo function LATTICESPOT (ESRI 1991). LATTICESPOT uses bilinear interpolation to compute surface values for each point in a point coverage from a lattice (raster coverage). Plot-level temperature values were used to compute temperature-based indices that approximate temperature conditions during the growing-season (SMRTMP) (fig. 3.f.) and cool-season (WTRTMP), as well as seasonal variability and continentality (CVTMP) (Table 5, fig. 3.g.).

Precipitation

Precipitation data were derived from 13 precipitation surfaces (mean annual and twelve mean monthlies) output from the model PRISM (Precipitation-elevation Regressions on Independent Slopes Model) (Daly et al. 1994), which I obtained in ArcInfo GRID format. PRISM distributes point measurements of precipitation to regularly spaced grid cells by: (1) using a DEM to estimate the orographic elevations of precipitation stations, (2) using the DEM and a windowing technique to group stations onto individual topographic facets, and (3) estimating precipitation at a DEM grid cell through a regression of precipitation versus DEM elevation developed from stations on the cell's topographic facet.

The surfaces were modeled from a 30-year (1961-1990) record of precipitation data from NWS stations. Grid-cell resolution was five minutes. This coarse spatial resolution is considered reasonable for precipitation, which responds to topographic features at a more coarse level than air temperature. Values from each precipitation grid were assigned to individual plot locations using the ArcInfo function LATTICESPOT (ESRI 1991), and transformed to natural logarithmic scale. Plot-level precipitation values were used to compute precipitation-based indices that approximate precipitation conditions during the growing-season (SMRPRE) (fig. 3.c.) and cool-season (WTRPRE), as well as seasonal variability and continentality (CVPRE and CONTPRE) (Table 5, figs. 3.d.-e.).

Solar Radiation

Solar radiation is closely related to site microclimate and frequently is an excellent predictor of vegetation (Peet 1981). Potential solar radiation was estimated for each plot based on the plot's latitude, elevation, aspect, and slope, using program SOLARPDX (Smith 1993). SOLARPDX computes total insolation, including direct insolation (direct beam) and indirect insolation (skylight), based on algorithms of Lowry and Lowry (1989). Calculations assume an average profile for atmospheric transmissivity and absorbtivity for humid, temperate climates. The algorithm does not adjust for cloud cover, which varies significantly across Oregon.

Geology

Data on lithology and geological age (Ptype) came from a geological map of Oregon (Walker and MacLeod 1991), obtained as an ArcInfo polygon coverage from the Corvallis Forestry Sciences Laboratory, USDA Forest Service, 3200 SW Jefferson Way, Corvallis, OR 97331. I used the INTERSECT command (ESRI

1991) to assign a Ptype to each field plot. I grouped the Ptypes into 14 generalized geological types (Appendix 3), which were treated as nominal variables in the analysis (Table 5, variables 20-32; fig. 4).

Spatial Position

Latitude (Y) and longitude (X) were obtained for each plot. To account for complex spatial trends, seven derived geographic variables were constructed by including all quadratic and cubic combinations of X and Y, as suggested by Borcard et al. (1992). Only five of the geographic variables were included in the analysis (Table 5), those which were identified in stepwise canonical correspondence analysis (CCA) (see below) as explaining the most variation in the species data.

I grouped the explanatory variables into five subsets for some of the analyses. Two of the subsets included factors measured at the local, plot level or thought to operate at a local scale (topography, L1, and disturbance, L2), two subsets included factors that operate or were measured at a broader, regional scale (macroclimate, R1, and geological type, R2), and one subset captured spatial position (latitude and longitude and transformations thereof, S) (Table 5).

Gradient Analyses

The primary analytical tool in my study was canonical correspondence analysis (CCA) (ter Braak 1986, 1987a-b, 1988), a relatively new ordination technique that has come into widespread use (Palmer 1993). CCA is a direct gradient analysis technique that represents a special case of multivariate regression. CCA is based on the correspondence analysis algorithm, but plot scores are constrained to be linear combinations of environmental variables. The statistical model underlying CCA is that a species' abundance or frequency is a unimodal (Gaussian) function of position along environmental gradients, which generally is accepted by ecologists. The CCA method has been shown to be robust to violations of this assumption, as well as to other characteristics of datasets that have caused problems for detrended correspondence analysis (DCA) (Palmer 1993, ter Braak and Prentice 1988). All CCA and DCA analyses were based on the CCA concept, using the program CANOCO version 3.12 (ter Braak 1987a). FORTRAN code was obtained, array sizes increased, and the program recompiled to handle large numbers of plots, species, and environmental variables.

CCA with Variance Partitioning

CCA with variance partitioning (Borcard et al. 1992, Okland and Eilertsen 1994, ter Braak 1988), or partial CCA, was conducted with the purpose of quantifying the relative contributions of various sets of explanatory variables to species variation. Species relative abundance was log-transformed cover; all other CANOCO defaults were used. All woody species were included, and all explanatory variables were included regardless of their significance or contribution to explained variation. All CCA plot scores in this paper are linear combinations, not weighted averages, as recommended by Palmer (1993).

Variance partitioning was conducted on several combinations of two sets of explanatory variables, denoted {A} and {B} in the general sense. The fraction of variation explained by a set of explanatory variables ({A} or {B}) was the sum of all constrained eigenvalues divided by the total inertia (TI). Total inertia is a measure of the total variation in the species data, equal to the sum of all unconstrained eigenvalues. Put differently, TI is the ratio of the dispersion of the species scores to the dispersion of the plot scores (ter Braak 1987a), and as such is a property of the species-by-plot data matrix. Species-by-plot data matrices with greater TI contain a more species with less overlap of species occurrence among plots (high beta diversity). The fraction of variation explained by {A} and not shared with {B} (A|B), was found by partial CCA using the variables in {B} as covariables and {A} as the constraining variables. The fraction of variation explained by {B}, not shared with {A} (B|A), was found by partial CCA using the variables in {A} as covariables and {B} as the constraining variables. Total variation explained (TVE, A∪B) is the ratio of the sum of all constrained eigenvalues to the total inertia. Calculation of components of the variation are summarized as follows:

A: variation explained by {A};
B: variation explained by {B};
A|B: variation explained by {A}, not shared by {B} = A - B∩A;
B|A: variation explained by {B}, not shared by {A} = B - A∩B;
A∩B: variation shared by {A} and {B} = A - A|B;
A∪B: total variation explained, TVE, by the variables {A∪B};
X: unexplained variation = 1 - A∪B.

CCA with variance partitioning was performed on the following combinations of sets of variables: (1) {L1∪L2∪R1∪R2} vs. {S}; (2) {L1} vs. {L2∪R1∪R2}; (3) {L2} vs. {L1∪R1∪R2}; (4) {R1} vs. {L1∪L2∪R2}; (5) {R2} vs. {L1∪L2∪R1}; (6) {L1∪L2} vs. {R1∪R2}. Set membership of the explanatory variables is shown in Table 5.

Stepwise CCA

For more in-depth CCA analyses, I identified a reduced set of explanatory variables. Spatial variables ({S}) were excluded from these analyses: the amount of explained variation attributable to spatial variables was relatively small (Tables 6-7), and distances among plots are large enough to avoid direct interactions among them. Stepwise CCA, available as an option in CANOCO, was performed on all woody species, tree species only, and shrub species only, for each geographic area. Variables were added to the model in the order of greatest additional

Table 6.--Results of partial CCAs of all woody species, by geographic area, using L and R explanatory variables, and using L, R, and S explanatory variables.[a] TI = total inertia; TVE = total variation explained; X = unexplained variation.

	No. plots	No. Spp.	TI	L∪R		L∪R∪S	
				TVE	X	TVE	X
				- Fraction (proportion) of TI -			
Oregon	2,443	192	24.924	2.510 (0.10)	21.814 (0.90)	2.959 (0.12)	21.365 (0.88)
Half-state:							
Western Oregon	1,233	158	15.468	2.086 (0.14)	13.382 (0.86)	2.305 (0.15)	13.163 (0.85)
Eastern Oregon	1,210	130	18.499	2.178 (0.12)	16.321 (0.88)	2.534 (0.14)	15.965 (0.86)
Subregion:							
Coast	461	97	9.705	1.549 (0.16)	8.156 (0.84)	1.702 (0.18)	8.003 (0.82)
Western Cascades	465	119	9.309	1.658 (0.18)	7.651 (0.82)	1.778 (0.19)	7.531 (0.81)
Klamath	307	124	10.565	2.156 (0.20)	8.409 (0.80)	2.308 (0.22)	8.257 (0.78)
Eastern Cascades	479	99	12.556	2.420 (0.19)	10.136 (0.81)	2.733 (0.22)	9.823 (0.78)
Blue Mountains	731	94	14.582	2.000 (0.14)	13.582 (0.86)	2.317 (0.16)	12.265 (0.84)

[a] See Table 5 for variable subset affiliations.

Table 7.--Total variation explained (TVE) in partial CCAs of all woody species, by geographic area. TI = total inertia; S = five spatial variables; E = 31 environmental (L and R) variables.[a]

	S|E	S∩E	E|S
	- - - - Fraction of TI - - - - (Proportion of TVE)		
Oregon	0.455 (0.15)	0.885 (0.30)	1.625 (0.55)
Half-state:			
Western Oregon	0.213 (0.09)	0.811 (0.35)	1.325 (0.56)
Eastern Oregon	0.358 (0.14)	0.566 (0.22)	1.615 (0.64)
Subregion:			
Coast	0.151 (0.09)	0.565 (0.34)	0.965 (0.57)
Western Cascades	0.123 (0.07)	0.510 (0.30)	1.078 (0.63)
Klamath	0.162 (0.07)	0.386 (0.18)	1.661 (0.75)
Eastern Cascades	0.320 (0.11)	0.660 (0.24)	1.825 (0.65)
Blue Mountains	0.321 (0.14)	0.391 (0.17)	1.605 (0.69)

[a] See Table 5 for variable subset affiliations.

contribution to TVE, but were added only if: (1) they were significant ($P \leq .01$), where significance was determined by a Monte Carlo permutation test using 99 permutations (H_0: additional influence of variable on vegetation is not significantly different from random); and (2) adding the variable did not cause inflation factors of that or other variables to exceed 20. In all analyses the addition of all significant variables resulted in excessively high inflation factors for several variables, especially among the precipitation and temperature variables.

Results were graphed as biplots (fig. 8), in which arrow length and the position of the arrowhead indicates the correlation between the explanatory variable and the CCA axes, arrow direction indicates how well the variable is correlated with the various species composition axes, the angle between arrows indicates correlations between variables, and the location of species scores relative to the arrows indicates the environmental preferences of each species (Palmer 1993).

Indirect Gradient Analyses

In order to more fully explore how successfully the explanatory variables used in the constrained ordination explained species variation, I analyzed the vegetation data using detrended correspondence analysis (DCA), an indirect gradient analysis method (Gauch 1982), and with detrended canonical correspondence analysis (DCCA) using the same sets of explanatory variables identified in the stepwise CCA analyses. I used detrending by segments with 26 segments for both DCA and DCCA. Detrending in CCA is probably necessary only when results are to be compared with DCA (Palmer 1993). Species relative abundance was log-transformed cover; all other defaults were used. I compared eigenvalues and gradient lengths from the two methods, and computed Spearman rank correlations (PROC CORR) (SAS Institute Inc. 1990) between DCA and DCCA plot scores on the first three axes. By rescaling in DCA and DCCA, gradient length is set equal to species turnover (standard deviations, SD) so as to make gradient length interpretable and readily comparable between different datasets (Peet et al. 1988).

Mapping Geographic Patterns of Dominant Gradients

Plot scores from axes 1-4 from stepwise CCA and axes 1-2 from DCA were kriged using ArcInfo command KRIGING (ESRI 1991). The Gaussian model was selected based on having the best fit between actual and predicted semivariograms for CCA axes 1-4 at the state level. Plot scores were interpolated to a lattice with 8,000-m spacing, and the lattice was contoured using command LATTICECONTOUR (ESRI 1991). The Blue Mountains subregion was kriged independently from the other four subregions. Sizes of the sampling windows and contour intervals were selected subjectively to standardize across the different axis lengths and achieve comparable appearance among maps.

Community Classification

All 2,443 vegetation plots were classified based on two-way indicator species analysis using program TWINSPAN (Hill 1979). All program defaults were accepted except only two pseudospecies levels were used, <5% and ≥5% cover. Only tree species were analyzed, as the objective was to obtain a regional-scale approximation of tree series and major forest zones. Whereas vegetation zones typically are defined based on climatic climax communities, I refer to "zones" as areas in which a single tree species would dominate late-successional forest, usage which is consistent with Franklin and Dyrness (1973). However, vegetation classes that I identified were by necessity typological, since they were based on existing vegetation spanning a range of successional stages and disturbance regimes.

RESULTS

Variance Partitioning Analyses

Results of the variance partitioning analyses were influenced by ecological differences among geographic areas, spatial scale (geographic extent), and sample size (numbers of plots and species). Total inertia (TI), sample size, and number of species increased, and the total amount of variation explained (TVE) decreased, with increasing geographic extent (Table 6, fig. 7). Sample size affected TI and TVE (see later discussion of sampling effects), but should not have affected the proportions of TVE attributable to different subsets of explanatory variables, so I confined my analysis to proportions.

Importance of Spatial Position and Environment

Spatial position (five spatial variables, S) alone contributed 7-15% of TVE (Table 7). At broader geographic scales, the importance of spatial position in explaining species variation was greater and the importance of environmental measures uncorrelated with spatial position was less (Table 7). Note that in this discussion, "environmental" variables include all independent variables, biotic and abiotic, exclusive of the spatial variables. Ecological differences among geographic areas (differences in physical environment, species present, and species-environment interactions) played a stronger role than scale (geographic extent) in influencing the relative fractions of TVE explainable by spatial position as opposed to environment (Table 7). A greater proportion of the TVE was attributed to spatial position in eastern Oregon (S|E = 0.14) and its subregions (S|E = 0.11-0.14) than in western Oregon (S|E = 0.09) and its subregions (S|E = 0.07-0.09). Also, environmental measures were less spatially structured in eastern Oregon (E|S =

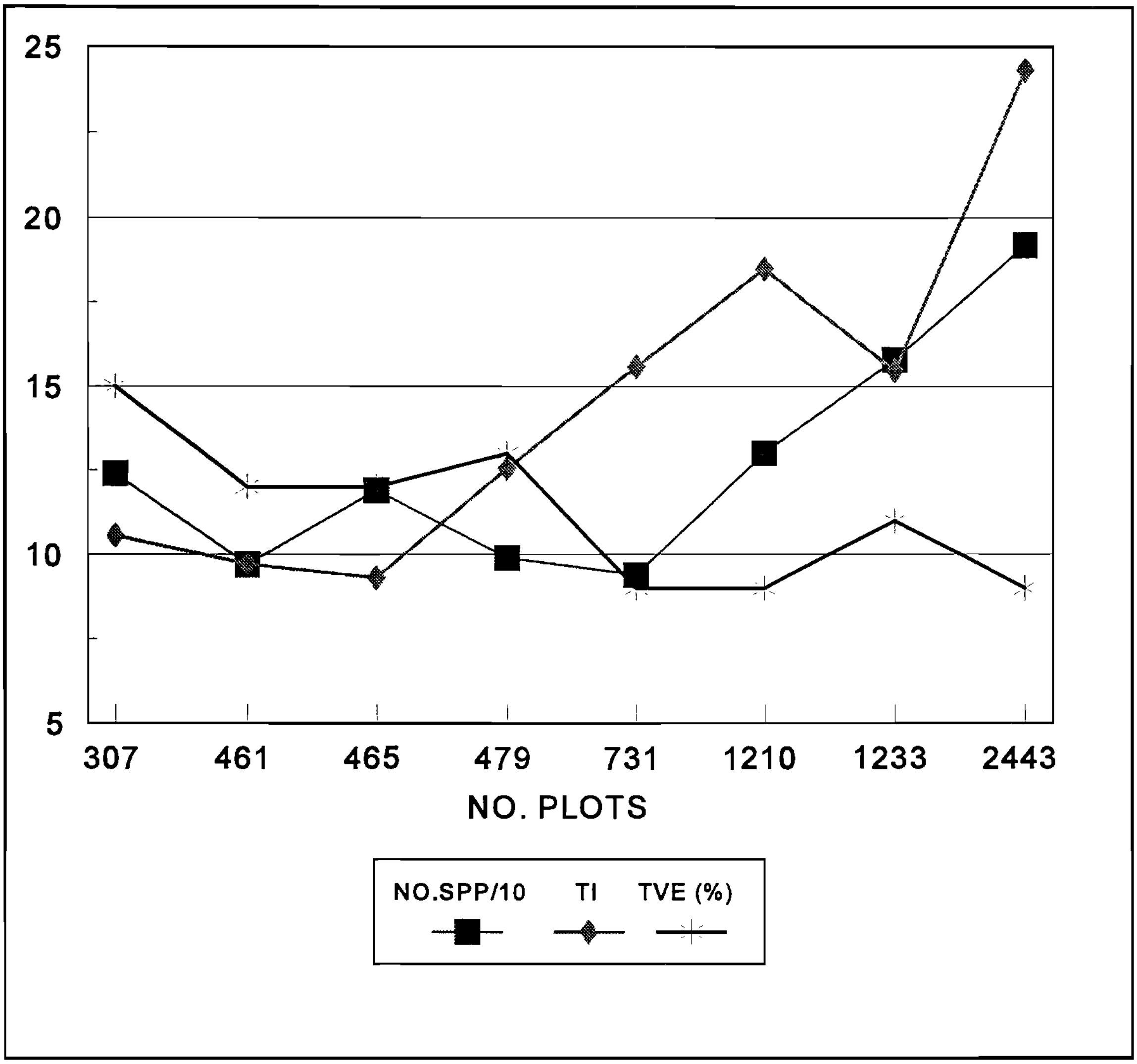


Figure 7. Relations between sample size (number of plots) and number of species, total inertia (TI), and total variation explained (TVE) for CCAs of all woody species. Samples are the five subregions, two half-states, and the entire State.

0.64) than in western Oregon (E|S = 0.56) (Table 7). The subregions also differed substantially in terms of proportions of TVE attributed to environmental measures uncorrelated with spatial position, with the Coast having the least (E|S = 0.57) and the Klamath having the most (E|S = 0.75). Given the secondary contribution of spatial position to TVE, spatial variables were not considered in the stepwise CCAs.

Importance of Local and Regional Explanatory Variables

Regional explanatory variables ($R1 \cup R2$) accounted for more of the TVE (70-79%) than local factors ($L1 \cup L2$) (10-20%) at all geographic scales of analysis (Table 8). The relative contributions of local and regional factors were influenced by both location and geographic scale. Overall, contributions of local measures were weaker at the state level (10% of TVE) than at the subregional level (14-20% of TVE) (Table 8), as hypothesized. However, contributions of regional measures were strong at all scales and did not increase with scale as hypothesized (Table 8). Local factors were especially strong contributors in the Blue Mountains subregion and hence in eastern Oregon. Contributions of local factors to explaining species variation were weakest (14% of TVE) and regional factors were strongest (78% of TVE) in the Coast subregion, where climate is most benign and where climatic gradients from the coast to the Willamette Valley margin are quite strong.

At all geographic scales and locations, macroclimate ({R1}) contributed far more to TVE (46-60%) than any other variable subset (Table 8), as hypothesized. Climate was particularly important (60% of TVE) in the Coast subregion. Geology variables ({R2}) were second to climate in overall contributions to TVE in all geographic areas, and contributions were unrelated to geographic extent (Table 8). Contributions of geologic variables were greater in western Oregon (19% of TVE) and its subregions (11-19%) than in eastern Oregon (16%) and its subregions (13-18%). Disturbance ({L2}) and topography ({L1}) contributed least to TVE (6-12% and 4-8%, respectively). Disturbance was more important in eastern Oregon than

Table 8.--Proportion of total variation explained (TVE) contributed by subsets of explanatory variables,[a] from partial CCA, all woody species, by geographic area. Local = $\{L1 \cup L2\} \mid \{R1 \cup R2\}$; regional = $\{R1 \cup R2\} \mid \{L1 \cup L2\}$; topography = $L1 \mid \{L2 \cup R1 \cup R2\}$; disturbance = $L2 \mid \{L1 \cup R1 \cup R2\}$; climate = $R1 \mid \{L1 \cup R2 \cup R2\}$; geology = $R2 \mid \{L1 \cup L2 \cup R1\}$.

	Local	Regional	Topography	Disturbance	Climate	Geology
	Proportion of TVE					
Oregon	0.10	0.72	0.04	0.06	0.49	0.15
Half-state:						
W. Oregon	0.10	0.79	0.04	0.06	0.50	0.19
E. Oregon	0.17	0.72	0.07	0.10	0.49	0.16
Subregion:						
Coast	0.14	0.78	0.05	0.09	0.60	0.11
W. Cascades	0.16	0.72	0.08	0.08	0.48	0.18
Klamath	0.16	0.76	0.06	0.09	0.46	0.19
E. Cascades	0.15	0.70	0.07	0.08	0.54	0.13
Blue Mtns.	0.20	0.70	0.08	0.12	0.48	0.18

[a] See Table 5 for variable subset affiliations.

in western Oregon, especially in the Blue Mountains (12% of TVE) (Table 8), probably because of the strong contribution of the overstory crown cover variable. Topographic variables showed a weak scale effect: $(\{L1\} \mid \{L2 \cup R1 \cup R2\})$ increased with decreasing geographic extent, from 4% at the state level to 5%-8% at the subregion level (Table 8), which was hypothesized.

Stepwise CCA

Gradient Structure

In each geographic area, TI was highest for shrub species, lowest for tree species, and intermediate for all woody species (Table 9). Total inertia increased with sample size and with geographic extent for each species group, ranging from 5.953 for trees in the western Cascades to 32.707 for shrubs in Oregon. Within each geographic area, TVE was highest for trees, lowest for shrubs, and intermediate for all woody species. TVE was highest for all woody species (0.15) and for shrubs (0.12) in the Klamath subregion, and for trees in the eastern Cascades (0.19). TVE generally but not always decreased with increasing geographic extent. Because sample size decreased at smaller geographic scales, it could not be discerned whether TVE differences (i.e., differences in explanatory power of the model) were because of change in scale or sample size.

Dominant Gradients at the State Level

At the state level, the dominant compositional gradient (CCA axis 1) in woody plant communities reflected a gradient from the high-rainfall, maritime climate of the Coast to the drier and more continental climate of the interior (Table 10, figs. 8.a. and 9.a.). With minor exceptions, the predominant compositional gradient tended to be longitudinal from the Coast to the foothills of the eastern Cascades, reflecting the strong climatic influence of the Pacific Ocean and the north-south orientation of the major physiographic features, the Coast and Cascade Ranges. In the Blue Mountain subregion, on the other hand, the dominant compositional gradient was more latitudinal. Forests in the northern part of the subregion receive a stronger

Table 9.--Summary of stepwise CCA results by species group and geographic area. TI = total inertia; TVE = total variation explained, expressed as a proportion of TI.

Geogr. Area	No. Plots	No. Spp.	TI	TVE (prop. of TI)	Eigenvalue			
					Axis 1	Axis 2	Axis 3	Axis 4
Oregon:								
Woody	2443	192	24.324	0.09	0.67	0.37	0.26	0.21
Trees	2443	51	14.084	0.13	0.64	0.39	0.23	0.18
Shrubs	2331	141	32.707	0.07	0.71	0.36	0.29	0.23
W.Oregon:								
Woody	1233	158	15.468	0.11	0.42	0.37	0.26	0.17
Trees	1233	46	10.066	0.16	0.44	0.36	0.25	0.16
Shrubs	1208	112	19.076	0.09	0.40	0.37	0.29	0.17
E.Oregon:								
Woody	1210	130	18.499	0.09	0.46	0.35	0.22	0.11
Trees	1210	37	10.301	0.13	0.44	0.26	0.17	0.12
Shrubs	1123	93	25.674	0.07	0.57	0.35	0.25	0.14
Coast:								
Woody	461	97	9.705	0.12	0.41	0.27	0.15	0.09
Trees	461	28	6.549	0.16	0.40	0.26	0.12	0.07
Shrubs	459	69	11.064	0.10	0.41	0.28	0.17	0.08
W.Cascades:								
Woody	465	119	9.309	0.12	0.45	0.21	0.16	0.09
Trees	465	34	5.953	0.16	0.47	0.22	0.11	0.05
Shrubs	445	85	12.161	0.08	0.41	0.20	0.15	0.10
Klamath:								
Woody	307	124	10.565	0.15	0.42	0.31	0.22	0.15
Trees	307	37	7.357	0.13	0.36	0.26	0.11	0.11
Shrubs	304	87	13.209	0.12	0.45	0.35	0.25	0.15
E.Cascades:								
Woody	479	99	12.556	0.13	0.51	0.32	0.22	0.16
Trees	479	30	7.127	0.19	0.49	0.35	0.19	0.13
Shrubs	453	69	18.713	0.07	0.48	0.26	0.24	0.16
Blue Mountains:								
Woody	731	94	15.582	0.09	0.46	0.34	0.13	0.09
Trees	731	24	7.746	0.14	0.47	0.29	0.12	0.09
Shrubs	670	70	20.180	0.06	0.44	0.40	0.11	0.09

Table 10.--Interset correlations (biplot scores) (X 1000) of explanatory variables selected in stepwise CCA, axes 1-4, all woody species, by geographic area. Variables are listed in order of descending correlation strength.

		Half-state				Subregion									
Oregon		Western Oregon		Eastern Oregon		Coast		Western Cascades		Klamath		Eastern Cascades		Blue Mountains	
Axis 1:															
CVTMP	897	ELEV	969	SMRPRE	765	SMRTSMRP	-869	ELEV	939	WTRPRE	917	TREOCOV	716	SMRTSMRP	720
MINTMP	-878	MAXTMP	-943	TREOCOV	619	ANNPRE	769	CVTMP	-791	CVTMP	-872	CONTPRE	-486	TREOCOV	-584
ELEV	871	MINTMP	-628	ANNPRE	588	CVTMP	-710	CVTMP	559	CONTPRE	-655	SMRPRE	440	SMRTMP	581
MAXTMP	-850	CVTMP	605	SMRTMP	-506	MAXTMP	-426	MAFY	413	MINTMP	618	SOLAR	-421	ELEV	-475
ANNPRE	-847	SMRTMP	-546	SOLAR	-340	CVPRE	-411	CLEARCUT	-401	ELEV	-361	SMRTMP	-416	TUFY	310
SMRPRE	-616	AGE	475	CVTMP	329	CONTPRE	312	PYRY	238	ANNTMP	-297	CVTMP	-240	AGE	-244
TREOCOV	-538	MAFY	427	AGE	290	TREOCOV	271	SLOPE	-160	UMAF	261	SLOPE	391	VOLC	-166
SLOPE	-360	SMRTSMRP	-420	SLOPE	269	MINTMP	271	SMRPRE	132	MAXTMP	180	MINTMP	341	SOLAR	92
CLEARCUT	-356	CLEARCUT	-403	MAXTMP	-215	SLOPE	212	TREOCOV	-126	AGE	178	AGE	317	SLOPE	60
MAFO	350	SOLAR	236	ELEV	210	CLEARCUT	-135	SOLAR	123	CLEARCUT	124	MAFO	-84	UMAF	-13
SOLAR	286	PYRY	234	VOLC	176	DEPO	-80	CVPRE	106	SOLAR	-118	ELEV	-70		
TUFY	173	UMAF	127	MINTMP	-155	ELEV	49			DEPO	-71	MAXTMP	34		
PYRY	143	CONTPRE	100	CVPRE	-123					SLOPE	-64				
TUFO	-142	CVPRE	94	SILV	-121					TREOCOV	23				
MAFY	118	TREOCOV	-53	PYRY	-111										
AGE	83	SLOPE	-46	SEDR	-30										
UMAF	-56	DEPO	-1	MAFY	-25										
SMRTSMRP	-50			UMAF	23										
DEPO	5														
Axis 2:															
SMRTSMRP	-849	SMRTSMRP	772	ELEV	-756	DEPO	698	SMRPRE	835	ELEV	899	ELEV	-817	ELEV	798
SMRPRE	590	SMRTMP	559	MAXTMP	722	ELEV	-560	TREOCOV	384	MAXTMP	-867	MAXTMP	781	SMRTMP	-612
MAXTMP	-439	CVTMP	409	SMRTMP	593	CVTMP	-554	SOLAR	-374	ANNTMP	-725	SMRTMP	649	SOLAR	544
ELEV	418	CVPRE	275	SLOPE	553	MINTMP	473	CVTMP	-300	MINTMP	-531	MINTMP	563	SMRTSMRP	-506
ANNPRE	371	TREOCOV	-208	SOLAR	-504	SLOPE	-385	PYRY	-261	AGE	412	CONTPRE	-269	SLOPE	-497
AGE	365	CONTPRE	-199	CVPRE	-352	TREOCOV	-256	ELEV	-188	CVTMP	363	CVTMP	-257	TREOCOV	-327
TREOCOV	270	MAFY	-170	ANNPRE	-227	CVPRE	238	SMRTMP	-185	CLEARCUT	-360	AGE	-192	VOLC	294
MAFY	236	SOLAR	157	MAFY	-189	CONTPRE	-234	CVPRE	-185	UMAF	335	SLOPE	191	TUFY	171
MINTMP	-211	UMAF	88	PYRY	-172	CLEARCUT	-226	CLEARCUT	168	SOLAR	191	SOLAR	-180	UMAF	41
CLEARCUT	-188	CLEARCUT	-64	VOLC	-141	ANNPRE	-173	MAFY	58	DEPO	-169	TREOCOV	159	AGE	-39
CVTMP	108	AGE	-63	TREOCOV	116	SMRTSMRP	170	SLOPE	40	WTRPRE	163	MAFO	75		
TUFY	-97	MAXTMP	60	CVTMP	115	MAXTMP	-155			CONTPRE	-97				
MAFO	61	PYRY	-56	MINTMP	113					SLOPE	-59				
PYRY	39	SLOPE	48	SMRPRE	68					TREOCOV	2				
SOLAR	-23	ELEV	47	SILV	-61										
UMAF	9	DEPO	-44	AGE	-33										
DEPO	9	MINTMP	-29	SEDR	29										
TUFO	-9			UMAF	-21										
SLOPE	-2														

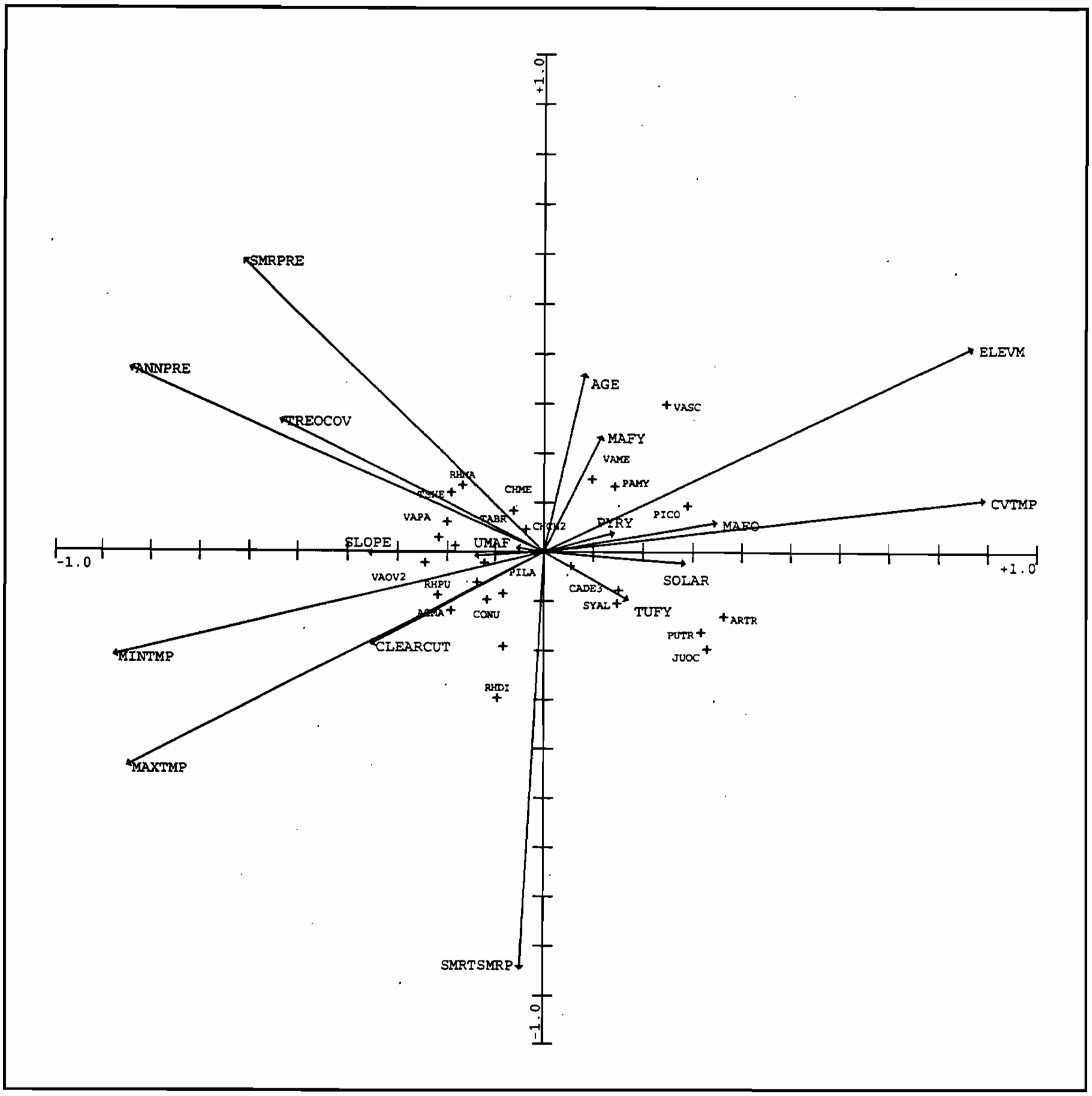
Table 10 (continued).

		Half-state				Subregion									
Oregon		Western Oregon		Eastern Oregon		Coast		Western Cascades		Klamath		Eastern Cascades		Blue Mountains	
Axis 3:															
UMAF	528	UMAF	678	CVTMP	-740	CVPRE	743	SLOPE	-622	UMAF	728	AGE	588	SLOPE	776
MAFO	-328	CONTPRE	-650	MINTMP	671	CONTPRE	-681	CLEARCUT	527	TREOCOV	-512	MAXTMP	-462	TREOCOV	-460
CVTMP	-302	CVTMP	-568	CVPRE	629	MAXTMP	-645	TREOCOV	-457	SOLAR	423	SMRPRE	440	SOLAR	-396
SOLAR	300	CVPRE	547	MAFY	459	ELEV	472	CVPRE	-410	SLOPE	-280	ELEV	439	SMRTSMRP	-241
MINTMP	268	MINTMP	471	SMRPRE	-407	SLOPE	444	PYRY	313	AGE	-134	CONTPRE	421	SMRTMP	-222
AGE	259	TREOCOV	-252	ELEV	-370	SMRTSMRP	-220	MAFY	248	CONTPRE	-126	SLOPE	414	TUFY	-138
SMRPRE	-245	SMRTMP	-249	TREOCOV	344	TREOCOV	-177	CVTMP	-241	MAXTMP	123	MAFO	352	UMAF	-128
CLEARCUT	-221	SMRTSMRP	-164	MAXTMP	332	DEPO	-103	ELEV	-213	DEPO	111	CVTMP	278	ELEV	113
MAXTMP	-164	CLEARCUT	-145	VOLC	-323	CLEARCUT	87	SOLAR	90	ELEV	-109	TREOCOV	-151	VOLC	92
ANNPRE	141	MAFY	-143	SMRTMP	223	ANNPRE	83	SMRPRE	13	CLEARCUT	-108	SMRTMP	97	AGE	81
ELEV	132	SOLAR	132	PYRY	160	MINTMP	-64	SMRTMP	2	MINTMP	60	SOLAR	-82		
PYRY	130	AGE	99	ANNPRE	115	CVTMP	-17			CVTMP	-51	MINTMP	-61		
MAFY	125	ELEV	-72	SEDR	-93					WTRPRE	-32				
TREOCOV	-107	MAXTMP	-67	AGE	78					ANNTMP	-3				
TUFO	-86	SLOPE	-29	SILV	78										
SLOPE	-66	PYRY	15	SOLAR	-69										
SMRTSMRP	-31	DEPO	8	UMAF	-14										
DEPO	21			SLOPE	-5										
TUFY	10														
Axis 4:															
SLOPE	-393	SLOPE	-566	SLOPE	556	MINTMP	-587	PYRY	822	SLOPE	-509	TREOCOV	-468	UMAF	767
TREOCOV	-350	TREOCOV	-396	TREOCOV	-507	TREOCOV	-539	MAFY	-277	CONTPRE	431	CONTPRE	-346	AGE	397
AGE	-347	DEPO	385	AGE	256	CVTMP	302	SMRTMP	251	DEPO	421	SOLAR	-273	TUFY	307
SMRTSMRP	-274	AGE	-375	SMRTMP	-223	CLEARCUT	255	SOLAR	-185	AGE	-408	ELEV	-245	TREOCOV	273
CVTMP	-226	CVPRE	-323	MAXTMP	-186	SLOPE	-255	TREOCOV	168	CLEARCUT	404	MAXTMP	220	SLOPE	258
DEPO	180	MAFY	277	SOLAR	-186	DEPO	251	SMRPRE	85	TREOCOV	-257	MINTMP	-208	ELEV	217
CLEARCUT	174	UMAF	-219	ELEV	160	CONTPRE	217	CLEARCUT	-60	MAXTMP	-250	SMRTMP	-201	VOLC	-116
SMRPRE	154	PYRY	219	UMAF	-131	ANNPRE	194	CVTMP	-49	SOLAR	139	SLOPE	200	SMRTMP	-114
ELEV	-151	CONTPRE	195	MAFY	81	CVPRE	-97	CVPRE	-39	CVTMP	-109	AGE	-179	SOLAR	-68
TUFY	147	CLEARCUT	155	PYRY	-80	ELEV	96	ELEV	-32	ELEV	108	MAFO	107	SMRTSMRP	-57
TUFO	-96	ELEV	-133	SILV	80	SMRTSMRP	-78	SLOPE	13	WTRPRE	-98	CVTMP	21		
PYRY	77	SMRTSMRP	119	SEDR	61	MAXTMP	77			UMAF	-79	SMRPRE	13		
SOLAR	49	SOLAR	91	SMRPRE	34					MINTMP	63				
MAXTMP	34	CVTMP	-85	MINTMP	34					ANNTMP	-63				
UMAF	34	MINTMP	-70	CVPRE	33										
MAFY	-23	SMRTMP	68	VOLC	-30										
MAFO	-18	MAXTMP	49	ANNPRE	-28										
MINTMP	13			CVTMP	-23										
ANNPRE	2														

maritime influence (fig. 3.g.), and were most similar in composition to forests of the Cascades (fig. 9.a.).

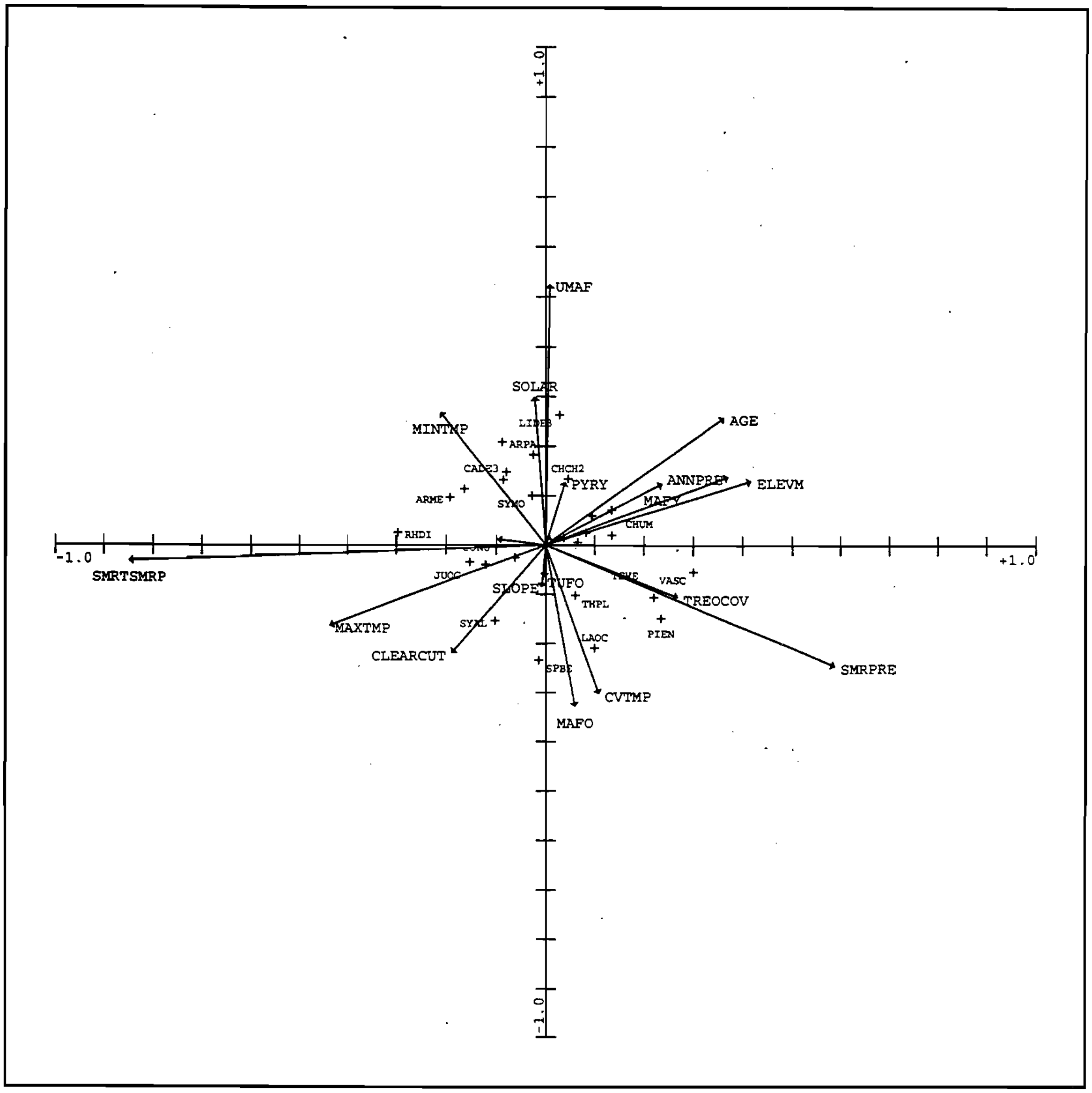
Plots with low scores on axis 1 occurred at lower elevations and were characterized by high rainfall, warm temperatures, and low seasonal variability in temperature (fig. 8.a.). These plots were concentrated along the length of the coast (fig 9.a.), and generally coincided with the Picea sitchensis zone of Franklin and Dyrness (1973). Widely distributed tree species (constancy ≥1%) with lowest scores on axis 1 included Picea sitchensis, Umbellularia californica, Alnus rubra, and Rhamnus purshiana; shrubs included Menziesia ferruginea, Vaccinium ovatum, V. parviflorum, Rubus spectabilis, Oplopanax horridum, and Sambucus racemosa, (Table 11, fig. 10, Appendix 4). Plots with high scores on axis 1 occurred at higher elevations and in areas of low precipitation, cool temperatures, and high seasonal variability in temperature (fig. 8.a.). The highest plot scores were concentrated along the eastern boundary of the eastern Cascades subregion south of Bend, and the southern boundary of the Blue Mountains subregion, where the two forested subregions meet the shrub-steppe of the High Lava Plains, Basin and Range, and Owhyee Upland provinces of southeat Oregon (fig. 9.a.). High-scoring plots fell largely within the Pinus ponderosa and Juniperus occidentalis zones of Franklin and Dyrness (1973). Widely distributed tree species with lowest scores on axis 1 included Juniperus occidentalis, Cercocarpus ledifolius, and Pinus contorta; shrubs included Artemisia tridentata, Chrysothamnus viscidiflorus, C. nauseosus, Haplopappus bloomeri, Purshia tridentata, Symphoricarpos oreophilus, and Ribes cereum (Table 11, fig. 10, Appendix 4).

