SUBALPINE AND MONTANE FORESTS ON GRANODIORITE IN THE CENTRAL KLAMATH MOUNTAINS OF CALIFORNIA

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SUBALPINE AND MONTANE FORESTS ON GRANODIORITE IN THE CENTRAL KLAMATH MOUNTAINS OF CALIFORNIA[1]

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Abstract. Study of montane and subalpine forests of the Klamath Region suggests the importance of local disturbance in maintaining high regional floristic diversity. The region's complex vegetation patterns including many relic and endemic species are generally understood. Previous explanations stress a long history of vegetational development in a physiographically and climatically complex environment to account for regional characters. These interpretations, though, do not adequately explain the complicated intra-regional patterns. Small, scattered populations of relic trees are of special interest in this respect.

A study of forest patterns on granitic parent materials allowed for an analysis of these relic populations as well. Significantly different forest patterns are found on the regionally extensive metasedimentary and ultrabasic parent materials. General reconnaissance pointed to the Russian Peak area as one of unusual interest with an exceptional concentration of 16 conifer species. Intensive sampling, ordination and classification analyses defined 11 forest types. These were then tested by sampling in 13 additional areas which led to the recognition of 16 regional forest types on granodiorites.

A reasonably predictable pattern emerged. Forests show decreasing geographic differentiation with increasing elevation. Zonation is more apparent in mature, floristically uniform, closed forests on deep soil habitats.

Diverse, open forests are found on heterogeneous, non-competitive habitats such as talus, rocky moraines and ridges. The relics are not habitat specific.

Even though the region has been geologically stable during the Cenozoic, various disturbances have occurred. Extensive disturbance which would cause floristic depauperization has not happened. Instead local disturbances have created a greater number of varied habitats and individualized species distributions. Existing vegetation patterns are complicated, and the relic populations are maintained. In this manner local history may be even more important than environmental constraints in determining existing patterns.

Key words: California, conifer distribution, floristics, forest types, Klamath Region, relics, vegetation patterns.

INTRODUCTION

The Klamath Region of northwestern California and southwestern Oregon has been recognized for its diverse forest patterns and rich flora which occupy a central role in the present western North American forest patterns. The few studies done reveal a flora rich in endemics and relics (Stebbins and Major 1965), creating complex vegetation patterns strongly controlled by parent material, physiography, and climate (Whittaker 1960). A long history of forest development comparable to that of the southern Appalachians (Braun 1950) is known for the Klamath Region forests, which represent the least modified examples of western North American Tertiary vegetation (Wolfe 1969).

Whittaker (1960) argues that current vegetation patterns are controlled primarily by parent materials, and secondarily by elevation and soil moisture as it relates to topography. His work was done primarily in the Oregon Siskiyou Mountains, and was concerned chiefly with low to middle elevation patterns. Whittaker's 1961 paper on the phytogeographic implications suggests that the region is a center of accumulated species of varied evolutionary history.

This interpretation is readily apparent from the distributions of several groups, notably the diverse complement of conifers growing in the region (Fig. 1).[1] The general pattern is one of a commingling of Northwest and California-centered species. Additionally many species are found in the Klamath Region as isolated stands characteristic of refugia. Scattered stands of trees regionally common in the Pacific Northwest (silver fir, Alaska yellow-cedar), the western interior (subalpine fir, Engelmann spruce), and the southern Sierra Nevada (foxtail pine) find their range limits here (Griffin and Critchfield 1972). Weeping spruce, once widespread (Wolfe 1969), is now endemic to the region. Redwood, western red-cedar, western hemlock, Port Orford-cedar show similar patterns at lower elevations.

Such generalized accounts fail to explain fully why the localized populations of these relics are scattered throughout the region in a variety of habitats at various elevations. To resolve this question we initiated a study of the ecological status of six relic conifers (silver fir, subalpine fir, Engelmann spruce, weeping spruce, Alaska yellow-cedar, foxtail pine). Compositional and habitat comparisons for 17 areas supporting one or more of these trees began in 1968 (Sawyer and Thornburgh 1969). The initial work demonstrated the primary control of parent materials over vegetation expression, as well as the

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[1]For brevity common tree names will be used. Figure 1 provides equivalent technical names.

general application of Whittaker's analyses. It also pointed out the need for more detailed descriptions to adequately define typical regional montane and subalpine forest patterns. The early work also suggested that the vegetation patterns of the Russian Peak area (Fig. 2) were the most floristically diverse (Sawyer et al. 1970). We began the regional characterization of high elevation forest types by first defining and describing those of the Russian Peak area. These forest types were then tested regionally against forests in other areas with similar parent material (Fig. 3), allowing the development of typical montane and subalpine regional forest types on granitic parent materials. The role of the relic conifers within the regional vegetation mosaic was then evaluated, since all six species grow on granitics although none is restricted to them.

Additional studies made in the Russian Peak area included an inventory of the vascular flora, a mapping of the locations and extent of the relic trees within the area, and an analysis of the soils of representative stands.

THE PHYSICAL SETTING

The Klamath Region is a geologically defined 30,560 km^2 area in northwestern California and southwestern Oregon. Although it is geographically contiguous with the Oregon and California Coast Ranges, its geological relations are with the Sierra Nevada and the Blue Mountains of the Pacific Province (Fennemen 1931). The surrounding lands of the coast ranges, Cascades, and Sacramento Valley are much younger geologically.

The Klamath Region is composed of a complex of mountain ranges, drained in California by the Smith River, the Klamath River, and its tributaries including the Scott, Salmon and Trinity Rivers (Fig. 3). The Klamath River begins outside the Region in the south-central Oregon Cascades. It generally flows west, then south until it meets the Trinity River, where it turns abruptly north to the Pacific Ocean.

To the north and west of the Klamath River lie the Siskiyou Mountains, whose west slopes are drained by the Smith River. The peaks of these rugged mountains range generally from 1,400 to 2,000m. Preston Peak (2,228m) is the prominent feature in California.

The central part of the Klamath Region includes a complex of poorly defined ranges in part drained by the Scott and Salmon Rivers as well as the North and East Forks of the Trinity River. These mountains have generally higher peaks and ridges (1,900 - 2,500m), and include the Marble

Mountains, nearest the Klamath River and the Salmon Mountains, which continue south and then west. To the south, the Salmon Mountains blend into the Scott Mountains and the Trinity Alps. The latter represent an expanse of heavily glaciated peaks culminating in Thompson Peak (2,744m).

South of the central area are less prominent ranges with only a few outstanding peaks, such as Bully Choop (2,122m) and North Yolla Bolly (2,397m). This area includes the headwaters of the South Fork of the Trinity River, the Trinity Mountains, and the South Fork Mountains. South Fork Mountain, a ridge some 64 km long, is considered the Region's western boundary. The western tributaries of the Sacramento River drain the eastern portion of the Region.

Rugged mountain topography prevails in this area. The Scott Valley is the only extensive one in the entire region. Considering the size of the rivers that drain the Region, the valleys are narrow and have small or non-existent floodplains. Canyons, high cliffs, and steep slopes are typical of low elevation landscapes.

At higher elevations the terrain is less rugged, though still highly dissected. The gentler slopes arch toward broad ridges and crests in unglaciated areas. On higher terrain (e.g., the Trinity Alps) alpine glaciation has created strong relief of sharp ridges, steep slopes, cirques, and U-shaped valleys.

CLIMATE

The steep climatic gradients typical of the Region (Whittaker 1960) are due to its location and physiography. The continental influence is shown (Table 1) by increasing seasonal temperature extremes from the western (maritime) side to the eastern (continental) side. Precipitation patterns follow accordingly (Table 1).

Increased sunshine, potential evapotranspiration, diurnal temperature changes, and decreased average humidities are associated with this general change from maritime to continental climates making the maritime climates significantly less droughty for trees (Waring 1969).

The Mediterranean climate of California is somewhat modified here by summer thunderstorms and occasional cyclonic activity. Summer precipitation is typical, especially at the higher elevations, but is not dependable from year to year.

The proximity to the Pacific Ocean accounts for the high precipitation experienced here. Large amounts of snowfall are common at middle and high elevations in the area. Deep snow melts slowly during the late spring and early summer, approximating environmental conditions at higher elevations in the Sierra Nevada and the Cascades. In years of heavy snow pack, snow fields may remain throughout the summer on north and east facing slopes above 1,850m. Permanent snowfields occupy the north slopes of Thompson Peak in spite of its modest elevation (Sharp 1960).

RECENT INFLUENCES

The area has a small, scattered population; Weaverville (population of 1,736) is the largest town. Extensive farming is restricted to the Scott Valley. The major environmental impacts come from timber removal, mining, and grazing on the Klamath, Shasta-Trinity, and Six Rivers national forests. Much of the area is not yet extensively modified by current land-use practices. The presence of the Marble Mountain Wilderness, the Yolla Bolly Wilderness, the Salmon-Trinity Alps Primitive Area, and 33 de facto wilderness areas here attest to its natural character. Nearly 3 x 10^5 ha are still roadless.