The second CCA axis was a gradient in growing-season moisture stress, from areas of warm, dry growing-seasons at lower elevations to areas of cool, wet growing-seasons at higher elevations (Table 10, figs. 8.a. and 9.b.). Moisture stress in Oregon generally is highest within the May-September period captured by SMRPRE, SMRTMP, and SMRTSMRP. Areas of low summer precipitation and high summer temperatures include the interior valleys of western Oregon,



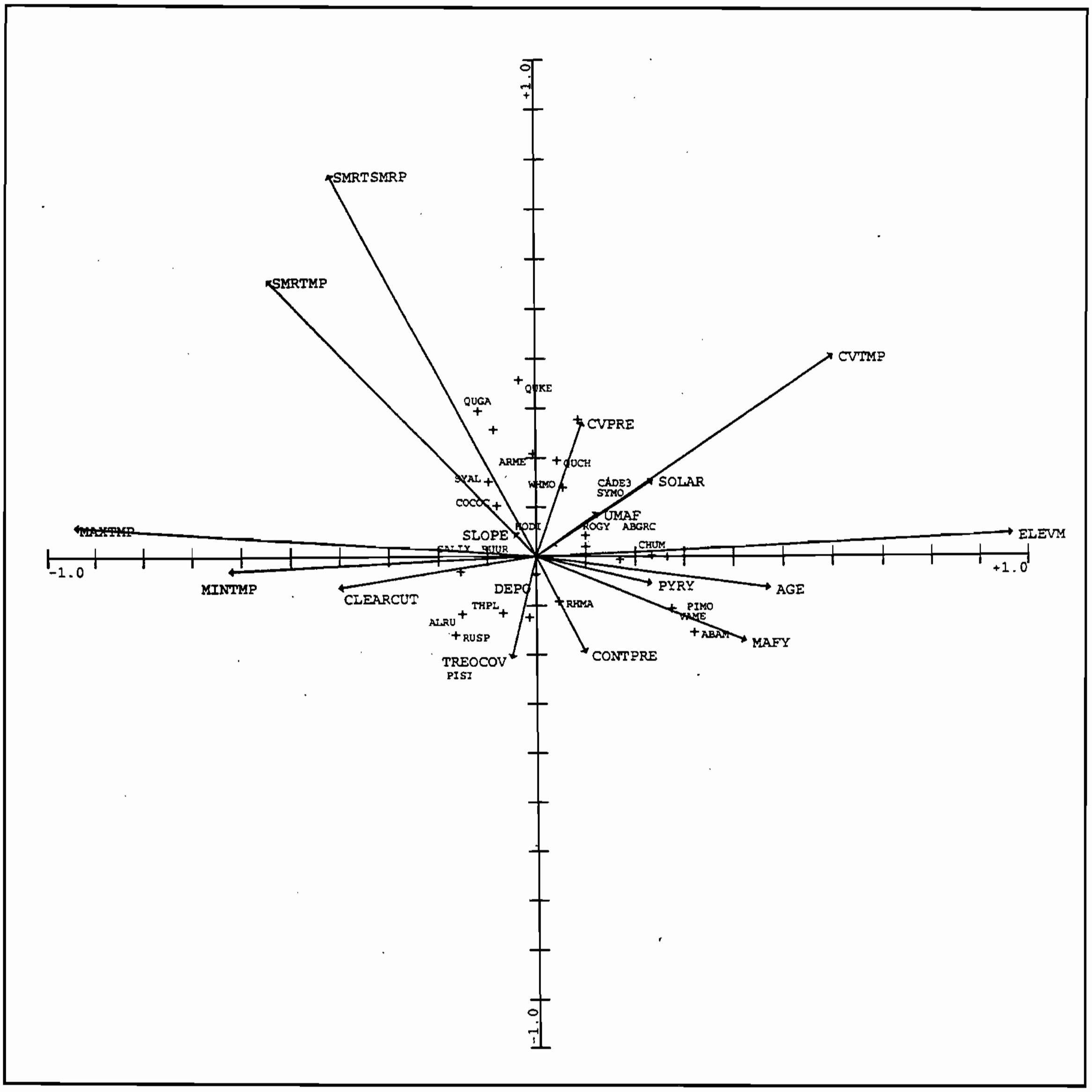
a.

Figure 8. Biplots from CCA of all woody species, showing species with ≥5% constancy. a. Oregon, axes 1 and 2; b. Oregon, axes 2 and 3; c. Western Oregon, axes 1 and 2; d. Eastern Oregon, axes 1 and 2; e. Coast subregion, axes 1 and 2; f. Western Cascades subregion, axes 1 and 2; g. Klamath subregion, axes 1 and 2; h. Eastern Cascades subregion, axes 1 and 2; i. Blue Mountains subregion, axes 1 and 2.



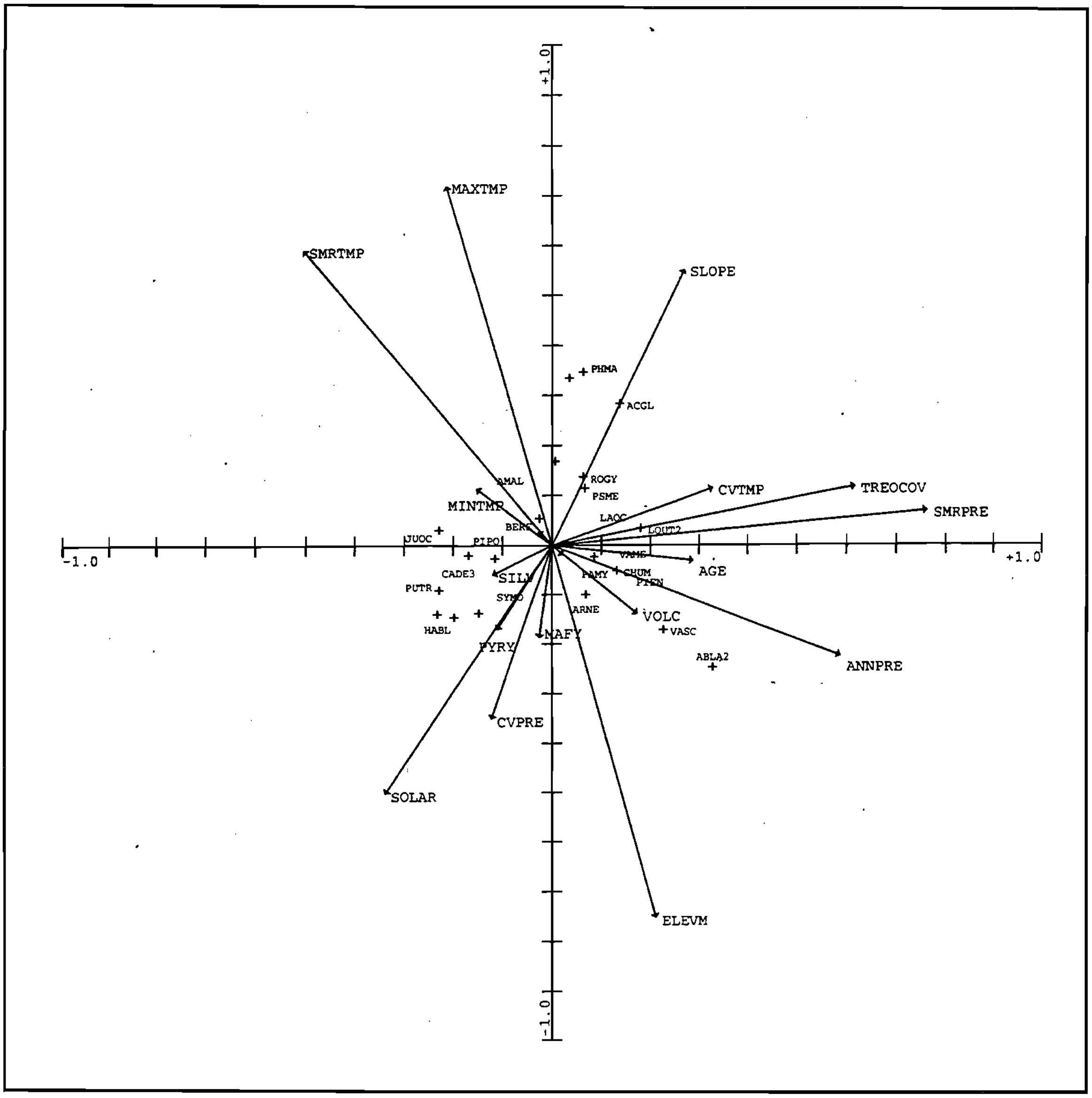
b.

Figure 8 (continued).



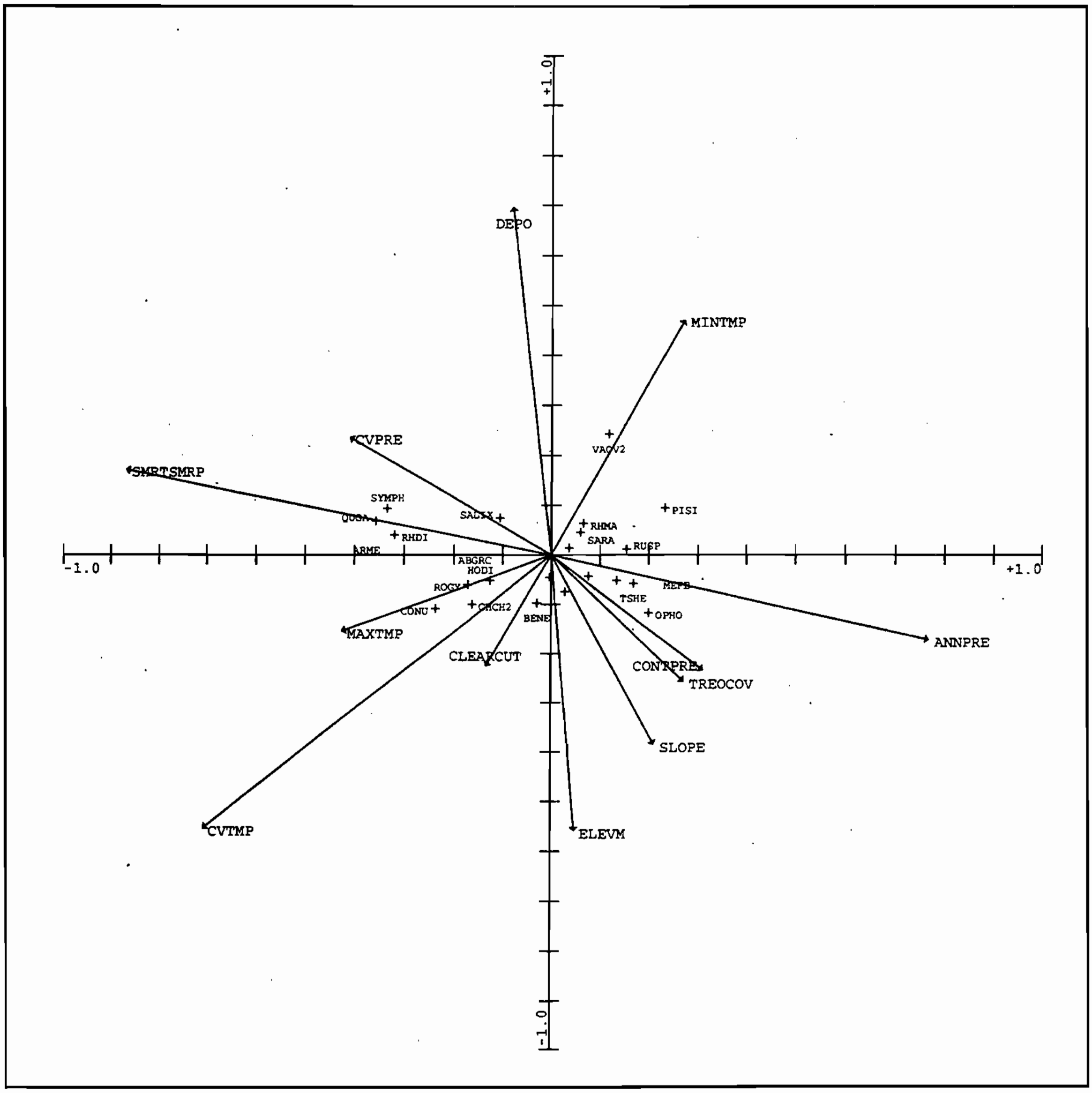
c.

Figure 8 (continued).



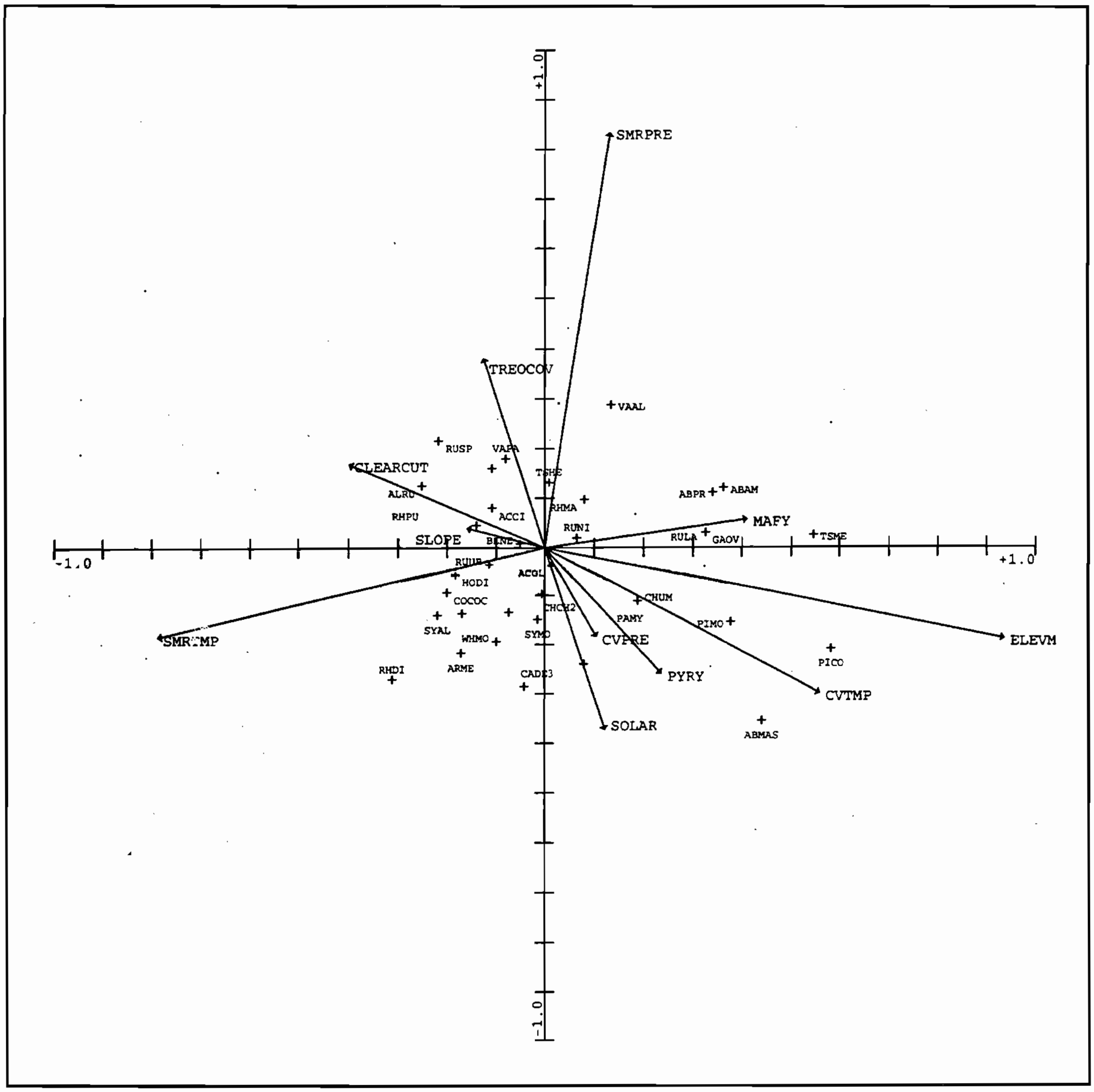
d.

Figure 8 (continued).



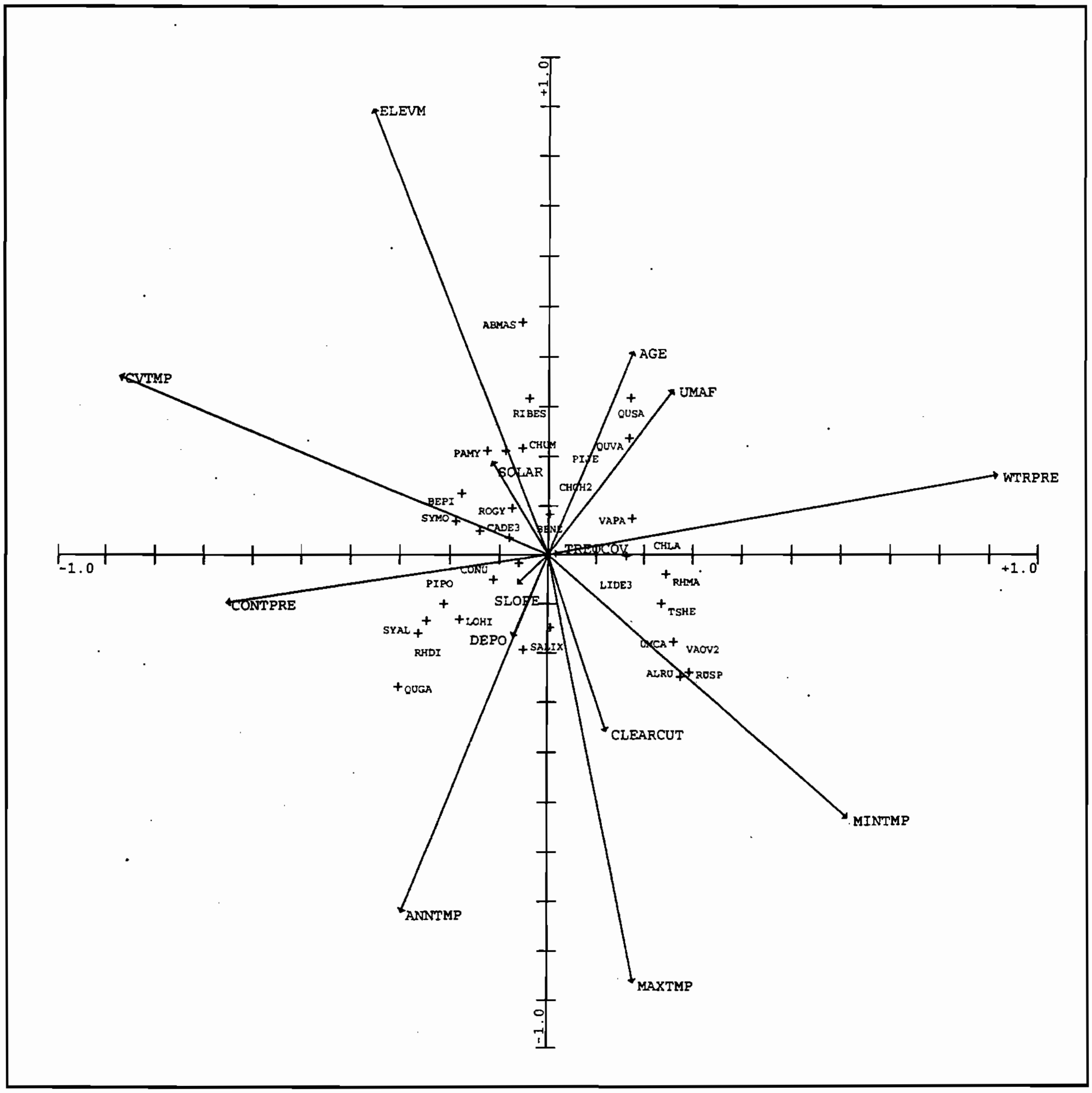
e.

Figure 8 (continued).



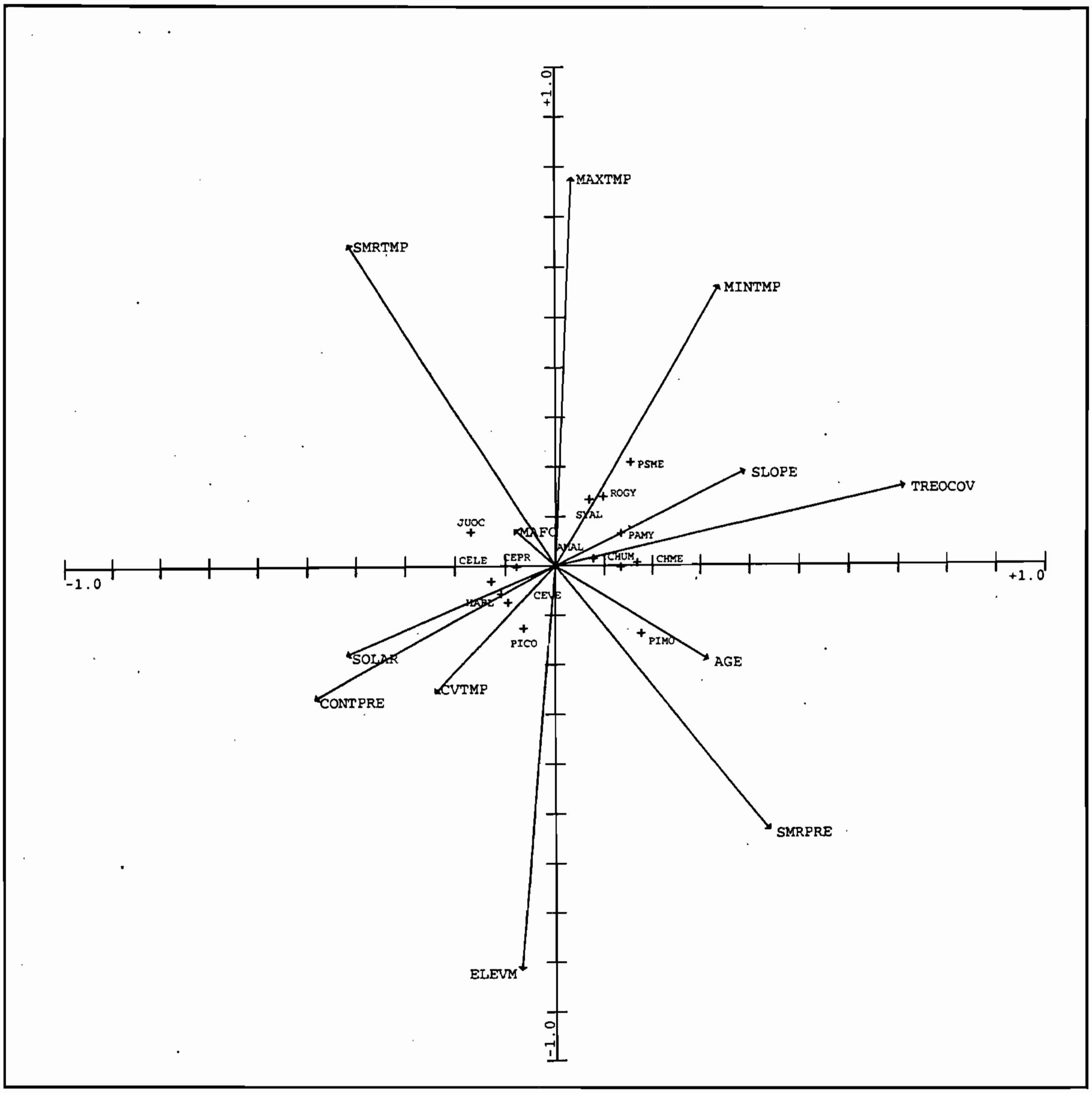
f.

Figure 8 (continued).



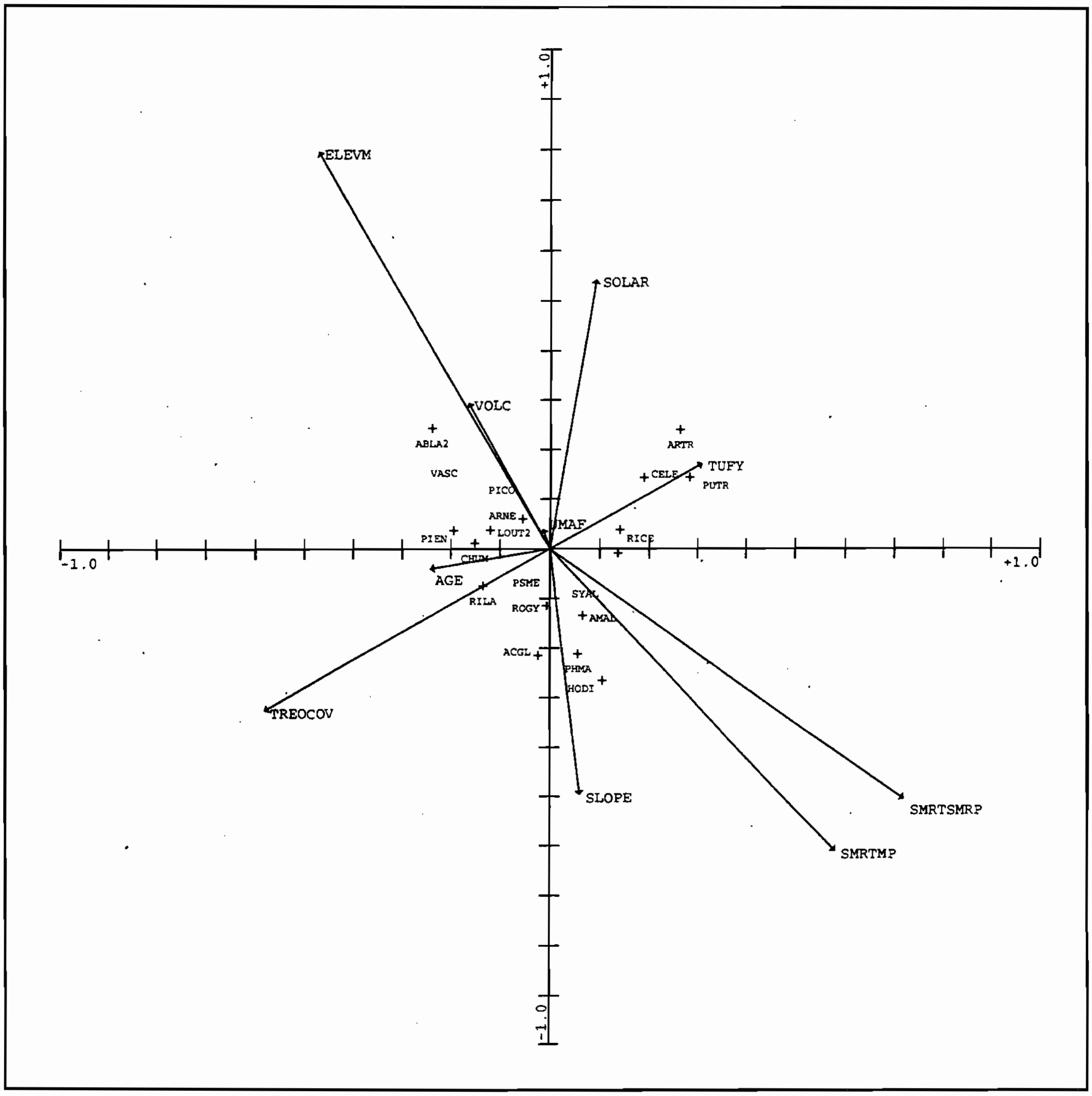
g.

Figure 8 (continued).



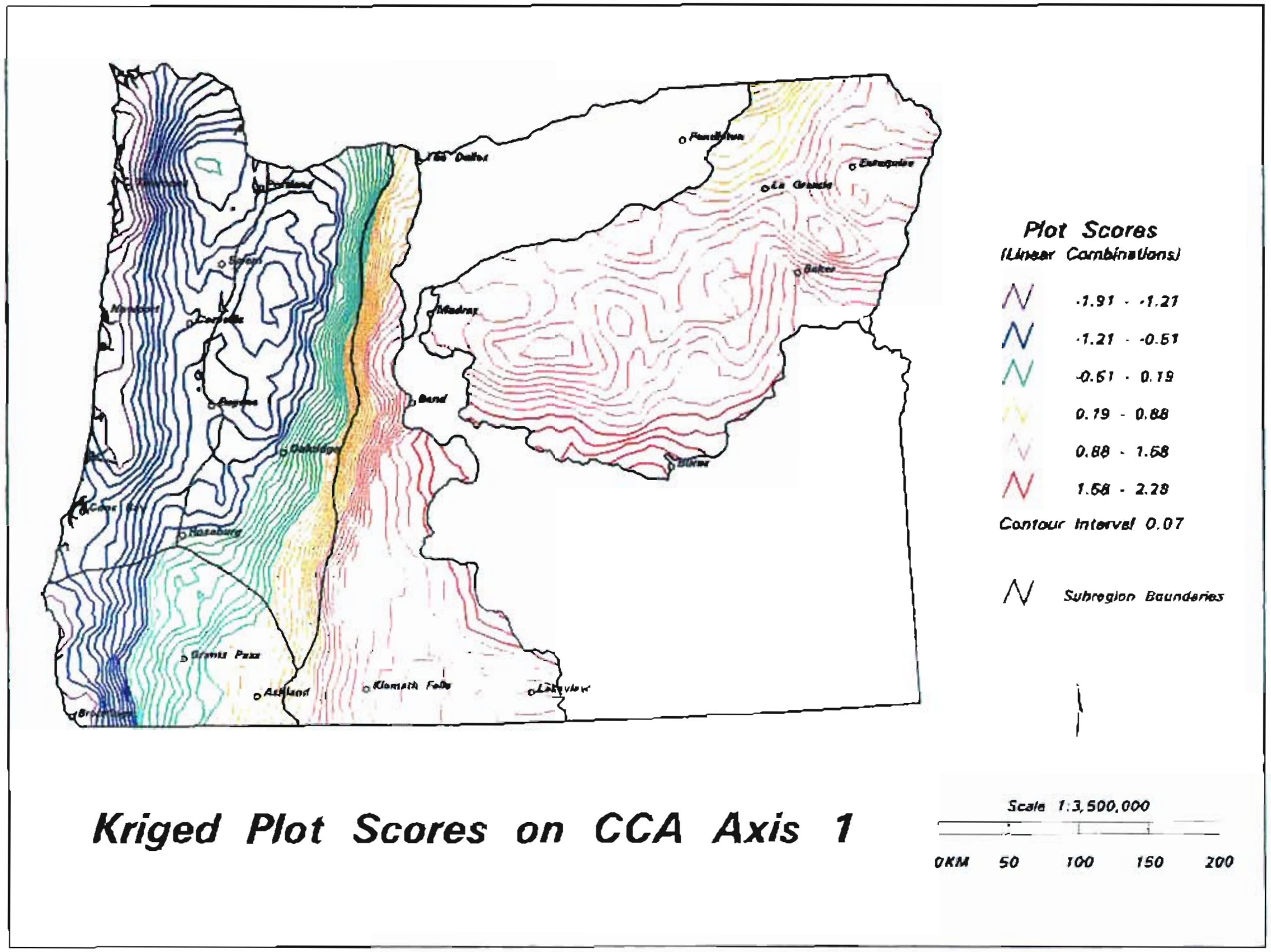
h.

Figure 8 (continued).



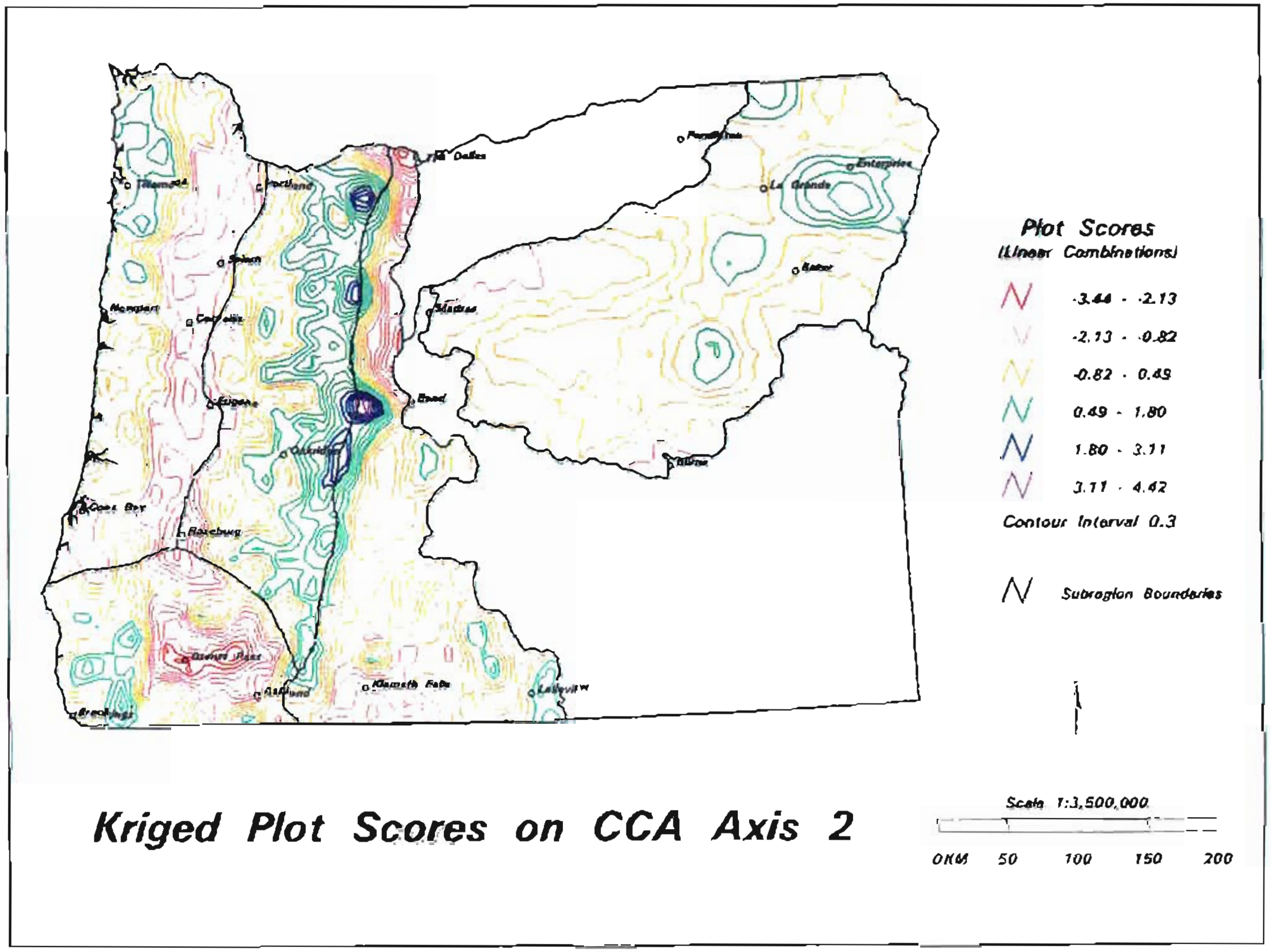
i.

Figure 8 (continued).



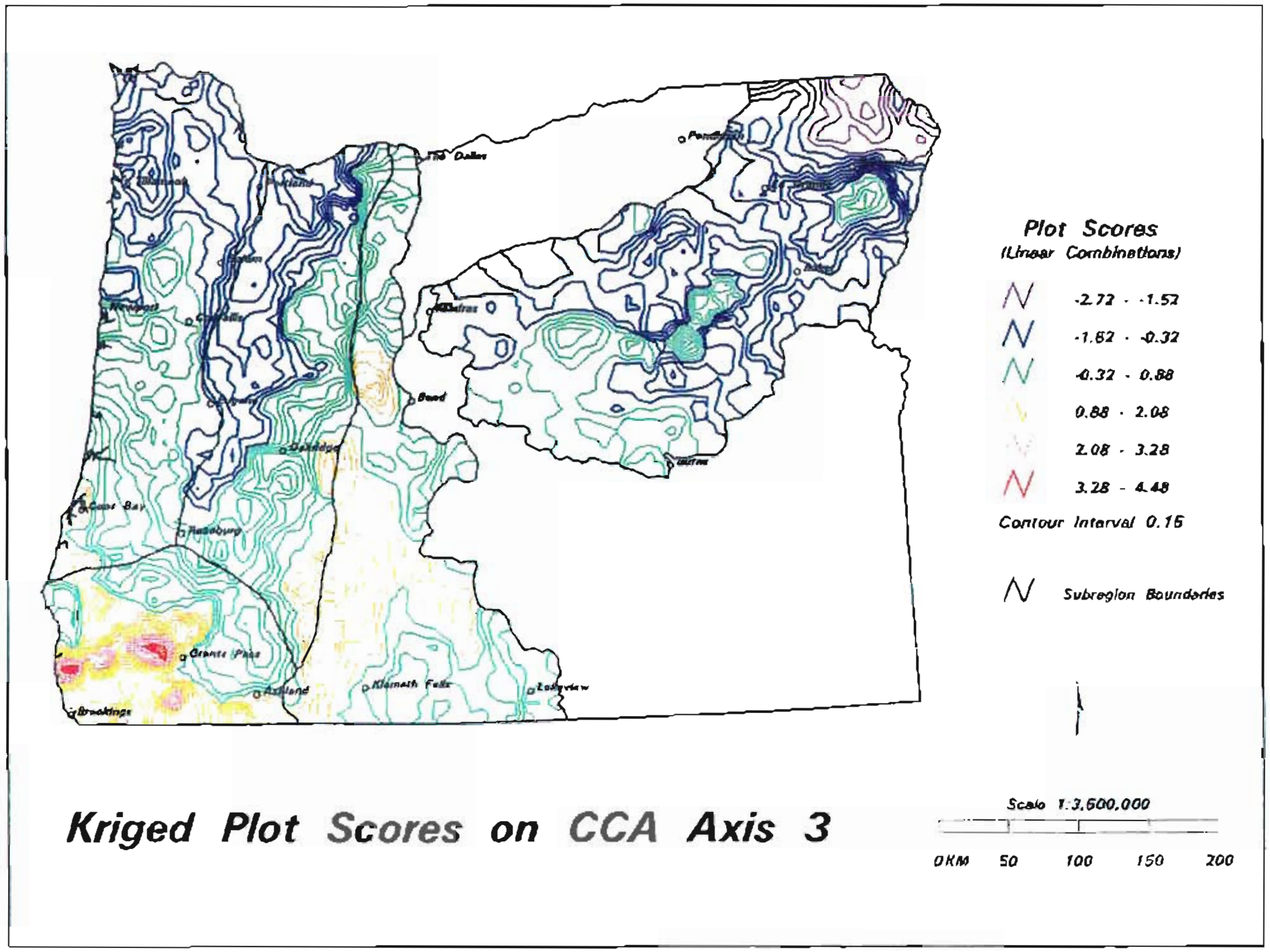
a.

Figure 9. Maps of plot scores (linear combinations) from canonical correspondence analysis (CCA) of all woody species, Oregon. a. axis 1; b. axis 2; c. axis 3; d. axis 4.



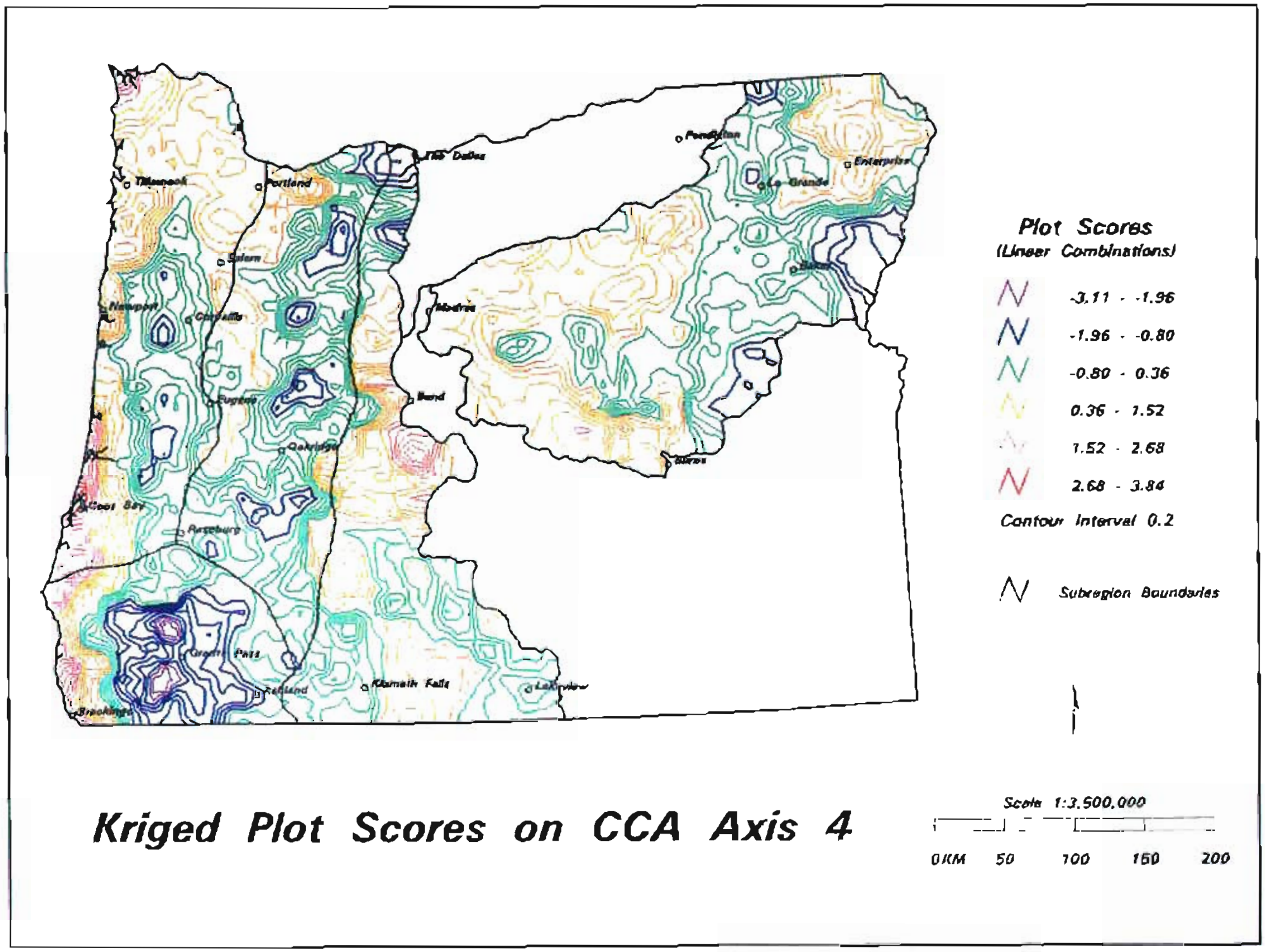
b.

Figure 9 (continued).



c.

Figure 9 (continued).



d.

Figure 9 (continued).

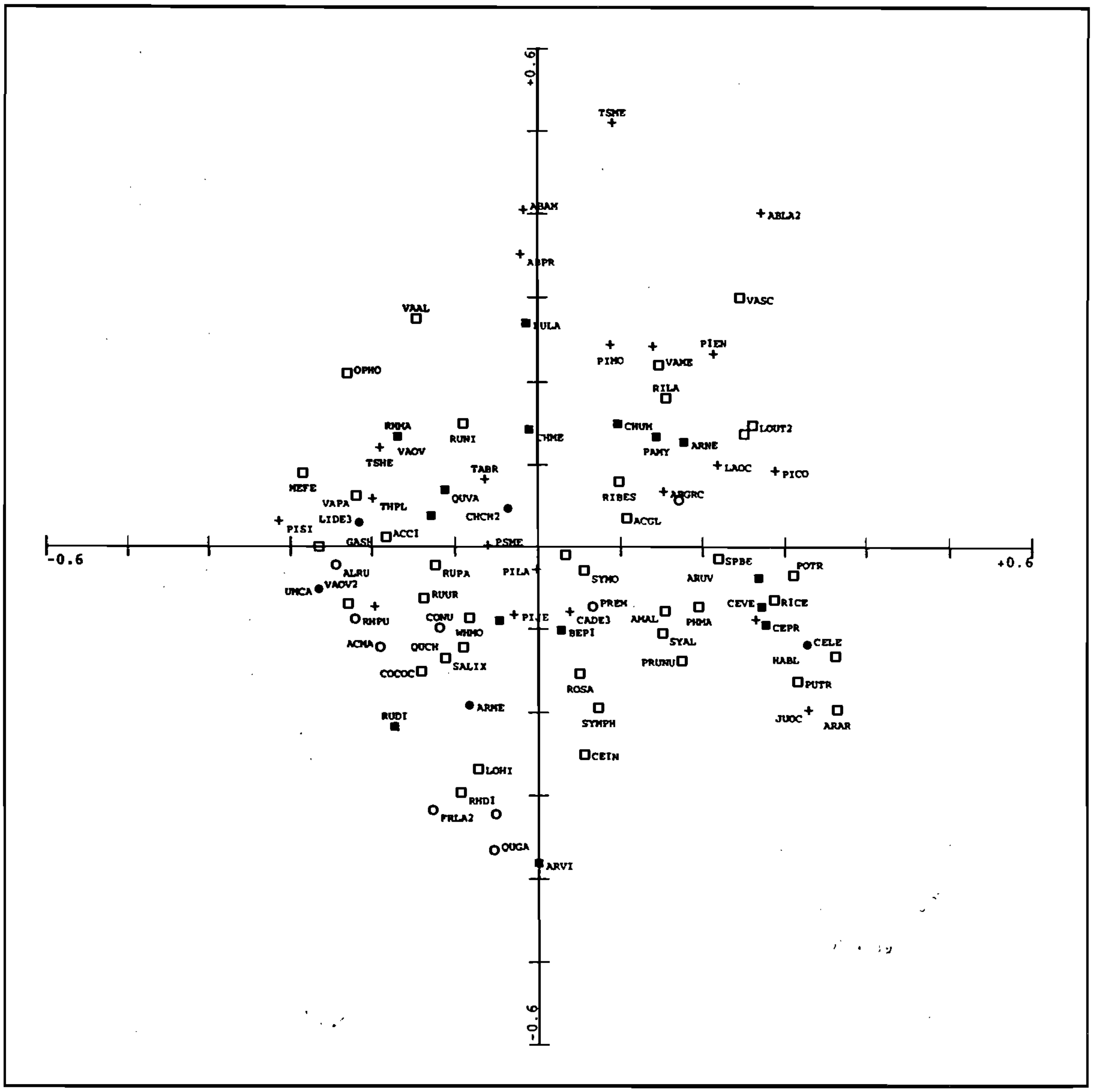


Figure 10. Scatterplot of species scores on first two axes from CCA of all woody species, Oregon, showing species with ≥1% weight. Symbols indicate membership to growth forms: cross = coniferous tree; solid circle = evergreen broadleaved tree; empty circle = deciduous broadleaved tree; solid square = evergreen broadleaved shrub; empty square = deciduous broadleaved shrub. (One needleleaved shrub, Juniperus communis, not shown.)

Table 11.--Tree species scores on first four CCA axes, all woody species, Oregon.

Species	Axis 1	Axis 2	Axis 3	Axis 4
Abies amabilis	-0.0777	1.8164	0.3464	-0.1082
Abies grandis, A. concolor	0.6789	0.2989	0.0293	-0.2854
Abies lasiocarpa	1.2120	1.8003	-0.4549	-0.0853
Abies magnifica var. shastensis	0.6209	1.0872	1.2062	-0.2993
Abies procera	-0.0921	1.5734	0.1788	-0.0033
Acer macrophyllum	-0.8561	-0.5425	-0.4089	-0.1546
Alnus rhombifolia	0.7258	-0.6805	-1.5607	-0.8726
Alnus rubra	-1.0961	-0.0970	-0.3909	0.7615
Arbutus menziesii	-0.3666	-0.8585	0.4328	-0.6910
Betula occidentalis	0.2895	0.0288	-1.6804	-0.5398
Calocedrus decurrens	0.1692	-0.3567	0.6677	-0.5387
Cercocarpus ledifolius	1.4691	-0.5267	0.1421	0.3077
Cercocarpus montanus	0.3407	-2.1115	0.3996	-0.9377
Chamaecyparis lawsoniana	-0.9361	0.1574	1.3956	0.4652
Chamaecyparis nootkatensis	0.1891	1.1693	0.5633	-0.7681
Chrysolepis chrysophylla	-0.1621	0.2085	0.6071	-0.5199
Cornus nuttallii	-0.5300	-0.4348	-0.0450	-0.7451
Cupressus bakeri	0.4210	-0.0706	0.4937	-0.0049
Fraxinus latifolia	-0.5675	-1.4204	-0.3499	0.3105
Juniperus occidentalis	1.4726	-0.8833	-0.1368	0.6072
Juniperus scopulorum	1.3324	0.7242	-0.6175	0.6872
Larix occidentalis	0.9756	0.4480	-0.9311	-0.0373
Lithocarpus densiflorus	-0.9722	0.1295	1.1792	0.1009
Picea breweriana	-0.3534	1.3464	1.2761	-1.7842
Picea engelmannii	0.9501	1.0454	-0.6635	-0.0592
Picea sitchensis	-1.4061	0.1392	-0.2571	1.3136
Pinus albicaulis	1.5773	2.2013	0.2157	-0.0193
Pinus attenuata	-0.7509	0.2994	3.2763	1.3608
Pinus contorta	1.2945	0.4180	0.2731	0.4087
Pinus contorta var. contorta	-0.8827	-0.3254	1.3713	2.7843
Pinus flexilis	1.3802	0.7542	-0.3461	0.6926
Pinus jeffreyi	-0.1306	-0.3688	3.0228	0.0593
Pinus lambertiana	-0.0080	-0.1205	0.8148	-0.8919
Pinus monticola	0.3891	1.0895	0.9072	0.0107
Pinus ponderosa	1.1817	-0.3957	-0.0354	0.2289
Populus tremuloides	1.3695	-0.0865	0.0914	-0.1576
Populus trichocarpa	-0.2006	-0.5776	-0.9074	0.6671
Prunus emarginata	0.2959	-0.3213	-0.0209	0.1076
Pseudotsuga menziesii	-0.2718	0.0102	-0.1147	-0.1516
Quercus chrysolepis	-0.4972	-0.5303	0.9304	-1.3049
Quercus garryana	-0.2361	-1.6356	-0.0088	-0.3336
Quercus kelloggii	-0.2343	-1.4438	0.2926	-1.2204
Rhamnus purshiana	-0.9880	-0.3935	-0.3777	0.3042
Robinia pseudo-acacia	-0.7516	-1.2765	-0.6443	0.0636
Salix scouleriana	0.7602	0.2525	-0.8086	-0.0607
Sequoia sempervirens	-1.2910	0.2899	1.6368	2.2537
Taxus brevifolia	-0.2838	0.3721	0.1125	-0.6843
Thuja plicata	-0.8923	0.2649	-0.4624	-0.0647
Tsuga heterophylla	-0.8570	0.5363	-0.2601	0.0681
Tsuga mertensiana	0.4022	2.2806	0.7225	0.1397
Umbellularia californica	-1.1903	-0.2282	0.9930	0.7161

especially the Rogue and Umpqua Valleys, the foothills of the eastern Cascades from Bend northward and into the Columbia Gorge, and lower-elevation areas of the Blue Mountains subregion. Lowest plot scores were concentrated in these areas as well as in the foothills of the Coast Range bordering the Willamette Valley, and in scattered locations throughout the Ochocos (fig. 9.b.). Widely distributed tree species with lowest scores on axis 2 were Quercus garryana, Q. kelloggii, and Fraxinus latifolia, and Juniperus occidentalis; shrubs included Arctostaphylos viscida, Rhus diversiloba, Lonicera hispidula, Ceanothus integerrimus, Rubus discolor, and Symphoricarpos spp. (Table 11, fig. 10, Appendix 4). In addition to R. discolor, several introduced species that occur primarily in the interior valleys of western Oregon and along the coast were among the lowest scoring species on axis 2 but had low constancy: Crataegus monogyna, Rosa eglanteria, and Cytisus scoparius. Highest plot scores on axis 2 occurred in subalpine forests in the Klamath, Cascade, Blue, and Wallowa Mountains and in high-elevation areas of the northern Coast Range and Siskiyou and Warner Mountains (fig. 9.b.). Widely distributed tree species with the highest scores on axis 2 included Tsuga mertensiana, Abies amabilis, A. lasiocarpa, A. procera, A. magnifica var. shastensis, and Pinus monticola; shrubs included Gaultheria ovatifolia, Vaccinium scoparium, V. alaskaense, and Rubus lasiococcus (Table 11, fig. 10, Appendix 4).

The explanatory variables most highly correlated with CCA axis 3 were geological (Table 10). Low-scoring plots often occurred on mafic rocks dating to the Miocene and older. High-scoring plots occurred on ultramafic parent materials, primarily concentrated in the Klamath subregion but also including ultramafic outcrops in the Aldrich Mountains-Strawberry Range in the Blue Mountains subregion (figs. 8.b., 9.c.). Climatically, axis 3 reflected a gradient from low to high potential solar radiation, from high to low seasonal variability in temperature, from high to low summer precipitation, and from low to high minimum temperatures (Table 10, fig. 8.b.). The gradient was latitudinal, with low scores in the north and high scores in the south (fig. 9.c.). Low-scoring species on axis 3 were those with affinities for moist or disturbed sites at forest edges or openings, and were predominantly species distributed east of the Cascade crest. Widely distributed trees included Larix occidentalis and Salix scouleriana; shrubs included Physocarpus malvaceus, Lonicera utahensis, Spiraea betulifolia, Philadelphus lewisii, Acer glabrum, Ribes lacustre, Oplopanax horridum, and Symphoricarpos albus (Table 11, Appendix 4). Highest-scoring tree species included Chamaecyparis lawsoniana (often associated with serpentine (Zobel 1990)), Abies magnifica var. shastensis, Lithocarpus densiflorus, Umbellularia californica, Quercus chrysolepis, and Pinus monticola; shrubs included Arctostaphylos viscida (serpentine associate), Berberis piperiana, Arctostaphylos patula, and Ceanothus prostratus. Several more of the highest-scoring species were serpentine associates that occurred with <1% constancy: Pinus attenuata, P. jeffreyi, Ceanothus pumilus, C. cuneatus, Garrya buxifolia, Berberis pumila, Rhamnus californica, Quercus vaccinifolia, and Juniperus communis (Table 11, Appendix 4).

Axis 4 was somewhat less interpretable than the first three axes. Strongest environmental correlates of axis 4 were measures of local site and disturbance (Table 10). Low-scoring plots occurred on steep slopes and stands were older with dense canopies, and were concentrated in the Klamath Mountains (fig. 9.d.). Widely distributed tree species with lowest scores on axis 4 were Quercus chrysolepis, Q. kelloggii, Pinus lambertiana, Cornus nuttallii, and Arbutus menziesii; shrubs included Lonicera ciliosa, L. hispidula, Arctostaphylos viscida, Berberis piperiana, and Whipplea modesta (Table 11, fig. 10, Appendix 4). High-scoring plots occurred on gentle terrain and stands were younger with sparse canopies, and were concentrated along the southern coast and in the Paulina Mountains of central Oregon (fig. 9.d.). Widely distributed tree species with the highest scores on axis 4 included Picea sitchensis, Alnus rubra, and Umbellularia californica; shrubs included Vaccinium ovatum, Rubus spectabilis, Sambucus racemosa, Menziesia ferruginea, Arctostaphylos uva-ursi, Chrysothamnus viscidiflorus, and Purshia tridentata (Table 11, Appendix 4).

Dominant Gradients at Half-State and Subregion Levels

Patterns of species variation in response to environment and disturbance varied substantially within the region. Differences in results from CCAs conducted at the half-state and subregion levels, presented below, illustrate shifts in the relative importances of explanatory variables in the models across the region as a function of the magnitudes of and interactions between the various factors, as well as with the changing identity and autoecology of the species present.

Western Oregon

When analyses were run separately at the half-state level, the dominant compositional gradients no longer were interpretable as continentality gradients. In western Oregon, the first axis was strongly correlated with elevation and temperature (Table 10, fig. 8.c.), with low plot scores on warm, low-elevation sites along the coast and in the interior valleys, and high scores at colder, high-elevation sites. Tree species with the lowest scores on axis 1 and ≥1% constancy were Picea sitchensis, Fraxinus latifolia, and Rhamnus purshiana; shrubs included Rubus discolor, R. spectabilis, Menziesia ferruginea, Sambucus racemosa, Myrica californica, Rosa spp., and Symphoricarpos spp.. Widely distributed tree species with the highest scores on axis 1 were Pinus contorta, P. monticola, Tsuga mertensiana, Abies magnifica var. shastensis, Picea engelmannii, and Abies amabilis; shrubs included Vaccinium scoparium, Ribes viscosissimum, Arctostaphylos nevadensis, and Gaultheria ovatifolia (Appendix 4).

The second axis was correlated with growing-season precipitation and temperature (Table 10, fig. 8.c.). Low scores were in areas of cool, wet summers along the coast and on Mt. Hood, and high scores in areas of hot, dry summers in the Rogue and Umpqua Valleys and in the eastern portion of the Columbia River Gorge. Tree species with the lowest scores on axis 2 and ≥1% constancy were

Picea sitchensis, Tsuga mertensiana, Abies amabilis, A. procera, and Pinus contorta; shrubs included Menziesia ferruginea, Oplopanax horridum, Vaccinium scoparium, V. alaskaense, and Rubus spectabilis. Tree species with the highest scores on axis 2 were Quercus kelloggii, Q. garryana, and Pinus ponderosa; shrubs included Ceanothus cuneatus, C. integerrimus, Arctostaphylos viscida, Lonicera hispidula, Rhus diversiloba, Amelanchier pallida, and Berberis piperiana (Appendix 4).

The geographic pattern of CCA scores on the first two axes for western Oregon did not differ notably from those of the state-level analysis. Gradients in some areas were more compressed or elongated than in the state-level analysis, but overall gradient directions were quite similar.

Eastern Oregon

When eastern Oregon was analyzed independently, important correlates of the first two axes were the reverse of those in western Oregon: the dominant compositional gradient followed a gradient in summer moisture stress, precipitation, and canopy cover, and the second axis was correlated with elevation and temperature (Table 10, fig. 8.d.). Axis 1 followed a gradient from areas of dry, warm summers, sparse canopies, and high moisture stress to areas of wet, cool summers, dense canopies, and low moisture stress (Table 10, fig. 8.d.). Geographic patterns and environmental correlates (Table 10) for axis 1 were quite similar to axis 2 for the eastern half of the state-level analysis. Lowest scoring tree species on axis 1 with $\geq 1\%$ constancy included Juniperus occidentalis and Quercus garryana; shrubs included Artemisia arbuscula, A. tridentata, Chrysothamnus nauseosus, C. viscidiflorus, Haplopappus bloomeri, Purshia tridentata, Arctostaphylos patula, and Ceonothus prostratus. Highest-scoring tree species on axis 1 included Tsuga mertensiana, Abies lasiocarpa, Pinus albicaulis, Taxus brevifolia, and Picea engelmannii; shrubs included Vaccinium scoparium, V.

membranaceum, Ribes lacustre, Sorbus scopulina, and Berberis nervosa (Appendix 4).

Axis 2 followed a gradient from areas of cool temperatures at higher elevations to warmer temperatures at lower elevations (Table 10, fig. 8.d.). In addition, topographic variables SOLAR and SLOPE were substantially more important here than in western Oregon, as hypothesized, with highest plot scores occurring on steep sites with low solar radiation (Table 10, fig. 8.d.). Low plot scores occurred on mountain peaks and in the southern portion of the eastern Cascades. Lowest-scoring tree species with ≥1% constancy were Pinus albicaulis, P. contorta, P. monticola, Tsuga mertensiana, Abies lasiocarpa, and A. magnifica var. shastensis; shrubs included Vaccinium scoparium, Arctostaphylos patula, Haplopappus bloomeri, and Ceanothus velutinus. Highest plot scores occurred in the northern portion of the eastern Cascades and Blue Mountains subregions, reflecting a latitudinal gradient. The highest-scoring tree species was Quercus garryana; shrubs included Philadelphus lewisii, Physocarpus malvaceus, Holodiscus discolor, Acer glabrum, Prunus virginiana, Ribes spp., Symphoricarpos albus, Spiraea betulifolia, and Rubus parviflorus (Appendix 4).

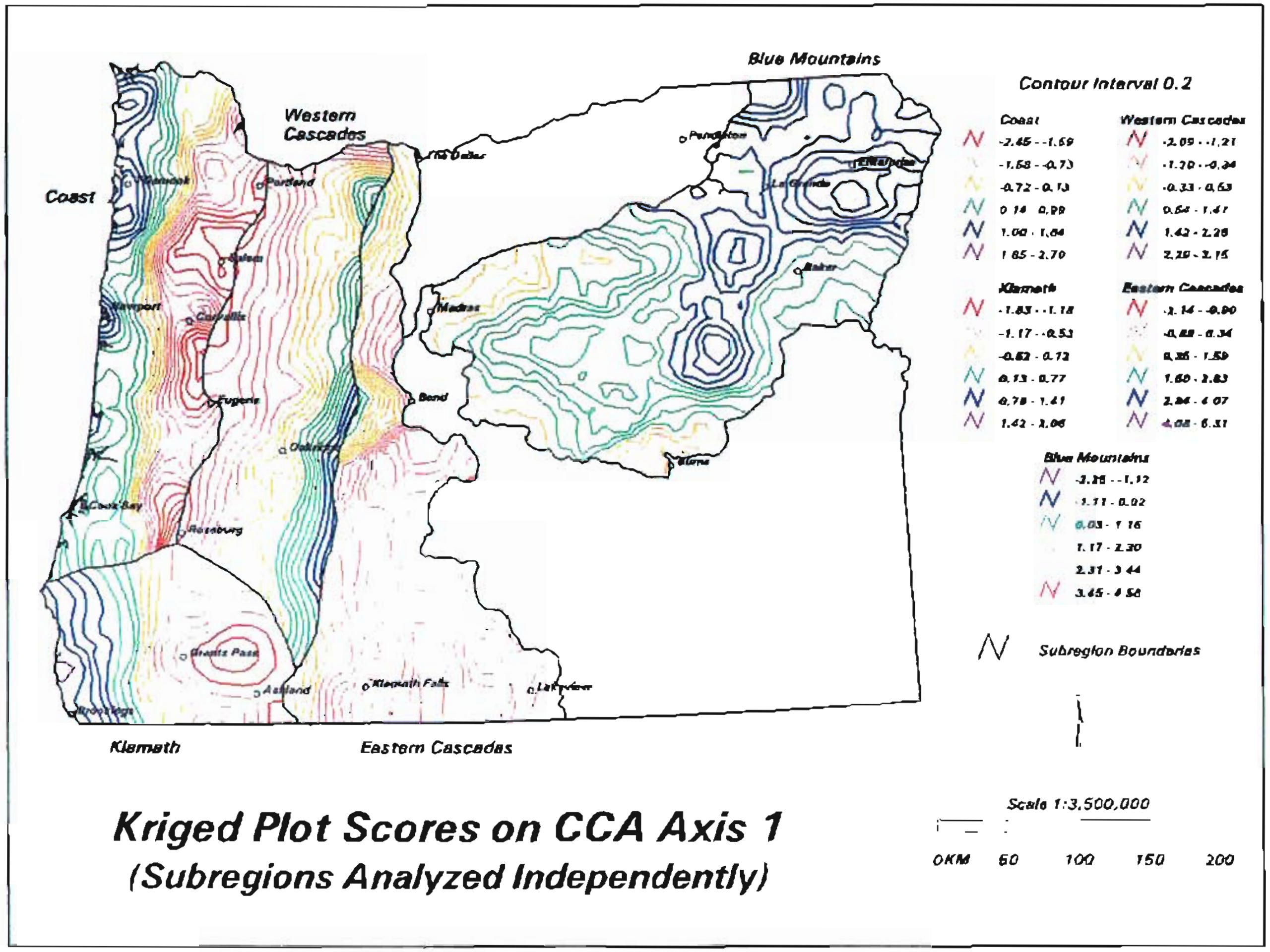
Coast Subregion

In the Coast, axis 1 reflected a gradient in summer moisture stress, annual precipitation, and seasonal temperature variability (Table 10, fig. 8.e.). Lowest plot scores were concentrated in the interior Umpqua and Willamette valleys (fig. 11.a.). Lowest-scoring tree species on axis 1 with ≥1% constancy included Quercus kelloggii, Q. garryana, Fraxinus latifolia, Arbutus menziesii, and Calocedrus decurrens; shrubs included Rosa eglanteria, R. spp., Amelanchier alnifolia, Symphoricarpos spp., and Rhus diversiloba. Highest plot scores were along the northwestern coast (fig. 11.a.). Highest-scoring tree species were Picea sitchensis, Chamaecyparis lawsoniana, Tsuga heterophylla, and Abies procera; shrubs included Menziesia ferruginea, Vaccinium alaskaense, V. membranaceum, Oplopanax horridum, Myrica californica, and Rubus spectabilis (Appendix 4).

Axis 2 was strongly influenced by geology and soil conditions (Table 10), especially by high-scoring plots in the coastal dunes, the Willamette Valley floor, coastal forests south of Coos Bay, and wet hardwood sites in the extreme northwest corner of the state (fig. 11.b.). Remaining plots were largely undifferentiated along this axis. Strongest environmental correlates of axis 2 were depositional soils, elevation, and seasonal temperature variability (Table 10, fig. 8.e.). Lowest-scoring tree species with ≥1% constancy included Abies procera, Cornus nuttallii, Castanopsis chrysophylla, and Prunus emarginata; shrubs included Vaccinium membranaceum, Oplopanax horridum, Berberis aquifolium, B. nervosa, Ribes spp., and Acer circinatum. Highest-scoring tree species were Pinus contorta var. contorta, Chamaecyparis lawsoniana, and Fraxinus latifolia; shrubs included Salix hookeriana, Arctostaphylos columbiana, Myrica californica, Baccharis pilularis, Cytisus scoparius, and Amelanchier alnifolia (Appendix 4).

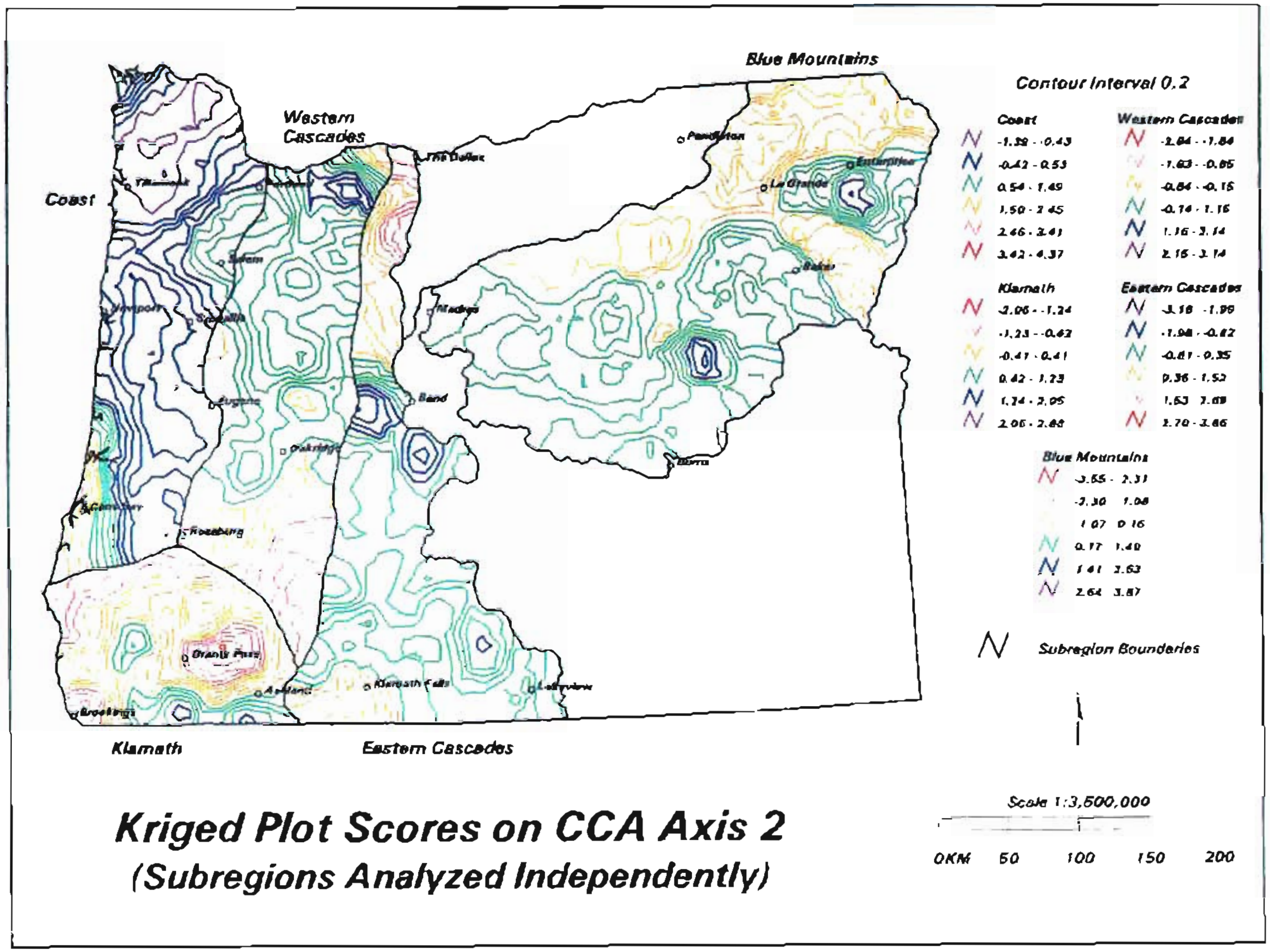
Western Cascades Subregion

The dominant compositional gradient in the western Cascades was strongly temperature-controlled (Table 10, fig. 8.f.): elevation, summer temperature, and seasonal temperature variability contributed 45% of TVE (Table 12). Lowest plot scores occurred along the margins of the Willamette and Umpqua Valleys (fig. 11.a.). All of the lowest-scoring tree species with ≥1% constancy were hardwoods, including Fraxinus latifolia, Quercus garryana, Q. kelloggii, Rhamnus purshiana, Acer macrophyllum, and Prunus emarginata; shrubs included Rubus discolor, R. laciniatus, Symphoricarpos spp., and Rhus diversiloba. High plot scores were found on the peaks of the Cascade Range (fig. 11.a.). Highest-scoring tree species on axis one included Abies lasiocarpa, A. magnifica var. shastensis, Pinus contorta, Tsuga mertensiana, and Picea engelmannii; shrubs included



a.

Figure 11. Maps of plot scores (linear combinations) from canonical correspondence analyses (CCA) conducted at the subregion level, all woody species. a. axis 1; b. axis 2.



b.

Figure 11 (continued).

Table 12.--Increase in total variation explained (TVE) by explanatory variables in stepwise CCA of all woody species, by geographic area. The magnitudes of increase in TVE reflects the order in which variables were added to the model. Increase in TVE = additional species variation explained by adding the variable after other variables already included, expressed as a proportion of TVE. Values are shown only for variables included by forward selection ($P<0.01$, where significance was determined by a Monte Carlo permutation test, H_0: additional influence of variable on vegetation is not significantly different from random), and where adding the variable did not result in inflation factors >20.

	Increase in Variation Explained							
Variable	Oregon	West. Oreg.	East. Oreg.	Coast	West. Casc.	Klam.	East. Casc.	Blue Mtns.
Topography:								
1 ASPECT	--	--	--	--	--	--	--	--
2 SLOPE	0.05	0.05	0.06	0.03	0.08	0.03	0.09	0.12
3 SOLAR	0.01	0.02	0.02	--	0.05	0.03	0.04	0.05
Disturbance:								
4 AGE	0.02	0.02	0.03	--	--	0.04	0.07	0.04
5 CLEARCUT	0.02	0.02	--	0.04	0.06	0.06	--	--
6 TREOCOV	0.04	0.03	0.11	0.06	0.05	0.05	0.20	0.16
Climate:								
7 ELEV	0.28	0.23	0.15	0.04	0.37	0.19	0.17	0.07
8 ANNPRE	0.17	--	0.08	0.03	--	--	--	--
9 WTRPRE	--	--	--	--	--	0.23	--	--
10 SMRPRE	0.10	--	0.19	--	0.15	--	0.04	--
11 CVPRE	--	0.08	0.02	0.06	0.04	--	--	--
12 CONTPRE	--	0.02	--	0.03	--	0.04	0.05	--
13 SMRTSMRP	0.03	0.17	--	0.28	--	--	--	0.27
14 ANNTMP	--	--	--	--	--	0.04	--	--
15 MAXTMP	0.03	0.03	0.03	0.13	--	0.03	0.04	--
16 MINTMP	0.02	0.02	0.03	0.03	--	0.04	0.06	--
17 WTRTMP	--	--	--	--	--	--	--	--
18 SMRTMP	--	0.05	0.06	--	0.04	--	0.11	0.15
19 CVTMP	0.06	0.06	0.05	0.18	0.04	0.05	0.08	--
Geology:								
20 VOLC	--	--	0.02	--	--	--	--	0.03
21 SILR	--	--	--	--	--	--	--	--
22 MAFO	0.01	--	--	--	--	--	0.04	--
23 MAFY	0.02	0.03	0.02	--	0.04	--	--	--
24 UMAF	0.07	0.10	0.05	--	--	0.10	--	0.06
25 PYRO	--	--	--	--	--	--	--	--
26 PYRY	0.01	0.03	--	--	0.09	--	--	--
27 SILV	--	--	--	--	--	--	--	--
28 META	--	--	--	--	--	--	--	--
29 SEDR	--	--	0.02	--	--	--	--	--
30 TUFO	0.01	--	--	--	--	--	--	--
31 TUFY	0.02	--	--	--	--	--	--	0.05
32 DEPO	0.01	0.02	--	0.08	--	0.06	--	--
TVE (prop. TI)	0.087	0.112	0.093	0.122	0.122	0.153	0.126	0.088

Vaccinium scoparium, Arctostaphylos nevadensis, Ribes viscosissimum, R. binominatum, and Sorbus sitchensis (Appendix 4).

The second axis was strongly correlated with summer precipitation and less so with overstory cover, solar radiation, and seasonal temperature variability (Table 10, fig. 8.f.). In contrast to state- and half-state-level analyses, plot scores were arrayed along a latitudinal gradient from low scores in the south to high in the north, culminating near Mt. Hood (fig. 11.b.). Lowest-scoring tree species were Quercus kelloggii, Q. garryana, Pinus ponderosa, and Abies magnifica var. shastensis; shrubs included Arctostaphylos nevadensis, A. patula, Berberis piperiana, Ribes binominatum, R. viscosissimum, and Lonicera hispidula. Highest-scoring tree species were Thuja plicata and Tsuga heterophylla; shrubs included Oplopanax horridum, Rubus pedatus, R. spectabilis, Vaccinium ovalifolium, V. alaskaense, V. parvifolium, Sambucus racemosa, and Oemleria cerasiformis (Appendix 4).

Klamath Subregion

In the Klamath subregion, axis one followed a gradient from east to west, from a continental climate in the eastern portion of the subregion to a maritime climate with low seasonal temperature variability, high winter precipitation, and high seasonal precipitation variability along the coast (Table 10, fig. 8.g.). The Klamath subregion was unique among the geographic areas studied in the strong influence of winter precipitation, which was added first in the stepwise procedure and contributed 23% of TVE (Table 12), as well as in the insignificance of variables that reflect summer moisture stress. This was surprising given that the interior valleys of southwest Oregon experience the hottest and driest summers in the State, and that SMRTSMRP was most variable of any geographic area studied (Table 3). Lowest plot scores on axis 1 were found in the Rogue Valley and eastward towards the Cascade crest (fig. 11.a.). Lowest-scoring tree species with ≥1% constancy were

Cercocarpus montanus, C. ledifolius, Quercus garryana, Q. kelloggii, and Fraxinus latifolia; shrubs included Ceanothus cuneatus, C. sanguineus, Symphoricarpos albus, and Ceanothus integerrimus. High plot scores were along the coast (fig. 11.a.). High-scoring tree species were Sequoia sempervirens, Pinus attenuata, Pinus contorta var. contorta, and Alnus rubra; shrubs included Berberis pumila, Juniperus communis, Rhododendron occidentale, Baccharis pulularis, Rhamnus californica, and Rubus spectabilis (Appendix 4).

Axis two followed a gradient from areas of low elevation and warm temperatures to high elevation and cool temperatures (Table 10, fig. 8.g.). Plots with low scores also tended to be in younger stands with a history of clearcutting. Low plot scores were clustered in the Rogue Valley, the southern end of the Umpqua Valley, and along the coast (fig. 11.b.). Lowest-scoring tree species on axis two included Fraxinus latifolia, Cercocarpus montanus, C. ledifolius, Quercus garryana, and Alnus rubra; shrub species included Rubus discolor, R. spectabilis, Baccharis pilularis, and Ceanothus thyrsiflorus. High plot scores were in the mountainous areas of the Siskiyous and southern Cascades (fig. 11.b.). Highest-scoring tree species included Abies magnifica var. shastensis and Pinus monticola; shrubs included Ribes binominatum, Acer glabrum, Vaccinium membranaceum, Quercus sadleriana, Arctostaphylos nevadensis, A. patula, and Ceanothus pumilus (Appendix 4). Despite contributing 10% of TVE (Table 12), ultramafic parent materials were not important until the third CCA axis (Table 10).

Eastern Cascades Subregion

In the eastern Cascades, axis 1 was most highly correlated with tree cover, which contributed 12% to TVE (Table 12) and entered first in the stepwise procedure, and precipitation variables (Table 10, fig. 8.h.). The axis was strongly dominated by high-scoring plots near the Three Sisters and Mt. Hood; most of the remaining plots were undifferentiated (fig. 11.a.). Low-scoring plots had sparse canopies and dry summers, but with a high proportion of total precipitation falling in summer (Table 10, fig. 8.h.), and were located throughout the mid- to low-elevation areas of the central Oregon Cascades (fig. 11.a.). Lowest-scoring tree species on axis 1 with ≥1% constancy included Juniperus occidentalis and Cercocarpus ledifolius; shrubs included Artemisia arbuscula, A. tridentata, Chrysothamnus viscidiflorus, C. nauseosus, Salix geyeriana, Purshia tridentata, Haplopappus bloomeri, and Spiraea douglasii. High-scoring plots had dense canopies and high summer rainfall (Table 10, fig. 8.h.), and were located along the crest of the Cascades, especially in the Three Sisters and Mt. Hood areas (fig. 11.a.). Highest-scoring tree species on axis one included Abies lasiocarpa, A. procera, and Tsuga mertensiana; shrub species included Vaccinium scoparium, V. membranaceum, Berberis nervosa, Acer circinatum, Spiraea betulifolia, Rubus ursinus, and Corylus cornuta var. californica (Appendix 4).

Axis 2 was a temperature gradient, correlated most strongly with elevation, high and low temperature extremes, and summer temperature (Table 10, fig. 8.h.). Lowest scores were located in the Three Sisters and Paulina Mountains (fig. 11.b.). Low-scoring tree species were Abies lasiocarpa, A. procera, Tsuga mertensiana, P. albicaulis, P. monticola, and P. contorta; shrubs included Vaccinium scoparium, Arctostaphylos nevadensis, Ribes viscosissimum, and Spiraea douglasii. Highest plot scores were in the extreme northern and southern portions of the subregion (fig. 11.b.). Highest-scoring tree species on axis two included Quercus garryana, Pseudotsuga menziesii, and Larix occidentalis; shrub species included Lonicera ciliosa, Corylus cornuta var. californica, Ceanothus integerrimus, Spiraea betulifolia, Holodiscus discolor, Symphoricarpos spp., and Berberis nervosa (Appendix 4).

Blue Mountains Subregion

The dominant compositional gradient in the Blue Mountains subregion reflected growing-season conditions and overstory canopy cover (Table 10, fig. 8.i.). Low plot scores occurred in areas of low summer moisture stress and dense canopies, primarily in high-elevation areas of the Wallowa and Blue Mountains (fig. 11.a.). Lowest-scoring tree species on axis 1 with ≥1% constancy included Abies lasiocarpa, Pinus albicaulis, P. contorta, Taxus brevifolia, and Picea engelmannii; shrubs included Chimaphila menziesii, C. umbellata, Vaccinium scoparium, Sorbus scopulina, and Lonicera involucrata. High plot scores occurred in low-elevation areas with low summer precipitation, high summer temperatures, and sparse canopies (Table 10, fig. 8.i.), primarily in the western and southern portions of the Ochocos (fig. 11.a.). Highest-scoring tree species were Juniperus occidentalis and Cercocarpus ledifolius; shrubs included Haplopappus bloomeri, Artemisia arbuscula, A. tridentata, A. rigida, Chrysothamnus nauseosus, C. viscidiflorus, Purshia tridentata, and Prunus spp. (Appendix 4).

The second axis was correlated with temperature and topography (Table 10, fig. 8.i.). Low plot scores occurred in areas of low elevation, hot and dry summers, steep slopes, and low solar radiation, and were concentrated in low-elevation canyons along the Snake River and in the Blue Mountains along the northern Oregon boundary (fig. 11.b.). Lowest-scoring tree species on axis 2 included Betula occidentalis and Taxus brevifolia; shrubs included Philadelphus lewisii, Holodiscus discolor, Berberis nervosa, Holodiscus discolor, Acer glabrum, Physocarpus malvaceus, Rubus parviflorus, Amelanchier alnifolia, and Rosa spp.. High plot scores were concentrated near the peaks of the Wallowa and Strawberry Mountains, and in the southern portions of the Ochocos (fig. 11.b.). Highest-scoring tree species on axis 2 included Pinus albicaulis, Abies lasiocarpa, and Juniperus occidentalis; shrubs included Artemisia tridentata, A. arbuscula, A. rigida, Chrysothamnus viscidiflorus, Vaccinium scoparium, Haploppapus bloomeri, and Purshia tridentata (Appendix 4).

Positions of Plant Growth Forms Along CCA Gradients

The regional scale of my study was sufficiently broad for the emergence of patterns in plant physiognomy, or growth form--here defined as the combination of habit (tree vs. shrub), needle-leaved (coniferous) vs. broadleaved, and evergreen vs. deciduous. Climate is the primary driver of physiognomic diversity, controlling the distribution of the major vegetation types of the world (Neilson et al. 1992, Woodward 1987). Climate exerts its influence both directly, through physiological effects on organisms, and indirectly by favoring certain growth forms in inter-specific competition. Although merely correlative, the relative positions of growth forms along environmental gradients in the ordination provide insights into mechanisms controlling species distributions. CANOCO output from CCA includes scores for species along each environmental axis. These scores are the maximum likelihood estimators of species modes under the assumption that species abundance is a Gaussian function of environmental gradients (ter Braak 1986). The Gaussian model underlying CA gradient methods, while principally concerned with individual species distributions along gradients, has implications for distributions of functional groups of species and of community-level variables as well (Gauch 1982).

Several important physiological differences among growth forms help explain species distributions, expressed as positions in ordination space (Table 13, fig. 10). Unfortunately, however, most research has focused on the dominant canopy layer, usually trees, and relatively little is known about physiognomic response of the understory. Minimum temperatures are important in controlling the spread of a species towards colder areas (Woodward 1987) (higher latitudes, higher elevations, or more continental climates). While mechanisms are not entirely understood, both sensitivity to frost drought and cell membrane sensitivity to low temperatures are thought to control plant survival, and hence species distribution (Woodward 1987). As a group, broadleaved evergreens are most cold-sensitive, followed by broad-leaved deciduous and coniferous species (Woodward 1987). Leaves and buds of

Table 13.--Means (standard errors) and P-values (PROC GLM) (SAS 1990) of weighted averages of species scores with respect to selected standardized environmental variables included in the stepwise CCA model for all woody species, Oregon, by growth form.