The summer-dry climate creates ideal conditions for frequent and extensive natural fires. Local Indians are considered to have used fire for hunting and warfare. More intense burning has been associated with prospecting activities of the mid-1800 gold rush period (Whittaker 1960). Fires continue to be a major environmental control of vegetation expression, but probably with reduced influence because of active fire supression by the U.S. Forest Service.

GEOLOGIC HISTORY

The Klamath Region is an area of mature topography resulting from a long, complex history of development. Its pre-Cenozoic history is similar to that of the Sierra Nevada, and in this respect the Klamath Region can be considered a northwesterly continuation of that range. However, the differences are significant. These lower mountains trend in several directions. The older Paleozoic and Triassic to mid-Jurassic rocks are exposed, and the major granitic intrusions are older. Additionally the Klamath mountains were not elevated so greatly during the Cenozoic (Oakeshott 1971, McKee 1972).

The Region's Paleozoic and Mesozoic development was followed by relative stability during the Cenozoic. Several periods of marine deposition by sedimentation and volcanism supplied the basic fabric of the Region. Mountain building, a result of compression as well as of ultrabasic and granitic intrusion during at least three periods, produced varying degrees of regional metamorphism (Davis 1966, Irwin 1966, Oakeshott 1971). The resulting Cretaceous land mass has not been subsequently submerged.

The early Tertiary mountains were eroded to a generally low relief by Miocene times. Uplift followed by erosion of this peneplain surface then occurred. Possibly two or more complete cycles of erosion followed by uplift are suggested by the elevations of accordant crests and ridge lines in the area (Irwin 1960); however, late Tertiary and Quarternary tilting, deformation, and erosion complicate interpretations (Irwin 1966).

Quarternary glaciation significantly eroded the higher mountains. Glaciers were most extensive in the central Trinity Alps surrounding Thompson and Sawtooth Peaks (Sharp 1960). More localized montane glaciers were characteristic of north and northeast tending drainages of the Trinity, Salmon, Marble, Scott, Siskiyou, and South Fork mountains, where cirques, steep rock walls, and tarns are now common.

RESULTING GEOLOGY

The resulting lithic pattern (Fig. 4) shows a series of north-south tending arcuate belts of distinctive rock assemblages of similar age and character. These sub-provinces are the Eastern Paleozoic, the Central Metamorphic, the Western Paleozoic and Triassic, and the Western Jurassic (Davis 1966). They include, and are more or less regionally separated by, faults and granitic and ultrabasic intrusions (Fig. 4). The Wolley Creek, the Ironside Mountain, and the Shasta Bally Batholiths are extensive. Ultrabasic intrusions, principally peridotite and dunite chiefly altered to serpentine, are common and may be extensive.

The composition of the sedimentary and volcanic rocks and the degree of metamorphism vary among the belts. This variability, along with that of the intruded ultrabasic and granitic rocks, results in a very high diversity of parent materials within the Klamath Region.

Of these materials, the granitics of the region are diorites. Hornblende diorite is found in the western part (Ironside Mountain Batholith, Siskiyou Mountains) and quartz diorite to granodiorite in the eastern part (Wolley Creek Batholith, Shasta Bally Batholith) (Irwin 1960).

These diorites were mainly intruded during the late Jurassic in contrast to the Sierra Nevada granitics, which were late Cretaceous.

PALEOBOTANY

Paleobotanical studies suggest that the Klamath Region and north coastal mountain ranges of California maintain forests most nearly equivalent to the western North American Arcto-Tertiary forests (Axelrod 1959, Chaney 1947, Whittaker 1961, Wolfe 1969). Some modification has resulted from segregation, recombination, and extinction of certain Arcto-Tertiary forest components, as well as evolution and introduction of other various taxa; nevertheless of all the forest regions in western North America the forests of the Klamath Region are the least modified.

Whittaker (1961) argues that the relative stability of the forests is the result of the Region's long history of mature topography, its regional lithic diversity, and central geographic location. These factors minimized the effects of a climatic shift from a summer-wet to summer-dry conditions. Additionally the Klamath Region has not undergone the significant geologic alterations (mountain building, volcanism, marine submergence) experienced over much of the West since the Miocene. Instead the maintenance of high regional habitat complexity through time has increased the Region's floristic and vegetational diversity. The shrinkage and differentiation of the mixed Arcto-Tertiary lowland and montane forests, in addition to assimilation of the Madro-Tertiary elements of woodland, chaparral, and grassland, could occur because diverse habitats were available. Wolf's (1969) reconstructions of late Miocene forests of the Columbia Plateau-Cascade Range and of Nevada include assemblages approximating present-day Klamath forests. For example, he includes in those interior assemblages weeping spruce, now a Klamath Region endemic, and Alaska yellow-cedar, which now attains its southern range limits here.

The cooler and drier climates of the Pliocene probably modified Miocene forests to more closely approximate modern patterns. Whittaker (1961) suggests that *Sequoia* was more restricted to coastal areas at that time. Actually relic stands of *Sequoia* still occur in the western parts of the Region (Griffin and Critchfield 1972).

Pleistocene glaciation significantly affected vegetation patterns. Since the glaciers were localized, subalpine and alpine vegetation was not eliminated to the extent experienced in other western mountain areas. The cooler Pleistocene climates no doubt also allowed the expansion of subalpine and montane forests to lower elevations. In this way the Klamath Region might have acted as a source for colonization of the surrounding, recently elevated mountains of the coastal ranges to the north and south, and even possibly the Sierra Nevada (Howell 1944).

Subsequent xerothermic periods probably caused local extinctions of some montane and subalpine species and so further modified vegetation patterns. But because of the region's high habitat complexity such localized extinctions and readjustments acted to complicate rather than to simplify the resulting floristic and vegetational patterns. The effects of fire in the summer-dry climates could have much the same effect, especially at low to middle elevations. As a result of this long, complicated history the Klamath Region now has one of the most highly complex vegetation patterns in North America.

METHODS

The field work was accomplished in the 1968-72 field seasons. A regional reconnaissance in 1968 indicated the importance of the Russian Peak area which was intensively studied in 1969-70. The resulting forest types were tested in 13 other granitic areas in 1971-72. Sampling was restricted to forests above 1,250m in the montane (1,250-1,950m) and subalpine (>1,950m) elevations.

Most areas at these elevations are not accessible by road. Plant collecting, vegetation, and soil sampling were accomplished by trail hiking or cross-country traverse. The required hiking added to the pleasure, if not the speed of gathering data. Over 2550 plant collections were made, 1300 in the Russian Peak Area alone. These are deposited in the Humboldt State University Herbarium. Some 458 relevés were taken, 221 within the Russian Peak area. In each relèvé we recorded species cover/abundance estimates using the standard 7-rank scale and procedures of continental phytosociologists (Shimwell 1972). In addition, we noted location, parent material, topographic position, percentage slope, aspect, soil depth and stonyness, litter characters, and disturbance. Stand characters of height in m and coverage in percent of the canopy, sapling, seedling, shrub, and herb layers were estimated.

The locations of the relevés were chosen not at random but to represent typical mature vegetation. Data analyses did not assume a random selective procedure.

RUSSIAN PEAK ANALYSES

Development of Russian Peak vegetation types

Quantitative analyses were undertaken in an attempt to determine major relationships between species distributions and environmental factors, and to objectively define species groups forming vegetation types. In these analyses the following designations were used: (1) the vegetation of each relevé as a stand, (2) the characteristics of the immediate environment of each relevé as a habitat, (3) a series of stands occupying points on a continuous scale as a vegetational gradient, (4) detected groupings of stands on vegetational gradients as vegetation types, and (5) the spatial arrangement of stands in relation to axes of variation as gradient analysis or ordination (Goodall 1954, Whittaker 1967). Direct gradient analysis employs environmental axes, whereas indirect gradient analysis utilizes compositional axes (Shimwell 1972).

The environmental characteristics of each relevé were transformed to numerical indices. A moisture equivalency index was derived, representing an estimate of the soil moisture availability for each community, considering topographic position and aspect (Table 2). This scale implies equivalent moisture conditions for locations of similar topographic position and aspect if other soil conditions are equal. The exposure scale developed by Whittaker (1961, 1967) was not used. Field estimates for the cover/abundance of the sampled species were transformed to percentages (1=1, 2=2, 3=6, 4=17, 5=37, 6=62, 7=87).

Direct gradient analysis of species

The average percent cover of 108 species was plotted in relation to elevation and the derived moisture equivalency gradient. Most species appeared to be limited to definite portions of this environmental space. Species with similar requirements generally occupied similar space, but some species that had overlapping distributions were often not found together in stands. Most species did not show distributions corresponding exactly to those of other species. Direct gradient analysis of conifers is reported (Fig. 5).

INDIRECT GRADIENT ANALYSIS

Since we could not readily identify species combinations by direct analysis using the elevation and moisture gradients alone, we attempted to identify relationships among different stands on the basis of vegetational similarity. The composition of the vegetation of a community is an indirect indication of the nature of the environment and of recent history. Compositional gradients should reflect environmental gradients insofar as species are limited in tolerance by those factors. Stands were arranged along gradients of varying vegetational composition by the ordination methods of Bray and Curtis (1957) as modified by Beals (1960).