Environmental Variable	Tree Species			Shrub Species[a]		
	Conifer (n=30)	Evergreen Broadleaf (n=7)	Deciduous Broadleaf (n=14)	Evergreen (n=41)	Deciduous (n=99)	P
AGE	0.29 (0.08)	0.11 (0.18)	-0.40 (0.08)	0.16 (0.04)	-0.07 (0.05)	<0.01
CLEARCUT	-0.29 (0.04)	-0.10 (0.08)	0.18 (0.12)	-0.12 (0.09)	-0.05 (0.06)	0.06
ELEV	0.47 (0.17)	-0.24 (0.26)	-0.51 (0.22)	-0.04 (0.13)	0.17 (0.09)	<0.01
ANNPRE	0.11 (0.15)	0.06 (0.33)	-0.11 (0.14)	0.23 (0.11)	-0.25 (0.08)	0.01
SMRPRE	0.18 (0.11)	-0.40 (0.29)	-0.18 (0.16)	-0.05 (0.11)	-0.15 (0.07)	0.13
SMRTSMRP	-0.67 (0.14)	0.54 (0.36)	0.74 (0.19)	-0.08 (0.15)	0.03 (0.08)	<0.01
MAXTMP	-0.55 (0.16)	0.22 (0.24)	0.53 (0.22)	0.02 (0.12)	-0.18 (0.08)	<0.01
MINTMP	-0.18 (0.18)	0.56 (0.32)	0.11 (0.22)	0.35 (0.12)	-0.23 (0.09)	<0.01
CVTMP	0.09 (0.19)	-0.40 (0.34)	0.01 (0.22)	-0.35 (0.12)	0.26 (0.09)	<0.01

[a] One coniferous shrub species, Juniperus communis, not included.

broad-leaved evergreens are irreversibly damaged below a mean annual minimum temperature of about -15° C. Below -15° C, only conifers are capable of evergreen physiognomy. Most hardwood trees in temperate regions cannot survive below -40° C, the temperature at which supercooled water changes from a liquid-crystalline to a gel state, although a few deciduous trees (e.g., Populus spp. and Betula spp.) show no lower temperature limit (Woodward 1987).

Mean positions of the growth forms differed significantly ($P<0.01$), and were ordered as predicted, along temperature axes (Table 13, fig. 10). Cold temperatures (MINTMP, CVTMP) most effectively separated broadleaved evergreen from other physiognomies: broadleaved evergreen trees and shrubs occupied the warmest sites on average, scoring highest for MINTMP and lowest for CVTMP, followed by broadleaved deciduous trees, conifers, and broadleaved deciduous shrubs (Table 13). Warm temperatures (MAXTMP) and elevation were most important in separating broadleaved from needleleaved physiognomies in trees: broadleaved deciduous and evergreen trees occupied the warmest and lowest sites and conifers the coldest and highest sites (Table 13, fig. 10).

Water relations also influence the geographic distribution of different growth forms, with the water budget (difference between precipitation and evapotranspiration) in the summer growing-season thought to be most critical (Woodward 1987, Waring and Franklin 1979). For example, broadleaved evergreens often demonstrate drought resistance through structural changes in cell membranes, increases in cryoprotectants, and other changes such as in cell-wall thickness and leaf morphology (e.g., sclerophylly) (Woodward 1987). In my study, the variable SMRTMP did not enter the stepwise CCA model at the state level ($P>0.01$) (Table 12), and separation of the growth forms along the SMRPRE axis was not significant ($P=0.13$). However, growth-form separation for the axis reflecting growing-season moisture stress as the combined influence of temperature and moisture (SMRTSMRP) was the most significant variable ($P=0.0001$) in separating growth forms, particularly for trees (Table 13). Conifers occupied sites with lowest summer moisture stress and broadleaved trees occupied the sites with greatest stress (Table 13, fig. 10). Differences in mean positions of the growth forms along the annual precipitation axis also were significant (P=0.01). In contrast to summer moisture conditions, annual precipitation was most important in separating deciduous and evergreen shrubs, and did not differentiate among the tree growth forms (Table 13).

It is an oversimplification to consider temperature and moisture effects separately. In western Oregon it is the combination of wet, mild winters and relatively dry summers that favors evergreen growth forms and needle-leaved conifers, by permitting extensive photosynthesis outside of the growing-season and reducing net photosynthesis during the summer months (Waring and Franklin 1979). Conifers, and evergreens in general, also use nutrients more efficiently. Relative positions of growth forms in ordinations are influenced by species interactions, disturbance, and other factors as well. For example, broadleaved deciduous trees were strongly associated with young stands and conifers with older stands (Table 13). Many early-successional, pioneer species in Oregon forests are broadleaved, such as Alnus rubra, especially in coastal and low-elevation sites. Although growth form positions along the clearcutting axis were not significantly different (P=0.06), ordering of the positions was the same as for stand age.

Positions of the tree growth forms along environmental axes showed greater separation and interpretability than did the shrubs. This suggests that explanatory variables included in the analysis were more relevant overall to trees than shrubs, as was hypothesized. Shrub response probably is more complex, given the greater number of shrub species and thus the greater variability in ecologic and physiologic traits represented. Understory light environment may be of equal or greater importance than micro- and macro-climate for shrubs. Because of their smaller stature, shrubs respond to the structure, composition, and processes of the tree overstory in addition to coarser-scale environmental signals, and to finer-scale variation in soils, litter depth, and canopy gaps. No good estimates were available for understory light environment and understory microclimate.

Spatial Patterns in Fit of the CCA Model

Residual analysis offers another means of evaluating performance of the CCA model in capturing gradients in species composition and environment. From the stepwise CCA of all woody species across Oregon, two notable features of plot-level residuals from the first four CCA axes emerged (fig. 12). First, there were concentrations of high residuals in geographic locations that represented the ends of the gradients of both of the first two CCA axes, where environmental features and community composition diverged most from regional norms. Most notably, these included the foothills of the Willamette Valley west of Salem; the interior valleys of southwest Oregon; a narrow strip along the coast north of Coos Bay, especially plots in the coastal dunes; and subalpine areas of the Three Sisters and Wallowa Mountains. It is possible that the climate models performed more poorly in these areas. Investigators often treat such sites as outliers and remove them from the dataset, but I chose not to do so in my study.

The second situation included extensive areas where plot residuals were generally larger and among-plot variability in residual score was great. The southern half of the Klamath subregion and most of eastern Oregon exhibited this "salt-and-pepper" pattern of residuals. Several possible explanations exist. Regional climate is more stressful for plant life in these areas--overly cold, hot, or dry. This constrains the suitability of species' habitats to smaller-scale variations in substrate, topography, and biotic interactions (Neilson et al. 1992), which are probably poorly captured by the explanatory variables of my study. In contrast, vast portions of the mid-elevation Coast and Cascade Ranges, where the CCA model performed well (fig. 12), are within the core of the biome where climate is benign and most fine-scale resource variation is within a given species' range of tolerance (Neilson et al. 1992). In these areas the CCA model, weighted heavily towards regional climate variables, would be expected to perform better than at the periphery. In addition, community data were "noisier" in general in eastern Oregon. Although species richness was lower in eastern Oregon, species turnover along

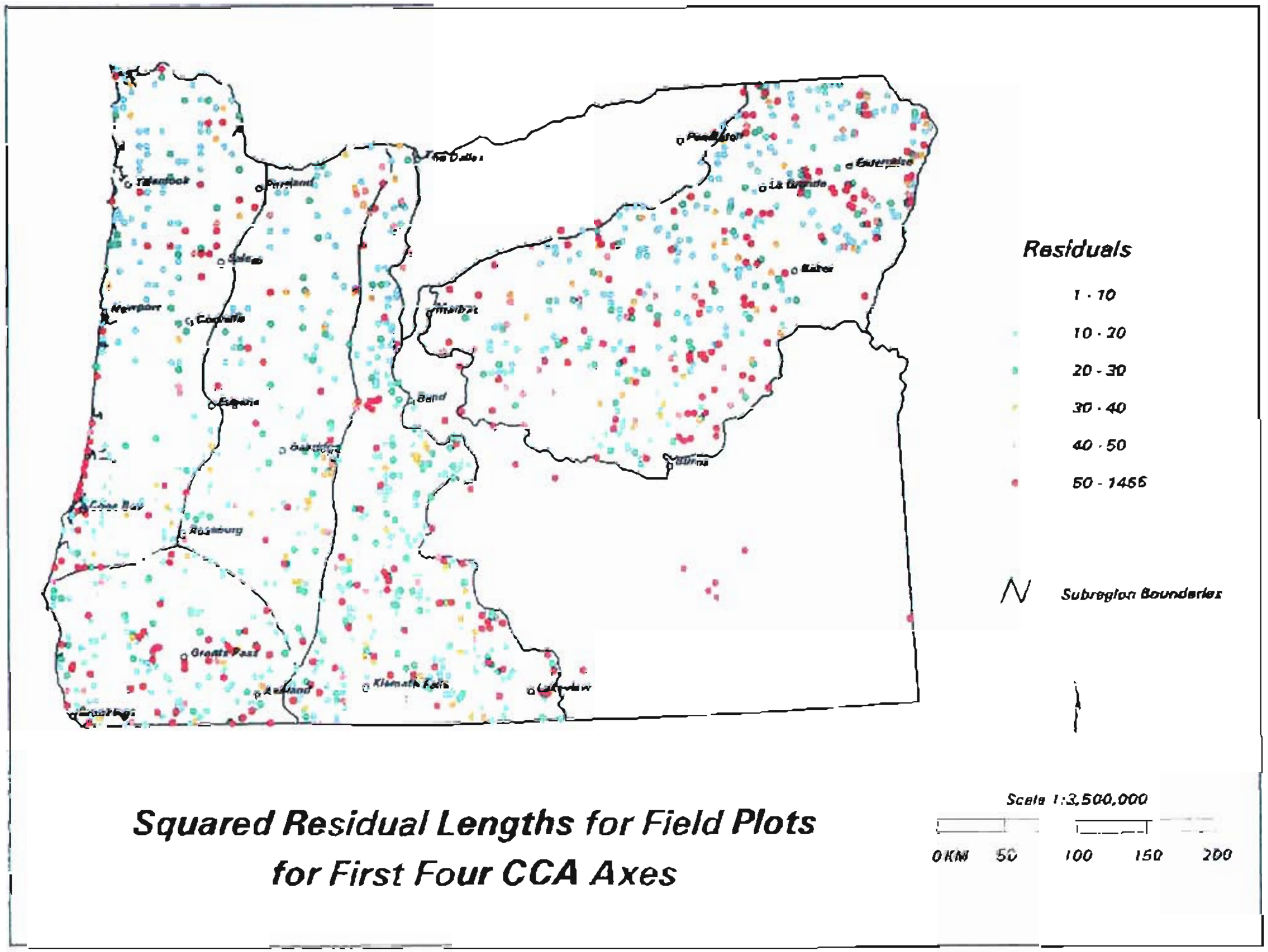


Figure 12. Residuals from first four axes from CCA of all woody species, Oregon.

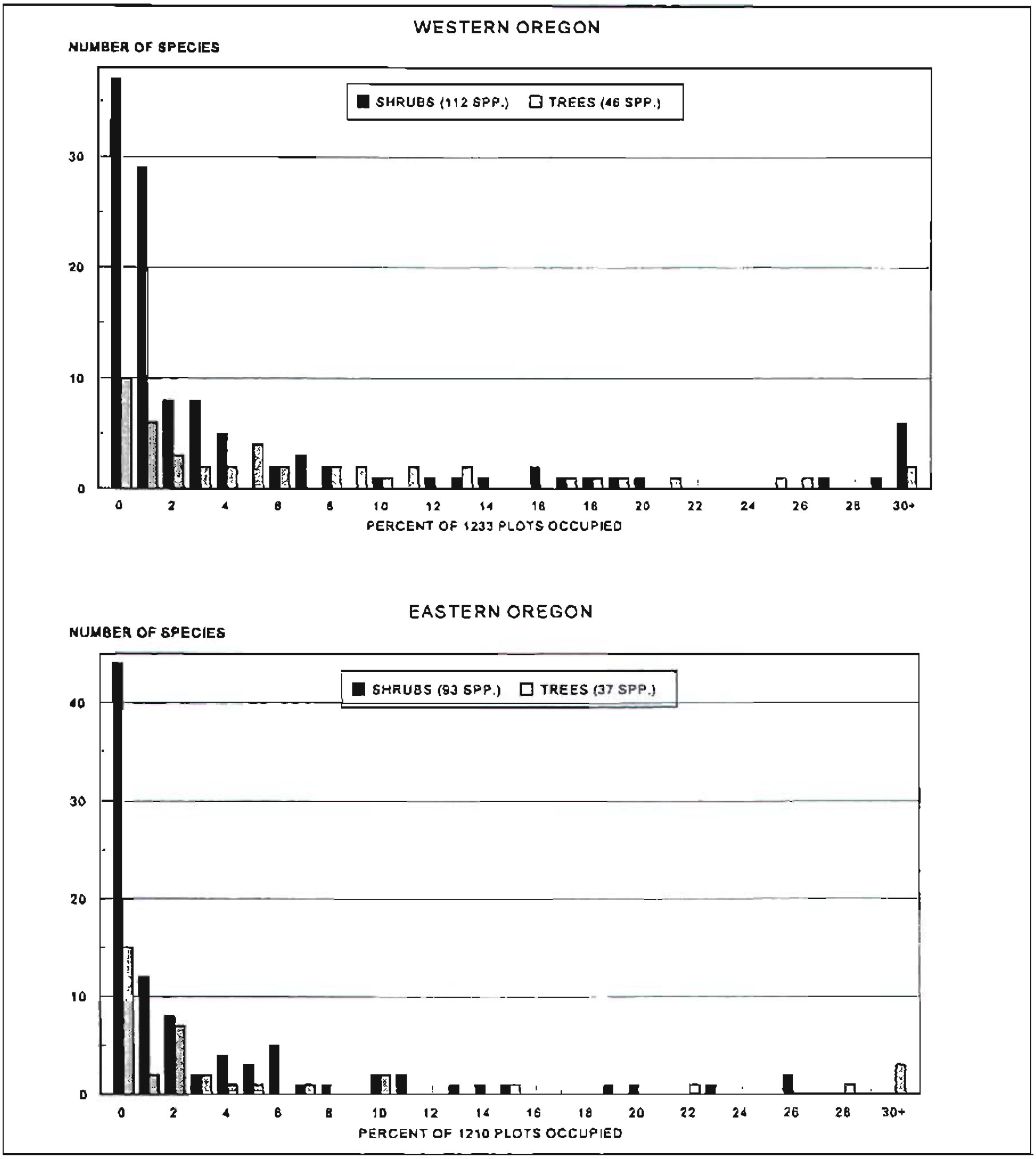


Figure 13. Distribution of tree and shrub species by constancy (percent of plots occupied) in western and eastern Oregon.

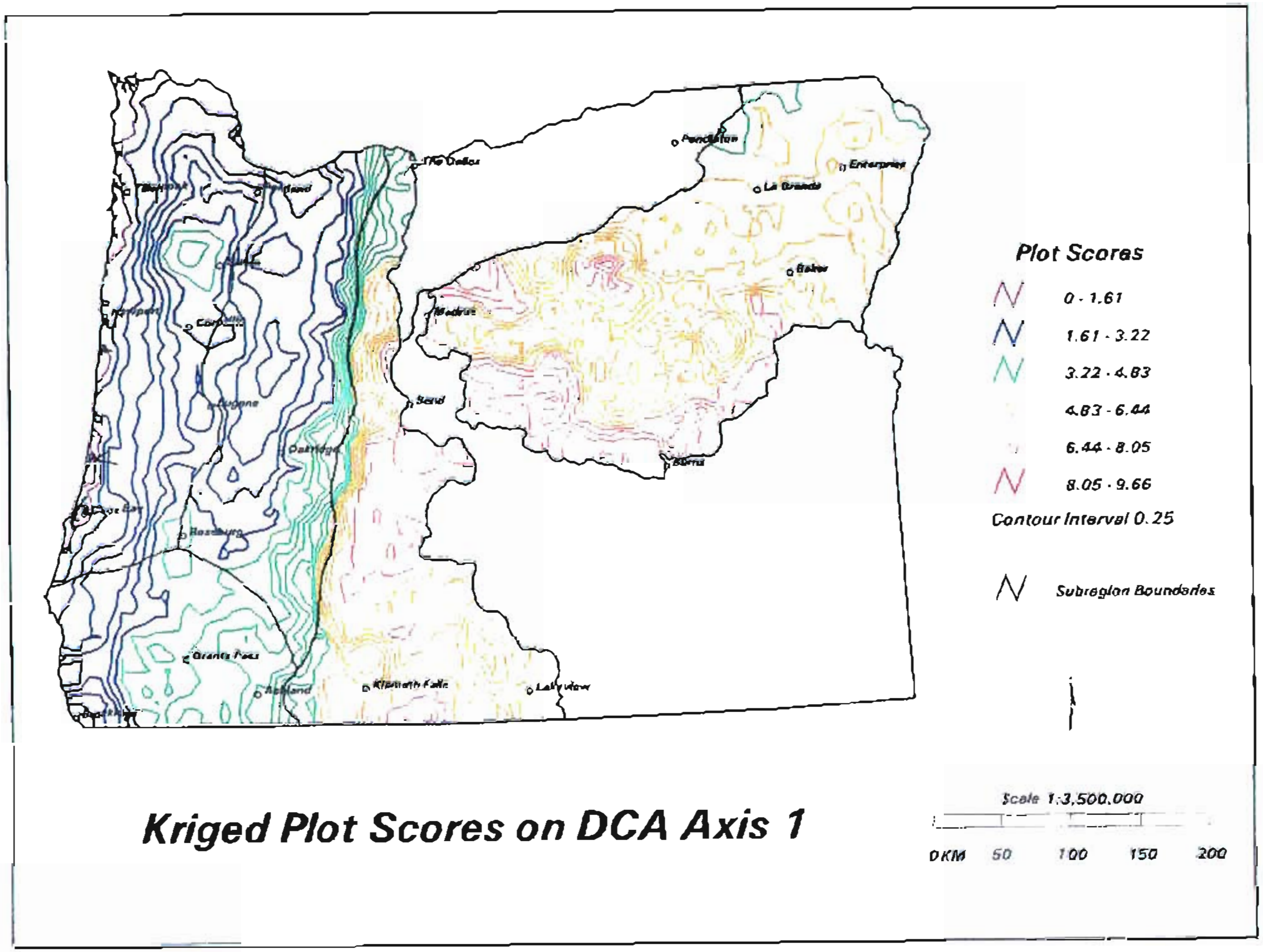
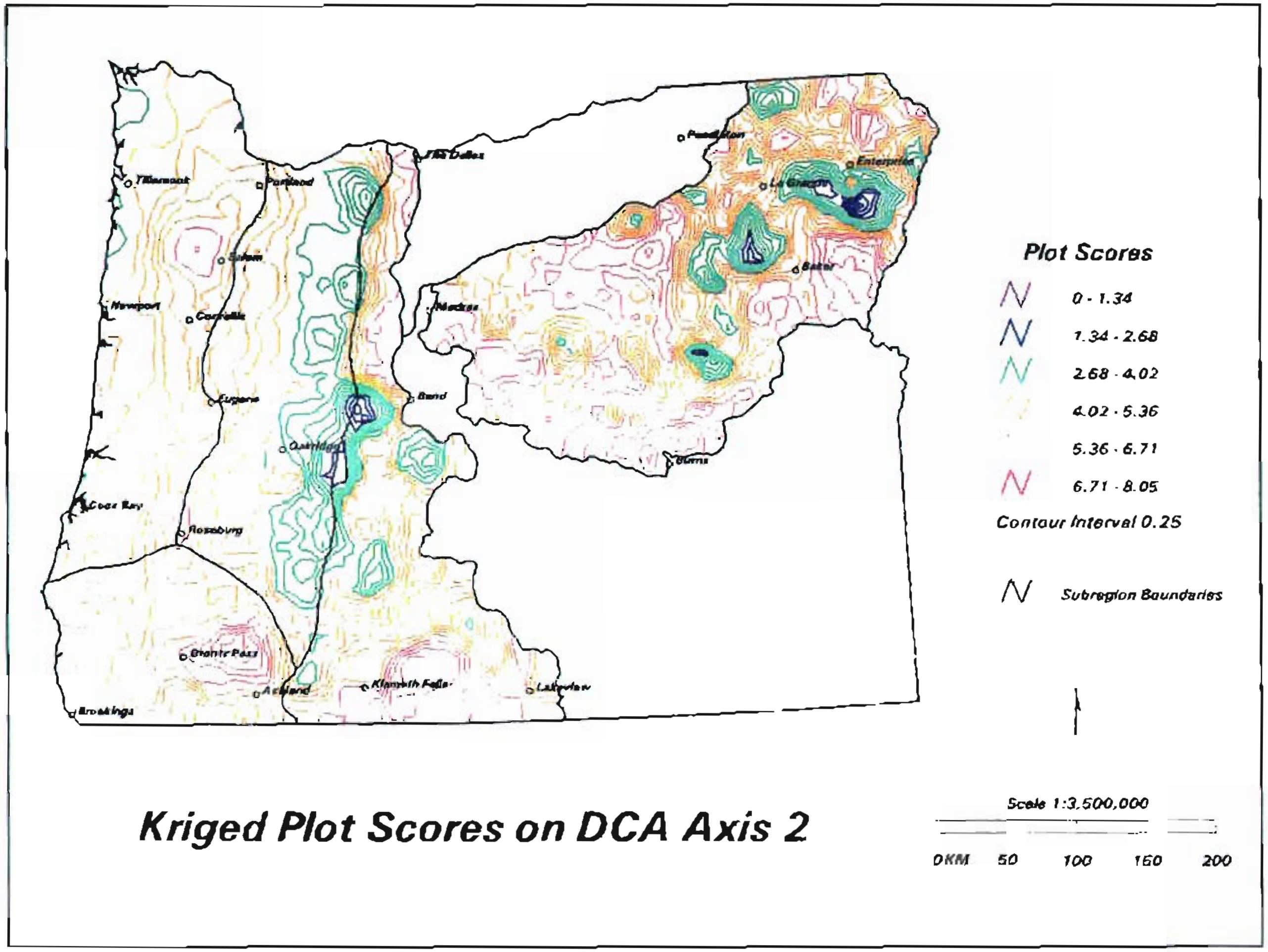


Figure 14. Maps of plot scores from detrended correspondence analysis (DCA) of all woody species, Oregon. a. axis 1; b. axis 2.



b.

Figure 14 (continued).

Table 14.--Total species (S) (gamma diversity), mean plot-level species richness (alpha diversity, α), and two measures of beta diversity (β_w = S/α-1, and total inertia), by geographic area and species group.

Geographic Area and Species Group	S	Mean α	Beta Diversity β_w	Beta Diversity Total Inertia
Oregon:				
Woody	192	8	23	24.324
Trees	51	3	16	14.084
Shrubs	141	4	34	32.707
W.Oregon:				
Woody	158	10	15	15.468
Trees	46	4	11	10.066
Shrubs	112	6	18	19.076
E.Oregon:				
Woody	130	6	21	18.499
Trees	37	2	18	10.301
Shrubs	93	3	30	25.674
Coast:				
Woody	97	8	11	9.705
Trees	28	3	8	6.549
Shrubs	69	5	13	11.064
W.Cascades:				
Woody	119	10	11	9.309
Trees	34	4	8	5.953
Shrubs	85	6	13	12.161
Klamath:				
Woody	124	11	10	10.565
Trees	37	4	8	7.357
Shrubs	87	6	14	13.209
E.Cascades:				
Woody	99	5	19	12.556
Trees	30	2	15	7.127
Shrubs	69	3	22	18.713
Blue Mtns.:				
Woody	94	6	15	15.582
Trees	24	2	11	7.746
Shrubs	70	3	22	20.180

Table 15. Eigenvalues, gradient lengths (SD), Spearman rank correlations, and P-values for first two axes from DCA and DCCA, all woody species, by geographic area.

Geographic Area	Axis	Eigenvalues		Gradient Length		Spearman Rank Correlation[a]	P
		DCA	DCCA	DCA	DCCA		
Oregon	1	0.78	0.67	9.664	5.237	0.9192	<0.01
	2	0.59	0.36	8.045	4.940	0.6575	<0.01
W. Oregon	1	0.62	0.42	7.557	3.715	0.7225	<0.01
	2	0.52	0.35	7.795	4.071	-0.4294	<0.01
E. Oregon	1	0.71	0.46	9.043	5.397	0.7401	<0.01
	2	0.54	0.32	4.693	4.569	0.4834	<0.01
Coast	1	0.59	0.41	6.537	3.653	0.7587	<0.01
	2	0.29	0.23	4.041	2.372	0.0623	0.18
W. Cascades	1	0.64	0.45	7.192	4.233	0.8832	<0.01
	2	0.36	0.20	4.136	2.789	0.7033	<0.01
Klamath	1	0.56	0.42	6.419	3.079	0.8060	<0.01
	2	0.51	0.23	4.988	2.697	0.3193	<0.01
E. Cascades	1	0.81	0.51	8.917	5.675	0.7812	<0.01
	2	0.61	0.28	5.317	3.375	0.5106	<0.01
Blue Mtns.	1	0.76	0.46	8.949	4.867	0.7750	<0.01
	2	0.54	0.30	2.127	4.086	-0.0825	0.03

[a] Sign reflects arbitrary selection of gradient direction by CANOCO.

Table 16. Spearman rank correlations for plot-scores by CA method, species group, CA axis, and geographic area. All correlations are significant (P<0.01).

Comparison	Spearman Rank Correlation[a] Axis 1	Axis 2	Axis 3	Axis 4
Within species groups, different CA methods:				
Oregon:				
DCA tree scores and DCCA tree scores	0.89	0.65		
DCA shrub scores and DCCA shrub scores	0.90	0.14		
Western Oregon:				
DCA tree scores and DCCA tree scores	0.71	0.72		
DCA shrub scores and DCCA shrub scores	0.73	0.73		
Eastern Oregon:				
DCA tree scores and DCCA tree scores	0.73	0.28		
DCA shrub scores and DCCA shrub scores	0.68	-0.37		
Between species groups, same CA method:				
Oregon:				
CCA tree scores and CCA shrub scores	0.99	0.79	0.66	0.77
DCA tree scores and DCA shrub scores	0.90	0.22		
Western Oregon:				
CCA tree scores and CCA shrub scores	0.71	0.68	0.82	0.62
DCA tree scores and DCA shrub scores	0.44	0.71		
Eastern Oregon:				
CCA tree scores and CCA shrub scores	0.57	-0.49	0.77	0.35
DCA tree scores and DCA shrub scores	0.62	0.30		

[a] Sign reflects arbitrary selection of gradient direction by CANOCO.

gradients was higher (Table 14), a greater proportion of species were rare (had low constancies) (fig. 13), and total inertia was higher (Table 9). Gradient methods are less efficient under such conditions, yielding lower TVEs (Table 9) and thus larger residuals (fig. 12).

Comparison of Direct and Indirect Gradient Analyses

Eigenvalues and gradient lengths for axes 1 and 2 were substantially higher for DCAs than DCCAs in all geographic areas, except for axis 2 gradient length in the Blue Mountains subregion (Table 15). Gradient lengths for DCCA averaged 56% and 81% of DCA across all geographic areas for axis 1 and 2, respectively (Table 15). Plot scores from DCAs and DCCAs of all woody species for the first axis were moderately to highly correlated (0.72-0.92) in all geographic areas, but correlations declined--often drastically, as in the Coast, Klamath, and Blue Mountains subregions--with second (Table 15) and subsequent axes. Nevertheless, for all woody species at the state level, overall geographic patterns for DCA scores (figs. 14.a.-b.) were quite similar to CCA (figs. 9.a.-b.) for the first two axes. One exception was the Siskiyou Mountains, which emerged as an area of high scores on CCA axis 2 (in green in fig. 9.b.) but did not emerge in DCA axis 2 (fig. 14.b.). DCA-DCCA comparisons for independent analyses of trees and shrubs showed similar patterns: correlations between plot scores were moderate to high (0.68-0.90) for the first axis, but low for the second axis for shrubs at the state level (0.14) and for both trees (0.28) and shrubs (-0.37) in eastern Oregon (Table 16).

Differences between gradient lengths and in the ordering of plots by DCA and DCCA might be caused by omission of one or more relevant explanatory variables, by errors in the explanatory variables used, or by vagaries of the DCA and DCCA algorithms. All probably were factors in my study. DCA is known to perform best when a single controlling factor dominates the data, and DCA results rarely are interpretable beyond the first two axes, whereas CCA performs well with greater than two-dimensional gradients (Palmer 1993). Palmer (1993) found that CCA generally performed better than DCA, but that DCA performed adequately on his simulated datasets. Other authors (e.g., Minchin 1987) have pointed out deficiencies in DCA performance.

The shorter gradient lengths from DCCA (Table 15) indicate that much of the species variation was not accounted for by the explanatory variables. However, DCCA gradient lengths were nearly as long or longer than for DCA on axis 2 in eastern Oregon and in the Blue Mountains (Table 15), suggesting poor performance of the DCA algorithm past the first axis in these areas. Differences in the ordering of plots by DCA and DCCA also appear to have been caused in part by declining performance of DCA beyond the first axis. DCA appeared to perform poorly in areas where gradients were long and species turnover was high (high beta diversity and high total inertia in the species-by-plot data matrix), which was especially true for eastern Oregon and its subregions (Table 14). The presence of discontinuities and outliers and the large number of zero values resulting from even moderate beta diversity have long been known to present problems in the analysis of large ecological datasets. Del Moral and Watson (1978) reported similar problems when ordinating community data for eastern Washington. More in-depth analysis of DCA performance with large and complex regional data is needed.

Comparison of Tree and Shrub Strata

The CCA models for trees and shrubs differed only slightly in terms of the significance and relative importances of explanatory variables, suggesting that both strata respond similarly to explanatory variables used in my study. Indeed, CCA plot scores were very strongly correlated between the two strata on the first two axes (0.99 and 0.79) at the state level, and moderately correlated for the third and fourth axes (0.66 and 0.77) (Table 16). Tree and shrub responses to the explanatory variables were moderately correlated at the half-state level, and were more tightly coupled in western than in eastern Oregon on all four CCA axes (Table 16).

Correlations between strata for the indirect gradient analyses were weaker than for CCA (Table 16). Correlations at the state level were strong (0.90) on DCA axis 1 but very weak (0.22) on DCA axis 2 (Table 16). At the half-state level, correlations were moderate to weak on both axes (Table 16). Correlations between strata on DCA axis 1 were stronger in eastern than in western Oregon, but the reverse was true for DCA axis 2 (Table 16). Although it could not be ascertained whether differences in DCA plot sequences for trees and shrubs were caused by differences in ecological response or to performance of the DCA algorithm, I hesitate to attribute ecological significance to stratum differences on DCA axis 2 given the questionable behavior of the DCA algorithm.

For DCA axis 1, the stronger correlation between trees and shrubs in eastern than in western Oregon was consistent with indirect gradient analyses conducted by del Moral and Watson (1978). They found that ordination scores of the trees and herbs were more strongly correlated in eastern than in western Washington, but they did not compare trees with shrubs. They hypothesized that the consistently denser canopies in western communities insulate the understory from responding to the broader physical environment in the same manner as the overstory; because the understory responds to overstory as well as to the broader physical environment, overall response patterns of the two strata diverge. Under conditions of more open canopies in the east, both canopy and understory respond to physical environment in the same way.

Interestingly, in the CCAs, where environmental factors including canopy density were considered directly, plot sequences for trees and shrubs were less similar in eastern than in western Oregon--the reverse of the pattern seen for DCA (Table 16). This does not necessarily refute the del Moral and Watson (1978) hypothesis, however, that overstory canopy contributes to regulating shrub response. The TREOCOV variable was substantially more important in the eastern than in the western Oregon CCA models for both trees and shrubs, yet it is likely that the strata responded to TREOCOV in different ways. Trees may respond to TREOCOV as an indicator of moisture conditions, whereas for shrubs the variable may reflect understory light conditions as well as moisture. It is widely believed that vegetation strata respond differently to environment, disturbance, and species interactions (Whittaker 1960), which is why ordinations often are conducted separately for tree and nontree vegetation. Further analyses of stratum differences in the Oregon dataset are warranted.

Overall study findings support conventional wisdom, and a hypothesis of my study, that trees are more consistent indicators of the regional environment, particularly climate, than are understory plants (Daubenmire 1989, Whittaker 1960). Shrubs and herbs respond at a finer scale to local conditions of light, moisture, and soil imposed by the tree overstory, and to fine-scale disturbances, as well as to the broader physical environment imposed by local topography and the regional climate. Because of their longer lifespans, trees also integrate conditions over a longer time and once established are less responsive to minor disturbances and changes in physical environment. In my study as elsewhere, tree species on average were more widely distributed regionally (fig. 13), were more locally abundant, and as a group had lower beta diversities (Table 14) than shrub species. From a methods standpoint, trees thus were more amenable to numerical methods of gradient analysis at the regional scale. Numerous studies have shown that widely distributed species are more locally abundant (Hanski et al. 1993), and vegetation studies are no exception (del Moral and Watson 1978, Whittaker 1960).

Community Patterns

The hierarchical division of the 2,443 plots based on the TWINSPAN algorithm (Hill 1979) is presented in fig. 15. Results are presented at either the fourth or fifth division, whichever was most comparable to series or major forest zones recognized in previous studies. It is important to note that the classes identified in my study were typological, since they were based on existing vegetation spanning a range of successional stages and disturbance histories. Nevertheless, results from CCA provide a strong rationale for comparing the tree-based types with forest zones and series that refer to species dominance at climax: at the state level, tree species responded fairly faithfully to climatic gradients and much less so to disturbance (Table 12).

The first TWINSPAN division distinguished western from eastern Oregon types (fig. 15). In western Oregon, classes identified at the second division and beyond were fairly distinct in the environmental space defined by summer moisture stress and temperature (fig. 16). The western Oregon types also were well segregated geographically (fig. 17). As hypothesized, the types corresponded well with the classification system used by Franklin and Dyrness (1973, p. 4), which was based on a combination of geographic location and potential and existing vegetation. At the second division, the four western Oregon classes could be characterized as subalpine forest of northwest Oregon, temperate coniferous forest of northwest Oregon, mixed conifer and mixed evergreen forest of southwest Oregon and the western interior valleys, and Quercus garryana woodland. At the fourth division, classes generally corresponded to major forest series or zones (fig. 15).

Except for the higher elevation, subalpine forest types (Abies lasiocarpa forest (5Ea, 6E, and 8Ea) and Tsuga mertensiana forest (8Eb)), the eastern Oregon types were much less distinct geographically (fig. 17) as well as in environmental space (fig. 16) than the western types. At no level in the community classification did types correspond one-to-one with existing classification systems, contrary to what was hypothesized. Because only some of the types at the fourth division corresponded to series or forest zones, types at the fifth division were utilized where necessary (fig. 15). Even then, types had to be combined to achieve correspondence with forest zones (e.g., Abies lasiocarpa forest occurred in three separate types, fig. 16).

The positions of the Oregon communities in relation to each other and to dominant environmental gradients of temperature and moisture (fig. 16) were comparable to those hypothesized by Franklin and Dyrness (1973, p. 50) (fig. 2), with a few exceptions. Data from my study suggest that summer moisture stress in Tsuga heterophylla forest is greater than hypothesized by Franklin and Dyrness (1973, p. 50) (fig. 2). Also, the low- to mid-elevation types in eastern Oregon were confined to a narrower range of environments than postulated by Franklin and Dyrness (1973, p. 50), suggesting that other factors not accounted for in my study may be more important in explaining floristic differences at low- to mid-elevations east of the Cascade crest. Differences between my findings and the Franklin and Dyrness (1973, p. 50) hypothesis may be attributed in part to use of different measures of temperature and moisture.

Results from the community classification corroborate findings from the ordinations. Tree species occurrence generally was more strongly associated with the environmental measures available for my study in western than in eastern Oregon. In CCA, the environmental variables explained somewhat more species variation in western (11%) than in eastern Oregon (9%), despite a larger sample size (Table 9). In the TWINSPAN analysis, the non-subalpine types of eastern Oregon were not segregated geographically, nor in the environmental space defined by annual temperature and summer moisture stress, as were the western types. The ordinations indicated that elevation, which was strongly correlated with annual temperature, was more important in explaining species variation in western than in eastern Oregon, and that the relative importance of elevation was particularly low in the Blue Mountains subregion (Table 12). Whereas separation of the eastern types was greater along the moisture axis than the temperature axis (fig. 16), the separation was less than expected based on the ordinations and on other studies (Franklin and Dyrness 1973).

Results from the classification analyses also corroborate the ordination findings that spatial patterns of species variation are more fine-grained east of the Cascade crest than in western Oregon. This was reflected in the patterns of residuals from the CCA models (fig. 12), which were low across broad areas of western Oregon but exhibited much fine-scale variation in eastern Oregon. Similarly, the TWINSPAN classes in eastern Oregon were not segregated geographically as they were in western Oregon (fig. 17).

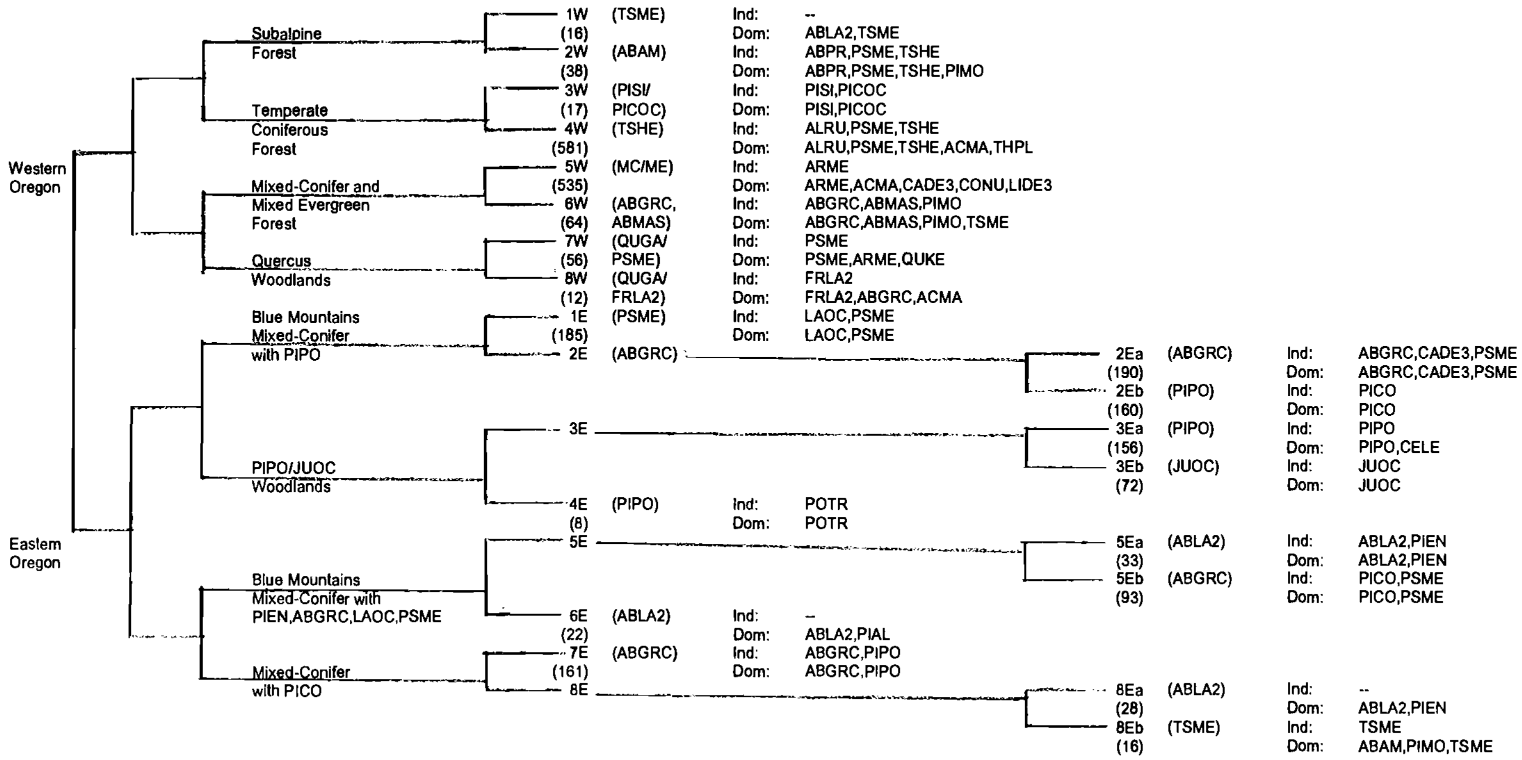


Figure 15. Dendrogram for the hierarchical TWINSPAN classification of tree species on 2,443 plots. The first dichotomy split western Oregon (W) from eastern (E) Oregon plots. Indicator (Ind) and dominant (Dom) species are listed for each type; species codes are defined in Table 1. Sample sizes are in parentheses under the community code. Related series or forest zones are shown in parentheses at right.

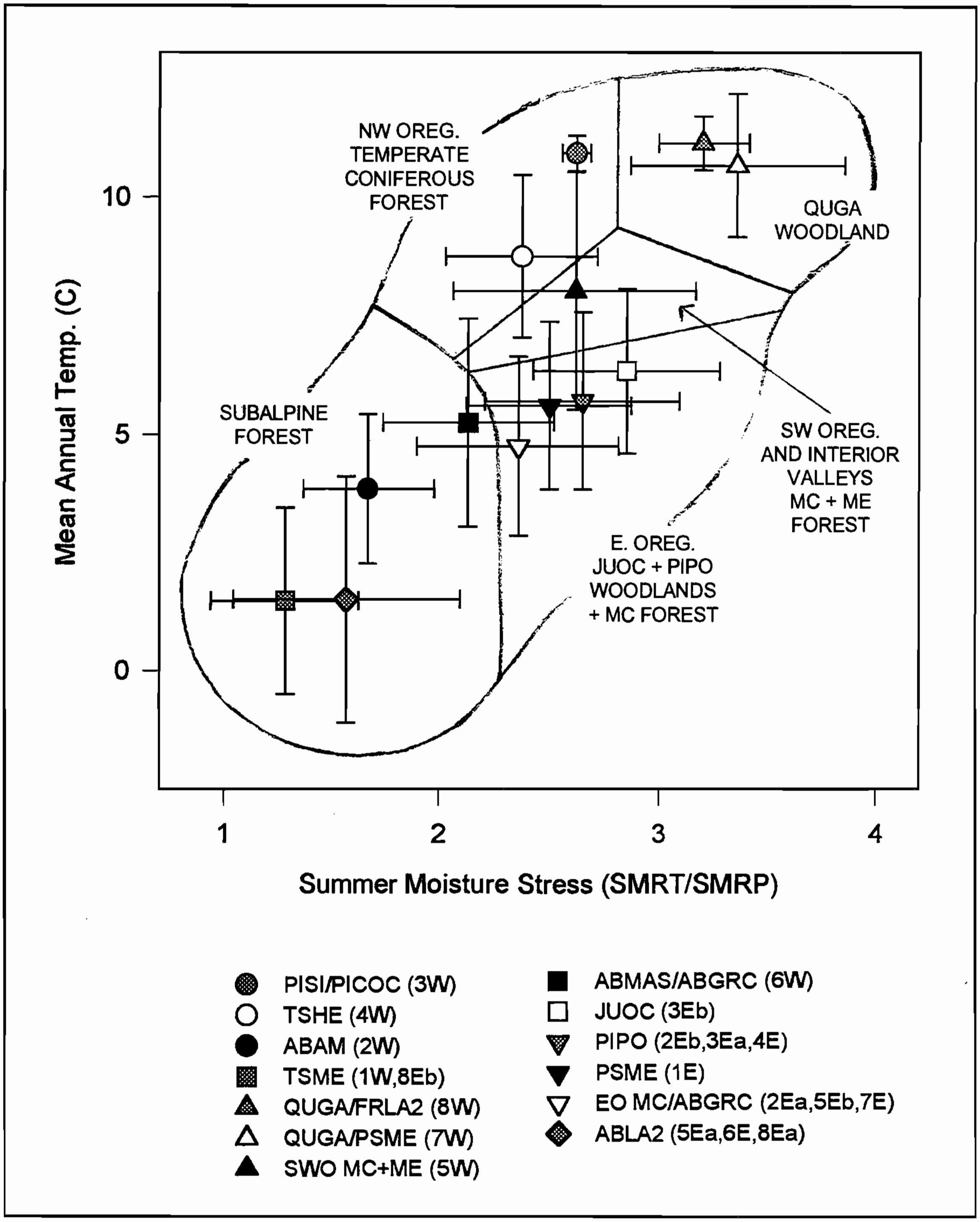


Figure 16. Distribution of community types from TWINSPAN classification in an environmental field defined by summer moisture stress (SMRTMP/SMRPRE) and mean annual temperature. Community codes are defined in fig. 15. Symbols indicate means and bars indicate standard deviations.

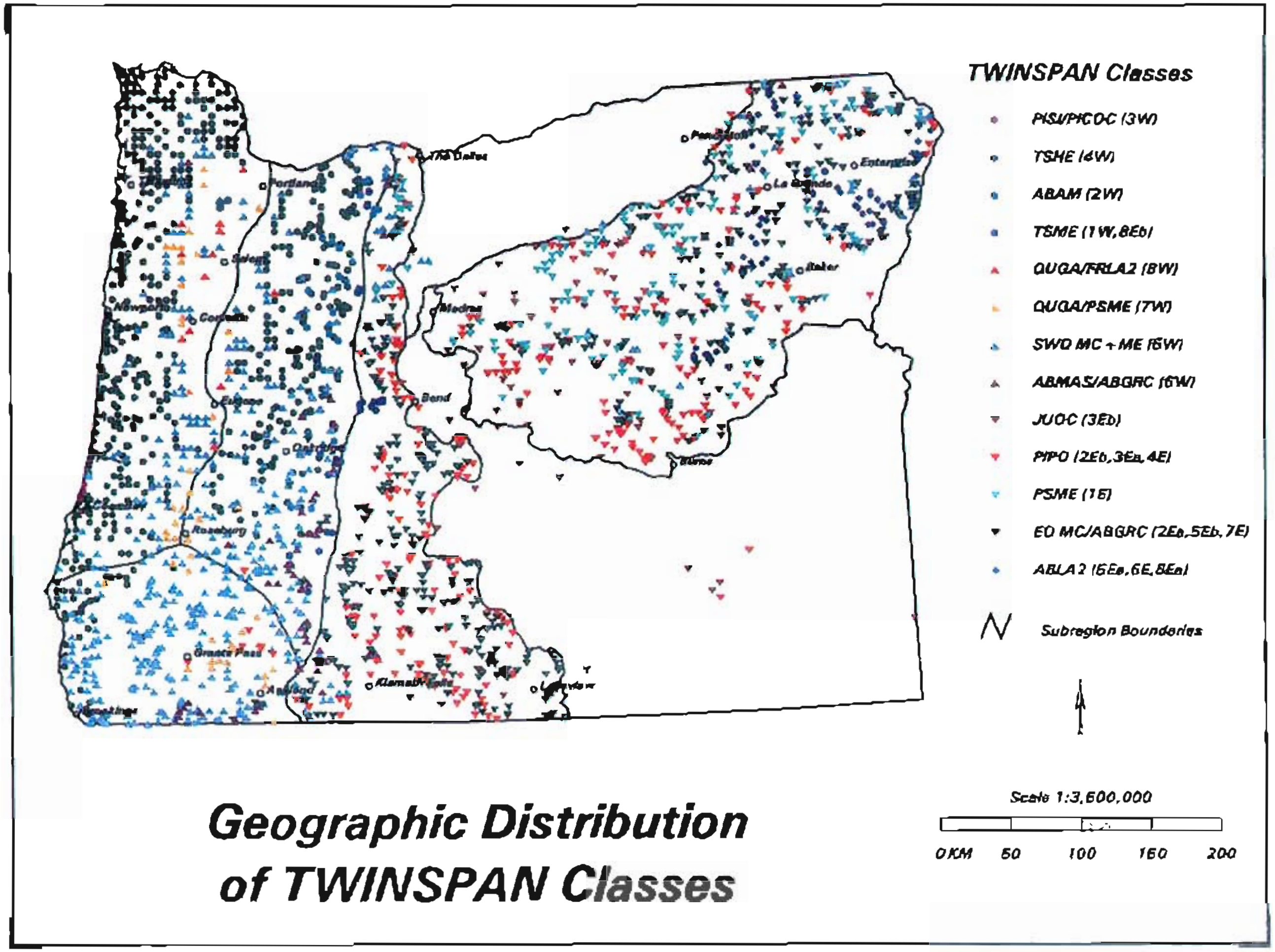


Figure 17. Geographic distribution of TWINSPAN classes. Community codes are defined in fig. 15.

Ecotones in Oregon Plant Communities

Regional-scale research provides an opportunity to observe broad-scale geographic patterns in community composition across very heterogeneous environments. The direction and rate of change in community composition are of ecological interest, particularly the location and nature of ecotones and the mechanisms that create them (Hansen et al. 1988, Holland et al. 1991). In plant ecology, an ecotone traditionally has denoted an intersection between plant communities where there is relatively abrupt change in vegetation structure or composition (Hansen et al. 1988), but more recently is considered any transitional area between adjacent ecological systems (Risser 1995). Vegetation scientists traditionally have avoided ecotones when sampling communities, both for convenience and because of organismic bias (Noss 1987, Risser 1995). In my study, ecotones were indicated by zones of rapid change in ordination scores or by transitions between mapped community types.

The hypothesis that ecotones correspond to gradients in environment is problematic to address. Current distributions of species, and hence communities, reflect a suite of environmental, disturbance, and historical factors that interact in complex ways. A lack of correspondence between vegetation and environment may indicate only that important environmental factors were excluded from the analysis. Historical and disturbance factors, which may be key to explaining zones of discordance between species and environmental gradients, are especially difficult to assess. Furthermore, any attempt to place boundaries between locations where resident species are distributed independently of one another must be recognized as arbitrary (McCoy et al. 1986). That said, a rigorous investigation of geographic pattern in the Oregon data still is possible to some extent (see review in McCoy et al. 1986), but is beyond the scope of this paper. Nevertheless, some general observations of pattern from both ordination and classification perspectives are discussed below. The reader should bear in mind that the Oregon data illustrate broad-scale patterns of variation in community structure across the region, but interpretation of fine-scale pattern is inappropriate. Sampling avoided local-scale boundaries: individual field plots were established within local areas of homogeneous vegetation, and plots were geographically separated from one another by an average of about 8 km.

Daubenmire (1968) defined four kinds of ecotones: (1) abrupt transitions caused by discontinuities in an underlying environmental gradient; (2) gradual blending of vegetation because of smooth environmental gradients; (3) mosaic ecotones where peninsulas and islands of each community extend into the other as the result of local heterogeneity in soil or microclimates; and (4) sharp transitions even on smooth environmental gradients because of biotic interactions among organisms. The first three kinds of ecotones are environmentally induced, but their observation also may be the result of scale of measurement. Daubenmire (1968) attributed the fourth kind of ecotone to biotic interactions, including disturbance, but at a regional scale environmentally-induced pattern also can be usurped by historical factors such as speciation and migration. Furthermore, biotic interactions or disturbance can obscure environmentally-induced boundaries as well as induce boundaries in the absence of an environmental gradient. For example, because of its superior competitive ability Pseudotsuga menziesii dominates forests across a wide variety of sites that in the absence of disturbance would be dominated by more shade-tolerant associates such as Tsuga heterophylla, Thuja plicata, and Abies spp. In conclusion, ecotones in the Oregon data can be identified and characterized, but determination of cause is necessarily speculative.

The dominant directional trend in species gradients was longitudinal, as reflected in axis 1 from both direct (fig. 9.a.) and indirect (fig. 14.a.) gradient analyses. The trend was more latitudinal in the Blue Mountains subregion. These directions of change corresponded to the major climate gradients driven by proximity to the Pacific Ocean, the north-south orientation of the Coast and Cascade Ranges, and the mountains in the northeastern corner of the Blue Mountains subregion.

The steepest gradient in species composition and environment, i.e. the most prominent ecotone, followed the crest of the Cascade Mountains, as indicated by the close spacing of contour lines for CCA axes 1 and 2 (figs. 9.a.-b.) and DCA axes 1 and 2 (figs. 14.a.-b.). The predominance of this ecotone was confirmed by the community classification, where the first TWINSPAN division separated western from eastern types (figs. 15 and 17). The Cascades ecotone was more gradual in the southern half of the range, indicated by wider spacing of the ordination contours (figs. 9.a. and 14.a.) and by the intermingling of community types (fig. 17). Ordinations indicated secondary ecotones between the Coast Range of northwest Oregon and the Willamette Valley (figs. 9.a. and 14.a.), in the Siskiyou Mountains (figs. 9.a. and 14.a.), in mountainous areas of eastern Oregon (figs. 9.b. and 14.b.), and in the interior valleys of southwest Oregon (figs. 9.b. and 14.b.). These areas also were characterized by strong gradients in environment (fig. 3).

Boundaries between the community types showed a variety of characteristics (fig. 17). Abrupt transitions, probably caused by discontinuities in an underlying environmental gradient, were most apparent in areas of extreme environmental conditions: the Picea sitchensis/Pinus contorta var. contorta type in the coastal dunes, the subalpine Tsuga mertensiana and Abies lasiocarpa types, and Quercus garryana and Juniperus occidentalis woodlands (fig. 17). The environmental control of boundaries between these and other types also was indicated by their distinct segregation within the temperature-moisture field (fig. 16). The southern boundary of the Tsuga heterophylla type in western Oregon also was quite distinct geographically (fig. 17), probably because of climate-limited distributions of some of the type's dominant species, such as Thuja plicata and Tsuga heterophylla. An example of gradual blending of vegetation because of smooth environmental gradients was observed in the transition from the Tsuga heterophylla type to the Abies amabilis type along the elevational gradient of the western Oregon Cascades (fig. 17).

Boundaries between community types over much of the mid-elevation forest in the eastern Cascades and Blue Mountains subregions showed a "mosaic" pattern (fig. 17). The Pinus ponderosa, Pseudotsuga menziesii, and mixed-conifer/Abies concolor types intermixed throughout their ranges, presumably because of fine-scale variation in habitat. In western Oregon, the northern boundary of the mixed-conifer/mixed evergreen type also showed a mosaic pattern, in contrast to the relatively distinct southern boundary of the adjacent Tsuga heterophylla type (fig. 17). Mosaic patterns such as the northern boundary of the mixed-conifer/mixed-evergreen type may in part be the legacy of shifting species distributions over geologic time. Species whose ranges are contracting or expanding as a result of change to less or more favorable climate may leave disjunct populations that could exhibit a mosaic pattern near the edge of their current range (Daubenmire 1968). The boundary of the range of a species that is expanding through dispersal and other population processes, on the other hand, would be more abrupt.

The overall gradient pattern from the indirect gradient analysis showed more fine-scale variation than direct gradient analysis in the first two ordination axes. Constraining the plot scores to be linear combinations of explanatory variables had the effect of "smoothing" the gradients across geographic space. This effect was especially notable in the eastern Cascades and Blue Mountains subregions, where CCA scores translated into broad areas of very gradual compositional change at mid- to low-elevations. Although the vegetation-based ordination showed more fine-scale ecotones in species composition (figs. 14.a.-b.), this effect was strongly influenced by the interpolation method and contour interval used. Contour maps based on kriged lattices can be misleading, and merely reflect the qualities of the underlying data. Interpretation needs to consider the accompanying variance lattices as well. For example, variance is higher in areas of sparse data, which in my study included areas of high elevation along the Cascade crest, large areas of nonforest such as the Willamette Valley, and the Kalmiopsis Wilderness area in the Siskiyou Mountains.

In conclusion, overall patterns in the Oregon data generally supported the hypothesis that ecotones in community composition coincide with zones of steep environmental gradients. Reasons behind the exceptions to environmental control pose interesting areas for further research. Areas of discordance between CCA- and DCA-based contour maps were one indicator of such exceptions. Perhaps the most notable example was in the Siskiyou Mountains of southwest Oregon, which emerged as an area of high scores in CCA axis 2 (fig. 9.b.), but was undistinguished in DCA axis 2 (fig. 14.b.). Another example was the location of the ecotone between the maritime forests of coastal northwest Oregon and the drier forests of the Willamette Valley in the rainshadow of the Coast Range. In CCA the area of highest scores was located farther north than in DCA (green in figs. 9.a. and 14.a.). In both CCA and DCA the same general species gradient was captured: high scores contain tree species such as Abies grandis, Acer macrophyllum, Arbutus menziesii, Cornus nuttallii, and Fraxinus latifolia, which occur much more frequently and with greater abundance in the rainshadow of the Coast Range. But in CCA the location of high scores was shifted to the north by the steeper environmental gradient imposed by the coastal mountains west of Portland, which are higher elevation than west of Salem.

Ecological Differences Between Land Ownerships

At the regional level in Oregon, where about 60% of forest land is publicly owned (Powell et al. 1993), many differences in vegetation characteristics and pattern are associated with differences in land ownership. These differences are important from the standpoint of forest policy formulation and evaluation. In regional-scale planning and policy decisions, land ownership is a pivotal point, and decisions must consider the mix of ownerships and the variety of benefits they provide. I therefore present a brief comparison of federal and nonfederal ownerships in terms of the species gradients and community types of my study. The reader must recall that the plot data were not a statistical sample, and strong inferences cannot be drawn to the larger populations of entire ownerships nor of all forested lands in Oregon. In particular, BLM lands in west-central and northwest Oregon were not represented in the data. Although proportions therefore are only approximate, they are indicative, and are the only information of this kind currently available.

Federal and nonfederal plots differed significantly in terms of mean positions along dominant environmental gradients (Table 17). Nonfederal lands were lower in elevation and experienced greater moisture stress during the growing season in every geographic area except the Coast subregion, where elevation did not differ between ownerships and nonfederal lands had less summer moisture stress (Table 17). The Coast also was unique in the predominance of nonfederal lands (65% of the plots) (Table 17).

Federal and nonfederal lands contrasted most greatly in terms of positions along dominant species gradients in the Coast and western Cascades subregions, western Oregon, and the state as a whole (Table 17). Plot scores for federal and nonfederal lands in eastern Oregon and in the Klamath, eastern Cascades, and Blue Mountains subregions did not differ significantly for CCA axis 1. Plot scores on CCA axis 2 differed significantly between federal and nonfederal lands in all geographic areas.

Differences in representation of the community types on federal and nonfederal lands were most pronounced for types at both extremes of the elevational gradient. High-elevation types (ABAM, TSME, ABMAS/ABGRC, and ABLA2) were concentrated on federal lands, and low-elevation types (PISI/PICOC, QUGA/FRLA2, QUGA/PSME, and JUOC) on nonfederal lands (Table 18). The mid-elevation and more widespread types were more evenly distributed between ownerships, with the exception of MC/ABGRC in eastern Oregon, which was concentrated on federal lands (Table 18).

Table 17.--Sample sizes and means of ELEV, SMRTSMRP, and CCA plot scores on the first two CCA axes for federal (Fed) and nonfederal (Nonfed) ownerships, by geographic area. All means differed significantly (P<0.01) between federal and nonfederal ownerships except numbers in parentheses.

	N		ELEV		SMRTSMRP		CCA1		CCA2	
	Fed	Nonfed	Fed	Nonfed	Fed	Nonfed	Fed	Nonfed	Fed	Nonfed
Oregon	1,594	849	1218	731	2.3355	2.6683	0.4368	-0.0041	0.2552	-0.6156
Half-state:										
Western Oregon	719	514	831	344	2.3433	2.6730	-0.5179	-0.8139	0.4196	-0.5791
Eastern Oregon	875	335	1,536	1,324	2.3291	2.6610	(1.2213)	(1.2385)	0.1201	-0.6714
Subregion:										
Coast	138	323	(263)	(268)	3.3235	2.6334	-1.2773	-0.9258	0.0227	-0.5657
Western Cascades	358	107	1,018	449	2.2367	2.5996	-0.2953	-0.7334	0.8952	-0.2617
Klamath	223	84	882	501	2.5266	2.9190	(-0.4054)	(-0.4863)	-0.0983	-1.0354
Eastern Cascades	351	128	1,542	1,344	2.5117	2.8379	(1.2934)	(1.2758)	-0.1194	-0.8665
Blue Mountains	524	207	1,533	1,312	2.2068	2.5517	(1.1730)	(1.2154)	0.2805	-0.5508

Table 18.--Number (proportion) of plots by community type from TWINSPAN analysis and by ownership in Oregon.

Community Type	Codes	Ownership			
		Federal		Nonfederal	
PISI/PICOC	(3W)	15	(88)	2	(12)
TSHE	(4W)	289	(50)	292	(50)
ABAM	(2W)	38	(100)	0	(0)
TSME	(1W,8Eb)	32	(100)	0	(0)
QUGA/FRLA2	(8W)	0	(0)	12	(100)
QUGA/PSME	(7W)	14	(25)	42	(75)
SWO MC/ME	(5W)	348	(65)	187	(35)
ABMAS/ABGRC	(6W)	62	(97)	2	(3)
JUOC	(3Eb)	23	(32)	49	(68)
PIPO	(2Eb,3Ea,4E)	221	(68)	103	(32)
PSME	(1E)	117	(63)	68	(37)
EO MC/ABGRC	(2Ea,5Eb,7E)	356	(80)	88	(20)
ABLA2	(5Ea,6E,8Ea)	79	(95)	4	(5)

DISCUSSION

Determinants of Vegetation on a Site

Spatial Structure in the Species and Environment Data

Spatial structure in the species and environmental data expressed ecological pattern, and presumably underlying processes, but as viewed through the lens imposed by the scale of the observations (field plots). The large fraction of TVE attributed to environmental factors ($S \cap E$ and $E|S$) (85-93%) (Table 7) indicated the importance of environment in determining vegetation on a site, at least for the particular suite of explanatory variables employed in my study. Much of the environmental variation was broad-scaled and geographically structured, as indicated by the large proportion of TVE attributed to spatial structure in the environmental variables ($S \cap E$) (17-34%) (Table 7). However, the $S \cap E$ component reflects correlations between species and environment that may or may not indicate real interactions.

The spatial matrix ($S|E$) quantifies spatial structure present in the data that is uncorrelated with environmental measures, and as such can be considered a synthetic descriptor of unmeasured underlying processes (Borcard et al. 1992). The greater amount of spatial pattern in the species data not shared by environmental variables ($S|E$) at broader geographic scales suggests that omitted measures of contagious biological processes or other factors were more important at the regional level. Given the broad scale of my study, these might include historical factors, evolutionary processes, and dispersal and migration, as well as local factors such as growth, reproduction, and interspecific competition. This scale effect also could have been an artifact of sampling, in that sampling was not intense enough (plots were spaced too widely) to detect finer-scale spatial pattern.

The trend of greater importance of spatially-uncorrelated environmental variables (E|S) at finer geographic scales (Table 7)probably reflected shifts across scales in the relative importances in the CCA models of explanatory variables (Tables 8 and 12). Measures of local environment such as topography and disturbance were more important at finer geographic scales (Tables 8 and 12). Pattern of spatial variation in local factors such as these is finer-grained than with "regional" variables such as climate and geology, and this fine-scale pattern would not be sensed as autocorrelated by the coarse sample of plots.

Geographic differences in spatial structure of the species and environment data were pronounced. Spatial pattern in the species data uncorrelated with environmental measures (S|E) was stronger in eastern Oregon, suggesting that the explanatory variables used in my study were less successful at explaining inherent community patterns east of the Cascade crest (Table 7). This interpretation was supported by the greater amount of TVE explained by environmental variables (S∩E and E|S) in western Oregon (91%) and its subregions (91-93%) than in eastern Oregon (86%) and its subregions (86-89%). Environmental factors in the Coast and western Cascades subregions (S∩E of 30-34%) were notably more spatially structured than in the Klamath, eastern Cascades, and Blue Mountains subregions (17-24%). It is interesting that the Klamath was more similar to the eastern than to the western Oregon subregions in this regard. Geographic differences in spatial structure of the species and environment data probably reflected shifts across the geographic areas in the relative importances of explanatory variables in the CCA models (Tables 8 and 12). For example, stand age was significant in CCA models for the Klamath, eastern Cascades, and Blue Mountains subregions, where spatial pattern in the AGE variable was not apparent (fig. 6). S∩E was greatest in the Coast subregion (Table 7), where climate variables contributed most to TVE (Table 8). As a group, the climate variables appeared to be most autocorrelated (fig. 3).

In summary, to the extent that the magnitude of S|E reflects omission of important explanatory factors, it appeared that the CCA models potentially could be improved slightly, with gains potentially greater in eastern Oregon. However, of the large amount of unexplained variation in the species data in my study (78-88%) (Table 6), current statistical methods cannot discriminate between "potentially explainable" variation and the "real" stochasticity in that unexplained variation.

Temperature and Moisture

Study findings for all locations and geographic scales (Tables 8 and 12) support the hypothesis of the primary importance of temperature and moisture and the secondary role of substrate (geology and soil factors) in controlling regional compositional gradients. These findings are consistent with other studies in the western U.S. and elsewhere (Allen et al. 1991; Allen and Peet 1990; Daubenmire and Daubenmire 1968; del Moral 1972; del Moral and Fleming 1979; del Moral and Watson 1978; Denton and Barnes 1987; Dyrness et al. 1974; Fonda and Bliss 1969; Franklin and Dyrness 1973; Minore 1972; Peet 1978, 1981; Riegel et al. 1992; Spies 1991; Spies and Franklin 1991; Whittaker 1960; Whittaker and Niering 1965; Zobel et al. 1976). However, because methods for measuring temperature and moisture at macro and local scales have differed substantially among studies, direct comparisons of specific environmental factors are problematic. Whereas virtually all other gradient studies have suggested that temperature and moisture are the primary habitat variables that control overall vegetation structure, none have addressed the relative contributions of macro- and micro-climate as was done in my study. Of the cited studies, only Zobel et al. (1976) measured air temperature, but at the scale of the plant rather than at a climatic scale as in my study. None of the studies measured precipitation. Most investigators have considered broad-scale climate only indirectly, usually by studying vegetation change with elevation or latitude, which are viewed as complex-gradients that are dominated by temperature but often are correlated with precipitation as well.

Moisture gradients are complex and not easily quantified, being the product of several covarying environmental factors that also vary in time. Not surprisingly, vegetation studies have differed in their methods for quantifying moisture, but most have emphasized local topography as an indirect measure of moisture stress through its relations to solar heating and dessication from wind exposure. Topography also influences moisture availability through hydrologic flows, soil processes, humidity, and so on. Geology influences moisture availability as well. Measurement of plant evapotranspiration stress, the actual measure of interest, is impractical to measure in landscape- (but see Zobel et al. 1976) and regional-scale studies. Unlike any of the other studies cited, my study assessed moisture input from precipitation, which indirectly indicates moisture availability to plants. Moisture stress, or water balance, was assessed indirectly by an interaction term between summer precipitation and summer temperature, topographic measures, air temperature, and overstory canopy cover, but humidity measures were unavailable.

The primary role of continentality in controlling the dominant state-level gradient in woody plant communities observed in my study is consistent with the major finding of del Moral and Watson's (1978) analysis spanning an east-west gradient across the Cascade Mountains in Washington, although they did not measure climate directly. Because continentality gradients contain interacting elements of temperature and moisture, it is simplistic to state which factor was most important, although my original hypothesis of the primary importance of temperature was supported by the greater contribution of temperature variables to TVE (Table 12). Continentality measures were more important in explaining compositional gradients in western than in eastern Oregon (Tables 10 and 12, fig. 8). Continentality measures were most important in the Coast subregion (Tables 10 and 12, fig. 8), which encompasses the strong influence of the Pacific Ocean, the orographic effects of the Coast Range, and the Willamette Valley in its rainshadow. Indeed, the influence of climate in general was especially strong in the Coast subregion, where elevation, temperature, and precipitation variables contributed 58% of TVE in CCA with variance partitioning (Table 8) and 75% of TVE in stepwise CCA (Table 12).

In all geographic areas, stepwise CCA results indicated that temperature contributed more to explaining species variation than precipitation, although the biplots and the order of variables added in the stepwise models suggest that temperature contributed more west of the Cascade crest and moisture stress in eastern Oregon (Table 12), as hypothesized. Temperature variables were more often significant ($P<0.01$) than were precipitation variables ($P\geq0.02$) in separating the positions of growth forms along environmental axes. Elevation contributed most to TVE, especially in the western Cascades (Tables 10 and 12). Elevation was highly correlated with all-time maximum temperature (-0.97 at the state level), and the two explanatory variables occupied nearly identical vectors in all biplots except the Coast (fig. 8). The primary importance of temperature and elevation was as expected given the broad scale of analysis, and is consistent with other authors who have pointed to temperature and elevation as most important in differentiating major vegetation zones. However, although I included elevation with the temperature variables for purposes of this analysis, elevation actually is a complex-gradient (sensu Whittaker 1965, 1960) that covaries with a host of climate and other environmental factors, and probably historical factors as well. For example, increasing elevation generally is associated with decreasing soil pH and percent base saturation, and increasing total nitrogen, on mountain slopes (Allen and Peet 1990), and increasing precipitation and amount and persistence of winter snowpack.

The characteristic warm, dry summers of the Pacific Northwest are the most critical period for plant moisture stress. Findings of my study bore this out: growing-season variables SMRPRE, SMRTMP, and SMRTSMRP were important everywhere except in the Klamath subregion (Table 10), contributing 13-42% of TVE elsewhere (Table 12). Axis 2 at the state-level and in western Oregon was interpreted as a gradient in moisture-stress during the growing-season, as was axis 1 in eastern Oregon and in the Coast and Blue Mountains subregions (Table 10, fig. 8). Moisture stress was especially important in explaining species gradients in eastern Oregon and its subregions (Table 10): SMRPRE was the first variable added in eastern Oregon, TREOCOV was added first in the Eastern Cascades subregion, and SMRTSMRP and TREOCOV were added first and second in the Blue Mountains (Table 12).

Response of community types in my study to the primary gradients of temperature and summer moisture stress are summarized in fig. 16. Although the array of community types corresponds well with other published accounts (e.g., fig. 2; Franklin and Dyrness 1973, p. 50), this portrayal of my results lacks the dimension of temporal variability in temperature and moisture (continental vs. maritime climate) that emerged as important in my study.

Topography

Topographic variables (aspect, slope, and solar radiation) contributed relatively little (4-8% of TVE) to explaining variation in species composition across Oregon (Table 8). The minor role of topography relative to climate measures in this regional-scale study was as hypothesized. The importance accorded topographic measures in other gradient studies can be attributed to the fact that most were conducted at smaller geographic scales, or that study areas were stratified into elevational bands before exploring the importance of topographic moisture (e.g., Allen et al. 1991; Allen and Peet 1990; Peet 1978, 1981). At regional and even landscape scales in mountainous terrain, topographic effects are blurred by the tendency for forest types to occupy different aspects in compensation for shifts in elevation (Daubenmire 1946, Zobel et al. 1976). Nevertheless, in my study topography did increase somewhat in importance in areas of greater climatic stress, as hypothesized. Also, topographic variables contributed less to TVE in the more benign climate of western Oregon (4% of TVE) than in eastern Oregon (7% of

TVE), where climate is more severe. Of the five subregions, topographic variables contributed least in the Coast (5% of TVE), the only geographic area where solar radiation was not significant (Tables 8, 10, and 12). Del Moral and Watson (1978) similarly found that topography more profoundly differentiated community composition on the eastern slopes of the Washington Cascades. Closer to the coast, climate is less stressful to plant growth. East of the Cascade crest, moisture is more limiting and temperatures are colder and more variable, topography is often deeply dissected, and topographic effects would be expected to be more pronounced (Neilson et al. 1992, del Moral and Watson 1978, Zobel et al. 1976).

Slope was the topographic variable most highly associated with community patterns in my study (Tables 10 and 12). Slope was significant in all geographic areas, contributing most to TVE in the western Cascades, eastern Cascades, and Blue Mountains subregions (Table 12). Nevertheless, slope never was strongly correlated with either of the first two CCA axes, was strong on axis 3 only in the western Cascades and Blue Mountains subregions, and was strong on axis 4 at the state and half-state levels in the Klamath subregion (Table 10). Interpretation is difficult because slope integrates a variety of hydrological and geomorphic processes, such as soil formation and movement (Swanson et al. 1988). Flat sites are more likely to be moist and have deeper soils, although low slopes also can occur on dry, rocky ridgetops. Steep sites are more likely to be dry with shallow, rocky soils. Slope integrates certain interactions between vegetation and soil formation, as well. Aspect was never selected in the stepwise procedure, but was one component in computing potential solar radiation. Solar exposure was significant in all geographic areas except the Coast, but contributed relatively little to explaining species variation (Table 12). Unfortunately, topographic position was not available for all plots in my study, and thus was not considered in the analysis.

Overstory Canopy Cover

Overstory cover was substantially more important in explaining species variation in eastern Oregon than in western Oregon (Table 12) and was strongly correlated with the first CCA axis in eastern Oregon and its subregions (Table 10). It is impossible in my study to discern to what degree this canopy measure reflects past disturbance, microsite environment, large-scale climate, or net primary productivity. I suspect TREOCOV probably captures a complex-gradient that is a combination of these and other factors, and that the variable carries different significance for the tree and shrub strata.

Water availability strongly influences leaf area index (LAI) in northwestern coniferous forests (Gholz 1982, Grier and Running 1977, Waring et al. 1978), and LAI probably is strongly correlated with the measure of canopy cover used in my study. Soil drought or high evaporative demand (high vapor pressure deficits) can limit canopy development as well as reduce photosynthesis, and hence growth, by causing stomatal closure (Runyon et al. 1994). These conditions are influenced by both microtopography and large-scale climate. In fact, the TREOCOV variable may better integrate factors influencing actual site moisture availability to plants than do the precipitation variables. The canopy cover vector was closely aligned with precipitation variables in biplots for all geographic areas except the eastern Cascades (fig. 8), where the vector is aligned with the other topographic variables and the variable contributes most (19%) to TVE (Table 12). However, the weighted correlations between canopy cover and the precipitation variables were low (e.g., 0.1675 for annual precipitation and 0.2530 for summer precipitation at the state level).

Del Moral and Watson (1978) attributed the major contrasts in community structure between eastern and western Washington to variation in overstory dominance, an indirect expression of a longer moisture gradient presented by climate and microtopography. They inferred that drought stress produced more open canopies in the drier forests of eastern Washington, and that the reduced canopy dominance in turn produced more heterogeneous conditions within stands with respect to light, moisture, and soil temperature and chemical properties. In their study this translated into a greater range of habitats east of the Cascades crest at both stand and subregional scales, which was associated with longer compositional gradients, greater species differentiation along gradients (beta diversity), and higher alpha diversity. Their view was mostly supported by my findings. Canopy cover was most dense on average, and least variable across the subregion, in the Coast and western Cascades (Table 3). Stands were substantially more open on average and cover was more variable across plots in the eastern Cascades and Blue Mountains, and the Klamath was intermediate (Table 3). These trends in canopy characteristics paralleled patterns of beta diversity but not alpha diversity (Table 14) in both trees and shrubs. Although alpha diversities were lower in eastern than in western Oregon in my study, in contrast to del Moral and Watson (1978), this probably was because of exclusion of the herbaceous stratum.

Regardless of the exact mix of environmental factors that TREOCOV integrates, the variable was measured locally and expresses local site conditions more than do the climate variables, so the variable was appropriately included with the local subset of variables for variance partitioning. The variable's membership to the topography, disturbance, or climate subset is less clear, however.

Disturbance

The importance of disturbance--particularly human-caused--relative to other factors in controlling compositional gradients in plant communities has not previously been addressed in landscape- to regional-scale gradient analyses. Most investigators have confined sampling to mid- to late-successional stands that originated following fire or other natural disturbance. The small contribution of disturbance variables to TVE in my study (6-12%) (Table 8) was less than expected given the extreme range of conditions sampled: from stands <10 yr old on recently clearcut sites to natural, old-growth forests over 1,000 yr old. In fact, disturbance variables were most important in the Blue Mountains (12% of TVE, Table 8), where clearcutting is seldom practiced. The contribution of disturbance variables to TVE would have been even less, particularly in eastern Oregon and its subregions, if canopy cover was not included in the subset of disturbance variables--a questionable affiliation as discussed previously.

Clearcutting significantly influenced species gradients in the western subregions (4-6% of TVE), where such harvesting methods are commonly practiced, but was less important at the half-state level (2% of TVE in western Oregon) and at the state level (2% of TVE) (Table 12). Only in the western Cascades was clearcutting strongly correlated (0.527, axis 3) with any of the first four CCA axes (Table 10). Tree species scoring the highest along the clearcut axis at the state level were predominantly early-successional hardwoods (Alnus rubra, Acer macrophyllum, Rhamnus purshiana, Prunus emarginata, Robinia pseudo-acacia, Populus trichocarpa, Fraxinus latifolia, Cornus nuttallii), and some conifers whose ranges are restricted to lower-elevation forest west of the Cascade crest (Picea sitchensis, Chamaecyparis lawsoniana). Highest-scoring shrub species along the clearcut axis were those associated with disturbed sites and forest openings and generally found at lower elevations in western Oregon: Ribes menziesii, Baccharis pilularis, Ceanothus thyrsiflorus, Pyrus spp., Cytisus scoparius, several species of Rubus (R. leucodermis, R. discolor, R. laciniatus, R. spectabilis, R. parviflorus, R. ursinus), Salix spp., Sambucus racemosa and S. cerulea, Vaccinium ovalifolium, Physocarpus capitatus, Corylus cornuta var. californica, Ribes sanguineum and R. bracteosum, Prunus spp., Acer circinatum, Holodiscus discolor, Oemleria cerasiformis, and Rhus diversiloba.

Time since major disturbance, to the extent it is reflected in stand age, was more important in explaining compositional gradients in eastern Oregon (4% of TVE) and its subregions (4-7% of TVE) than in western Oregon (2% of TVE), where stand age was significant only in the Klamath subregion (4% of TVE) (Table 12).

Nowhere was stand age important in either of the first two CCA axes, and only in the eastern Cascades was age strongly correlated with CCA axis 3. Age was important on axis 4 in the Blue Mountains, in both half-states, and at the state level (Table 10). The secondary importance of stand age likely is because of the fact that species presence, rather than relative abundance, has the strongest influence on ordinations at subregional to regional scales. While empirical evidence is scanty, existing studies suggest that disturbance exerts its influence on the relative abundances of species within a local area, and that few species are completely eliminated from a site by disturbance in general or by logging in particular (Bailey et al. in prep., Bolsinger et al. in press, Halpern and Spies 1995; Ohmann and Bolsinger 1991). Most species that are early invaders on disturbed sites are herbaceous (Bailey et al. in prep., Halpern and Spies 1995), and were not included in my study.

Tree species scoring lowest along the stand age axis were Cercocarpus montanus, Alnus rhombifolia and A. rubra, Cupressus bakeri, Fraxinus latifolia, and Populus trichocarpa. Shrub species included Ribes menziesii, Baccharis pilularis, Ceanothus thyrsiflorus, Rubus spp. (R. laciniatus, R. discolor, R. leucodermis, R. spectabilis), Cytisus scoparius, Salix spp., Crataegus spp, Pyrus spp., Rosa eglanteria, Myrica californica, and Sambucus racemosa. Highest-scoring tree species were Chamaecyparis nootkatensis, Tsuga mertensiana, Taxus brevifolia, Abies amabilis, and Abies magnifica var. shastensis. The low contribution by stand age in explaining community composition at the regional scale addressed in my study is consistent with the findings of Spies (1991) and Spies and Franklin (1991), who found ecological differences among physiographic provinces more important than stand age in explaining many aspects of community composition in Douglas-fir forests of Oregon and Washington. This is not to say that stand age does not control other important characteristics of ecosystem structure and function that were beyond the scope of my study.

The low amounts of species variation explained by stand age and clearcutting may in part reflect the inadequacy of these measures in capturing the relevant influences of disturbance on community structure. The identification and measurement of appropriate attributes of site disturbance history and successional development are especially problematic in regional studies. Inconsistencies across the component plot datasets limited the disturbance measures available for analysis. Where both stand age and clearcutting were included in CCA (Oregon, western Oregon, and the Klamath subregion), their vectors occupied different positions in the biplots (fig. 8). This is to be expected if one assumes that kind of disturbance is an important influence on successional trajectory. Stands of a given age in my study arose from a wide array of disturbance histories. In addition, the analysis did not distinguish between overstory and understory tree species composition. Relative abundance (cover) values for overstory and understory trees were combined by species for analysis, which may have masked some successional changes in community composition.

The geographic and environmental distribution of vegetation plots in my study also confounded attempts to distinguish the effects of clearcutting from elevation. The two variables occupied nearly identical vectors in the CCA biplots for most geographic areas (fig. 8). Stand age, on the other hand, was positively correlated with elevation but the two variables occupied different vectors in the CCA biplots (fig. 8). The tight coupling of the clearcutting and elevation vectors probably was an artifact of sampling. Virtually all plots on nonfederal lands at lower elevations have been heavily disturbed by logging, and most stands are very young. Plots on National Forest lands were higher in elevation (Table 17) and almost all were placed in older, natural stands. An ideal sample would be evenly distributed across the multivariate space defined by stand age and disturbance history. In reality, however, very little of the forest landscape at any elevation is in early successional, natural forest (Hansen et al. 1991), and late-successional forests at low elevations are virtually nonexistent. The vegetation dataset could be made more balanced, however, by the addition of samples from young, managed stands at higher elevations.

I conducted several supplementary analyses in an attempt to control for major climatic sources of species variation, thereby reducing sampling influences, and to explore disturbance effects more explicitly. Separate CCAs were conducted for plots within strata defined by subregion and by 500-m elevation classes. However, contributions of disturbance variables (AGE and CLEARCUT) did not differ in any consistent way from analyses on the unstratified data. Two additional CCAs were conducted on plots <500 m elevation in the Coast and western Cascades subregions, which I stratified by stand age (0-39 yr and 40-79 yr). Again, contributions of the CLEARCUT variable were unchanged or even less than in CCAs of the unstratified data. Similarly, CCAs where variation attributed to AGE was partialled out (AGE was treated as a covariable) yielded no change in the importance of clearcutting.

These attempts to isolate disturbance effects still appear to have been thwarted by limitations of the sample, which was revealed in a more in-depth look at species-level responses. For the western Cascades subregion, I computed mean cover for widely distributed (≥5% constancy) tree species on cut and uncut plots (Table 19), where the CLEARCUT variable was significant in the CCA model for trees but not for shrubs. Of the six species that scored lowest on the CLEARCUT axis, only one species occurred on one plot that had been clearcut (Table 19). Even for the six highest-scoring species on the CLEARCUT axis, differences in mean cover between cut and uncut plots were only marginally significant for three hardwoods (Alnus rubra, Acer macrophyllum, and Rhamnus purshiana) (P=0.02-0.04), which increased with clearcutting, and for Pseudotsuga menziesii (P=0.02), which decreased with clearcutting (Table 19). Mean elevation of clearcut plots was lower than uncut plots, and species scoring lower on the clearcutting axis occurred at much higher elevations than those with high scores (Table 19). In conclusion, the geographic and environmental separation of cut and uncut plots in this dataset precluded any solid conclusions about the role of disturbance and succession on regional patterns of community composition. Nevertheless, results suggest that

Table 19.--Mean elevation, mean (standard error) canopy cover, P-values (PROC GLM) (SAS 1990), and sample size (N) of widely distributed tree species (constancy ≥5%) scoring highest and lowest on CLEARCUT axis, for clearcut and uncut plots <80 years old in the western Cascades subregion.

	Mean Elevation (m)		Mean (SE) Percent Cover			N	
Species	Uncut	Cut	Uncut	Cut	P	Uncut	Cut
Lowest CLEARCUT scores:							
Pinus contorta	1557	--	20.4 (5.0)	--	--	25	0
Abies magnifica var. *shastensis*	1543	--	30.9 (3.9)	--	--	23	0
Pinus lambertiana	921	--	6.3 (1.1)	--	--	44	0
Tsuga mertensiana	1518	--	28.8 (3.0)	--	--	66	0
Abies amabalis	1285	--	24.9 (2.3)	--	--	113	0
Pinus monticola	1356	823	5.5 (0.6)	2.0 (NA)	--	66	1
Highest CLEARCUT scores:							
Alnus rubra	547	469	7.1 (2.1)	15.2 (2.5)	0.03	21	36
Acer macrophyllum	581	410	8.3 (1.3)	14.5 (2.4)	0.02	73	40
Rhamnus purshiana	516	365	2.9 (0.7)	8.4 (3.9)	0.04	28	11
Arbutus menziesii	792	459	4.0 (0.6)	4.4 (1.7)	0.79	42	9
Pseudotsuga menziesii	899	496	43.0 (1.3)	35.7 (3.0)	0.02	345	77
Thuja plicata	707	510	14.0 (1.3)	15.0 (4.3)	0.79	111	20

disturbance effects on patterns of tree community composition in the landscapes studies have thus far been relatively minor.

Geology

Geology was second only to climate measures in explaining regional compositional gradients (Table 8). A greater number of geology variables were significant at broader spatial scales, from one to three at the subregion level to seven at the state level (Tables 10 and 12). Geologic variables contributed most to TVE in western Oregon (19%) and in the Klamath, western Cascades, and Blue Mountains subregions (18-19%) (Table 8). However, as hypothesized, geology played a secondary role in controlling species variation: geology variables were never important in the first CCA axis in any geographic area, and were important in the second CCA axis only in the Coast subregion (depositional substrates) (fig. 8). Ultramafic parent materials were strongly correlated with axis 3 in the Klamath subregion, western Oregon, and at the state level, and with axis 4 in the Blue Mountains subregion (Table 10). Four of the 13 geological types were most strongly correlated with compositional gradients for woody species: ultramafic rocks; mafic rock of the Pliocene and later; mafic pyroclastic rock, ash, ejecta, and vent deposits of the Pliocene and later; and depositional soils (Table 12, fig. 8). My study could not determine which properties of the parent materials influenced community composition.