Ordination of middle elevation forests

Sixty-eight stands chosen from midelevations (1,280-1,770m) were first ordinated. The resulting pattern for canopy trees shows a general gradient from ponderosa pine-dominated to white fir-dominated stands. The inclusion of higher elevation species complicates this simple pattern. The following categories are recognized (Fig. 6). A great overlap is seen when these types, based on canopy patterns, are directly ordinated in relation to the elevation and moisture index gradients. The mixed forests (I, III) tend to be restricted to the lower elevations and to drier habitats at higher elevations. The enriched mixed forests (IV, VI) descend to about 1,370m on edaphically wet habitats.

Analysis of reproduction data of the same 68 stands shows a more definite pattern. Only types III and V are recognized by the definitions used in the canopy ordination. These show close correlation with the elevation and moisture index gradients (Fig. 7), suggesting that the reproductive layer better represents the potential patterns and past stand history influences canopy composition. Fig. 7 also suggests that these two objectively defined forest types are distinct on the basis of elevation and moisture gradients alone. This supports Whittaker's (1960) conclusions that, after parent material, elevation and topographic moisture are the major environmental controls.

Ordination of all stands

After the success of midelevation analysis, another ordination was attempted for the complete area. Calculation of similarities among 221 stands based on 64 chosen species produced a matrix of similarities from which major axes of variation were extracted.

The x-axis was constructed from two stands typifying the predominant observable environmental gradient from a low-elevation, moist alluvial terrace habitat to a high-elevation, dry-ridge habitat. The y-axis, approximately perpendicular to the x-axis, represents the variation between a high-elevation, moist habitat and a low-elevation, dry habitat. Stands are arranged on the z-axis representing a gradient from a deep-soil, densely canopied forest to a shrub field over thin rocky soil with very low tree coverage.

When arranged on these nearly perpendicular axes the stands form distributions that approximate interstand similarities in the calculated similarity matrix (Fig. 8). There is a close relationship between ordination distance and calculated similarity among more marginal stands. However, those stands nearer the center are not arranged in significant patterns by the axes of this ordination. Other combinations of axis end-points were attempted, but they resulted in the same problems, and created groupings with less information.

An attempt to test the relationship between the calculated similarity and ordination for 299 pairs of randomly selected stands showed a low positive correlation (r=0.109 for P<.05 with N=299). Stand similarity and distance in the ordination are not as highly correlated as expected. The non-Euclidean nature of the interstand differences prevents the exact representation of the matrix of calculated similarities by ordination distances (Swain 1970, Gauch and Whittaker 1972, Gauch 1973). Since the axes representing gradients were constructed in relation to the vegetation of the end-points, the description of vegetation occupying the center of each gradient was inexact. Species present in the center of an ecologically important gradient may not be present in stands at either end-point. The presence or absence of such species from a stand would not significantly affect stand position on an ordination axis. This reduces the ecological significance of the ordination procedure here. It also accounts for the greater success on the earlier mid-elevation forest ordination.

The arrangement of all stands by significant similarities was a means of helping to create categories based on vegetational similarity. Stands close to each other in the ordination and separated from other groups of stands represent naturally occurring species combinations. Stands between groupings represent intermediates, although inexactly. Some groups represent types which had been recognized in the field. Other groups provided evidence for natural combinations that were not so evident and thus helped in defining the described vegetation units. Although the indirect ordination failed to adequately differentiate all units, it did help to distinguish trends and reoccurring species combinations not readily apparent.

RUSSIAN PEAK FOREST TYPES

The vegetation of the middle and high elevations are conveniently categorized into four elevational zones according to the dominant climax trees of the mesic habitats. These zones are then divided into a series of vegetation types reflecting distinctive environments.

White Fir Zone

Two forest types are recognized between 1,280 and 1,650m, where white fir is the climax dominant. They are Abies concolor/Berberis nervosa on mesic slopes, and Abies concolor/Ceanothus prostratus on xeric slopes and ridges.

Abies concolor/Berberis nervosa.- White fir dominates a typical assemblage of mid-elevation conifers including Douglas-fir, incense-cedar, sugar pine, and ponderosa pine. Together they form moderate to dense forests. Reproduction shows heavy dominance of white fir and incense cedar. Douglas-fir, sugar pine and ponderosa pine are found growing in openings in the mature forest canopy enabling them to maintain populations, although a more important role for white fir with increasing maturity is suggested. Cornus nuttallii, Quercus chrysolepis, Q. kelloggii, Acer macrophyllum, and Taxus brevifolia are common understory associates. A moderately developed shrub layer is dominated by Berberis nervosa, Rubus ursinus, R. parviflorus, Salix scouleriana, Cornus nuttallii, Rosa gymnocarpa, Symphoricarpos hesperius, and Paxistema myrsinites. The moderately developed ground layer characteristically includes Arnica cordifolia, Apocynum pumila, Campanula prenanthoides, Disporum hookeri, Goodyera oblongifolia, Chimaphila umbellata, Hieracium albiflorum, Pteridium aquilinum, Linnaea borealis, Adenocaulon bicolor, Pyrola picta, and Festuca occidentalis. This forest is generally found below 1,650m on mesic habitats with deep soils (Fig. 9).

Abies concolor/Ceanothus prostratus.- The generally open to moderately dense forest is dominated by ponderosa pine. White fir and Douglas-fir are common secondary dominants along with sugar pine and incense-cedar. A secondary layer of Quercus chrysolepis, Q. kelloggii, and Chrysolepis chrysophylla is common, especially along ridges. The reproductive layer is generally dominated by Douglas-fir and white fir, but ponderosa pine, incense-cedar, and sugar-pine are reproducing well. The understory is mainly sclerophyllous shrubs, Ceanothus prostratus, Chrysolepis sempervirens, and Quercus vaccinifolia often forming dense patches under canopy openings along with Rosa gymnocarpa and Symphoricarpos hesperius. Herbs are uncommon except for the ubiquitous Chimaphila umbellata, Pyrola picta, and Pteridium aquilinum. This forest is generally found below 1,950m on dry, middle to upper slopes and ridges (Fig. 9).

<u>Shasta Fir Zone</u>

Four types are recognized between 1,650 and 1,950m, where Shasta fir dominates successional trends, if not the canopy. Both open and closed forests are found at these elevations, creating more variety than is found in the White Fir Zone. Two closed forests, the mesic *Abies magnifica/ Linnaea borealis* and the streamside *Abies magnifica/ Leucothoë davisiae*, are common on the well-developed soils. The open forests form a heterogenous grouping of communities, described as *Abies magnifica/Quercus vaccinifolia*. They are found on talus and moraines characterized by spotty soil development among large rocks. The south-facing colluvium is covered by montane chaparral stands, *Quercus vaccinifolia-Arctostaphylos patula*.

Abies magnifica/Leucothoë davisiae.- Engelmann spruce, along with Shasta fir and white fir, dominates the dense forests. Other important associates are white pine, mountain hemlock, incense-cedar, and lodgepole pine. Occasional weeping spruce and subalpine fir are found at higher elevations, as are sugar pine and ponderosa pine at lower elevations. The reproductive layer is dominated by Engelmann spruce along with abundant white pine, mountain hemlock, white fir, and Shasta fir. All canopy species except ponderosa pine were found reproducing. The rich shrub layer is dominated in many areas by *Leucothoë davisiae*, *Ribes lacustre*, *Alnus tenuifolia*, *Sorbus californica*, and *Salix scouleriana* border the streams.

Taxus brevifolia covers many alluvial flats. Other common shrubs are *Rosa gymnocarpa*, *Symphoricarpos hesperius*, *Vaccinium arbuscula*, and *Ledum gladulosum*. The ground layer is varied. Common species are *Anemone deltoidea*, *Adenocaulon bicolor*, *Clintonia uniflora*, *Disporum hookeri*, *Streptopus amplexifolius*, *Viola glabella*, *Senecio triangularis*, *Smilacina stellata*, *Trillium ovatum*, *Listera convallarioides*, *Pyrola picta*, *Goodyera oblongifolia*, and *Pteridium aquilinum*. This forest is restricted to wet streamside terraces, meadow margins and seeps below 2,100m (Fig. 9).

Abies magnifica/*Linnaea borealis*.- An open to moderately dense forest is surprisingly characterized by 12 conifers. Although as many as 10 may occur in a single stand, 7 or 8 is the normal complement. The canopy diversity results from the 5 midelevation species being enriched by as many as 7 high elevation species. The dominants are Douglas-fir, white fir, and Shasta fir. White fir characteristically shows the highest canopy cover. The 9 other species in order of prominence are white pine, weeping spruce, mountain hemlock, sugar pine, ponderosa pine, incense-cedar, Engelmann spruce, lodgepole pine, and occasionally subalpine fir. The midelevation species gradually decline in importance with elevation. All species reproduce in this type, although reproduction is mostly Shasta fir, white fir, Douglas-fir, weeping spruce, and mountain hemlock. A characteristically well-developed shrub layer is dominated by *Chrysolepis* sempervirens, Quercus vaccinifolia, Rosa gymnocarpa, Symphoricarpos hesperius, Rubus parviflorus, Ribes lobbii, Acer glabrum, and Amelanchier pallida. The ground layer is well developed, with Linnaea borealis, Adenocaulon bicolor, Clintonia uniflora, Anemone deltoidea, Goodyera oblongifolia, Arnica spp., Galium triflorum, Pteridium aquilinum, Chimaphila spp., and Hieracium albiflorum common. This forest has a general range from 1,650 to 1,950m but is more restricted at low elevations (Fig. 9).