Within-Region Variation in Patterns of Community Structure and Environment

An important finding, although not unexpected, was the degree of contrast in species-environment associations that was observed among the geographic subregions. As observed by Whittaker (1960), coenocline differentiation (community change along environmental gradients) is a complex expression not only of the range of environments that occur in a place, but also of the kinds of communities that develop in those environments. Results illustrated that geographic areas within Oregon differ in several important ways: community- (plot-) level structure (number and identities of species present); subregion-level attributes (beta diversity, gamma diversity, and species-area relations); and environmental correlates of these vegetation patterns. Yet my study demonstrated that despite strong contrasts among subregions, it was still possible to characterize patterns of variation in community composition and environmental correlates in a unified way at a regional scale. This lends credence to the idea that apparent contradictions in findings among landscape-scale vegetation studies can be attributed to real differences in species and ecological relations among places, as well as to the scale of analysis.

Whereas subregions were delineated *a priori* for my analysis, boundaries closely followed widely accepted geographic boundaries. An alternative approach, which could be pursued in future analyses, would be to use results of the state-level analyses as the basis for subregion delineation.

Overall, the greatest contrast in vegetation was between the more maritime, moist climate of the Coast and western Cascades and the drier, continental climate of the eastern Cascades and Blue Mountains. The Klamath subregion was intermediate in character, showing affinities to the western subregions for some ecological characteristics and to the eastern subregions for others. This reflected the Klamath's "central" nature to forest flora of the western U.S. from both historical and climate perspectives (Whittaker 1960).

I have discussed the subregional differences in the relative importances of various environmental factors in explaining species variation earlier in this paper. Chief among these was the greater influence of moisture conditions in eastern Oregon, reflected in greater contributions of precipitation, local topography, and canopy cover variables to the ordinations. Overall findings also suggested that vegetation complexity from several perspectives and scales increases from the equable, maritime climate of the Coast to the more erratic and drier climate of eastern Oregon. Beta diversity increased markedly from west to east (Table 14), for both tree and shrub strata, as has been observed in other vegetation studies in the Pacific Northwest (del Moral and Watson 1978, Whittaker 1960). In contrast to these studies, however, alpha diversity was higher in western Oregon, especially in the western Cascades and Klamath subregions, and lowest in the eastern Cascades and Blue Mountains subregions, for both tree and shrub strata (Table 14). This can be explained by the exclusion from my study of herbaceous species, the most species-rich of the vegetation strata. Gamma diversity, the total number of species sampled within the subregion, did increase and decrease in parallel with alpha diversity (Table 14). Many more species were "rare" in eastern Oregon, as well, which is discussed in more detail later in this paper.

My study findings support the observation by Whittaker (1960) that the extent of change in community composition (beta diversity) was correlated with the extent of environmental contrast along the topographic-moisture gradient. This was corroborated by the spatial complexity of vegetation patterns observed in eastern Oregon, as well, as discussed previously. Variation was finer-grained (fig. 12), probably because of the greater importance of local factors such as topography and its role in moisture stress. Also, community types were more intermixed in eastern Oregon and more segregated in western Oregon (fig. 17).

Sampling and Scale Effects

The two major origins of community structure as observed through direct gradient analysis are interactions between organisms and their environment, and sampling imperfections (Gauch 1982). Several aspects of the latter deserve comment.

Sample Size and Rare Species

The relations that I observed between sample size (numbers of plots), numbers of species, total inertia, and amount of variance explained (fig. 7) suggest that CCA comparisons must be approached with caution, because sample size confounds interpretation. Del Moral and Watson (1978) reported similar problems in comparing geographic areas because of the effects of high or even moderate beta diversity on their ordination methods, although CCA was not available at that time. It is inappropriate to compare the performance of CCA models by comparing magnitudes of variance explained. In other words, greater TVEs may be the result of either smaller sample sizes or of stronger associations between the species data and explanatory variables. Sample size did not seem to influence CCA biplots in terms of relative positions of species, plots, and principle axes, nor the lengths and directions of environmental vectors. I therefore limited comparisons of CCAs across geographic areas and species groups to these measures. The influence of sampling on assessments of community structure are well known (Hanski et al. 1993, Magurran 1988). Sampling issues as they pertain to CCA have not been addressed in the literature, however, and merit further investigation. Palmer (1993) found CCA to perform well on simulated datasets with properties that usually cause problems for DCA, but he did not address sample-size effects.

One likely mechanism behind the sample-size effect is that greater numbers of plots sample an increasing number of species as more "rare" species are encountered. Rare species may be those with small geographic ranges, narrow habitat specificity, or small, non-dominant population sizes (Rabinowitz 1981). Two almost universal "laws" in community ecology can account for this sampling effect: the species-area relationship and the positive relationship between species distribution and species abundance (Hanski et al. 1993). Current models of regional species distribution (Levins 1969, Brown 1984, Collins and Glenn 1991) predict that most species are locally distributed (regionally rare) and only a few species will be found at all sites. This large-scale model of species distribution represents a logical extension of intracommunity models to the regional scale (Collins and Glenn 1991). In addition, it has been documented for many taxa that species with more extensive distributions tend to be more abundant locally than species with more restricted distributions (Hanski et al. 1993). Because locally rare species are more difficult to detect than are locally abundant species, the number of sites at which a species is found with some fixed scheme of sampling is a monotonically increasing function of the average abundance of the species (Hanski et al. 1993). The increase in numbers of plots (and hence species) can be either through more intensive sampling within a study area of given size, or by sampling an increasingly larger area at a constant intensity. Broader geographic areas encompass a greater variety of habitats, and the frequency of occurrence of any given species would be expected to decrease. Adding species to a dataset increases the amount of inertia (total variation present in the species-by-plot data matrix) in CCA, but the very nature of the uncommonness of these species means their presence or abundance is unlikely to be explainable by available environmental variables. Hence, TVE would not increase, and actually would be expected to decrease as a proportion of total inertia.

It is an important distinction that the sample-size effect was not attributable purely to numbers of species, but rather to the shape of the frequency distribution of the species across plots (i.e., how many of the species are common and how many are rare; see fig. 13). The influence of rare species on CCA would be expected to vary among geographic areas according to the area's beta diversity and the particular shape of the species-area curve. In my study, both alpha and gamma diversity were higher in western Oregon, but beta diversity was higher in eastern Oregon (Table 14) and more species were rare (fig. 13). Since total inertia measures the dispersion of species abundances among plots, it is one indicator of relative numbers of rare vs. common species in the species-by-plot data matrix. Indeed, for each geographic area, total inertia was highest and TVE lowest for CCA of shrubs alone, whereas the CCA of all woody species included the greatest number of species (Table 9). For all species groups, species rarity increased with both geographic extent and with sampling intensity (number of plots per unit area) in my study (figs. 13 and 18). At the subregion level, 28-44% of species had constancies of <1%, whereas 50% of species were this rare at the state level.

At the state level, the shape of the frequency distribution of species occurrence (fig. 18) was consistent with Brown's (1984) model of regional species distribution and with other plot-level plant datasets that span regions similar in geographic extent to my study (reviewed in Collins and Glenn 1991). The effect of rare species on CCA results was more pronounced for shrubs than for trees, as there were nearly twice as many shrub species and a greater proportion were rare (fig. 13); at the state level, 15 (29%) of the tree species and 81 (55%) of the shrub species had constancies of <1%. Greater sampling intensity within a constant geographic area also was associated with increased species rarity (and TI): a greater proportion of species were rare in the entire 10,000-plot dataset than in the 2,443-plot subsample (fig. 18). Many of the mechanisms proposed to underly the species-area and distribution-abundance relationships (Connor and McCoy 1979, Hanski et al. 1993) probably contributed to the patterns of species abundance observed in my study. More research is needed to understand regional patterns of species distribution and abundance.

Effects of Geographic Scale

In this discussion, "scale" refers to geographic extent. Because numbers of plots and species increased with increasing geographic extent, differences in TVE among geographic areas of different size could not definitively be attributed to changes in geographic scale. Different sample-sizes aside, one might expect lower TVEs at broader geographic scales (Table 9), because of the stronger role that historic factors such as speciation and climate change play at broader scales of analysis. Such factors are problematic to quantify or assess, and were poorly or only very indirectly represented in the explanatory variables of my study.

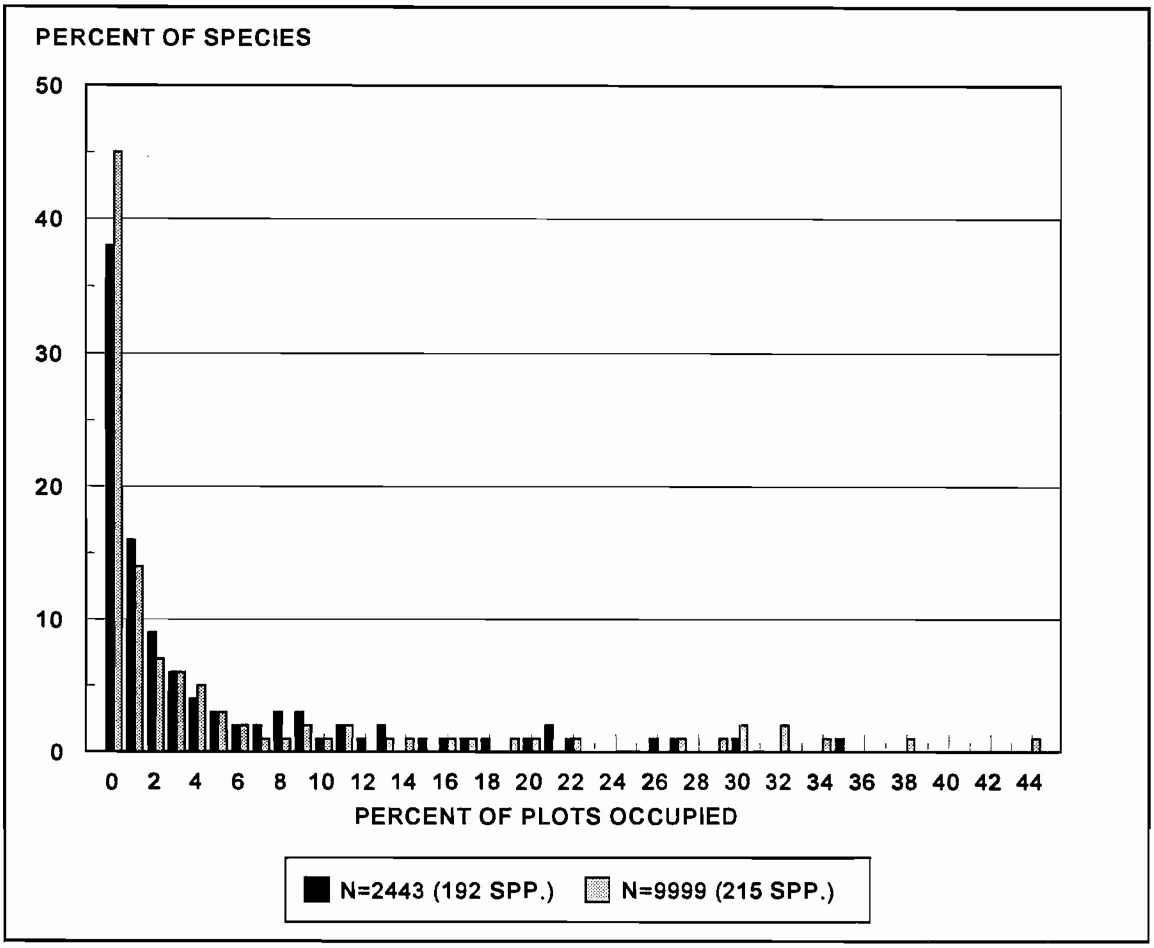


Figure 18. Distribution of woody plant species by constancy (percent of plots occupied) in Oregon, for 9,999 plots and for a subsample of 2,443 plots. Does not include Pseudotsuga menziesii (occurs on 62% of 2443-plot sample and 76% of 9999-plot sample).

Conversely, TVEs might be expected to be higher at larger geographic scales because of the greater importance of climate, which was well-represented in the explanatory variables.

The influence of geographic extent on CCA results can be evaluated by the degree to which proportions of TVE contributed by different variables change with geographic scale of analysis. Although the relative contributions of different variable subsets were most strongly influenced by ecological differences among geographic areas, some effects of geographic extent were observed (Table 8).

Contributions of variable subsets that reflect local conditions and controls over species composition were more important at smaller geographic scales of analysis (Table 8). Furthermore, community composition was more responsive to local measures in eastern Oregon, where climate is more stressful. Topographic variables showed the clearest scale effect: $(\{L1\}|\{L2 \cup R1 \cup R2\})$ increased with decreasing geographic extent, from 4% at the state level to 6%-8% at the subregional level (Table 8).

The contribution of local factors to TVE was small even at the subregion level, the finest geographic scale of analysis (Tables 8 and 12). This suggests that broad-scale factors, climate in particular, are the primary drivers of community-level composition across the range of spatial scales addressed in my study. It is likely that local factors would assume greater significance at much smaller geographic scales. I explored this hypothesis by conducting CCAs on five datasets consisting of plots with five EMAP hexagons, which at 63,500 ha still are larger than many landscape-scale studies. Unfortunately, small sample sizes (N between 21 and 55) caused unstable results. Very few explanatory variables were significant, and SOLAR was added in only one of the models.

It also is likely that some compositional patterns occur on scales finer than those reflected in the explanatory variables (Okland and Eilertsen 1994), which could account for some of the unexplained variation in the species data. Explanatory variables used in my study were weighted heavily towards macroclimate, which may be more important at broader scales and more relevant to trees than shrubs. Even the finest-scaled environmental variables, the topographic variables and overstory cover, do not express within-plot variation. The assumption that environmental variables are constant within a site is a major limitation of CCA, and a general problem of all direct gradient analyses (Palmer 1993). In particular, measures such as soil properties (e.g., nutrient availability, pH, texture, depth), litter, down logs, and presence of canopy gaps resulting from fine-scale disturbances such as windthrow show considerable within-stand variation and affect community structure, but were not accounted for in my study. One might expect shrubs as a group to respond to finer-grained variation in the environment than trees because of their smaller stature, greater number of species, and greater variation in life history characteristics represented. This could explain higher TVEs for trees than for shrubs, but this is obscured by the effects of differences in numbers of species.

Resolution of the Species Data

The question of optimal transformation of species abundances in CCA has not yet been fully addressed (M. Palmer and R. Neilson, pers. comm.), but clearly will hinge on study objectives. Transformation changes the grain of the data, which amounts to changing the scale (Allen and Starr 1982, p. 137). Relative abundance, log- or square-root-transformed abundance, and presence/absence fall along a continuum from heavy weighting of dominant species to equal weighting of all species. Logarithm and square-root transformations dampen but do not remove the effects of dominant species. Relative abundance emphasizes peaks in species performance, thus focusing analysis on the effects of short segments of multivariate environmental gradients; whereas presence emphasizes a coarse environmental grain at the mean tolerance range for the species (Allen and Starr 1982). Because presence of a species reflects survival and integrates conditions over a longer time period, presence/absence may be a more relevant metric for studies that address broad spatial scales or longer timeframes. In their study in the west-central Cascades of Oregon, Zobel et al. (1976) noted that within vegetation zones most species were widely distributed, and that shifts in their relative abundance were the basis for community differentiation except on the most extreme sites. Spies (1991) and Spies and Franklin (1991) made the same observation in their study of Pseudotsuga menziesii forests. In contrast, species turnover along gradients in my study was substantial (9.629 SDs in DCA at the state level) (Table 15), and positions of plots in the ordinations were strongly influenced by which species were present. This may partially explain the secondary importance of local factors such as topography, disturbance, and overstory canopy cover in explaining compositional gradients at the regional and subregional scales in my study. Use of log-transformed cover in my study was a compromise. A CCA of all woody species at the state level using presence/absence yielded very similar results to log-transformed cover.

Limitations and Sources of Unexplained Variation

Community data are notoriously noisy, containing much variation in species' abundances not coordinated with other species' abundances (Gauch 1982). Biological, statistical, and sampling causes of noise are numerous and complex, and it is typical to explain only 10-50% of species variation in gradient analysis (Gauch 1982, Palmer 1993). Explained variation in my study fell on the low end of this range, probably because of the large number of plots and species, and high beta diversity (inertia), in the dataset (see earlier discussion of sample size and rare species). Investigators commonly remove outliers (species or plots) and rare species, which contribute to high species variation, from their datasets. Very few plots in my dataset were established in special habitats (coastal dunes, serpentine soils, pumice soils, and subalpine areas being a few exceptions). These plots as well as those at the extreme ends of environmental and compositional gradients were retained in my study. Exploratory analyses that removed plot outliers did not appreciably change the CCA results.

Given the large size of the vegetation dataset, and the great number of individuals involved in its collection and management, errors in species identification and coding are inevitable. The sheer size of the dataset renders such errors insignificant insofar as their effect on overall conclusions. Limitations of CCA (and multiple linear regression in general) are the assumption that relevant independent (environmental) measures were used, and that the independent variables are measured without error, when in fact there exist several known and unknown sources of error in data for my study. Particularly worth mentioning are errors in the geographic locations of plots (both accuracy and precision). Locational errors translate into errors in values of the climatic and geologic variables assigned to the plots. Of course, those digital data contain errors of their own.

There were several important gaps in the study data. The most notable sampling gaps were reserved areas (parks and wildernesses) and managed forests on federal lands at higher elevations. Soils data, which were unavailable for all plots, were perhaps the most serious omission in terms of potentially important explanatory variables. Characteristics such as nutrient availability, pH, texture, and depth have been shown to be associated with vegetation patterns in many locations, although usually at a secondary level, and their omission certainly contributed to the unexplained variation of my study. For example, in areas of limited moisture Pinus ponderosa is more common on coarse-textured soils, probably because roots can better develop (Franklin and Dyrness 1973). The geologic map used in my study (Walker and MacLeod 1991) provided only an indirect approximation of site-level soil conditions. Furthermore, the digital version does not show locations of ash deposits. These deposits are known to be a particularly important influence on vegetation pattern within portions of the eastern Cascades subregion--i.e., the Pinus ponderosa-Pinus contorta complex on Mazama pumice in south-central Oregon. Also important to forest community structure in central Oregon are frost pockets in local microtopography that would not register in the 500-m-resolution temperature data. Nonetheless, CCA successfully captures relations in available data even when important environmental variables are left out (Palmer 1993).

Lastly, it is important to remember limitations on the study and interpretation of results that are imposed by the scale of the observations. Although the purpose of my study was to infer regional-scale pattern, observations of community structure were based on field plots of specific size and shape. A further complication was that plot sizes and configurations varied among the component datasets and thus with geographic location (Table 4, Appendix 1), a fact that was ignored in the analysis. Other sampling and measurement approaches may in fact be better suited to many of the ecological questions addressed in my study, and such issues are topics of needed research. Fire history, through interactions with site and species, certainly plays a strong role in regulating community composition, yet regional data were unavailable.

Summary of Research Hypotheses

My findings as they relate to study objectives and hypotheses are summarized below.

Objective One

Temperature and moisture, as expressed in macroclimate, are the primary factors controlling regional patterns of community composition. Temperature is most important in differentiating forest zones. Study findings for all locations and geographic scales generally supported the hypothesis of the primary importance of climate in explaining regional species variation. This was true of results from CCA with variance partitioning, stepwise CCA, and analysis of positions of the growth forms in ordinations. Contrary to what was hypothesized, community types were separated along both temperature and moisture axes that defined an environmental field, and the eastern Oregon types showed greater separation along the moisture axis.

Macroclimate contributes more to explained variation at larger geographic scales than at smaller scales. Contributions of regional measures were strong at all scales addressed in my analyses, and did not increase with scale as hypothesized.

Local factors are secondary to climate at the regional level, but contribute more to explained variation at smaller scales. This hypothesis generally was supported by my findings. Topographic and disturbance variables contributed relatively little to explaining variation in species composition across Oregon, and contributions of local measures were weaker at the state level than at the subregional level as hypothesized. However, only the topographic measures showed the expected scale effect. Evaluation of the role of disturbance was hindered by the inadequacy of the available disturbance measures in capturing relevant influences on community structure, and by sampling effects.

Substrate is a secondary control on community composition at broad (regional) spatial scales, but may assume local importance. My findings supported the hypothesis that geology is secondary to climate measures in explaining regional compositional gradients. It was not possible to analyze the contributions of geology at local scales.

Moisture assumes greater importance in eastern Oregon and at lower elevations in western Oregon, where climate is drier. This hypothesis was strongly supported by my findings. The greater importance of moisture in explaining species gradients in eastern Oregon, indicated by the greater contributions of precipitation, local topography, and canopy cover variables to the ordinations, was a key finding of this study. Relative contributions of variables among areas within western Oregon were not be assessed in the analysis.

The influence of microclimate, topography, and substrate on community composition is stronger in eastern Oregon and to a lesser extent the Klamath subregion, where climate is more stressful, particularly because of moisture limitations. Effects are most muted nearest the coast and in northwest Oregon, where climate generally is more benign. This hypothesis was supported by my findings for microclimate and topography, but not for substrate (geology). Local factors were especially strong contributors in the Blue Mountains subregion and in eastern Oregon. Contributions of local factors were weakest and regional factors were strongest in the Coast subregion. Contributions of geology variables were not associated with climatic stress.

Tree growth forms and species more faithfully reflect regional gradients than do shrubs. This hypothesis generally was supported by results from both gradient and classification analyses. Trees and shrubs responded similarly to the environmental variables available, but less variation in shrub species was explained. Shrub response to regional variables was moderated by overstory cover. Tree species on average were more widely distributed regionally and more locally abundant, and as a group had lower beta diversities than shrubs, and thus were more amenable to regional gradient analysis. Further analyses of stratum differences are warranted.

Community types at one level in a classification are analogous to the series level in site classification and to the forest zones of Franklin and Dyrness (1973). This hypothesis generally was supported for western Oregon but much less so for eastern Oregon, where the types also were less distinct geographically and within a temperature-moisture field. This was consistent with results from the gradient analyses, which indicated that tree species responded fairly faithfully to regional climatic gradients and much less so to disturbance.

Objective Two

Rate-of-change in community composition varies geographically and is not constant. Steeper gradients (sharper ecotones) alternate with areas of relatively little change. This hypothesis was supported by my findings. Presence of ecotones were indicated by zones of rapid change in the ordination scores as well as by transitions between mapped community types.

Ecotones in community composition coincide with steep environmental gradients. The hypothesis that ecotones correspond to gradients in environment is problematic to address, but was supported by my findings in a general sense. The dominant directional trends and locations of steep species gradients corresponded to major climate gradients and physiographic features. Exceptions to this rule pose interesting areas for further research.

IMPLICATIONS FOR CONSERVATION AND RESOURCE MANAGEMENT

Findings from regional-scale ecological research can be brought to bear on a wide array of problems in conservation and natural resource planning and policy. Regional studies such as this one provide context and a scientific basis for both research and management efforts at finer landscape and watershed scales. Understanding the structure and function of communities and ecosystems along environmental gradients will improve the ability to manage these systems.

Regional Biodiversity Conservation Strategies

Regional gradient studies in general, and my study in particular, provide important new information for regional- to local-scale planning for the conservation of biological diversity. Long-term maintenance of diversity requires a strategy that considers regional biogeography and landscape pattern above local conditions (Noss 1983, 1987). Study findings and data are particularly relevant to coarse-filter approaches (TNC 1982), which involve establishing a set of reserves that contain representative examples of the various types of communities within an area. The assumption is that, if the array is reasonably complete, it will protect populations of most species. Representative reserves also serve a function as baselines for evaluating experiments in ecosystem management. Findings from my study provide a regional-scale, empirical basis for identifying the types, locations, and extents of forest communities, for quantifying variation within the types, for identifying important ecotones in community composition and environment, for evaluating the degree to which a particular site is representative of conditions across a broader region, and for considering diversity at a range of levels from alpha (within-stand) to beta (across gradients) to gamma (within a region).

My study data possess several strengths for potentially improving upon current coarse-filter approaches (Hunter 1991): they spanned environment and species gradients across upland forests of all ownerships; they considered both communities and the physical environments they occupy (i.e. was "ecosystem-based"); they provided fine-resolution information on the regional-scale distributions of species and communities that cannot be obtained with remote-sensing methods (indeed, the data could be used to characterize mapped polygons based on satellite or other data); and they provided plant community information below the level of the tree overstory. Interestingly, study results suggest that disturbance and succession may be less of a confounding factor than has commonly been thought (Hunter 1991), at least from a regional perspective of species gradients in woody plant communities, and especially if the conservation strategy adopts a long-term view. Findings do not discount the critical importance of considering disturbance in the management of local landscapes and reserves, however.

An early step in focusing a coarse-filter strategy often is to delineate biophysical regions, or ecoregions. Ecoregions generally define relatively homogeneous units based on their climate, landform and geology, and potential vegetation. Ecoregion maps provide a geographic framework, or stratification tool, for a variety of activities that, in addition to conservation planning, include resource management, ecosystem modeling, inventory and monitoring, and ecological and resource assessment. As such, ecoregions can provide an important link between regional- and landscape-scale studies. Whereas subregions were delineated *a priori* for my study, data and results provide a strong quantitative and empirical basis for more in-depth analyses aimed specifically at delineating ecoregions within Oregon's forested uplands, in cases where more explicit consideration of vegetation pattern is desired. Most ecoregion mapping efforts published to date have been conducted at a considerably broader, continental scale (e.g., Bailey 1995). Published maps of comparable extent to my study in the Pacific Northwest (Franklin and Dyrness

1973, Omernik and Gallant 1986) have incorporated only very generalized information on vegetation.

The next step often advocated in a coarse-filter conservation approach is to inventory communities in relation to existing reserves in order to identify "gaps" in protection (Scott et al. 1987, Scott et al. 1993). Comparisons between current and historical (pre-European settlement) conditions also help identify vegetation types that have experienced greatest declines (e.g., Noss et al. 1995). Attention also must be given to conditions in the landscape matrix--the complex of semi-natural lands within which most reserve systems will be embedded (Franklin 1993, Hunter 1991, Noss and Harris 1986). These ecosystems have been subject to intensive uses such as logging or grazing but still remain essentially natural ecosystems. Information on woody plant communities from my study provide a basis for gap analysis and reserve selection, as well as for characterizing biodiversity across the landscape matrix.

A major challenge to ecosystem management is planning for a mix of land uses and values across a regional landscape that encompasses land ownerships with differing management objectives. An important issue in the western United States is the roles of federal and nonfederal lands in providing these benefits. My study is the first to provide quantitative information on patterns of species composition in forests across all ownerships in the State, and thus provides valuable biodiversity information to policymakers. Of particular interest from a regional perspective are areas of contrast in vegetation between federal and nonfederal forests. Most notable in my study were the two ends of the elevational gradient. Current reserves, as well as other areas where biodiversity conservation is a management objective, are concentrated almost exclusively on federal lands, where high-elevation types are overrepresented regionally and low-elevation types are underrepresented. This has implications for the conservation of forest communities and species concentrated at lower elevations and on nonfederal ownerships across the state, especially in western Oregon. Broad segments of regional gradients in community composition currently are not protected in reserves, nor even contained on federal lands where management for biodiversity conservation is more likely, so baselines for evaluating effects of forest management activities are lacking. Contrasts between forest communities on federal and nonfederal lands are less in eastern Oregon, where the community types intermix at a finer scale and are less segregated elevationally and geographically. This implies that appropriate spatial configurations of habitat patches and corridors will differ across the regional landscape.

Caution is advised in applying study results to regional conservation strategies. Whereas it is tempting to use information on geographic distributions of woody plant species and communities as a basis for biodiversity planning, it is largely unknown to what degree these patterns coincide with those of other taxa. It is hypothesized but unproven that plant communities can be used as surrogates for other species that are difficult or expensive to measure and monitor directly, and some evidence indicates plant communities are poor surrogates. The simultaneous consideration of physical environment--climate, geology, and topography--improve the odds that forest ecosystems identified in my study are relevant to other organisms. For example, in the Pacific Northwest the diversity of forest vertebrates is strongly associated with elevation (Harris 1984) and probably ecosystem productivity.

Planning for Global Climate Change

Study results also provide a basis for planning forest management and conserving biodiversity under alternative future scenarios of global change. My study quantified relations of species and communities with current climate, which provides a strong empirical basis for modeling efforts that predict future patterns under altered climate, but not under changing atmospheric concentrations of carbon dioxide. Also, some have argued that reserve design should capture the range of variation in physical environment (landform, geology, soils), as the particular suite of species and communities occupying those sites is dynamic (Hunter et al. 1988). My study provides information relevant to such an approach.

Monitoring Biodiversity in Forest Ecosystems

Findings from my study have several implications for regional inventory and monitoring efforts, and hence regional assessments, that consider biodiversity. These recommendations are part of an adaptive management loop: inventory plot data were used in this analysis, and the analysis provides the basis of recommendations for continuing inventory efforts. My recommendations are aimed primarily at extensive, sample-based inventories.

My study reinforces the value of collecting biodiversity data that are reasonably consistent across all lands, spanning boundaries between ownerships as well as biophysical boundaries at the biome and finer scales. Major limitations were imposed on my study by gaps in data for forest lands in reserved areas (parks and wildernesses), BLM lands in western Oregon, and managed stands on National Forests, for example. During the course of my study, the permanent sampling grid of plots was extended across federal lands, a major step forward for future analyses. However, it would be extremely useful if vegetation were sampled across boundaries between forest and other biomes, most notably the shrub-steppe and other grasslands, as well. Monitoring shifts in these ecotones, hypothesized to be important indicators of changing climate and other land-use practices, currently may be accomplished using remote sensing, but regional-level species data are unavailable.

Consistency in plot design and data elements across ownerships and biomes also is critical to regional biodiversity assessments. For example, newly established plots on the permanent grid will lack data on the forest understory, which is a major limitation. A key finding of my study was the contrasting responses of tree and shrub strata to environment, and differences likely are even more pronounced for herbaceous species. Other key elements missing from some or all of the plots that would add greatly to regional biodiversity studies such as this one are data on a plot's soils, topographic position, landscape context, and disturbance history.

Findings from my study underscore the critical importance of accurate tallies of species presence/absence on a plot, as opposed to obtaining precise and accurate measures of species relative abundance, at least from the perspective of regional gradient analyses. This view is tempered somewhat as it pertains to the remeasurement of permanent plots, where successional changes in relative abundance become more critical.

Finally, regional gradient analyses such as my study provide a basis for considering plant communities in the delineation of ecoregions, as discussed earlier. These ecoregions can be used as a sampling framework for inventories, and as the basis for stratifying plot data for ecological analysis and assessment.

CONCLUSIONS

My study represents the first quantification and synthesis of vegetation-environment gradients across Oregon's forests based on an empirical dataset. Findings generally were consistent with, and provide a broader context for, the divergent results from ordination and classification studies at smaller, landscape scales across the State. Patterns of variation in species composition across the region were complex and multidimensional, and the relative importance of climate, geology, topography, and disturbance factors in explaining species variation shifted with location, geographic scale, and vegetation stratum.

Broad-scale climate was the primary control on community composition at all scales examined. At the state level, the two dominant gradients were temperature-moisture complexes: continentality (CCA axis 1) and moisture stress during the growing-season (CCA axis 2). This was an emergent property at the regional scale to the extent that the relative contributions of various factors diverged at finer geographic scales of analysis. At all scales and locations, geology, topography, and disturbance were significant but secondary factors in explaining species variation.

Whereas the relative importance of regional and local explanatory factors shifted somewhat with geographic scale of analysis, community composition was more strongly related to geographic location. The most striking contrast in vegetation within the region was between the wetter and more maritime climate of the Coast and western Cascades in northwest Oregon with the drier and more erratic climate of eastern Oregon. The Klamath subregion of southwest Oregon was intermediate in vegetation character, showing some affinities with northwestern and some with eastern Oregon. In eastern Oregon, both climatic and topographic moisture were substantially more important in explaining compositional gradients, and local site factors assumed greater importance in the drier and less equable climate, as hypothesized. Elevation and topographic effects were minimal in areas where climate is most benign, especially in the Coast subregion. Although there were fewer species in eastern Oregon at both alpha and gamma levels, compositional gradients were longer, species turnover along gradients (beta diversity) was greater, and more species were rare. This could in large part be attributed to the area's finer-scale heterogeneity in environment and to the greater importance of moisture and of local factors (topography, disturbance, and canopy cover as an integrator of both site moisture and the sub-canopy light environment). These differences were more pronounced for shrubs than for trees.

Geographic patterns of compositional gradients generally tracked spatial variation in the environment. With a few exceptions, which pose interesting areas for further research, major ecotones in community composition coincided with the major physiographic and climatic features in the State.

Results suggest that disturbance is of only secondary importance in explaining regional compositional gradients in Oregon, but limitations imposed by sampling indicate that further investigation is warranted. In particular, research is needed into successional patterns based on the remeasurement of permanent plots, or at minimum based on chronosequence data that are better balanced across the major disturbance and environmental gradients.

The environmental variables employed in my study were more successful in explaining patterns of community composition in western than in eastern Oregon. My study findings also suggested that trees respond more faithfully to regional environmental gradients, particularly climate. Attempts to explain species variation were less successful in eastern Oregon and for shrubs, cases where beta diversity (species turnover along gradients) was greater and patterns of variation appeared finer-grained and more complex.

Much of the species variation across the community samples was unexplained in my study, which is not unusual in gradient analyses of forest vegetation. Nevertheless, spatial structure in the species data that was uncorrelated with the explanatory variables, as well as the longer gradient lengths for indirect (DCA) than for direct (DCCA) gradient analyses, suggest there is potential to improve the CCA models. This was especially true for eastern Oregon. The greater amounts of spatial structure found at broader geographic scales may be attributable to regional-scale historical processes, such as species evolution and migration and climate change, that are problematic to incorporate in regional gradient analyses.

Findings from my study provide a strong quantitative and empirical basis for generating hypotheses about regional vegetation patterns that could be tested in a variety of ways. Additional CCAs could be performed in a formal hypothesis-testing, rather than exploratory, framework using another independent, random subsample of the 10,000-plot vegetation dataset. However, more research is needed on the influence of sample size and rare species on CCA and on the interpretation of results, particularly in the context of regional studies spanning long and complex gradients. Hypotheses could be tested through regional experiments or field trials, as well, to determine mechanisms driving patterns observed in my study. Multivariate analysis of community data is no substitute for experimentation, but it has its own unique advantages, and the strongest research strategy employs both approaches. Much information remains to be exploited through additional exploratory analysis of the dataset compiled for my study. Indeed, my study illustrates the tremendous potential for employing dual approaches of multivariate and geographic analysis of community patterns based on extensive, plot-level datasets.

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APPENDICES

Appendix 1--Sources, Dates, and Sample Designs of Vegetation Datasets

Inventory and Economics (IE) Inventory Plots

Source.--Manuals for field procedures and inventory compilation for Occasion 3 w. Oreg., Occ. 2 w. Oreg., Occ. 2 treatment opportunity plots in w. Oreg., Occ. 3 central Oreg. regression plots (1986), Occ. 3 central Oreg. and Blue Mtns. On file with Inventory and Economics RD&A, Portland Forestry Sciences Lab, Portland, OR.

Dates.--1984-1986 (western Oregon), 1986-1987 (eastern Oregon).

Sample design.--Field plots established on all lands except NFs, BLM lands in w. Oreg., and reserved areas. Plots sampled all forest land regardless of condition. Design is double sampling for stratification (Cochran 1977). Secondary sample was a grid of permanent field plots spaced at 6 K intervals. Grid was originally laid out on base maps in 1961 (w. Oreg.) and 1957-1969 (e. Oreg.), transferred to aerial photos, and then established on ground.

Field plot design.--laid out in relatively homogeneous vegetation as defined by size and density of overstory tree layer. Cover ocularly estimated by species and canopy layer. Layers were plot-specific, up to 3 tree layers and shrub layers, except where otherwise noted. Plot size and configuration depended on location and site:

Forest sites unsuitable for timber production (usually wet sites, some rocky sites), w. Oreg. and e. Oreg..--1-point 17-m radius circular plot; 908 m^2; 0.09 ha. Ocular cover estimates for all tree layers and shrubs.

Timberland, low productivity, oak and juniper woodlands; w. Oreg.--Cluster of 5 subplots over 2.7 ha. At each subplot: circular 5-m radius plot; 79 m^2 x 5 = 393 m^2 = 0.04 ha. Ocular cover estimates for all tree layers and shrubs. [Trackable tree tally not used in thesis data base: circular 2.35-m radius plot for trees <12.5 cm dbh; 7 M BAF variable-radius plot for trees 12.5-89.9 cm dbh; circular 17-m radius plot for trees ≥90.0 cm dbh.]

Juniper woodlands, e. Oreg.--Cluster of 5 subplots over 2.7 ha. For shrubs, used ocular cover estimates from circular 3.37-m plots (36 m^2 x 5 = 178 m^2 = 0.02 ha). For trees, used relative stocking computed from tree tally: circular 3.37-m plot for trees <12.5 cm dbh; 15 BAF variable-radius for trees 12.5-62.9 cm dbh; circular 16.95-m plot for trees ≥63.0 cm dbh (902.59 m^2 * 5 = 4513 m^2 = 0.45 ha).

Timberland--hardwood stands (sample kind 3), w. Oreg. (except Clatsop and Columbia Counties).--Tree tally from cluster of 10 subplots over 0.4 ha, measured in 1973-1976 and projected to 1984-1986 (dbhs and heights projected, tree expansion factors adjusted by mortality factors). 80 BAF (18.4 M) variable-radius plot for trees ≥5 inches (12.7 cm) dbh; circular 4.9-foot (1.49-m) plot for trees <12.7 cm dbh (6.97 m^2 * 10 = 70 m^2 = .007 ha). Ocular estimates of shrub cover collected on temporary treatment opportunity (TOP) plots, which consisted of 10 points over about 10 ac, or 4 points if tract <10 ac (except 5 points in Douglas Co.). In Douglas Co. (1973): circular 55.6-ft plots at each point (902.59 m^2 * 10 = 9026 m^2 = 0.9 ha); recorded the percentage of the plot occupied by "each major species of inhibiting vegetation." In southwest Oreg. (1974): circular 11.1-ft plots at each point; recorded the percentage of the plot occupied by "each major species of inhibiting vegetation;" recorded species, height (ft), and percent cover by quadrat. In west central Oreg. (1975) and northwest Oreg. (1976): circular 11.1-ft (3.38-m) plots at each point (35.89 m^2 * 10 = 359 m^2 = 0.04 ha); veg. profile included all tall and low shrubs; recorded species, height (ft), and cover class (1-10, 11-20, 21-30, etc.).

Timberland and low productivity, central Oreg., sample kind 2 (1986): Cluster of 5 subplots over 2.7 ha. In central Oreg., prism factor and associated fixed plots determined by site stockability. If stockability not limited: circular 2.41-m plot for trees <12.5 cm dbh, and for cover estimates; 30 BAF for trees 12.5-89.9 cm dbh; circular 16.95-m for trees ≤90.0 cm dbh. If stockability limited: circular 2.96-m plot for trees <12.5 cm dbh and for cover estimates; 20 BAF for trees 12.5-89.9 cm dbh; circular 20.73-m (1350 m^2 * 5 = 6750 m^2) for trees ≥90.0 cm dbh. For thesis data base used ocular cover estimates for all tree layers and shrubs on 2.41-m (18 m^2 x 5 = 91 m^2 = 0.01 ha) and 2.96-m plots (28 m^2 x 5 = 138 m^2 = 0.01 ha).

Timberland, low productivity, and oak woodland, central Oreg. and Blue Mtns., not sample kind 2 (1987): Cluster of 5 subplots over 2.7 ha. For shrubs, used ocular cover estimates from circular 2.41-m radius plots (if 30 BAF prism) and circular 2.96-m radius plots (if 20 BAF prism). (Cover estimated for tree seedlings only on these plots.) For trees, used relative stocking, computed based on projected dbhs and heights from tree tally. (See above discussion of sample kind 2 plot sizes. In Blue Mtns., 30 BAF prism and associated fixed plots always used.)

Forestry Intensive Research (FIR) Study

Source.--Data collected by Brad Smith (obtained from Tom Atzet and Lisa McCrimmon). Procedures generally followed Hawk et al. (1979).

Dates.--1980-1983.

Sample Design.--Sampled BLM lands in southwest Oregon. Sampled older, relatively undisturbed stands, mostly >100 years old. Purpose was to develop plant association (climax) guide across range of all forest lands. Used circular, 500 m^2 plots. (B. Smith, pers. comm.). Visually estimated cover by species, and by size class (for trees only).

Region 6 Ecology Program

According to B. Smith (pers. comm.), The Ecology Program generally used a 1/10-acre (405 m^2) circular plot for species data. Tree measurements for site index, gba, etc., were done using a grid system copied from inventory procedures. The 1/10-ac plot is seldom laid out on the ground by experienced crews. Size and boundaries are estimated to approx. 1/10-ac. This was done to increase speed and maximize plot numbers. Some ecologists did vary plot size by vegetation (e.g., Henderson in Area 1), although 1/10-ac was the usual minimum.

Western Oregon

Area 5: Rogue River, Siskiyou, and Umpqua NFs. Sampled oldest and most stable stands they could find. [No methods section in plant association guides.] For the recon (extensive plots, in surveying the vegetation (trees, shrubs, herbs, and grasses) they did not use a fixed-size plot, but rather they covered an area of roughly 1/3 acre (1349 m^2) centered around plot center. Sometimes more area was covered and sometimes less. For the intensive plots they used 5 points from the old 10-point inventory cluster. They used whichever 5 would fit in the same plant association. Again, the vegetation was what was around the 5 points but no fixed area was used. For the productivity data they used variable-radius plots centered on the 5 points. (L. McCrimmon, pers. comm.).

Area 6: Siuslaw and Willamette NFs. Procedures discussed in Hemstrom et al. (1987). Plant association and management guide, Willamette NF. Publ. R6-Ecol-257-B-86. Sampled relatively undisturbed, natural stands >70 years old with uniform vegetative composition. Plant associations were not sampled proportional to their occurrence. For reconnaissance plots: one circular 12.61-m (41.38-ft) plot; 0.05 ha; 500 m^2. Ocular cover estimates for all vascular species. For intensive plots: cluster of 10 subplots over about 0.4 ha; same circular plot for cover estimates. [Trees also tallied using 40 BAF, but data not used in thesis data base.]

Area 7: Mt. Hood NF. 1979-1985 plots used in data base. Plots done in relatively undisturbed, yet representative and accessible stands $\geq$40-50 years old (mostly >80 years). Plots selected "subjectively without preconceived bias." Methods described in Topik et al. (1988). Same recon and intensive plot data as Area 6. No clusters were used on the Mt. Hood NF (N. Diaz, pers. comm.)