Abies magnifica/Quercus vaccinifolia.- These open forests are dominated by mountain hemlock and Shasta fir. White fir, weeping spruce, white pine, and lodgepole pine are common at the lower elevations. At higher elevations whitebark pine associates in open forests lacking white fir and lodgepole pine. Reproduction indicates continuance of the present canopy assemblages in most areas. In canopy openings and among rocks are patches of Arctostaphylos patula, A. nevadensis, Amelanchier pallida, Chrysolepis sempervirens, Ceanothus velutinus, Prunus emarginata, and Rosa gymnocarpa. Herb composition varies with microhabitat influences. The common high elevation species of dry areas are Penstemon newberryi, Phlox diffusa, and Polygonum davisiae, along with such typical montane forest herbs as Chimaphila spp., Pyrola picta, Goodyera oblongifolia, Apocynum pumila, Kelloggia galioides, and Monardella odoratissima. This forest is of general extent on moist moraines and talus above 1,860m, but similar forests occur on cool, upper slopes approaching 2,440m on soils too thin to support closed stands (Fig. 9).

Quercus vaccinifolia-Arctostaphylos patula.- Patches of generally dense sclerophyllous shrubs about 1m tall cover the dry slopes. White pine, Shasta fir, and white fir are scattered among the shrubs. Lodgepole pine, incense-cedar, sugar pine, and Jeffrey pine are less common. Although any tree species may be locally abundant. Amelanchier pallida, Arctostaphylos patula, A. nevadensis, Ceanothus velutinus, Holodiscus microphyllus, Prunus emarginata and Quercus vaccinifolia dominate the chaparral in varying degrees. Lonicera conjugialis, Garrya fremontii, Acer glabrum, Chrysolepis sempervirens are important secondary species and may be locally abundant. Common herbs found scattered among the shrubs are Senecio integerrimus, Monardella odoratissima, Phlox diffusa, Castilleja appelgatei, Penstemon newberryi, P. procerus, Eriogonum umbellatum, and Smilacina racemosa var. glabra. This type, also referred to as montane chaparral, covers dry slopes with thin, rocky soils above 1,830m (Fig. 9).

Mountain Hemlock Zone

Four forests with important tree components are recognized between 1,950 and 2,200m. The distinction between open and closed forests used in the Shasta Fir Zone is convenient here as well. The two closed forest types are vegetationally simple and very closely related. Described as a "complex" to emphasize their similarities, they may be divided by canopy dominance of mature stands into Abies magnifica/Pyrola picta and Tsuga mertensiana/Pyrola picta. Streamside, meadow, lake margins, and seepage areas are characterized by Tsuga mertensiana/Phyllodoce empetriformis. On glacially polished rock, soil develops in areas of particle accumulation such as cracks, crevices, or concave surfaces. Such areas have a distinctive form of chaparral described here as Pinus monticola/Holodiscus microphyllus.

Tsuga mertensiana/Phyllodoce empetriformis.- Locally these forests are dominated by subalpine fir and occur in two characteristic habitats. They form extensive dense forests bordering wet meadows and streams. The type also occurs in local seeps and along streamlets where subalpine fir forms krummholz to 2m on otherwise dry slopes. In both phases subalpine fir shares dominance with mountain hemlock and lodgepole pine. Other common associates are white pine and Shasta fir. Occasional weeping spruce, Engelmann spruce, and white fir occur around wet meadows. Reproduction is heavy for mountain hemlock and subalpine fir with the others reproducing less abundantly. All trees are actively invading many wet meadows. Phyllodoce empetriformis, Vaccinium scoparium, V. arbuscula, Lonicera conjugialis, Leucothoë davisiae, and Ribes lacustre dominate the shrub layer. Ledum glandulosum and Kalmia polifolia are common at lake margins. The ground layer is composed of wet meadow herbs, Senecio triangularis, Veratrum californicum, Dodecatheon jeffreyi, and Carex spp. mingling with such forest associates as Pyrola picta and Chimaphila umbellata, under the trees. Sedum obtusatum, Phlox diffusa, and Cryptogramma acrostichoides grow in the xeric microhabitats which are especially characteristic of the seepage phase. This forest is restricted to 1,950 to 2,130m within the zone (Fig. 9).

Tsuga mertensiana-Abies magnifica/Pyrola picta complex.- The deeper high elevation soils support moderate to dense forests. Canopy dominance is typically shared by mountain hemlock and Shasta fir. White pine is a constant companion of minor importance. On the drier habitats, Shasta fir increases in dominance and may be the only tree in the stand (Abies magnifica/Pyrola picta). Such forests are typical on south to southwest-facing slopes and ridges with deep soil. On the cooler aspects mountain hemlock may dominate or be found without Shasta fir (Tsuga mertensiana/Pyrola picta). Pure mountain hemlock forests are typical of upper slopes with east to northeast aspect. Middle and lower slopes usually maintain both, so the two types are conveniently segregated depending on canopy dominance. Occasionally other trees such as whitebark pine, subalpine fir, lodgepole pine and weeping spruce are found. These forests usually tend towards the more open Abies magnifica/Quercus vaccinifolia. Shrub and herb coverage is extremely light, and in many cases non-existent. Shrubs such as Ribes viscosissimum are scattered and restricted to canopy openings. Depauperate individuals of Arctostaphylos patula, A. nevadensis, Chrysolepis sempervirens, Holodiscus microphyllus, or Quercus vaccinifolia may be found. Wet areas support small stands of Vaccinium scoparium or Leucothoë davisiae. The ground layer is equally depauperate in both types. Pyrola picta is the most consistently associated, but only in small quantities. A few individuals of Pyrola secunda, Penstemon newberryi, Chimaphila umbellata and Polygonum davisiae may be found. These types occur above 1,950m on all but the driest ridges and summits, if the soil is developed well enough to support a closed forest (Fig. 9).

Pinus monticola/Holodiscus microphyllus.- Groves of white pine, Shasta fir and lodgepole pine are scattered along drainage courses and in small areas of soil accumulation on polished bedrock slopes. Individual trees, especially of lodgepole pine, support themselves in small fissures. A discontinuous, low shrub layer is scattered among the patches of herbs and bare rock. The chaparral component is dominated by Arctostaphylos patula, A. nevadensis, Holodiscus microphyllus, and Amelanchier pallida. Typical dry habitat herbs are Achillea lanulosa, Arenaria congesta, Sedum obtusatum, Chielanthes gracillima, Juncus parryi, Phlox diffusa, Calyptridium umbellatum, Lewisia cotyledon, and Penstemon newberryi. This open forest is best represented on south-facing slopes between 2,070 and 2,290m (Fig. 9).

Whitebark Pine Zone

The environment above 2,200m is restricted to ridges and summits where the Pinus albicaulis/Holodiscus microphyllus open forest type is recognized. The foxtail pine stand found above Little Duck Lake is included.

Pinus albicaulis/Holodiscus microphyllus.- Ridge crests, summits and upper southwesterly slopes support a dwarfed, open woodland where trees exceed 6m only among the sheltered rocks. Whitebark pine dominates the canopy with mountain hemlock and Shasta fir as common associates. White pine, Jeffrey pine, foxtail pine and lodgepole pine grow in some stands. Stand reproduction suggests a continuation of this pattern. Shrubs, typically wind trained and pruned at less than 1m, grow on gravel slopes or among the rocks. Holodiscus microphyllus, Haplopappus greenei, along with Arctostaphylos patula, Ceanothus velutinus, and Prunus emarginata are common. Juniperis communis shows local dominance. One shrubby population of Populus tremuloides was found. Herbs, at best, are scattered. Arenaria congesta, Achillea lanulosa, Phlox diffusa, Penstemon newberryi, Draba howellii, and Polemonium pulcherrimum are scattered among the rocks above 2,225m (Fig. 9).

KLAMATH REGION FOREST TYPES

A reconnaissance of additional areas with granitic parent materials (Fig. 2) allowed regional evaluation of the 11 forest types developed from the Russian Peak analyses. This expanded sampling also made possible the development of additional regional types, and the modification, when necessary, of those local descriptions. Association tables were produced for the analysis of these regional types using 458 relevés from 14 areas. The data are summarized as presence tables which also include average cover/abundance for trees and shrubs, and for herbs attaining greater than 10 percent presence.

Sixteen vegetation types dominated by trees are primarily segregated by elevation and secondarily by soil moisture availability. The degree of canopy closure is another significant variable. Elevation zones are named according to the dominant climax tree of the mesic habitat (Table 3). Species used to characterize types are not necessarily restricted to a type or zone.