Eastern Oregon

Data for Ecology plots in eastern Oregon were those included in the Eastside Data Base, provided by Brad Smith. Original data files and supplemental data provided for Area 3 and Blue Mountains plots by Charlie Johnson and Rod Clausnitzer. According to S. Simon (pers. comm.), some of the central and northeast Oreg. plots sampled early- and mid-successional (as well as late-).

<u>Area 3:</u> Wallowa-Whitman NF. Sampling focused on mid- and late-successional forests. See Johnson and Simon (1987). For thesis data base, used cover plot from both recon and intensive plots: circular 10.97-m (36-ft) radius plot; 378 m^2; 0.04 ha. Overstory trees were classified by crown class (either dominant/codominant or intermediate/suppressed); understory trees were classified as poles (4-11 in dbh), saplings (<4 in dbh, >1 m tall), or seedlings (<4 in dbh, <1 m tall).

<u>Area 4:</u> No fixed-area plot was used. Cover by species was ocularly estimated for an undefined area (W. Hopkins, pers. comm.).

<u>Blue and Ochoco Mountains:</u> From 1958 to 1968 they sampled for "range condition guides" as follows: a 1/5-acre tree plot (when in trees) on top of a 100 x 100 foot plot with two 100-foot, 3-step transects in the middle of the plot. After 1968 we used a 10-factor prism for tree sampling within a 1/4-acre plot, usually measuring 3-5 trees with a prism count near each tree; ground vegetation cover (trees, shrubs, herbs, mosses, and lichens on ground) was estimated on a 1/5-acre (809 m^2) plot centered in the 1/4-ac plot, with (when dug) a soil hole in the center. Prism sampling often included trees on a 0.35-acre area. Plot selection was biased toward best range condition vegetation--plots were not randomly or systematically distributed. The purpose was to sample the best condition (least disturbed) vegetation so as to build a foundation of "good condition types" so range condition guides could be developed. They were also distributed over variations in topography and soils to encompass as much inherent variability as possible. (F. Hall, pers. comm.).

<u>Central Oreg. Pumice Zone:</u> No fixed-area plot was used. Cover by species was ocularly estimated for an undefined area (W. Hopkins, pers. comm.).

Appendix 2--Derivation of Temperature, Precipitation, and Solar Radiation Variables

Temperature

Extraction of Temperature Data for National Weather Service Stations.--For National Weather Service (NWS) stations, I extracted temperature data using queries (DAILY, HISTORY, and EXTREME views) from the EarthInfo CD-ROM and DOS software provided by John Kimball at EPA (503-754-4495; e-mail JohnK@snow.cor.epa.gov). The source data were summarized by EarthInfo using NCDC standards: a month is invalid if missing >9 days [similar to John Kimball's "30% rule"]; a year is invalid if it has any invalid months. Temperature (T) data were extracted for the period Jan. 1981-Dec. 1992, chosen to match availability of SNOTEL data, although the EarthInfo dates are calendar years (SNOTEL data are water-years). I extracted data for all stations in Oregon and Washington, and any stations in Idaho, Nevada, and California that were north of 40 degrees latitude and west of -115 degrees longitude. Numbers of stations were: Washington 157, Oregon 190, California 59, Idaho 80, Nevada 41.

The HISTORY view provided the following variables for each station: station ID (STAID), station name, elevation (ft), beginning date (mo and yr), ending date (mo and yr), latitude and longitude (deg, min, sec), and county. In cases where the elevation or latitude/longitude for a given station changed over time, I used the data most representative of 1981-1992 (latitude/longitude rarely changed, and elevation usually changed by <10 ft).

I used T data from the DAILY view to derive mean monthly Ts. I changed a few STAID codes in order to eliminate duplicate codes across states. From the DAILY view, I used the monthly mean Ts provided in the output for each station and year; I did NOT recompile the daily data (i.e., I accepted whatever error-checking and assumptions were incorporated in the EarthInfo monthly summaries). I then computed a multi-year mean for each month, using whatever years were available over the 12-yr period for a given station and month. I.e., monthly mean Ts for different stations are based on different years and different numbers of years; for a given station, mean Ts for different months are based on different years. For any given month, only 11-16 stations lacked a valid mean T. I computed the mean annual T as a mean of the mean monthly Ts. Of the total 527 stations, 24 annual mean Ts were based on less than 12 yearly values.

T data from the EXTREME view were used to identify each station's all-time maximum (MAXTMP) and minimum (MINTMP). MAXTMPs and MINTMPs were based on each station's entire recorded history (which varies by station), not the 1981-1992 period. Only those stations present on the HISTORY view were used.

Extraction of Temperature Data for SNOTEL Stations.--Data were provided by Dana Kuiper (Water Supply Forecasting Staff, Soil Conservation Service (SCS), 511 NW Broadway, Rm 248, Portland, OR 97209-3489; 503-326-2843). Data were in multiple files spanning 18 3.5" diskettes. I requested data for all SNOTEL stations in Oregon and Washington, and any stations in Idaho, Nevada, and California that were north of 40 degrees latitude and west of -115 degrees longitude. No stations in Idaho or Nevada met these criteria. Numbers of stations were: Washington 40, Oregon 68, California 3. I requested data for October 1981 (earliest date available) through September 1992. For most stations, however, T data were not present for the entire period (1989 forward was most common).

There were two kinds of files: site files (STAID, station name, elevation (ft), latitude and longitude (deg, min, sec) and weather data files (including variables labeled as "pill" [snow-water equivalent], "prec" [accumulated precipitation], "prcp" [supposedly bogus], "Tmax," "Tavg," and "Tmin"]). Values for Tmax, Tavg, and Tmin were for midnight of the previous day, in degrees C. Weather data files were in a report format, with one report per station/year, with the STAID included only in the report header. Report formats varied among station/years, so no standard file format could be used. I concatenated and edited the files to delete extraneous stuff and to associate STAIDs with data records.

On the original files, data that were missing or questionable were coded "-99.9" by SCS. Unfortunately, many questionable values were NOT edited out by SCS. E.g.: Tmaxs >100 degrees, Tmin's <-50. I assumed a questionable value for any of the T variables (Tmax, Tavg, Tmin) made the entire record suspect, so I deleted any daily record where any of the three variables met at least one of the following: (1) =-99.9; (2) <-45; (3) >50; (4) Tmax<Tavg; (5) Tmax<Tmin; (6) Tavg<Tmin.

I computed mean monthly Ts for each station and yr, using the Tavg variable, considering a month to be valid if it had at least 21 valid daily values. I then averaged these monthly mean Ts across multiple years, considering the mean valid if at least one year was present. Unfortunately, these means were quite commonly based on three or fewer years. Only two station-months lacked valid monthly means. As with the EarthInfo data, monthly mean Ts for different stations are based on different years and different numbers of years; for a given station, mean Ts for different months are based on different years. The mean annual T was computed as the mean of the mean monthly Ts.

The MAXTMP and MINTMP values were identified from the daily Tmax and Tmin values over the period of record (Oct. 1981-Sept. 1992), generally significantly shorter than for the EarthInfo stations.

Input Files for Potential Temperature Model.--Geographic locations of NWS and SNOTEL stations were converted in ArcInfo from degrees (latitude/longitude) to northings and eastings in Albers projection (1st parallel 29 30 00, 2nd parallel 45 30 00, central meridian -96, lat of origin 23, false easting 0 and false northing 0; based on phone consultation to EPA Lab). Two model input files were created: (1) POTTMO.FIX, containing average monthly temperatures, with October as the first month. (2) POTTANN.FIX, containing the same "header" information (STAID, elevation (m), X coordinate (Albers), Y coordinate (Albers), and parameter), followed by mean annual temperature (mean of all the mean monthly temperatures included in POTTMO.FIX), and lastly by the all-time minimum temperature and all-time maximum temperature. Alphanumeric STAIDs (e.g., 17A20S) denoted SNOTEL stations; all other STAIDs denoted NWS stations. Missing values were indicated by -9999, as per John Kimball's instructions.

Model Output.--The temperature surfaces were created by Barbara Marks (Oregon State University, Corvallis Forestry Sciences Lab (FSL)) using the temperature model developed by Danny Marks and John Kimball. Temperature surfaces are stored at Corvallis FSL (server tilia.fsl.orst.edu, subdirectory /data/strix/temp500/mean10yr). The images are in ERDAS (*.GIS) format, Albers equal area projection, with a grid cell size of 500m by 500m. The images are 8-bit files (i.e., data values of 0 to 255 are possible). The data were scaled such that an image value of 0 corresponds to a temperature of -40 degrees C and 255 corresponds to a temperature of +40 degrees C.

Conversion of Model Output to Portland FSL GIS.--The temperature surfaces (ERDAS images) were transferred (remote FTPed) from the Corvallis system to the Portland FSL's DG system, then FTPed to the SUN workstation. ERDAS image files were converted to ArcInfo grids. Temperature (Z) values were rescaled from the ERDAS 8-bit values (0-255) to degrees C using the formula: TEMPC = -40 + (0.313725*TEMP8BIT). There is one temperature grid for each month of the year, one mean annual, one all-time minimum, and one all-time maximum.

Assigning Temperature Values to Plot Locations.--To assign values from the temp. surfaces to individual plot locations I used the ArcInfo function LATTICESPOT, within the TIN module. LATTICESPOT computes surface values for each point in a point coverage by interpolating from a lattice (raster coverage), using bilinear interpolation. (ESRI 1991.) Two plots (FI57 10 and A6122678) fell outside the OR/WA "mask" used by Barbara Marks to clip output from the original runs of the temperature model. For these plots I used temperature parameters of the nearest plots (FI57 11 and A6122679, respectively).

Computing Temperature Measures and Indices.--I computed the following temperature measures and indices for each plot:

<u>Mean monthly, annual, and seasonal temperatures:</u> JANT (January), FEBT (February), MART (March), APRT (April), MAYT (May), JUNT (June), JULT (July), AUGT (August), SEPT (September), OCTT (October), NOVT (November), DECT (December), WARMMOT (warmest month, usually August), COLDMOT (coldest month, usually January), ANNTMP (mean of the 12 monthly means), WTRTMP (mean of NOVT, DECT, JANT, FEBT, and MART), SMRTMP (mean of MAYT, JUNT, JULT, AUGT, and SEPT).

Extreme temperatures: MAXTMP (all-time maximum temperature over a station's record), MINTMP (all-time minimum temperature over a station's record).

Seasonal temperature variability: SDALLT (standard deviation of 12 monthly means), CVALLT (coefficient of variation of 12 monthly means), SDMXMNT (standard deviation of WARMMOT and COLDMOT), CVTMP (coefficient of variation of WARMMOT and COLDMOT), SDJANAUG (standard deviation of JANT and AUGT), CVJANAUG (coefficient of variation of JANT and AUGT), DFMXMNT (difference between WARMMOT and COLDMOT) (continentality index), DFJANAUGT (difference between JANT and AUGT) (continentality index).

Heat sums, measures of growing season length, and measures of interannual (among-year) variability could not be calculated from temperature surfaces generated by the temperature model.

Precipitation

Data Source.--Fourteen ArcInfo GRID coverages generated by the precipitation model PRISM (Daly et al. 1994)were obtained from the Corvallis FSL (contact: George Lienkaemper): a mean P coverage for each month of the year, a mean annual precipitation coverage created by adding the mean monthly values for each cell, and a mean annual precipitation coverage that was modeled directly as an annual value. The grids were in geographic coordinates (latitude and longitude in decimal degrees). The precipitation surfaces were modeled from 30-year (1961-1990) record of precipitation data from weather stations. PRISM was run using a 5-minute DEM; precipitation grid cells are 5 minutes on a side (about 8 km, 73 by 109 pixels). This coarse spatial resolution is considered reasonable for precipitation, which "responds" to major changes in topography, as opposed to temperature, where spatial pattern has finer grain. The Oregon coverages used here are of finer spatial resolution than those developed by Daly for the western U.S., (the monthly surfaces for the NW have not been adequately reviewed). The Oregon ppn. surfaces have received extensive review and editing by Chris Daly and George Taylor (state climatologist) and are considered much more accurate than previously published maps. Units of the Z values in the original coverages were in inches, which I converted to mm.

PRISM does not use slope and aspect directly. The model assigns a "topographic facet" (N, S, E, or W) to each DEM cell. Facets are at least 2 DEM cells wide. PRISM uses weather station data only if from the same facet as the estimation cell.

I assigned values from the precipitation surfaces to plot locations using the ArcInfo function LATTICESPOT, within the TIN module. LATTICESPOT computes surface values for a point by interpolating from a lattice (raster coverage), using bilinear interpolation.

Computing Precipitation Measures and Indices.--I obtained values for each plot for the following precipitation measures and indices:

Mean monthly, annual, and seasonal precipitation: JANP (January), FEBP (February), MARP (March), APRP (April), MAYP (May), JUNP (June), JULP (July), AUGP (August), SEPP (September), OCTP (October), NOVP (November), DECP (December), ADDP (sum of January - December precipitation grids), ANNP (mean annual precipitation modeled with PRISM), WTRPRE (natural logarithm of mean annual precipitation during the cool season, November-March), SMRPRE (natural logarithm of mean annual precipitation during the growing-season, May-September).

Seasonal variability in precipitation: SDALLP (standard deviation of 12 monthly means), CVALLP (coefficient of variation of 12 monthly means), SDMXMNP (standard deviation of the months of maximum and minimum mean monthly precipitation), CVPRE (coefficient of variation of the months of maximum and minimum mean monthly precipitation), SDDECJLP (standard deviation of mean December and July precipitation), CVDECJLP (coefficient of variation of mean December and July precipitation), DFMXMNP (difference between months of maximum (usually December) and minimum (usually July) precipitation), DFDECJLP (difference between mean December and July precipitation), CONTP1 (continentality index 1, the difference between May-July precipitation and August-October precipitation), CONTP2 (continentality index 2, the difference between May-September precipitation and November-March precipitation), CONTP3 (named "CONTPRE" in manuscript) (continentality index 3, the percent of mean annual precipitation that falls in June-August: [(JUNP+JULP+AUGP)/ANNP]*100), CONTP4 (continentality index 4, P_S/P_W, where P_S = ppn. in 6 warmest ("summer") months and P_W = ppn. in 6 coldest ("winter") months).

Data on interannual (among-year) variability in precipitation could not be calculated from output from the PRISM model.

Index for Growing Season Moisture Stress

An index of moisture stress during the growing season was computed as SMRTMP/SMRPRE.

Solar Radiation

Solar radiation was estimated for each plot location using program SOLARPDX, written and distributed by Brad Smith (area ecologist, Okanogan National Forest, 1240 South 2nd St., Okanogan, WA 98840) (Smith 1993). SOLARPDX estimates components of solar insolation for a given combination of latitude, elevation, aspect, and slope. The components estimated by SOLARPDX are direct insolation (direct beam), indirect insolation (skylight), total insolation (direct and indirect), and a two-part solar insolation index. The first index is total insolation in Joules divided by 10^9. The second index is the average number of hours each day to reach peak insolation on a given slope-aspect combination, aimed at accounting for diurnal timing of insolation. In the northern hemisphere the east slopes receive their peak load in the morning while moisture may still be available, and west slopes in the afternoon after the slope has been heated and moisture lost. Ecologists have noted that the driest vegetation is often on southwest slopes while the most mesic is on northeast slopes.

Most of the algorithms used by SOLARPDX were taken from Lowry and Lowry (1989). I ran the program using the "monthly" precision option, which estimates insolation on the 15th day of each month and expands the estimate by the number of days in the month. (The "daily" option estimates insolation for each day of the period, so is more precise but runs considerably more slowly.) All calculations use a transmissivity profile through the atmosphere and an absorbtivity profile. With increasing elevation more light is received for direct beam calculations (transmissivity) and absorbtivity is reduced (reducing skylight). These profiles are set internally to average values for humid, temperate conditions. The assumption of a constant profile is not critical as long as comparisons are made between sites within the same general climatic regime. If sites are gathered from very different climatic areas then insolation estimates will not be as comparable.

Appendix 3--Map Symbol, Geological Age-Epoch, and Lithology of Ptypes by Geology Type

Source: Walker, G.W.; MacLeod, N.S. 1991. Geologic map of Oregon. U.S. Geological Survey, scale 1:500,000; 2 sheets. Question marks ("?") appear below as they do in source documents.

VOLC	Igneous: Volcanic and intrusive Rocks (Unspecified)	
Jv	Jurassic	volcanic rocks
KJdv	Lower Cretaceous and upper Jurassic	volcanic rocks, Dothan Formation
KJi	Cretaceous and Jurassic	intrusive rocks
Thi	Miocene?	Hypabyssal intrusive rocks
Ti	Tertiary	intrusive rocks [not in key]
Tia	Oligocene and Eocene	alkalic intrusive rocks
TRPv	Triassic and Permian	volcanic rocks
TRv	upper Triassic	volcanic and metavolcanic rocks
Tsr	middle and lower Eocene and Paleocene	Siletz River volcanics and related rocks
Tstv	Pliocene?, Miocene	Strawberry volcanics
Ttv	upper and middle Eocene	Tillamook volcanics
Ttvm	upper and middle Eocene	Tillamook volcanics: marine facies

SILR	Igneous: Silicic Rocks (Granite, Diorite, Rhyolite, Dacite)	
JTRgd	Jurassic and Triassic	granite and diorite
KJg	Cretaceous and Jurassic	granitic intrusive rocks
Qrd	Holocene, Pleistocene	rhyolite and dacite intrusives
Tr	Miocene, upper Eocene?	rhyolite and dacite domes and flows and small hypabyssal intrusive bodies
Trh	Pliocene?, Miocene	rhyolite and dacite

MAFO	Igneous: Mafic Rocks (Basalt, Basaltic Andesite, Andesite, Gabbro) --Miocene and Older	
Jc	Jurassic	Chetco Complex (igneous and metamorphosed volcanic rocks, including gabbro, metagabbro, quartz diorite, and amphibolite)
Jub	Jurassic	basaltic volcanic and sedimentary rocks
Tb	upper and middle Miocene	basalt
Tba	Miocene	basalt and andesite
Tbaa	upper and middle Miocene	basaltic and andesitic rocks
Tbas		andesitic and basaltic rocks on Steens Mountain

Tc	Miocene	Columbia River basalt group and related flows
Tca	lower Oligocene?, Eocene, Paleocene?	clastic rocks and andesite flows
Tcg	middle and lower Miocene	Grande Ronde basalt
Tci	lower Miocene	Imnaha basalt
Tcp	middle and lower Miocene	Picture Gorge basalt
Tcs	upper and middle Miocene	Saddle Mountains Basalt
Tcw	middle Miocene	Wanapum basalt
Tfeb	Oligocene and upper Eocene	basaltic rocks
Tib	Pliocene, Miocene, Oligocene?	basalt and andesite intrusions
Tig	Oligocene and Eocene	intrusive gabbroic rocks
Tim	Pliocene, Miocene	mafic and intermediate intrusive rocks
Tob	Pliocene, Miocene	olivine basalt
Tpb	upper Eocene	pyrophyritic basalt
Trb	Pliocene, upper Miocene	ridge-capping basalt and basaltic andesite
TRPzg	Triassic and Paleozoic	ultramafic and mafic intrusive rocks and serpentinized equivalents: gabbroic rocks
Tub	Miocene, Oligocene	basaltic lava flows
MAFY	**Igneous: Mafic Rocks (Basalt, Basaltic Andesite, Andesite, Gabbro) --Pliocene and Younger**	
Qa	Holocene, Pleistocene	andesite
Qb	Holocene, Pleistocene	basalt and basaltic andesite
Qba	Holocene?, Pleistocene	basaltic andesite and basalt
Qlb	Holocene or upper Pleistocene	late basalt
QTa	Pleistocene, Pliocene	andesite
QTb	Pleistocene, Pliocene	basalt
QTba	Pleistocene, Pliocene	basalt and basaltic andesite
QTib	Pleistocene, Pliocene, Miocene	intrusive basalt and andesite
Qyb	Holocene	youngest basalt and basaltic andesite
UMAF	**Igneous: Ultramafic Rocks (Serpentine)**	
Ju	Jurassic	ultramafic and related rocks of ophiolite sequences
KJgu	Cretaceous and Jurassic	gabbro and ultramafic rocks associated with granitic plutons
TRPzu	Triassic and Paleozoic	ultramafic and mafic intrusive rocks and serpentinized equivalents: ultramafic rocks

PYRO	**Igneous: Mafic Pyroclastic Rock, Ash, Ejecta, Vent Deposits --Miocene and Older**	
Qmp	Holocene	Mazama pumice deposits
Tmv	Miocene	mafic vent complexes
Tp	lower Pliocene?, Miocene?	pyroclastic rocks of basaltic cinder cones: basaltic and andesitic ejecta
Tps	lower Pliocene?, Miocene?	pyroclastic rocks of basaltic cinder cones: subaqueous pyroclastic rocks of basaltic cinder cones
Tvi	Eocene?	mafic vent and intrusive rocks
Tvm	Pliocene?, Miocene	mafic and intermediate vent rocks

PYRY	**Igneous: Mafic Pyroclastic Rock, Ash, Ejecta, Vent Deposits --Pliocene and Younger**	
Qma	Holocene	Mazama ash-flow deposits
QTmv	Pleistocene, Pliocene, Miocene	mafic vent complexes
QTp	Holocene, Pleistocene, Pliocene, Miocene?	pyroclastic rocks of basaltic and andesitic cinder cones: basaltic and andesitic ejecta
QTps	Holocene, Pleistocene, Pliocene, Miocene?	pyroclastic rocks of basaltic and andesitic cinder cones: subaqueous basaltic and andesitic ejecta
QTvm	Pleistocene, Pliocene, Miocene?	mafic vent deposits

SILV	**Igneous: Silicic Vent Deposits**	
QTvs	Pleistocene, Pliocene	silicic vent deposits
Tsv	Pliocene, Miocene, upper Oligocene	silicic vent complexes
Tvs	Pliocene, Miocene, Oligocene, Eocene?	silicic vent rocks

META	**Metamorphic**	
bc	Mesozoic or Paleozoic	ampibolite of Briggs Creek
cm	Triassic? or Paleozoic?	Condrey Mountain schist
cs	Mesozoic or Paleozoic	Colebrooke schist
mc	Paleozoic	May Creek schist
Psv	Permian, Permian?	sedimentary and volcanic rocks, partly metamorphosed
Pzs	Paleozoic	sedimentary rocks, partly metamorphosed
Pzsv	Paleozoic	sedimentary and volcanic rocks, partly metamorphosed

TRPsv	Triassic and Permian	sedimentary and volcanic rocks, partly metamorphosed
TRPzm	Triassic or Paleozoic	melange of Dutchmans Peak (heterogeneous texture)
TRPzsn	Triassic and Paleozoic	sedimentary rocks, partly metamorphosed: marble
TRPzs	Triassic and Paleozoic	sedimentary rocks, partly metamorphosed
SEDR	**Sedimentary: Siltstones, Sandstones, Mudstones, Conglomerates**	
Js	Jurassic	sedimentary rocks
Jss	Jurassic	sedimentary rocks
JTRs	Jurassic, upper Triassic	sedimentary rocks
Kc	upper and lower Cretaceous	clastic sedimentary rocks
KJds	lower Cretaceous and upper Jurassic	Dothan Formation and related rocks: sedimentary rocks
KJm	lower Cretaceous and upper Jurassic	Myrtle Group (conglomerate, sandstone, siltstone, and limestone)
Ks	Cretaceous	sedimentary rocks
QTs	Pleistocene, Pliocene	sedimentary rocks
Ta	Oligocene and upper Eocene	Alsea Formation
Tco	upper and middle Eocene	Cowlitz Formation (micaceous, arkosic to basaltic marine sandstone, siltstone, and mudstone)
Tcss	upper and middle Miocene	continental sedimentary rocks
Tm	lower Pliocene? and upper Miocene	marine sedimentary rocks
Tms	middle and lower Miocene	marine sedimentary rocks
Tmsc	lower Eocene	marine siltstone, sandstone, and conglomerate
Tmsm	lower Eocene and Paleocene?	marine sandstone, siltstone, and mudstone
Tmss	middle Eocene	marine sandstone and siltstone
Tmst	middle Miocene, upper Eocene	marine sedimentary and tuffaceous rocks
Tn	Eocene	nonmarine sedimentary rocks
TRs	upper Triassic?, upper and middle Jurassic	marine sedimentary rocks
Tsd	Oligocene and upper Eocene	sedimentary rocks
Tsm	lower Miocene, Oligocene	marine sedimentary rocks
Tt	middle Eocene	Tyee Formation (sandstone with thin, inter-bedded mudstones)
Tus	Miocene, Oligocene	undifferentiated tuffaceous sedimentary rocks, tuffs, and basalt: sedimentary and volcaniclastic rocks

Ty	upper and middle Eocene	Yamhill Formation and related rocks
TUFO	**Sedimentary: Tuffaceous Rocks and Tuffs, Pumicites, Silicic Flows --Miocene and Older**	
Tct	lower Oligocene?, Eocene	predominantly tuffaceous facies of Clarno Formation
Tfc	Miocene	flows and clastic rocks, undifferentiated
Tfee	Oligocene, upper Eocene	Fisher and Eugene Formations and correlative rocks: marine Eugene Formation (tuffaceous)
Ts	Pliocene, Miocene	tuffaceous sedimentary rocks and tuff
Tsf	lower Miocene, Oligocene, uppermost Eocene?	rhyolitic tuff, tuffaceous sedimentary rocks, and lava flows
Tsff	???	thin flows of basalt and andesite, part of John Day Formation
Tsfj	lower Miocene, Oligocene, uppermost Eocene?	John Day Formation of east-central Oregon (soft rock composed of ash and welded tuffs)
Tss	upper and middle Eocene	tuffaceous siltstone and sandstone
Tts	Miocene	tuffaceous sedimentary rocks, tuffs, pumicites, and silicic flows
Tu	Miocene, Oligocene	undifferentiated tuffaceous sedimentary rocks, tuffs, and basalt
Tut	Miocene, Oligocene	undifferentiated tuffaceous sedimentary rocks, tuffs, and basalt: tuff
Twt	upper? and middle Miocene	welded tuffs and tuffaceous sedimentary rocks
Tyq	lower Miocene and upper Oligocene	Yaquina Formation (thick- to thin-bedded sandstone, conglomerate, and tuffaceous siltstone of deltaic origin)
TUFY	**Sedimentary: Tuffaceous Rocks and Tuffs, Pumicites, Silicic Flows --Pliocene and Younger**	
QTst	lower? Pleistocene or Pliocene	tuffaceous sedimentary rocks and tuffs
Tat	lower Pliocene, upper Miocene	silicic ash-flow tuff
DEPO	**Depositional: Dune Sand, Alluvial, Glacial, Glaciofluvial, Loess, Landslide and Debris Flow, Playa, Lacustrine, Fluvial**	
OW	Unknown [not in key]	outwash [not in key]
Qal	Holocene	alluvial deposits
Qd	Holocene	dune sand
Qf	Holocene?, Pleistocene	fanglomerate
Qg	Pleistocene	glacial deposits

Qgf	Pleistocene	glaciofluvial deposits
Qgs	Holocene, Pleistocene	glaciofluvial, lacustrine, and pediment sedimentary deposits
Ql	Holocene, Pleistocene	loess
Qls	Holocene, Pleistocene	landslide and debris-flow deposits
Qpl	Holocene	playa deposits
Qs	Pleistocene	lacustrine and fluvial sedimentary rocks
Qt	Pleistocene	terrace, pediment, and lag gravels
QTg	Pleistocene, Pliocene	terrace and pediment gravels
Tlf	Miocene	lacustrine and fluvial deposits
MIXR	**Mixed Rocks (Unspecified)**	
Jm	Jurassic	melange
Jop	upper Jurassic	Otter Point Formation and related rocks
JTRsv	Jurassic, upper Triassic	sedimentary and volcanic rocks
mr	Mesozoic and Paleozoic	mixed rocks
Tas	Miocene? and Oligocene	andesite and dacite and sedimentary rocks
Tfe	Oligocene and upper Eocene	Fisher and Eugene Formations and correlative rocks
TRsv	upper? Triassic	sedimentary and volcanic rocks

Appendix 4--Species Scores on CCA Axes by Geographic Area

Oregon

Species	Axis 1	Axis 2	Axis 3	Axis 4
Abies amabilis	-0.0777	1.8164	0.3464	-0.1082
Abies grandis or A. concolor	0.6789	0.2989	0.0293	-0.2854
Abies lasiocarpa	1.212	1.8003	-0.4549	-0.0853
Abies magnifica var. shastensis	0.6209	1.0872	1.2062	-0.2993
Abies procera	-0.0921	1.5734	0.1788	-0.0033
Acer circinatum	-0.8199	0.0534	-0.3634	-0.0006
Acer glabrum	0.4776	0.1567	-0.8602	-0.5781
Acer macrophyllum	-0.8561	-0.5425	-0.4089	-0.1546
Alnus incana	0.7595	1.1564	-1.1021	-0.7107
Alnus rhombifolia	0.7258	-0.6805	-1.5607	-0.8726
Alnus rubra	-1.0961	-0.097	-0.3909	0.7615
Alnus sinuata	0.6215	0.1616	-0.5788	-0.0407
Amelanchier alnifolia	0.6807	-0.3477	-0.2468	-0.1854
Amelanchier pallida	0.1456	-0.5197	1.5365	-0.837
Arbutus menziesii	-0.3666	-0.8585	0.4328	-0.691
Arctostaphylos cinerea	-0.0693	-1.327	1.9656	-0.1295
Arctostaphylos columbiana	-0.681	-0.4258	0.8452	1.729
Arctostaphylos nevadensis	0.7895	0.5701	0.6324	0.2859
Arctostaphylos patula	1.2453	-0.3984	0.9318	0.3466
Arctostaphylos uva-ursi	0.8765	-0.0818	0.1158	0.7905
Arctostaphylos viscida	0.	-1.7087	1.6767	-0.9321
Artemisia arbuscula	1.6283	-0.8873	-0.0319	0.9065
Artemisia cana	1.4085	0.0622	0.2934	0.2978
Artemisia rigida	1.4193	-0.5093	-0.3006	0.6644
Artemisia spinescens	1.4226	-0.5474	0.5595	-0.0412
Artemisia tridentata	1.6234	-0.5883	-0.0504	0.4968
Baccharis pilularis	-1.0083	-0.998	0.907	1.9261
Berberis aquifolium	-0.2088	-0.3973	0.0711	-0.5139
Berberis nervosa	-0.5781	0.1677	0.0651	-0.4128
Berberis piperiana	0.1246	-0.456	1.0474	-0.8584
Berberis pumila	-0.9595	0.8927	3.601	1.9267
Berberis repens	1.2006	-0.1655	-0.4121	0.0854
Betula occidentalis	0.2895	0.0288	-1.6804	-0.5398
Calocedrus decurrens	0.1692	-0.3567	0.6677	-0.5387
Ceanothus cuneatus	0.2783	-2.1541	1.3316	-0.7556
Ceanothus integerrimus	0.2483	-1.1258	0.5555	-0.6
Ceanothus prostratus	1.2355	-0.4219	0.9133	0.3121
Ceanothus pumilus	-0.3519	-0.3091	4.1851	-0.1536
Ceanothus sanguineus	0.4724	-0.7521	-0.642	-0.0883
Ceanothus spp.	-0.0749	-2.1174	0.7898	-0.6615
Ceanothus thyrsiflorus	-0.8934	-0.7888	0.8185	1.3302
Ceanothus velutinus	1.211	-0.3254	0.6793	0.32
Cercocarpus ledifolius	1.4691	-0.5267	0.1421	0.3077
Cercocarpus montanus	0.3407	-2.1115	0.3996	-0.9377
Chamaecyparis lawsoniana	-0.9361	0.1574	1.3956	0.4652
Chamaecyparis nootkatensis	0.1891	1.1693	0.5633	-0.7681
Chimaphila menziesii	-0.0457	0.6365	0.3831	-0.5252
Chimaphila umbellata	0.43	0.6677	0.2226	-0.3983
Chrysolepis chrysophylla	-0.1621	0.2085	0.6071	-0.5199
Chrysothamnus nauseosus	1.513	-0.6979	0.2872	0.5639
Chrysothamnus viscidiflorus	1.5681	-0.7225	-0.0633	0.7368
Clematis columbiana	0.9741	0.3446	-1.7107	0.6843

Species	Axis 1	Axis 2	Axis 3	Axis 4
Cornus nuttallii	-0.53	-0.4348	-0.045	-0.7451
Cornus stolonifera	0.4621	0.1968	-0.5362	-0.2072
Corylus cornuta californica	-0.6285	-0.6772	-0.1521	-0.2971
Crataegus douglasii	-0.1641	-0.7529	-0.6828	1.2511
Crataegus spp.	0.168	-1.3375	-0.8689	0.113
Cupressus bakeri	0.421	-0.0706	0.4937	-0.0049
Cytisus scoparius	-0.6795	-1.	-0.0374	0.9524
Fraxinus latifolia	-0.5675	-1.4204	-0.3499	0.3105
Garrya buxifolia	-0.4185	0.0565	3.6359	0.4945
Garrya fremontii	-0.0947	-0.5413	0.8028	-0.6418
Gaultheria humifusa	0.2995	2.3295	0.9157	0.1126
Gaultheria ovatifolia	-0.082	1.3888	0.4576	-0.0989
Gaultheria shallon	-0.8544	0.0077	0.0182	0.1342
Haplopappus bloomeri	1.4585	-0.6013	0.6464	0.5525
Holodiscus discolor	-0.3974	-0.544	-0.1856	-0.212
Ilex spp.	-0.8333	-0.928	-0.3053	0.8954
Juniperus communis	-0.4355	1.0247	2.9661	1.7019
Juniperus occidentalis	1.4726	-0.8833	-0.1368	0.6072
Juniperus scopulorum	1.3324	0.7242	-0.6175	0.6872
Larix occidentalis	0.9756	0.448	-0.9311	-0.0373
Ledum glandulosum	-0.2386	0.1319	0.6647	2.4465
Leucothoe davisiae	-0.8297	1.4282	2.8795	-1.5691
Lithocarpus densiflorus	-0.9722	0.1295	1.1792	0.1009
Lonicera ciliosa	-0.1457	-0.6391	0.3521	-0.9919
Lonicera conjugialis	0.2638	1.0814	1.9343	-0.5656
Lonicera hispidula	-0.3234	-1.198	0.4498	-0.8718
Lonicera involucrata	0.2858	0.3752	-0.3302	0.2583
Lonicera spp.	-0.1922	-0.8343	0.0683	-0.839
Lonicera utahensis	1.1656	0.6604	-1.1737	0.195
Malus spp.	-0.5672	-0.6843	-0.6724	-0.0051
Menziesia ferruginea	-1.2789	0.4036	-0.434	0.8722
Myrica californica	-0.9844	-0.6529	1.0009	3.0321
Oemleria cerasiformis	-0.7046	-0.6242	-0.643	0.2138
Oplopanax horridum	-1.0295	0.9344	-0.7412	0.3818
Pachistima myrsinites	0.6404	0.5983	0.0918	-0.2581
Peraphyllum ramosissimum	1.1259	-0.8867	-0.8591	-0.7157
Philadelphus lewisii	-0.1121	-0.7095	-0.9978	-0.558
Phyllodoce empetriformis	1.0311	2.4092	0.1915	0.0116
Physocarpus capitatus	-0.327	-0.3315	0.0083	0.1705
Physocarpus malvaceus	0.8661	-0.3233	-1.5636	-0.0722
Picea breweriana	-0.3534	1.3464	1.2761	-1.7842
Picea engelmannii	0.9501	1.0454	-0.6635	-0.0592
Picea sitchensis	-1.4061	0.1392	-0.2571	1.3136
Pinus albicaulis	1.5773	2.2013	0.2157	-0.0193
Pinus attenuata	-0.7509	0.2994	3.2763	1.3608
Pinus contorta	1.2945	0.418	0.2731	0.4087
Pinus contorta var. contorta	-0.8827	-0.3254	1.3713	2.7843
Pinus flexilis	1.3802	0.7542	-0.3461	0.6926
Pinus jefferyi	-0.1306	-0.3688	3.0228	0.0593
Pinus lambertiana	-0.008	-0.1205	0.8148	-0.8919
Pinus monticola	0.3891	1.0895	0.9072	0.0107
Pinus ponderosa	1.1817	-0.3957	-0.0354	0.2289
Populus tremuloides	1.3695	-0.0865	0.0914	-0.1576
Populus trichocarpa	0.2006	-0.5776	-0.9074	0.6671
Prunus emarginata	0.2959	-0.3213	-0.0209	0.1076
Prunus spp.	0.7768	-0.6164	-0.3787	0.2892
Prunus virginiana	0.2132	-0.7474	-0.8274	-0.055

Species	Axis 1	Axis 2	Axis 3	Axis 4
Pseudotsuga menziesii	-0.2718	0.0102	-0.1147	-0.1516
Purshia tridentata	1.418	-0.7305	0.5187	0.7352
Quercus chrysolepis	-0.4972	-0.5303	0.9304	-1.3049
Quercus garryana	-0.2361	-1.6356	-0.0088	-0.3336
Quercus kelloggii	-0.2343	-1.4438	0.2926	-1.2204
Quercus sadleriana	-0.5454	1.0543	2.0982	-0.5153
Quercus vaccinifolia	-0.5016	0.3047	3.0462	0.2074
Rhamnus californica	-0.8246	0.5257	3.1242	1.0489
Rhamnus purshiana	-0.988	-0.3935	-0.3777	0.3042
Rhododendron albiflorum	0.0976	1.7559	-0.2845	0.4278
Rhododendron macrophyllum	-0.7538	0.5987	0.3239	-0.0247
Rhododendron occidentale	-0.8536	0.4627	3.4636	1.3778
Rhus diversiloba	-0.4178	-1.3326	0.1107	-0.5365
Rhus glabra	0.6305	1.5353	-1.1996	-1.0216
Ribes binominatum	0.7004	0.8981	1.2712	-0.3424
Ribes bracteosum	-1.0991	-0.6623	-0.1589	0.7741
Ribes cereum	1.2821	-0.2874	-0.035	0.3567
Ribes cruentum	-0.026	0.0434	0.4148	-0.599
Ribes lacustre	0.6902	0.8103	-0.7532	-0.0067
Ribes lobbii	0.2912	0.1269	1.2704	-0.4272
Ribes menziesii	-1.2817	-0.6663	0.9476	1.843
Ribes montigenum	1.4966	2.0687	-0.5966	-0.8513
Ribes niveum	0.4278	-0.5953	-2.3139	-0.5425
Ribes sanguineum	0.3443	-0.0073	0.117	0.0916
Ribes spp.	0.4369	0.3562	-0.3559	0.0493
Ribes velutinum	-0.0674	0.127	0.3586	-0.7209
Ribes viscosissimum	1.1214	0.6148	-0.091	-0.1327
Ribes watsonianum	0.2578	1.2932	0.5771	-1.0617
Robinia pseudo-acacia	-0.7516	-1.2765	-0.6443	0.0636
Rosa eglanteria	-0.52	-1.4238	-0.2828	0.1823
Rosa gymnocarpa	0.1431	-0.0423	-0.0767	-0.3748
Rosa nutkana	1.028	-0.2169	-0.584	-0.247
Rosa spp.	0.2242	-0.6884	-0.5112	0.0173
Rosa woodsii	0.8893	-0.3192	-1.0224	0.1885
Rubus discolor	-0.7792	-0.9757	-0.5856	0.5276
Rubus idaeus	0.9535	0.4794	-2.3204	0.7938
Rubus laciniatus	-0.73	-0.4914	-0.8238	0.6721
Rubus lasiococcus	-0.0595	1.2046	0.3726	-0.1792
Rubus leucodermis	-0.5156	-0.6195	-0.0581	0.0514
Rubus nivalis	-0.4035	0.6685	0.1525	-0.4809
Rubus parviflorus	-0.5561	-0.1013	-0.3536	0.2639
Rubus pedatus	-0.3973	1.6531	-0.5288	0.2788
Rubus spectabilis	-1.1925	0.0011	-0.348	1.0163
Rubus spp.	-0.4018	-0.7934	-0.1085	0.0206
Rubus ursinus	-0.6122	-0.2771	-0.1121	-0.0032
Salix geyeriana	1.317	-0.5547	1.0579	0.0836
Salix hookeriana	-0.9738	-0.5433	0.9286	3.0186
Salix phylicifolia	1.1072	-1.0533	0.3478	0.5513
Salix scouleriana	0.7602	0.2525	-0.8086	-0.0607
Salix spp.	-0.4994	-0.6085	-0.2921	0.3499
Sambucus cerulea	-0.2013	0.1085	-0.6756	0.9301
Sambucus racemosa	-1.0289	-0.3091	-0.4702	0.9242
Sambucus spp.	-1.0802	-0.887	1.2038	1.5469
Sequoia sempervirens	-1.291	0.2899	1.6368	2.2537
Shepherdia canadensis	1.2	0.2783	-0.662	-0.0796
Sorbus scopulina	1.21	0.8629	-1.1888	-0.3568
Sorbus sitchensis	0.0292	1.4374	0.2321	-0.3945

Species	Axis 1	Axis 2	Axis 3	Axis 4
Spiraea betulifolia	0.9776	-0.0639	-1.0556	-0.139
Spiraea densiflora	1.2562	-0.7688	0.4159	-0.2185
Spiraea douglasii	0.8774	-0.5304	0.6887	0.6346
Symphoricarpos albus	0.6703	-0.4662	-0.6982	-0.0169
Symphoricarpos mollis	0.2453	-0.1297	0.4469	-0.6172
Symphoricarpos oreophilus	1.3949	-0.1538	-0.6535	-0.1082
Symphoricarpos spp.	0.3207	-0.8777	-0.526	0.1433
Taxus brevifolia	-0.2838	0.3721	0.1125	-0.6843
Tetradymia canescens	1.5644	-0.8142	-0.1933	-0.6551
Thuja plicata	-0.8923	0.2649	-0.4624	-0.0647
Tsuga heterophylla	-0.857	0.5363	-0.2601	0.0681
Tsuga mertensiana	0.4022	2.2806	0.7225	0.1397
Umbellularia californica	-1.1903	-0.2282	0.993	0.7161
Vaccinium alaskaense	-0.6528	1.2328	-0.3221	-0.084
Vaccinium caespitosum	1.0048	0.8742	1.0234	0.0446
Vaccinium membranaceum	0.6503	0.9874	-0.4743	-0.08
Vaccinium myrtillus	1.1312	0.3231	1.5267	0.3712
Vaccinium occidentale	1.2149	-0.1752	0.8774	0.1596
Vaccinium ovalifolium	-0.795	0.5323	-0.0642	0.3365
Vaccinium ovatum	-1.2013	-0.1602	0.6617	1.0446
Vaccinium parvifolium	-0.9806	0.2777	-0.1744	0.2656
Vaccinium scoparium	1.0989	1.344	-0.2425	0.1751
Vaccinium spp.	0.8729	1.0179	-0.5376	-0.1423
Vaccinium uliginosum	-0.9648	-0.6001	0.9706	3.1044
Whipplea modesta	-0.3656	-0.3856	0.5955	-0.7766