Montane zones show regional differences recognized by Waring (1969). These differences become less at higher elevations as reflected in the following classification:

WHITE FIR ZONE

Types characteristic of the western subregion:

<u>Abies concolor/Trillium ovatum</u> - closed forests of streamside terraces, moist slopes, seeps.

Abies concolor/Vicia americana - closed forests of mesic slopes.

Abies concolor/Chimaphila umbellata - closed forests of xeric slopes.

Types characteristic of the eastern subregion:

Abies concolor/Berberis nervosa - closed forests along streams, mesic slopes.

Abies concolor/Ceanothus prostratus - open forests of xeric slopes.

SHASTA FIR ZONE

Abies magnifica/Leucothoë davisiae - closed forests along streamside terraces, wet meadows.

Abies magnifica/Linnaea borealis - closed forests of mesic slopes.

Abies magnifica/Chimaphila umbellata - closed forests of xeric slopes.

Abies magnifica/Quercus vaccinifolia - open forests of mesic slopes.

Quercus vaccinifolia-Arctostaphylos patula - montane chaparral of xeric slopes.

MOUNTAIN HEMLOCK ZONE

Tsuga mertensiana/Phyllodoce empetriformis - open to closed forests along streams, wet meadow, lake margins.

Tsuga mertensiana/Quercus vaccinifolia - open forests of mesic slopes.

Tsuga mertensiana/Pyrola picta - closed forests of mesic slopes.

Abies magnifica/Pyrola picta - closed forests of xeric slopes.

Pinus monticola/Holodiscus microphyllus - open forests of xeric slopes.

WHITEBARK PINE ZONE

Pinus albicaulis/Holodiscus microphyllus - open forests of xeric slopes, ridges.

White Fir Zone

Subregional differences are enough to recognize two sets of forest types at midelevations. In the western subregion three types, Abies concolor/Trillium ovatum, Abies concolor/Vicia americana, Abies concolor/Chimaphila umbellata, dominated by Douglas-fir and white fir, occupy streamside, mesic and xeric slopes respectively. In the eastern subregion ponderosa pine and sugar pine play more important roles, thereby producing mixed forests. The mesic and xeric types described for the Russian Peak area are characteristic.

Abies concolor/Trillium ovatum.- Douglas-fir and white fir dominate these tall, dense forests typical of draws, streamside terraces, seeps and lower slopes with deep soils. Forests approaching this type may also occur on some upper slopes. The dominance of Douglas-fir and white fir in the canopy and white fir in the understory is typical. Douglas-fir consistently reproduces in smaller numbers as well. Sugar pine and incense-cedar are common secondary conifers. Chrysolepis chrysophylla and Taxus brevifolia are common understory trees above well-developed shrub and ground layers. The shrub layer is diverse including up to 15 species of common regional shrubs in a single stand (Table 4). Holodiscus discolor, Rosa gymnocarpa, Corylus cornuta, Symphoricarpos spp., Rubus parviflorus, Paxistema myrsinites, Cornus nuttallii, Berberis nervosa, and Quercus sadleriana are common. The ground layer is rich in species covering most of the soil. Some typical herbs are *Trillium ovatum*, *Anemone deltoidea*, *Adenocaulon bicolor*, *Asarum caudatum*, *Linnaea borealis*, *Smilacina stellata*, *Clintonia uniflora*, *Fragaria californica*, *Osmorhiza chilense*, *Trientalis latifolia*, *Achlys triphylla*, *Viola glabella*, *Corallorhiza maculata*, *Galium triflorum*, *Whipplea modesta*, *Chimaphila umbellata*, *Pyrola picta*, *Disporum hookeri*, *Heiracium albiflorum*, *Penstemon anguinus*, and *Vancouveria hexandra*. This forest type commonly grades into the *Abies concolor/Vicia americana* of mid-slopes, but can be differentiated from it by the extensively developed shrub layer here. At higher elevations it grades into *Abies magnifica/Leucothoë davisiae* and *Abies magnifica/Linnaea borealis*.

Abies concolor/Vicia americana.- Douglas-fir and white fir dominate these dense forests on mesic slopes. These forests also characteristically include occasional sugar pine and incense cedar, but ponderosa pine is rare. The reproduction is dominated by white fir, although all species reproduce. *Chrysolepis chrysophylla* and *Quercus chrysolepis* are common understory trees. The shrub layer is diverse, but of low coverage. Common shrubs include *Rubus parviflorus*, *Cornus nuttallii*, *Berberis nervosa*, *Rosa gymnocarpa*, *Symphoricarpos* spp., and *Corylus cornuta* (Table 4). The ground layer is diverse and typically well-developed. Common associates include *Achlys triphylla*, *Trientalis latifolia*, *Lupinus adsurgens*, *Adenocaulon bicolor*, *Galium triflorum*, *Heiracium* *albiflorum*, *Vicia americana*, *Disporum hookeri*, *Corallorhiza maculata*, *Pteridium aquilinum*, *Chimaphila umbellata*, *Pyrola* spp., and *Campanula prenanthoides*. This type is intermediate in character between the more moist *Abies concolor/Trillium ovatum* and the xeric *Abies concolor/Chimaphila umbellata*. It is distinctive with a shrub layer of low coverage and a ground layer with high coverage.

Abies concolor/Chimaphila umbellata.- White fir dominated forests, including Douglas-fir, sugar pine, ponderosa pine, and incense-cedar as less important associates, grow on drier slopes and ridges with deep soils. The open character of the mature forests allows reproduction of all five conifers. *Quercus chrysolepis* is a component at lower elevations. A distinctive character of the type is the depauperate shrub and ground layer (Table 4). Low coverage of a few shrubs as *Corylus cornuta*, *Rosa gymnocarpa*, and *Symphoricarpos hesperius* and herbs as *Goodyera oblongifolia*, *Corallorhiza maculata*, *Chimaphila* spp., and *Pyrola* spp. is typical. Even these relatively common species show low presence. It is distinguished from *Abies concolor/Ceanothus prostratus* by the low coverage of sclerophyllous shrubs. Immature forests are typically dense stands of white fir which eliminate early-seral species. The more open character of the *Abies concolor/Ceanothus prostratus* sere allows maintenance of the chaparral. Intermediate stands between these two types are also regionally common. This forest type also grades not only into *Abies concolor/Vicia americana*, but also the equivalent *Abies magnifica/Chimaphila umbellata* of the Shasta Fir Zone.

Abies concolor/Berberis nervosa.- The forest description for the Russian Peak area is typical of mesic habitats in the eastern Klamath region. The mixture of canopy species rather than white fir and Douglas-fir dominance, a mingling of mesophytic and xerophytic shrubs and a less developed ground layer distinguish it from *Abies concolor/Trillium ovatum* and *Abies concolor/Vicia americana* forests found on comparable habitats in the western subregion. On the drier slopes it merges with *Abies concolor/Ceanothus prostratus* (Table 4).

Abies concolor/Ceanothus prostratus.- Described for the Russian Peak area this forest is typical of the eastern Klamath Region on dry, rocky slopes with thin soils. The shrub layer may include *Lithocarpus densiflora* var. *echinoides*, not found in the Russian Peak stands. Successional trends show a mix of mid-elevation conifers gradually growing through and overtopping montane chaparral. The open, mixed character of the mature forest allows the light demanding species to continue to reproduce well. The lack of a dense shade stage found in *Abies concolor/Chimaphila umbellata* accounts for the understory differences between these types with mature forests of similar canopy composition. In addition these forests do not show the more nearly complete white fir dominance of the relatively more mesic *Abies concolor/Chimaphila umbellata* (Table 4).

Shasta Fir Zone

Subregional differences described in the White Fir Zone are not as evident at these elevations. Consistent differences do occur, but not to a degree warranting typal distinction. In contrast to Russian Peak stands, regional forests typically show white fir and Shasta fir dominance with varying associates. In the western subregion Quercus sadleriana plays a role in several types. Also the ecologically equivalent noble fir is considered to grow in the Siskiyou Mountains (Munz 1959). Noble fir is included in the Shasta fir data. Field determination is difficult without the rarely available mature cones. Taxonomic differentiation, especially in the Klamath Region, is in dispute (Franklin and Dryness 1973, Critchfield and Griffin 1972). Alaska-yellow-cedar was also sampled in this zone in the central Siskiyou Mountains.

Russian Peak types generally apply to the regional Shasta fir forests, but with a more narrow definition of Abies magnifica/Quercus vaccinifolia. In addition a closed forest type of xeric slopes with deep soils, Abies magnifica/Chimaphila umbellata, is also described.

Abies magnifica/Leucothoë davisiae.- Forests along streams and around wet meadows and seeps maintain the herb and shrub composition (Table 5) described in the Russian Peak area, but generally lack the diverse complement of conifers. Instead the common forests have the canopy and reproductive layers dominated by Shasta fir and white fir. White pine, mountain hemlock, and lodgepole pine are common regional associates. Engelmann spruce and subalpine fir are restricted to the Russian Peak area. This type most commonly grades into *Abies magnifica/Linnaea borealis* forests within the zone. At higher elevations it is associated with *Tsuga mertensiana/Phyllodoce empetriformis* where it may be found on mesic slopes. At lower elevations it is restricted to streamside locations where it is associated to some extent with *Abies concolor/Berberis nervosa*, but more commonly it grades into *Abies concolor/Trillium ovatum*.

Abies magnifica/Linnaea borealis.- White fir and Shasta fir dominate these forests rich in herbs and shrubs on moist, lower slopes. Douglas-fir, sugar pine, incense-cedar and white pine are also regionally common. The relative open, conifer rich stands described for the Russian Peak area are rarely encountered. Examples in the eastern Trinity Alps, eastern Marble Mountains and central Siskiyou Mountains have been sampled. They are found on rocky, though moist moraines rather than on the uniformly deep, moist soils which are regionally typical. *Quercus sadleriana* is a common dominant in the western subregion. Otherwise the herb and shrub layers (Table 5) are comparable to those described for the Russian Peak stands. This type grades into *Abies magnifica/Leucothoë davisiae* or the open forests of the Shasta Fir Zone as well as *Tsuga mertensiana/Quercus vaccinifolia* at higher elevations.

Abies magnifica/Chimaphila umbellata.- On drier middle to upper slopes and ridges with deep soils dense white fir, Shasta fir forests are common. Douglas-fir, sugar pine, white pine, and lodgepole pine are less important than in the more mesic forests at these elevations. Reproduction is also dominated by white fir and Shasta fir. Shrub and ground layers exhibit lower coverage and less variety than do the more mesic forests (Table 5). Common shrubs include Rubus parviflorus, Quercus sadleriana, and Rosa gymnocarpa. The ground layer is distinctive in its poor development rather than composition. Pyrola spp., Pteridium aquilinum, and Chimaphila spp. are most common. The forest is ecologically equivalent to the lower Abies concolor/Chimaphila umbellata, but distinguished by the major role played by Shasta fir. White fir dominated forests are found in the Shasta Fir Zone, but trends indicate them to be seral as Shasta fir is heavily represented in the understory. At higher elevations white fir is rare in the Abies magnifica/Pyrola picta which is found in comparable habitats. The mid-seral phase of dense white fir canopy may account for the lack of early seral shrubs continuing into the more open mature forests. Within the zone this type also grades into the mesic forests with white fir and Shasta fir canopy dominance.

Abies magnifica/Quercus vaccinifolia.- The open forest as described in the Russian Peak area is typical of moraines and talus throughout the region. The Russian Peak analyses suggested that this type occurred not only in the Shasta Fir Zone, but also in the higher Mountain Hemlock Zone. Regional sampling shows significant elevational differences requiring a redefinition of Abies magnifica/Quercus vaccinifolia (Table 5).

An open forest dominated by Shasta fir, white fir, Douglas-fir, and with sugar pine, white pine, weeping spruce, and lodgepole pine as common associates occurs within the limits of the Shasta Fir Zone. The canopy is composed of scattered groups of trees. Shrubs cover the open, rocky slopes. Arctostaphylos patula, A. nevadensis, Quercus vaccinifolia, are dominant along with Rosa gymnocarpa and Acer glabrum. Other sclerophylls as Amelanchier pallida, Ceanothus velutinus, and Holodiscus microphyllus play a less dominant role than in the drier Quercus vaccinifolia/Arctostaphylos patula. Herbs associated with the mesic forests, as Pteridium aquilinum, Pyrola picta, and Chimaphila spp., are common. Additionally Apocynum pumila, Kelloggia galioides, and Monardella odoratissima are most abundant, but others as Senecio integerrimus, Castilleja appelgatei, and Penstemon newberryii are less abundant than in the drier habitats. It gradually changes with elevation into Tsuga mertensiana/Quercus vaccinifolia, and on the drier habitats of the Shasta Fir Zone into Quercus vaccinifolia/Arctostaphylos patula.

Quercus vaccinifolia-Arctostaphylos patula.- The montane chaparral described in the Russian Peak area is well represented in the region (Table 5). Quercus sadleriana plays a major role in the western subregion, and Quercus garryana var. breweriana may be locally abundant as well. Montane chaparral is less restricted elevationally than others in the Shasta Fir Zone and is developed to a lesser extent in the White Fir and Mountain Hemlock Zones. It grades into Pinus monticola/Holodiscus microphyllus at higher elevations, into Abies magnifica/Quercus vaccinifolia within the zone, and into Abies concolor/Ceanothus prostratus at lower elevations where chaparral of similar composition is also seral.

Mountain Hemlock Zone

The general lack of midelevation conifers, except occasionally in open forests, characterizes these mountain hemlock-dominated high elevation forests. The Russian Peak descriptions apply regionally. In addition to them Tsuga mertensiana/Quercus vaccinifolia is described creating three closed and two open forest types for this zone. Stands of silver fir are found in Tsuga mertensiana/Pyrola picta and Tsuga mertensiana/Quercus vaccinifolia forests in the English Peak area of the Marble Mountains (Table 6).

Tsuga mertensiana/Phyllodoce empetriformis.- Forests growing along streams, lake margins and in local seeps are regionally dominated by mountain hemlock, Shasta fir, and white pine. Subalpine fir and Engelmann spruce are restricted to the Russian Peak area. The understory of the Russian Peak description is typical (Table 6). The type grades into *Abies magnifica/Leucothoë davisiae* at lower elevations, but more commonly into *Tsuga mertensiana/Quercus vaccinifolia* surrounding it in many areas. The seep phase is generally higher in elevation forming a mosaic with *Pinus monticola/Holodiscus microphyllus*.

Tsuga mertensiana/Pyrola picta and *Abies magnifica/Pyrola picta*.- These forests as described for the Russian Peak area are regionally uniform in their simplicity and pattern. Species dominance is consistently correlated with habitat differences, the dry slopes dominated by Shasta fir and the moist slopes by mountain hemlock. The lack of understory development is also characteristic (Table 6). Noble fir replaces Shasta fir in the Siskiyou Mountains and silver fir grows mixed with mountain hemlock on north-facing slopes in the English Peak area. These types merge into *Tsuga mertensiana/Quercus vaccinifolia* and *Pinus albicaulis/Holodiscus microphyllus*.

Tsuga mertensiana/Quercus vaccinifolia.- Such open forests grow on moraines, talus and cool upper slopes with soils too thin to support closed stands. White pine, Shasta fir and mountain hemlock tend to dominate such habitats. Weeping spruce is most commonly found in this type. Lodgepole pine and to a lesser extent silver fir and white fir are also associates. These trees are scattered around the boulders and shrubs. A well developed shrub layer (Table 6) includes _Vaccinium arbuscula_ in seepage areas. _Quercus vaccinifolia_, _Arctostaphylos nevadensis_, _A. patula_, _Holodiscus microphyllus_, and _Amelanchier pallida_ mix with others throughout the stands. The ground layer is a mixture of mesophytic species, as _Arnica latifolia_, _Penstemon duestus_, _Clintonia uniflora_, juxtiposed with xerophytic species, _Penstemon newberryi_, _Monardella odoratissima_, _Sedum obtusatum_, _Senecio integerrimus_, and _Phlox diffusa_, in the same stand. This microhabitat variability is more characteristic of this type than of _Abies magnifica/Quercus vaccinifolia_ which lacks the moist microhabitat complement. In this respect this type is as much an open, high elevation extension of the open phases of _Abies magnifica/Linnaea borealis_ and _Abies magnifica/Leucothoë davisiae_ as it is the drier _Abies magnifica/Quercus vaccinifolia_. Additionally it grades into the closed mountain hemlock, Shasta fir forests as well as _Pinus monticola/Holodiscus microphyllus_.

Pinus monticola/Holodiscus microphyllus.- The Russian Peak description is typical of these woodlands most commonly found in the Trinity Alps. White pine and lodgepole pine dominate them, but Jeffrey pine may be locally abundant. _Vaccinium arbuscula_ is found in localized seepage areas which are not sufficiently developed for _Tsuga mertensiana/Phyllodoce empetriformis_ (Table 6). It grades into _Quercus vaccinifolia-Arctostaphylos patula_ at lower elevations, but differs in that _Arctostaphylos nevadensis_ and _Holodiscus microphyllus_ dominate and *Quercus vaccinifolia* is only a minor component. It also merges into *Tsuga mertensiana/Quercus vaccinifolia* or into meadow communities within the zone, or *Pinus albicaulis Holodiscus microphyllus* on the higher ridges and summits.

Whitebark Pine Zone

A single woodland type is recognized at the highest elevations. Other habitats are occupied by a series of meadow communities. The Russian Peak description is typical of these woodlands best represented in the Trinity Alps.