Western Oregon

Species	Axis 1	Axis 2
Abies amabilis	1.6573	-0.8031
Abies grandis or Abies concolor	0.8311	0.4062
Abies lasiocarpa	2.7228	-0.9627
Abies magnifica shastensis	2.151	-0.0661
Abies procera	1.4242	-0.7297
Acer circinatum	-0.3221	-0.2706
Acer glabrum	0.9009	0.204
Acer macrophyllum	-0.6664	0.2029
Alnus rubra	-0.7897	-0.6056
Alnus sinuata	0.3649	0.3923
Amelanchier alnifolia	0.3873	0.7407
Amelanchier pallida	0.8855	1.3305
Arbutus menziesii	-0.0285	1.0804
Arctostaphylos cinerea	0.2293	1.9818
Arctostaphylos columbiana	-0.3516	-0.1184
Arctostaphylos nevadensis	1.5834	-0.2659
Arctostaphylos patula	1.3056	0.9184
Arctostaphylos uva-ursi	0.5663	-0.5285
Arctostaphylos viscida	0.145	2.3727
Baccharis pilularis	-0.8906	-0.1442
Berberis aquifolium	-0.127	0.4116
Berberis nervosa	0.151	0.0005
Berberis piperiana	0.8244	1.1652
Berberis pumila	0.6092	-0.8928
Berberis repens	-0.0591	1.8994

Species	Axis 1	Axis 2
Calocedrus decurrens	0.5712	0.8002
Ceanothus cuneatus	0.1114	2.7855
Ceanothus integerrimus	0.1493	1.7304
Ceanothus prostratus	0.7445	0.705
Ceanothus pumilus	0.8915	1.051
Ceanothus sanguineus	0.1599	1.2395
Ceanothus spp.	-0.2746	2.5098
Ceanothus thyrsiflorus	-0.6297	0.0581
Ceanothus velutinus	0.1394	0.64
Cercocarpus ledifolius	0.0448	2.2193
Cercocarpus montanus	-0.3236	2.9274
Chamaecyparis lawsoniana	-0.0202	-0.3068
Chamaecyparis nootkatensis	1.3043	-0.7141
Chimaphila menziesii	0.8688	-0.0354
Chimaphila umbellata	1.2099	0.0161
Chrysolepis chrysophylla	0.5175	0.2246
Chrysothamnus nauseosus	1.0648	2.8343
Chrysothamnus viscidiflorus	2.4413	-0.6169
Cornus canadensis	2.0096	-0.4536
Cornus nuttallii	-0.1074	0.5901
Cornus stolonifera	-0.0152	0.6059
Corylus cornuta californica	-0.4153	0.5281
Crataegus douglasii	-1.0634	-0.3143
Crataegus spp.	-1.1127	0.9829
Cupressus bakeri	1.0834	0.9499
Cytisus scoparius	-0.7789	0.4142
Fraxinus latifolia	-0.923	1.019
Garrya buxifolia	0.8915	0.4315
Garrya fremontii	0.5335	0.9919
Gaultheria humifusa	2.6356	-0.9451
Gaultheria ovatifolia	1.5589	-0.6648
Gaultheria shallon	-0.2896	-0.2331
Holodiscus discolor	-0.2931	0.4008
Ilex spp.	-1.056	0.3194
Juniperus communis	0.7348	-0.8134
Larix occidentalis	1.2087	0.7502
Ledum glandulosum	-0.9682	-0.3825
Leucothoe davisiae	1.2941	-0.3098
Lithocarpus densiflorus	-0.0531	-0.2181
Lonicera ciliosa	0.2751	0.9012
Lonicera conjugialis	2.0077	0.0674
Lonicera hispidula	-0.1425	1.4361
Lonicera involucrata	-0.8894	-0.7619
Lonicera spp.	0.0494	1.2691
Malus spp.	-0.8507	0.3949
Menziesia ferruginea	-0.9398	-1.2099
Myrica californica	-0.9165	-0.5976
Oemleria cerasiformis	-0.7025	0.2582
Oplopanax horridum	-0.2399	-1.1422
Pachistima myrsinites	1.3759	0.0046
Philadelphus lewisii	-0.7849	1.0043
Phyllodoce empetriformis	3.1167	-1.2489
Physocarpus capitatus	-0.2723	0.1639
Picea breweriana	1.4462	-0.0269
Picea engelmannii	1.9687	-0.5507
Picea sitchensis	-1.031	-1.1641
Pinus albicaulis	3.1391	-1.2128

Species	Axis 1	Axis 2
Pinus attenuata	0.4637	-0.1974
Pinus contorta	2.6327	-0.7812
Pinus contorta var. contorta	-0.5759	-0.6033
Pinus jefferyi	0.8687	0.984
Pinus lambertiana	0.5959	0.7389
Pinus monticola	1.7178	-0.3749
Pinus ponderosa	0.4431	1.4403
Populus tremuloides	-0.8557	0.9559
Populus trichocarpa	-0.7851	0.3209
Prunus emarginata	-0.4702	0.139
Prunus spp.	-0.9273	0.4297
Prunus virginiana	-0.8766	0.3072
Pseudotsuga menziesii	-0.0302	-0.0177
Quercus chrysolepis	0.2278	1.0092
Quercus garryana	-0.6132	1.5295
Quercus kelloggii	-0.1841	1.8478
Quercus sadleriana	1.0896	-0.1927
Quercus vaccinifolia	0.8281	0.2691
Rhamnus californica	0.4812	-0.3328
Rhamnus purshiana	-0.7945	-0.1635
Rhododendron macrophyllum	0.2387	-0.4785
Rhododendron occidentale	0.4712	-0.3802
Rhus diversiloba	-0.4424	1.3359
Ribes binominatum	2.0266	0.3492
Ribes bracteosum	-1.0164	-0.216
Ribes cereum	1.0496	-0.183
Ribes cruentum	0.7811	0.5836
Ribes lacustre	1.1572	-0.6741
Ribes lobbii	1.2472	0.67
Ribes menziesii	-0.9698	-0.5304
Ribes sanguineum	0.176	0.4384
Ribes spp.	0.9561	-0.1291
Ribes velutinum	0.558	0.1964
Ribes viscosissimum	1.6837	0.0274
Ribes watsonianum	1.7958	0.0782
Robinia pseudo-acacia	-1.1083	0.8925
Rosa eglanteria	-0.8676	1.2156
Rosa gymnocarpa	0.4183	0.4
Rosa spp.	-0.8366	1.0114
Rubus discolor	-0.9569	0.3872
Rubus laciniatus	-0.7326	0.0217
Rubus lasiococcus	1.3593	-0.3414
Rubus leucodermis	-0.2693	0.4284
Rubus nivalis	0.6503	-0.2213
Rubus parviflorus	-0.382	-0.2172
Rubus pedatus	0.9002	-1.0418
Rubus spp.	-0.3145	0.7358
Rubus ursinus	-0.2296	0.1598
Rubus spectabilis	-0.8558	-0.8286
Salix hookeriana	-0.8949	-0.5883
Salix scouleriana	-0.334	-0.0447
Salix spp.	-0.6258	0.1579
Sambucus cerulea	-0.5755	-1.0118
Sambucus racemosa	-0.9267	-0.4715
Sambucus spp.	-0.8067	-0.1126
Sequoia sempervirens	-0.3989	-1.2112
Sorbus sitchensis	1.5056	-0.3565

Species	Axis 1	Axis 2
Spiraea betulifolia	0.8298	0.9758
Spiraea douglasii	-1.0575	0.4209
Symphoricarpos albus	-0.5015	0.788
Symphoricarpos mollis	0.5563	0.7584
Symphoricarpos spp.	-0.8166	0.9052
Taxus brevifolia	0.5173	0.1026
Thuja plicata	-0.3317	-0.4302
Tsuga heterophylla	-0.0749	-0.6361
Tsuga mertensiana	2.404	-0.9084
Umbellularia californica	-0.5993	-0.3521
Vaccinium alaskaense	0.5322	-0.896
Vaccinium caespitosum	3.1167	-1.2489
Vaccinium membranaceum	1.4183	-0.5556
Vaccinium ovalifolium	0.0348	-0.5976
Vaccinium ovatum	-0.6867	-0.569
Vaccinium parvifolium	-0.3561	-0.5961
Vaccinium scoparium	2.8534	-1.1079
Vaccinium uliginosum	-0.908	-0.5833
Whipplea modesta	0.2851	0.7192

Eastern Oregon

Species	Axis 1	Axis 2
Abies amabilis	3.5302	-1.0242
Abies grandis or A. concolor	0.3933	-0.1097
Abies lasiocarpa	1.529	-1.1616
Abies magnifica shastensis	0.3069	-1.0818
Abies procera	2.372	-0.6105
Acer circinatum	0.7612	-0.1884
Acer glabrum	0.6358	1.3095
Alnus incana	1.2211	-0.3556
Alnus rhombifolia	0.1529	1.406
Alnus rubra	0.5284	-0.238
Alnus sinuata	0.4955	0.5319
Amelanchier alnifolia	-0.1953	0.5742
Amelanchier pallida	0.7131	0.4911
Arctostaphylos nevadensis	0.3187	-0.4643
Arctostaphylos patula	-0.9232	-0.6798
Arctostaphylos uva-ursi	-0.2607	-0.0889
Artemisia arbuscula	-1.2318	-0.1084
Artemisia cana	-0.3259	-0.6941
Artemisia rigida	-0.7647	-0.0767
Artemisia spinescens	-0.8542	-0.4137
Artemisia tridentata	-1.0026	-0.2676
Berberis aquifolium	-0.1673	-0.0297
Berberis nervosa	0.8508	0.3599
Berberis piperiana	0.5448	0.1685
Berberis repens	-0.1238	0.2586
Betula occidentalis	1.117	1.9861
Calocedrus decurrens	-0.6479	-0.1899
Ceanothus integerrimus	-0.2687	-0.2908
Ceanothus prostratus	-0.8539	-0.5141
Ceanothus sanguineus	-0.0208	1.4921
Ceanothus velutinus	-0.6845	-0.6346

Species	Axis 1	Axis 2
Cercocarpus ledifolius	-0.78	-0.0972
Cercocarpus montanus	-1.4157	-0.5872
Chamaecyparis nootkatensis	1.4439	0.3208
Chimaphila menziesii	0.5915	-0.3534
Chimaphila umbellata	0.6052	-0.2441
Chrysolepis chrysophylla	0.1686	-0.6201
Chrysothamnus nauseosus	-1.1404	-0.1823
Chrysothamnus viscidiflorus	-0.8936	-0.0915
Clematis columbiana	0.8023	1.4062
Cornus nuttallii	0.3478	-0.0471
Cornus stolonifera	0.9761	0.7083
Corylus cornuta californica	0.0155	0.8855
Crataegus douglasii	-0.1383	1.9323
Crataegus spp.	-0.809	0.8601
Haplopappus bloomeri	-1.0741	-0.6484
Holodiscus discolor	0.157	1.5524
Juniperus communis	0.865	-0.7933
Juniperus occidentalis	-1.0584	0.1447
Juniperus scopulorum	0.4813	0.1441
Larix occidentalis	0.7739	0.2316
Ledum glandulosum	2.2644	-2.5974
Lonicera ciliosa	-0.1217	1.0838
Lonicera involucrata	0.6518	-0.2094
Lonicera utahensis	0.839	0.1649
Malus spp.	-0.3045	0.7239
Menziesia ferruginea	2.2904	-0.2968
Pachistima myrsinites	0.6042	-0.2054
Peraphyllum ramosissimum	-0.8088	1.5949
Philadelphus lewisii	0.8051	2.198
Phyllodoce empetriformis	1.739	-1.9548
Physocarpus capitatus	-0.6056	0.1697
Physocarpus malvaceus	0.2971	1.6116
Picea engelmannii	1.1197	-0.2731
Pinus albicaulis	1.439	-2.2321
Pinus contorta	-0.0473	-0.8479
Pinus flexilis	0.3873	0.0781
Pinus jefferyi	-0.3796	-0.8968
Pinus lambertiana	-0.3097	-0.4525
Pinus monticola	0.5518	-0.8228
Pinus ponderosa	-0.4304	0.0152
Populus tremuloides	-0.5391	-0.5313
Populus trichocarpa	0.2152	0.7342
Prunus emarginata	-0.6347	-0.3313
Prunus spp.	-0.517	0.3721
Prunus virginiana	-0.3592	1.1481
Pseudotsuga menziesii	0.3073	0.5316
Purshia tridentata	-1.0562	-0.4219
Quercus garryana	-0.9257	1.1705
Quercus kelloggii	0.9503	0.5309
Rhamnus purshiana	0.0804	2.1145
Rhododendron albiflorum	3.0522	-0.3691
Rhododendron macrophyllum	2.1778	-1.0115
Rhus glabra	1.9915	0.2952
Ribes binominatum	0.05	-0.8107
Ribes cereum	-0.5263	-0.1159
Ribes lacustre	0.9623	0.2908
Ribes lobbii	-0.1928	-0.5722

Species	Axis 1	Axis 2
Ribes montigenum	1.6352	-1.504
Ribes niveum	0.8598	2.9478
Ribes sanguineum	-0.1604	-0.9892
Ribes spp.	0.5422	0.9081
Ribes velutinum	-0.8494	-0.8281
Ribes viscosissimum	0.3238	-0.3001
Rosa gymnocarpa	0.2974	0.6423
Rosa nutkana	-0.1268	0.4537
Rosa spp.	0.1498	0.7349
Rosa woodsii	0.2211	0.8468
Rubus idaeus	1.1198	1.4513
Rubus lasiococcus	2.7332	-0.5035
Rubus parviflorus	0.7904	0.7679
Rubus ursinus	0.4747	-0.1343
Salix geyeriana	-1.1087	-0.8059
Salix phylicifolia	-0.7366	0.0827
Salix scouleriana	0.4938	0.3453
Salix spp.	-0.3993	0.5992
Sambucus cerulea	0.3864	1.3844
Sambucus racemosa	-0.2737	-0.0127
Shepherdia canadensis	0.315	-0.0033
Sorbus scopulina	0.8586	0.1012
Sorbus sitchensis	2.5496	-0.034
Spiraea betulifolia	0.2564	0.7817
Spiraea densiflora	-0.987	-0.131
Spiraea douglasii	-0.9899	-0.8817
Symphoricarpos albus	0.0281	0.7895
Symphoricarpos mollis	-0.2005	-0.4116
Symphoricarpos oreophilus	-0.176	0.3057
Symphoricarpos spp.	-0.3299	0.5522
Taxus brevifolia	1.3456	0.4871
Tetradymia canescens	-0.9411	-0.2908
Thuja plicata	0.8912	-0.5414
Tsuga heterophylla	1.1829	-0.1106
Tsuga mertensiana	2.4312	-1.7935
Vaccinium caespitosum	-0.5348	-1.0926
Vaccinium membranaceum	0.9508	-0.01
Vaccinium myrtillus	-0.3526	-1.342
Vaccinium occidentale	-0.5684	-0.773
Vaccinium parvifolium	-0.0873	0.3277
Vaccinium scoparium	1.0525	-0.7947
Vaccinium spp.	1.1972	-0.7141

Coast Subregion

Species	Axis 1	Axis 2
Abies amabilis	0.7471	-0.779
Abies grandis or Abies concolor	-0.9037	-0.0286
Abies procera	0.6772	-0.8527
Acer circinatum	0.1289	-0.3231
Acer macrophyllum	-0.5447	-0.2216
Alnus rubra	0.4273	-0.1103
Amelanchier alnifolia	-1.524	0.5895
Arbutus menziesii	-1.4659	0.1153

Species	Axis 1	Axis 2
Arctostaphylos columbiana	0.0956	3.2921
Arctostaphylos uva-ursi	0.0811	3.92
Arctostaphylos viscida	-0.4982	-0.822
Baccharis pilularis	0.1904	1.4455
Berberis aquifolium	-0.4722	-0.4896
Berberis nervosa	-0.13	-0.427
Calocedrus decurrens	-1.3723	-0.291
Ceanothus integerrimus	-1.3321	0.1011
Ceanothus sanguineus	-0.9766	-0.0962
Ceanothus thyrsiflorus	0.3211	1.8255
Ceanothus velutinus	-0.985	0.5833
Chamaecyparis lawsoniana	0.7789	1.9879
Chimaphila menziesii	1.1553	-0.3358
Chrysolepis chrysophylla	-0.7137	-0.4388
Cornus nuttallii	-1.0366	-0.476
Corylus cornuta californica	-0.857	-0.0597
Crataegus douglasii	-0.146	1.7476
Crataegus spp.	-1.5173	0.6032
Cytisus scoparius	-0.7581	0.7615
Fraxinus latifolia	-1.5346	1.0419
Gaultheria shallon	0.1598	0.0671
Holodiscus discolor	-0.445	-0.0651
Ilex spp.	-0.7023	0.4633
Ledum glandulosum	0.246	3.0176
Lithocarpus densiflorus	0.0882	-0.4539
Lonicera ciliosa	-0.3314	0.2588
Lonicera hispidula	-1.3443	0.1654
Lonicera involucrata	0.6985	1.8629
Lonicera spp.	1.1963	-0.4554
Malus spp.	-1.3927	-0.2644
Menziesia ferruginea	1.1266	-0.1324
Myrica californica	0.6982	2.8436
Oemleria cerasiformis	-0.8677	0.3439
Oplopanax horridum	0.8686	-0.5095
Philadelphus lewisii	-1.2637	0.3984
Physocarpus capitatus	-0.974	-0.3247
Picea sitchensis	1.0109	0.4135
Pinus contorta var. contorta	0.4961	3.0792
Pinus monticola	-0.1624	-0.5125
Pinus ponderosa	-1.4607	-0.0213
Populus trichocarpa	-1.7571	1.9792
Prunus emarginata	-0.3078	-0.3372
Prunus spp.	-1.0078	0.3933
Prunus virginiana	-1.1464	0.0008
Pseudotsuga menziesii	-0.0104	-0.2009
Quercus garryana	-1.5671	0.296
Quercus kelloggii	-1.7206	-0.0729
Rhamnus purshiana	-0.0361	-0.0075
Rhododendron macrophyllum	0.2891	0.2693
Rhus diversiloba	-1.3968	0.171
Ribes bracteosum	0.3801	0.0065
Ribes cereum	0.3705	-0.5631
Ribes lacustre	-0.0532	-0.1333
Ribes sanguineum	-0.0816	-0.4067
Ribes spp.	0.4789	-0.4723
Robinia pseudo-acacia	-1.9247	1.2357
Rosa eglanteria	-1.5345	0.3089

Species	Axis 1	Axis
Rosa gymnocarpa	-0.7436	-0.2612
Rosa spp.	-1.4863	0.4762
Rubus discolor	-0.9636	0.4148
Rubus laciniatus	-1.0658	-0.098
Rubus lasiococcus	-0.6408	-0.0547
Rubus leucodermis	-0.7182	-0.0893
Rubus nivalis	0.4265	1.2207
Rubus parviflorus	0.2668	-0.2493
Rubus spectabilis	0.6728	0.0519
Rubus spp.	-1.2446	0.0572
Rubus ursinus	-0.5318	0.0115
Salix hookeriana	0.2968	3.5852
Salix scouleriana	0.0627	-0.7514
Salix spp.	-0.4664	0.3231
Sambucus cerulea	1.1209	-0.6116
Sambucus racemosa	0.2646	0.2032
Sambucus spp.	0.1387	2.3453
Spiraea douglasii	-1.5821	2.5036
Symphoricarpos albus	-1.146	-0.0249
Symphoricarpos mollis	-1.1209	-0.0883
Symphoricarpos spp.	-1.4582	0.4068
Taxus brevifolia	-0.8339	0.0235
Thuja plicata	0.3333	-0.1922
Tsuga heterophylla	0.7356	-0.2474
Umbellularia californica	0.2541	0.4481
Vaccinium alaskaense	1.1239	0.037
Vaccinium membranaceum	1.0473	-0.5462
Vaccinium ovalifolium	0.453	-0.234
Vaccinium ovatum	0.511	1.0683
Vaccinium parvifolium	0.5859	-0.2231
Vaccinium uliginosum	0.2869	3.6981
Whipplea modesta	-0.8011	-0.3085

Western Cascades Subregion

Species	Axis 1	Axis 2
Abies amabilis	1.2429	0.4121
Abies grandis or Abies concolor	0.2765	-0.8289
Abies lasiocarpa	2.3176	0.4438
Abies magnifica shastensis	1.5153	-1.2167
Abies procera	1.1642	0.3794
Acer circinatum	-0.3713	0.2793
Acer glabrum	0.0486	-0.1322
Acer macrophyllum	-0.9797	0.1091
Alnus rubra	-0.8629	0.434
Alnus sinuata	1.3315	0.9786
Amelanchier alnifolia	0.0935	-0.5885
Amelanchier pallida	1.382	-1.2271
Arbutus menziesii	-0.589	-0.7412
Arctostaphylos columbiana	0.2234	-0.1797
Arctostaphylos nevadensis	1.5808	-1.4685
Arctostaphylos patula	0.44	-1.443
Arctostaphylos uva-ursi	1.7646	-0.3508
Arctostaphylos viscida	-0.6198	-0.4651

Species	Axis 1	Axis
Berberis aquifolium	-0.3342	-0.3301
Berberis nervosa	-0.1725	0.0246
Berberis piperiana	-0.0759	-1.3838
Berberis repens	-1.7267	-2.6973
Calocedrus decurrens	-0.0455	-0.9611
Ceanothus integerrimus	-0.4459	-2.0492
Ceanothus prostratus	1.8022	-1.7697
Ceanothus spp.	0.0359	-0.9438
Ceanothus velutinus	-0.4741	-0.4825
Chamaecyparis nootkatensis	0.973	0.6239
Chimaphila menziesii	0.3373	-0.0123
Chimaphila umbellata	0.643	-0.383
Chrysolepis chrysophylla	-0.0592	-0.3704
Chrysothamnus viscidiflorus	1.8022	-1.7697
Cornus canadensis	1.2448	-1.7786
Cornus nuttallii	-0.5749	-0.4713
Cornus stolonifera	1.2535	0.4346
Corylus cornuta californica	-0.6853	-0.3214
Crataegus spp.	-1.2723	-0.7085
Cytisus scoparius	-1.0553	0.2224
Fraxinus latifolia	-1.3243	-0.4214
Garrya fremontii	0.4409	-0.7162
Gaultheria humifusa	2.1638	0.1522
Gaultheria ovatifolia	1.117	0.1081
Gaultheria shallon	-0.4844	0.1548
Holodiscus discolor	-0.6272	-0.1941
Juniperus communis	2.7399	1.4703
Larix occidentalis	0.532	-1.1579
Lithocarpus densiflorus	-0.0999	-0.3517
Lonicera ciliosa	-0.2929	-0.8708
Lonicera hispidula	-0.7154	-1.0218
Lonicera involucrata	-1.3991	0.4967
Lonicera spp.	-0.786	-1.2193
Malus spp.	-1.3203	0.2352
Menziesia ferruginea	-1.3585	0.1923
Oemleria cerasiformis	-0.6692	0.5156
Oplopanax horridum	0.3273	1.7414
Pachistima myrsinites	0.7388	-0.528
Philadelphus lewisii	-1.2379	-0.5259
Phyllodoce empetriformis	2.9244	0.8268
Physocarpus capitatus	-0.6627	0.2691
Picea engelmannii	1.3027	-0.3145
Pinus albicaulis	2.8215	1.1858
Pinus contorta	2.0059	-0.7141
Pinus lambertiana	-0.1452	-0.979
Pinus monticola	1.2957	-0.528
Pinus ponderosa	-0.163	-1.3588
Populus tremuloides	-1.357	-0.4623
Populus trichocarpa	-0.6945	0.5075
Prunus emarginata	-0.9117	-0.4006
Prunus spp.	-0.6304	0.4199
Prunus virginiana	-1.3762	-0.029
Pseudotsuga menziesii	-0.1374	0.0757
Quercus chrysolepis	0.2019	-0.9203
Quercus garryana	-1.217	-0.9842
Quercus kelloggii	-0.9606	-1.4913
Rhamnus purshiana	-0.9853	0.1434

Species	Axis 1	Axis 2
Rhododendron macrophyllum	0.2712	0.3336
Rhus diversiloba	-1.0652	-0.9321
Ribes binominatum	1.355	-1.3439
Ribes cereum	1.2225	-0.9215
Ribes cruentum	0.7035	-0.7878
Ribes lacustre	1.1543	0.3987
Ribes lobbii	0.859	-0.7471
Ribes sanguineum	-0.3666	-0.982
Ribes spp.	0.5712	-0.637
Ribes velutinum	0.0268	-0.1418
Ribes viscosissimum	1.5054	-1.1665
Ribes watsonianum	1.2142	-0.4018
Rosa eglanteria	-1.3154	-0.2428
Rosa gymnocarpa	-0.0186	-0.3386
Rubus discolor	-1.3819	-0.2983
Rubus laciniatus	-1.0727	-0.08
Rubus lasiococcus	1.114	0.0533
Rubus leucodermis	-0.3315	-0.3688
Rubus nivalis	0.221	0.0653
Rubus parviflorus	-0.2519	-0.4636
Rubus pedatus	0.6848	1.426
Rubus spectabilis	-0.7425	0.7486
Rubus ursinus	-0.3942	-0.12
Salix scouleriana	-0.9514	-0.4391
Salix spp.	-0.5915	0.2601
Sambucus racemosa	-0.8378	0.5479
Sorbus sitchensis	1.4974	0.3499
Spiraea betulifolia	0.006	-1.0491
Spiraea douglasii	-1.357	-0.4623
Symphoricarpos albus	-0.7583	-0.4849
Symphoricarpos mollis	-0.0445	-0.508
Symphoricarpos spp.	-1.2922	-0.7667
Taxus brevifolia	-0.0292	-0.1055
Thuja plicata	-0.3741	0.5519
Tsuga heterophylla	0.0341	0.4478
Tsuga mertensiana	1.8762	0.0872
Vaccinium alaskaense	0.4611	0.9936
Vaccinium caespitosum	2.9244	0.8268
Vaccinium membranaceum	1.1793	0.1706
Vaccinium ovalifolium	0.7756	1.0097
Vaccinium ovatum	1.2752	-2.18
Vaccinium parvifolium	-0.2724	0.6215
Vaccinium scoparium	2.3097	-0.0443
Whipplea modesta	-0.3424	-0.6659

Klamath Subregion

Species	Axis 1	Axis 2
Abies grandis or Abies concolor	-0.3642	0.859
Abies magnifica shastensis	-0.221	1.912
Acer circinatum	0.1419	-0.0003
Acer glabrum	-0.5466	1.382
Acer macrophyllum	0.0237	-0.6042
Alnus rubra	1.1317	-1.0127

Species	Axis 1	Axis 2
Alnus sinuata	0.1424	-0.0899
Amelanchier alnifolia	-0.7838	0.2334
Amelanchier pallida	-0.7127	0.4915
Arbutus menziesii	-0.5163	-0.3673
Arctostaphylos cinerea	-0.4096	-0.3592
Arctostaphylos columbiana	0.3302	-0.3329
Arctostaphylos nevadensis	1.0139	1.2686
Arctostaphylos patula	-0.3774	1.2358
Arctostaphylos viscida	-0.8609	-0.4136
Baccharis pilularis	1.3545	-1.1974
Berberis aquifolium	-0.9092	-0.2391
Berberis nervosa	0.0119	0.3389
Berberis piperiana	-0.7198	0.5158
Berberis pumila	1.7948	0.8835
Berberis repens	-0.5181	-0.2052
Calocedrus decurrens	-0.577	0.1968
Ceanothus cuneatus	-1.2654	-0.646
Ceanothus integerrimus	-0.9993	-0.5512
Ceanothus prostratus	0.6037	0.4145
Ceanothus pumilus	0.5262	1.0932
Ceanothus sanguineus	-1.2051	0.0546
Ceanothus spp.	-0.9344	-1.2559
Ceanothus thyrsiflorus	0.5704	-1.0825
Ceanothus velutinus	-0.9317	0.2931
Cercocarpus ledifolius	-1.3024	-0.9764
Cercocarpus montanus	-1.4355	-1.281
Chamaecyparis lawsoniana	0.8389	0.0508
Chimaphila menziesii	-0.0023	0.7572
Chimaphila umbellata	-0.2201	0.883
Chrysolepis chrysophylla	0.037	0.5899
Chrysothamnus nauseosus	-1.434	0.5055
Cornus canadensis	1.0038	1.6033
Cornus nuttallii	-0.4468	-0.1071
Cornus stolonifera	-0.766	-1.586
Corylus cornuta californica	-0.4517	-0.2081
Crataegus douglasii	1.1165	-1.8471
Cupressus bakeri	-1.0036	0.6397
Fraxinus latifolia	-0.9936	-1.4352
Garrya buxifolia	0.6684	1.0513
Garrya fremontii	-0.5968	-0.0285
Gaultheria ovatifolia	0.5012	-0.0246
Gaultheria shallon	0.6661	-0.0081
Holodiscus discolor	-0.3767	-0.0811
Juniperus communis	1.7934	0.8819
Leucothoe davisiae	1.1156	1.7571
Lithocarpus densiflorus	0.7823	-0.2292
Lonicera ciliosa	-0.7579	-0.0337
Lonicera conjugialis	-0.1027	2.1893
Lonicera hispidula	-0.7358	-0.5345
Lonicera spp.	-1.1456	-0.447
Oemleria cerasiformis	-1.2642	-0.0921
Pachistima myrsinites	-0.5095	0.8629
Philadelphus lewisii	-1.3264	-1.3788
Physocarpus capitatus	0.3494	0.9451
Picea breweriana	0.1456	1.7016
Picea engelmannii	-0.9049	1.0909
Picea sitchensis	1.2352	-1.2142

Species	Axis 1	Axis 2
Pinus attenuata	1.2237	0.58
Pinus contorta var. contorta	1.1649	0.7171
Pinus jefferyi	0.1362	0.8672
Pinus lambertiana	-0.2656	0.3721
Pinus monticola	0.7977	1.0531
Pinus ponderosa	-0.9033	-0.1131
Populus tremuloides	-1.0272	-0.8725
Prunus emarginata	-0.5517	2.0069
Prunus virginiana	1.4315	-0.5801
Pseudotsuga menziesii	0.0301	0.033
Quercus chrysolepis	-0.2469	-0.0716
Quercus garryana	-1.2334	-1.1014
Quercus kelloggii	-1.0201	-0.6663
Quercus sadleriana	0.6976	1.2923
Quercus vaccinifolia	0.6919	0.9664
Rhamnus californica	1.2479	0.6718
Rhamnus purshiana	0.8945	-0.961
Rhododendron macrophyllum	1.0062	-0.1664
Rhododendron occidentale	1.4114	0.6284
Rhus diversiloba	-0.8146	-0.7521
Ribes binominatum	-0.4288	1.7187
Ribes cereum	-1.1253	0.4588
Ribes cruentum	-0.6855	0.096
Ribes lacustre	1.3792	-0.9851
Ribes lobbii	-0.4951	0.954
Ribes menziesii	1.1555	-1.4428
Ribes sanguineum	-0.9994	0.7962
Ribes spp.	-0.1641	1.293
Ribes velutinum	-0.7134	-0.1346
Ribes viscosissimum	0.0015	0.9754
Rosa eglanteria	-1.1983	-1.7845
Rosa gymnocarpa	-0.3062	0.3876
Rosa spp.	-1.5274	-1.4489
Rubus discolor	-0.1905	-1.2235
Rubus lasiococcus	-0.2705	0.6809
Rubus leucodermis	-0.3482	-0.168
Rubus nivalis	-0.2732	0.946
Rubus parviflorus	-0.329	0.1393
Rubus spectabilis	1.2087	-0.9863
Rubus spp.	-0.3221	0.4911
Rubus ursinus	-0.0237	-0.1155
Salix scouleriana	1.4686	-0.5118
Salix spp.	-0.2002	-0.7895
Sambucus cerulea	0.6822	-0.8919
Sambucus spp.	1.0496	-0.8643
Sequoia sempervirens	1.6315	-0.7034
Sorbus sitchensis	-0.0339	-0.2047
Symphoricarpos albus	-1.07	-0.6551
Symphoricarpos mollis	-0.7738	0.2797
Symphoricarpos spp.	-1.0896	-0.5227
Taxus brevifolia	-0.2683	0.4235
Thuja plicata	0.6154	0.7851
Tsuga heterophylla	0.9639	-0.4032
Tsuga mertensiana	-0.1382	2.2745
Umbellularia californica	1.072	-0.7209
Vaccinium membranaceum	-0.5788	1.3663
Vaccinium ovalifolium	0.4319	-0.9674

Species	Axis 1	Axis 2
Vaccinium ovatum	1.1173	-0.7652
Vaccinium parvifolium	0.7148	0.3076
Vaccinium scoparium	0.6617	1.6593
Whipplea modesta	-0.351	0.0417

Eastern Cascades Subregion

Species	Axis 1	Axis 2
Abies amabilis	4.6512	-1.3908
Abies grandis or Abies concolor	0.3694	-0.0872
Abies lasiocarpa	3.5896	-2.2218
Abies magnifica shastensis	0.9819	-0.4177
Abies procera	3.3658	-0.5095
Acer circinatum	1.6608	0.8266
Acer glabrum	1.4068	1.9839
Alnus rubra	1.2848	0.5068
Amelanchier alnifolia	-0.0655	0.289
Amelanchier pallida	1.7866	1.191
Arctostaphylos nevadensis	0.6651	-0.8793
Arctostaphylos patula	-0.4265	-0.1516
Arctostaphylos uva-ursi	-0.1362	-0.057
Artemisia arbuscula	-1.0671	0.0247
Artemisia cana	-0.2505	-0.5567
Artemisia rigida	-0.9421	-0.6344
Artemisia spinescens	-0.3958	-0.1389
Artemisia tridentata	-0.7074	-0.1917
Berberis aquifolium	0.7548	0.9302
Berberis nervosa	1.6743	0.9779
Berberis piperiana	1.584	1.3633
Berberis repens	-0.0721	0.1148
Calocedrus decurrens	0.0241	0.4912
Ceanothus integerrimus	0.7477	1.949
Ceanothus prostratus	-0.4039	-0.0106
Ceanothus velutinus	-0.3084	-0.2227
Cercocarpus ledifolius	-0.6497	0.0348
Cercocarpus montanus	-0.9254	0.4941
Chimaphila menziesii	1.0383	0.0377
Chimaphila umbellata	0.7068	-0.0143
Chrysolepis chrysophylla	0.8955	0.0363
Chrysothamnus nauseosus	-0.6829	-0.1744
Chrysothamnus viscidiflorus	-0.879	0.0329
Cornus nuttallii	1.2477	1.0263
Cornus stolonifera	1.1769	-0.5605
Corylus cornuta californica	1.0796	2.2666
Haplopappus bloomeri	-0.5826	-0.299
Holodiscus discolor	1.0758	1.3998
Juniperus occidentalis	-0.8964	0.3691
Larix occidentalis	0.9078	0.96
Lonicera ciliosa	1.014	2.5319
Lonicera involucrata	0.3927	-0.37
Lonicera utahensis	0.4267	0.5691
Pachistima myrsinites	0.7147	0.3496
Phyllodoce empetriformis	3.1601	-2.8368
Picea engelmannii	0.8379	-0.3295

Species	Axis 1	Axis 2
Pinus albicaulis	0.5906	-1.5116
Pinus contorta	-0.3289	-0.6683
Pinus jefferyi	0.2755	0.3872
Pinus lambertiana	0.3239	0.0754
Pinus monticola	0.9422	-0.7303
Pinus ponderosa	-0.319	0.0309
Populus tremuloides	-0.3585	-0.4041
Prunus emarginata	-0.1815	-0.1028
Prunus spp.	-0.4519	-0.0999
Prunus virginiana	0.0575	0.5278
Pseudotsuga menziesii	0.8231	1.1089
Purshia tridentata	-0.6422	-0.0719
Quercus garryana	0.1465	2.4884
Quercus kelloggii	2.2101	1.2755
Rhododendron albiflorum	4.2493	-0.7432
Rhododendron macrophyllum	2.6826	-0.2561
Ribes binominatum	0.5937	-0.0333
Ribes cereum	-0.4968	-0.4008
Ribes lacustre	0.265	-1.2654
Ribes lobbii	0.8085	-0.0393
Ribes sanguineum	0.2477	-0.9666
Ribes velutinum	-0.5561	-0.7342
Ribes viscosissimum	0.6642	-0.7302
Rosa gymnocarpa	0.5201	0.7457
Rosa spp.	0.5806	-0.1624
Rosa woodsii	0.8275	1.875
Rubus lasiococcus	3.8615	-0.6217
Rubus parviflorus	0.7117	0.6121
Rubus ursinus	1.3856	0.5637
Salix geyeriana	-0.6617	-0.4117
Salix phylicifolia	0.1548	0.7545
Salix scouleriana	0.7877	0.9944
Salix spp.	0.1024	0.8102
Sambucus cerulea	0.2219	-0.0432
Sambucus racemosa	-0.534	-0.4373
Sorbus sitchensis	5.3092	-2.5515
Spiraea betulifolia	1.5188	1.7597
Spiraea densiflora	-0.717	0.4241
Spiraea douglasii	-0.5766	-0.4513
Symphoricarpos albus	0.3681	0.7153
Symphoricarpos mollis	0.4128	0.0714
Symphoricarpos spp.	-0.0167	1.3826
Taxus brevifolia	1.783	0.7613
Thuja plicata	1.7181	0.3206
Tsuga heterophylla	2.2463	0.8546
Tsuga mertensiana	2.8575	-2.1715
Vaccinium caespitosum	-0.1486	-0.3811
Vaccinium membranaceum	2.092	-0.4217
Vaccinium myrtillus	0.0606	-0.4868
Vaccinium occidentale	-0.2497	-0.1438
Vaccinium parvifolium	0.946	1.4804
Vaccinium scoparium	2.3736	-2.4354
Vaccinium spp.	2.6826	-0.2561

Blue Mountains Subregion

Species	Axis 1	Axis 2
Abies amabilis	-1.6119	2.4572
Abies grandis or Abies concolor	-0.5138	-0.1338
Abies lasiocarpa	-1.1998	1.2229
Acer glabrum	-0.1155	-1.0782
Alnus incana	-0.8082	0.2438
Alnus rhombifolia	0.1761	-1.2436
Alnus sinuata	0.1693	-0.1896
Amelanchier alnifolia	0.3365	-0.681
Arctostaphylos nevadensis	-0.2699	0.2963
Arctostaphylos uva-ursi	-0.1738	-0.143
Artemisia arbuscula	1.5852	1.136
Artemisia rigida	1.1568	0.9656
Artemisia tridentata	1.3131	1.2071
Berberis nervosa	-0.5331	-1.38
Berberis repens	0.2679	-0.0383
Betula occidentalis	-0.5846	-2.1901
Ceanothus integerrimus	-1.1033	0.9594
Ceanothus sanguineus	0.3192	-0.7755
Ceanothus velutinus	0.3866	0.2144
Cercocarpus ledifolius	0.9479	0.7109
Chamaecyparis nootkatensis	-1.1049	-0.8769
Chimaphila menziesii	-0.9998	-0.185
Chimaphila umbellata	-0.758	0.0539
Chrysothamnus nauseosus	1.491	0.5479
Chrysothamnus viscidiflorus	1.1309	0.9857
Clematis columbiana	-0.5495	-0.9514
Cornus stolonifera	-0.6135	-1.5583
Crataegus douglasii	0.6621	-1.099
Crataegus spp.	0.7246	-0.3427
Haplopappus bloomeri	1.5926	0.7538
Holodiscus discolor	0.5333	-1.3301
Juniperus communis	-0.5995	1.3357
Juniperus occidentalis	1.4156	0.7198
Juniperus scopulorum	-0.4019	0.3905
Larix occidentalis	-0.4915	-0.169
Ledum glandulosum	-2.114	2.1474
Lonicera involucrata	-0.7236	-0.1712
Lonicera utahensis	-0.6046	0.1901
Malus spp.	0.6358	-0.06
Menziesia ferruginea	-1.864	0.6155
Pachistima myrsinites	-0.6735	0.1183
Peraphyllum ramosissimum	1.4303	-0.4081
Philadelphus lewisii	0.0631	-2.0752
Phyllodoce empetriformis	-1.482	1.9639
Physocarpus capitatus	0.7431	0.7686
Physocarpus malvaceus	0.2822	-1.0628
Picea engelmannii	-0.9775	0.188
Pinus albicaulis	-1.1897	2.8086
Pinus contorta	-0.6999	0.615
Pinus flexilis	-0.3193	0.5015
Pinus monticola	-1.1542	-0.5391
Pinus ponderosa	0.4463	0.0209
Populus tremuloides	0.0871	0.3941
Populus trichocarpa	-0.158	-0.772
Prunus emarginata	0.4406	-0.0871

Species	Axis 1	Axis 2
Prunus spp.	0.9258	-0.0296
Prunus virginiana	0.6556	-0.5414
Pseudotsuga menziesii	-0.0351	-0.3145
Purshia tridentata	1.4797	0.7153
Rhamnus purshiana	0.3371	-1.7029
Rhus glabra	-0.7247	-0.1986
Ribes cereum	0.703	0.1918
Ribes lacustre	-0.6734	-0.3667
Ribes montigenum	-1.4242	1.7877
Ribes niveum	0.0186	-2.5496
Ribes spp.	-0.0965	-0.372
Ribes viscosissimum	-0.124	0.276
Rosa gymnocarpa	-0.0254	-0.5807
Rosa nutkana	0.451	-0.113
Rosa spp.	0.2829	-0.6609
Rosa woodsii	-0.0038	-0.2121
Rubus idaeus	-0.8173	-1.0425
Rubus parviflorus	-0.3947	-0.8411
Rubus ursinus	0.384	0.0959
Salix scouleriana	-0.2544	0.0028
Salix spp.	0.6907	-0.1965
Sambucus cerulea	0.1816	-1.5397
Sambucus racemosa	-0.0719	-0.0083
Shepherdia canadensis	-0.0728	0.329
Sorbus scopulina	-0.7721	0.2241
Sorbus sitchensis	-1.2826	-0.9175
Spiraea betulifolia	0.0894	-0.4199
Spiraea densiflora	0.6306	-0.5291
Symphoricarpos albus	0.3538	-0.5583
Symphoricarpos mollis	0.7609	-0.0291
Symphoricarpos oreophilus	0.4274	0.4113
Symphoricarpos spp.	0.6846	-0.0488
Taxus brevifolia	-0.9906	-0.8604
Tetradymia canescens	1.3804	1.54
Tsuga mertensiana	-1.8328	0.7921
Vaccinium membranaceum	-0.6511	0.0861
Vaccinium occidentale	0.2548	0.5449
Vaccinium scoparium	-0.8712	0.7841
Vaccinium spp.	-0.466	0.7398