Pinus albicaulis/Holodiscus microphyllus.- Shasta fir and mountain hemlock are the common associates with whitebark pine. Foxtail pine is not restricted to this type, to the elevation zone, or even to granitic parent materials. Instead foxtail pine woodlands are better developed on ultrabasics. Shrub and herb composition is similar to *Pinus monticola/ Holodiscus microphyllus*, although *Ceanothus velutinus*, *Chrysolepis sempervirens*, and *Haplopappus greenei* are more common (Table 6). *Cercocarpus ledifolius* is restricted to these high ridges and summits, at least on granitics. *Polemonium pulcherrimum* and *Draba howellii* are also restricted to these woodlands. Below 2,225m this woodland most commonly grades into *Pinus monticola/Holodiscus microphyllus* and the closed mountain hemlock-Shasta fir forests of the Mountain Hemlock Zone.

DISCUSSION

The regional forest patterns on granitic parent materials are reasonably predictable in spite of the complex mosaic throughout the Region. If only the mature forests on deep soils are considered, the pattern is readily apparent: a series of elevationally zoned forests dominated by one to several tree species. Within each elevational zone understory development decreases with increased habitat dryness. Forests rich in herbs and shrubs along the streams give way to simple forests barren of understories on the dry slopes. The pattern is similar to that of other western mountain areas (Daubenmire and Daubenmire 1968, Franklin and Dryness 1973) but is less obvious because of the lack of habitat continuity. In addition to the strong climatic, topographic, and lithic diversity, a variable fire history creates a variety of confusing seral stages. For this reason the understory composition is more indicative of habitat conditions and more regionally consistent than is canopy composition.

Regional patterns show decreasing geographic differentiation with increasing elevation. Subregional differences are greatest at the low elevations. In the western subregion low-elevation Douglas-fir,tan oak forests give way to white fir,Douglas-fir forests, then to Shasta fir,white fir forests and to mountain hemlock,Shasta fir forests with increasing elevation. In the eastern subregion the pattern is similar, but with ponderosa pine-dominated forests at low elevations. The subregional differences are not as extreme within the White Fir Zone as the classification suggests. White fir,Douglas-fir forests are typical and best developed in the west at these elevations, but can be found anywhere on suitable habitats. Likewise Abies concolor/ Ceanothus prostratus forests can be found in the Siskiyou Mountains. Subregional differences in the Shasta Fir Zone are not great enough for recognition of types, although some consistent variation has been described. The forests of the Mountain Hemlock and Whitebark Pine zones are regionally uniform in their simplicity in spite of being highly discontinuous.

Elevational zonation is more apparent in mature, closed forests than in comparable open forests, where individual species show greater environmental ranges, e.g. white fir and Douglas-fir growing on a ridge at 2,1?5m with foxtail pine and whitebark pine. The greater restriction in the closed forests can be considered a function not only of differences in individual tolerances, but to a greater degree, of differential competitive advantages. In this way the number of occupiable habitats for each species is reduced, and zonation results, as expected from ecological theory (Odum 1971).

The lessened degree of competitive interaction among individuals of the open forests may also account for some of the greater stand-to-stand variability observed for those types. It follows that areas with open forests would be expected to have greater floristic variety than comparable ones with only closed forests, and that a mosaic of both kinds within a single area or zone would be expected to have the greatest.

Additionally, some forests grow on more physically variable habitats. The xeric/hydric mosaic of microhabitats described for *Tsuga mertensiana*/*Quercus vaccinifolia* are illustrative. Thus within-habitat complexity also leads to floristic diversity.

Competitive restriction of regionally common species growing on mesic habitats is modified not only by the presence of less competitive, open habitats, but also by disturbance. The maintenance of seral stands allows species to grow in additional areas not available to them when the site is occupied by climax forests. For example, lodgepole pine grows not only in the open forests at higher elevation but also in seral communities on mesic habitats, where it will potentially be replaced by Shasta fir and mountain hemlock. Fire plays a significant role in maintaining midseral stages, especially in the White Fir and Shasta Fir zones, but possibly not to the extent suggested for the Sierra Nevada (Kilgore and Briggs 1972). Some disturbance, then, will maintain floristic diversity on uniform habitats. Other factors such as seed source and dispersal abilities will also determine forest composition under such conditions and create compositional variability in spite of habitat uniformity.

One a longer time scale disturbance such as glaciation will create new and different habitats, such as moraines, cirque basins, talus, and filling lakes at the higher elevations, all of which will be less competitive because of their variable and poorly developed character. Such disturbance has increased habitat variability in the Klamath Region since glacial action was localized, although widespread.

In addition, this disturbance would lead to localized and differential extinctions in various parts of the Region depending on local topography and preglacial floristic patterns. The result would be to further complicate patterns by individualizing species distributions. Warm, dry periods would have the same effects, especially for midelevation floras. The chance of total extinction in the Klamath Region would be low, since this topographically diverse area would have a maximum number of suitable habitats that could act as refuges and subsequent centers of dispersal when environmental conditions change. Regional habitat diversity could also allow successful introductions from adjacent regions, further enriching the flora. The presence of xerophytic shrubs of the California chaparral and woodlands can be accounted for in this manner. A Great Basic element (e.g., Cercocarpus ledifolius-Haplopappus spp.-Artemesia tridentata) is also present in the eastern subregion.

By contrast, areas of extensive and severe disturbance would be expected to show a simplification of floristic patterns. Extensive glaciation would result in a less diverse flora to vegetate the newly created habitats. Fire, if it were extensive and frequent, would simplify in a similar manner.

In areas where knobcone pine forests are extensive other forests tend to be simpler lacking such trees as the supposedly fire-sensitive weeping spruce, even though suitable habitats are available.

Throughout the Cenozoic the Klamath Region has continuously maintained a diverse set of habitats occupied by a corresponding array of forests. During the Tertiary a change from summer-wet to summer-dry climates occurred, floristic segregation followed with increasing habitat differentiation. Summer-dry climates accentuate habitat differences in moisture availability and resulting effective growing seasons. Additionally regional upwarp produced increased floristic differentiation. Such a history allowed not only for maximum retention of Arcto-Tertiary elements, but for an assimilation of Madro-Tertiary elements as well.

Pleistocene glaciation and climatic cooling resulted in localized extinctions and range differentiation of individual species. In some areas, such as the Central Trinity Alps, the effects were severe and extensive. In response to warming trends and deglaciation, community associations were rearranged depending on local topography, climate, available populations, and the dispersal abilities of the individual species, a process which continues today in response to continuing environmental change.

Fire has further modified this vegetational response by eliminating species from areas where they could potentially grow. A countereffect is that fire has also maintained extensive, less competitive seral stands throughout the region where some species could have potentially been eliminated.

Time for dispersal, competitive interactions, and habitat development have been sufficient to reduce local influences, and regional patterns are therefore evident, especially for the closed forests. The associated open forests are more variable in floristic composition, particularly trees. These open forests tend to grow on environmentally heterogeneous habitats, where competitive interactions are less realized. The most diverse forests are found under such conditions except where water is severaly limiting. Such habitats are the exception, but do tend to occur in the Shasta Fir and Mountain Hemlock zones.

When these environmental conditions are encountered, forest composition is unpredictable. For example, Shasta fir,white fir stands are typical of Abies magnifica/Linnaea borealis. At higher elevations mountain hemlock and Shasta fir are common dominants of Tsuga mertensiana/Quercus vaccinifolia. But in certain areas - the eastern Trinity Alps, eastern Marbles, central Siskiyous, and especially the Russian Peak area - floristically varied forests are found in these and other types. That these specific areas show such exceptional richness, a variety created by the accumulation of populations of several relic species growing together, must be due to distinctive local history, since comparable habitats are regionally available. Such local history also accounts for the stands of silver fir in the southern Marbles and Alaska yellow-cedar in the central Siskiyous.

Pleistocene distribution of these trees may have been patchy throughout the Region. Pleistocene glaciers destroyed most populations. In the Russian Peak area, however, subalpine fir survived as krummholz on cliffs above ice margins, subsequently repopulating hydric habitats created by glacial retreat. Englemann spruce survived along streams below the glaciers, and later repopulated streamside habitats. Range maps (Fig. 10, 11) suggest such interpretations. Suitable habitats for other populations remained in the area as well. The habitats along the cool east tending streams would reduce fire intensity and frequency allowing the maintenance of populations of weeping spruce. Low fire frequency should result in the competitive elimination of shade-intolerant species like lodgepole pine, but suitable open habitats are available on moraines and dry slopes. Thus the higher than normal diversity is maintained in the Russian Peak area, and to a lesser extent in a few other locations within the Region.

The general similarity of the Region to the southern Appalachian forests suggests a similar history. In the Klamath Region variety in vegetation patterns and floristic composition may be due not so much to the long period of environmental stability, but to the perturbations which have kept the area in a continuing state of development. These maintain high habitat complexity and continued rearrangement of floristic elements through time. However the perturbations are not regionally severe nor uniform, thus allowing local maintenance of individual species in certain areas with suitable habitats. Such areas, especially Russian Peak, have been favored by just enough disturbance to maintain habitat complexity, but not enough to destroy continuing relic populations. Other parts of the Region have had extensive or highly restricted disturbance, leading to either a degradation in floristic composition or a competitive elimination of species on extensive uniform habitats. Relatively simple forests would result in either case. In the Klamath Region more intermediate situations are typical, and the result is a highly diverse vegetation mosaic.

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TABLE 1. Climate records for selected stations in the central Klamath Region. Stations ordered from western, maritime influenced to eastern, continental influenced locations. No long-term data available for middle and high elevations except Mt. Hebron Ranger Station. U.S. Dept. Commerce Annual Summ. 1973. Climatological Data 77(13).

Station	Elev. m	Normal temp., °C. Ann.	Jan.	Jul.	Annual Precip., mm
Klamath	8	11.2	7.1	13.9	2,684
Orleans	124	14.6	5.3	23.5	1,766
Happy Camp	350	13.4	3.2	23.6	1,692
Sawyers Bar	661	12.3	2.3	23.1	1,358
Callahan	971	10.4	1.2	20.4	527
Yreka	800	11.7	0.8	23.3	452
Mt. Hebron R.S.	1,295	6.9	-3.3	17.7	331

Table 2. Habitat moisture equivalency index used in the direct ordinations. Soil moisture conditions are equivalent if factors other than topographic position and aspect are equal. A - indicates inclusion of intermediate aspects along the following scale: NNE, NE, N, ENE, NNW, E, NW, ESE, WNW, SE, W, SSE, WSW, S, SW, SSW.

INDEX	SEEPS	LOW ALLUVIAL TERRACES	HIGH ALLUVIAL TERRACES	RAVINES	LOWER SLOPES	MIDDLE SLOPES	UPPER SLOPES	RIDGES	SUMMITS
1	X								
2		X							
3			X	NNE-SE					
4				W-SSW	NNE,NE				
5					N,ENE				
6					NNW,E	NNE,NE			
7					NW,ESE	N,ENE			
8					WNW,SE	NNW,E	NNE,NE		
9					W,SSE	NW,ESE	N,ENE		
10					WSW,S	WNW,SE	NNW,E		
11					SW,SSW	W,SSE	NW,ESE		
12						WSW,S	WNW,SE	NNE-ENE	
13						SW,SSW	W,SSE	NNW-NW	
14							WSW,S	ESE-SW	
15							SW,SSW	W-WSW	
16								S-SSW	X

TABLE 3. Ecological roles played by middle and high elevation trees in White Fir, Shasta Fir, Mountain Hemlock, and Whitebark Pine zones. Equivalent scientific names for conifers (Fig. 1). Chinquapin (*Chrysolepis chrysophylla*), Canyon live oak (*Quercus chrysolepis*), Bigleaf maple (*Acer macrophyllum*), California black oak (*Quercus kelloggii*).

Table 4. Presence (Prs %) and modal cover/abundance (C/A)[a] for shrubs with > 10% presence[b] and herbs with > 20% presence in the White Fir Zone types.

Forest types[c]	WF/Trov	WF/Viam	WF/Ptaq	WF/Bene	WF/Cepr
No. relevés	20	17	17	16	26
Species	Prs·C/A	Prs·C/A	Prs·C/A	Prs·C/A	Prs·C/A
Shrubs					
Vaccinium membranacium	15·3				
Quercus sadleriana	35·4				
Arctostaphylos nevadensis				19·2	
Rubus ursinus	20·2			6·2	
Berberis dictyota	15·2			6·2	
Ribes lacustre	15·3			13·3	
Holodiscus discolor[1]	15·3	6·3			
Cornus stolonifera	15·3	16·2		6·2	
Ribes lobbii	35·3	29·2		6·2	
Rubus parviflorus	75·4	39·2		19·2	
Ribes sanguineum	10·2	12·3		25·3	
Salix scouleriana	10·3	12·2		25·3	11·3
Amelanchier pallida	5·3	16·3		31·2	7·3
Cornus nuttallii	30·3	24·3		63·2	4·3
Berberis nervosa	45·3	41·3	13·2	88·3	
Corylus cornuta[2]	65·4	59·3	38·3	25·4	
Rosa gymnocarpa	95·3	76·3	25·3	81·3	27·2
Symphoricarpos hesperius	45·3	24·2	31·2	50·3	23·2
Paxistema myrsinites	55·3	12·2	6·3	44·3	11·3

Ceanothus velutinus	25·2	6·2	25·2	6·3	11·3
Symphoricarpos mollis	30·3	24·3		6·3	23·3
Chrysolepis sempervirens	5·4	6·2	19·2	44·3	50·5
Quercus vaccinifolia	15·3	6·2	6·3	25·3	46·4
Ceanothus prostratus			19·2	13·3	65·4
Berberis repens					15·3
Herbs					
Trillium ovatum	60·3				
Asarum caudatum	24·2				
Achlys triphylla	60·4	29·3			
Trientalis latifolia	55·3	29·3			
Penstemon anguineus	35·3	24·3			
Viola glabella	35·3	24·3			
Vancouveria hexandra	25·3	16·3			
Osmorhiza chilensis	25·3	24·2			
Smilacina racemosa[3]	20·3	24·3			
Smilacina stellata[4]	30·3				11·3
Lupinus andersonii		29·3			
Adenocaulon bicolor	50·4	53·3		40·3	
Galium triflorum	50·3	41·3		27·2	
Fragaria californica	35·3	12·2		27·2	
Clintonia uniflora	50·4	12·3		20·3	
Anemone deltoidea	30·3	16·3		20·2	
Hieracium albiflorum	25·3	47·3		20·3	
Pyrola secunda	25·3	12·2		27·2	
Linnaea borealis[5]	35·3	12·2		33·3	
Arnica cordifolia[6]	10·2	12·2		20·2	

Calypso bulbosa		12·2		20·2	
Vicia americana[7]		59·3		20·2	
Disporum hookeri[8]	45·3	35·3	19·2	40·2	
Corallorhiza maculata	25·2	29·2	31·2	12·2	
Apocynum pumila	30·2	24·3	19·2	33·2	
Campanula prenanthoides	10·2	29·3	12·2	12·2	
Stellaria jamesiana	10·2	24·3	19·2		
Goodyera oblongifolia	40·3	41·3	25·2	20·2	11·2
Pteridium aquilinum[9]	45·3	35·3	12·2	53·3	34·3
Chimaphila umbellata[10]	70·3	53·3	56·3	67·3	69·3
Pyrola picta[11]	50·3	29·2	31·2	67·2	46·2
Chimaphila menziesii	20·3	29·3	31·2	27·2	15·2
Bromus marginata		12·3	19·2	20·2	11·2
Festuca occidentalis			12·2	27·2	

a 1 = one individual, 2 = rare, 3 = < 10%, 4 = 10-25%, 5 = 25-50%, 6 = 50-75%, 7 = > 75%.

b Shrubs with < 10% presence: WF/Trov; Berberis aquifolium, Acer circinatum, Rhamnus californica, Lithocarpus densiflora, Prunus emarginata. WF/Bene; Alnus tenuifolia, Acer glabrum, Leucothoë davisiae. WF/Cepr; Ribes roezlii, Berberis piperiana, Lithocarpus densiflora var echinoides, Chrysothamnus nauseosus, Ceanothus integerrimus.

c WF/Trov = Abies concolor/Trillium ovatum, WF/Viam = Abies concolor/Vicia americana, WF/Ptaq = Abies concolor/Pteridium aquilinum, WF/Bene = Abies concolor/Berberis nervosa, WF/Cepr = Abies concolor/Ceanothus prostratus.

[1]including *H. d.* var *franciscanus*, [2]*C. c.* var *californica*, [3]*S. r.* var *amplexicaulis*, [4]including *S. s.* var *sessifolia* in WF/Cepr, [5]*L. b.* ssp *longiflora*, [6]including *A. c.* var *alata* and *A. c.* var *pumila*, [7]*V. a.* var *oregona*, [8]*D. h.* var *trachyandrum*, [9]*P. a.* var *lanuginosum*, [10]*C. u.* var *occidentalis*, [11]including *P. p.* forma *aphylla* and *P. p.* ssp *dentata* with sp.

Table 5. Presence (Prs %) and modal cover/abundance (C/A)[a] for shrubs with > 10% presence[b] and herbs with > 20% presence in the Shasta Fir Zone types.

Forest types[c]	RF/Leda	RF/Libo	RF/Ptaq	RF/Quva	Quva/Arpa
No. relevés	27	24	21	23	27
Species	Prs·C/A	Prs·C/A	Prs·C/A	Prs·C/A	Prs·C/A
Shrubs					
Kalmia polifolia[1]	11·3				
Ledum glandulosum[2]	37·3				
Rhamnus californica		12·2			
Ribes lacustre	59·3	8·2			
Alnus tenuifolia	59·4	8·2			
Vaccinium arbuscula	30·3	17·3			
Alnus sinuata	26·3	17·3			
Berberis nervosa	11·3	25·2			
Vaccinium membranacium	7·4	17·3	10·3		
Leucothoë davisiae	85·7	8·3		4·3	
Salix scouleriana	37·3	29·3		13·3	
Spiraea douglasii	15·3	8·2		4·3	
Rosa gymnocarpa	33·2	67·3	29·3	26·3	
Symphoricarpos hesperius	37·3	67·3		17·3	7·4
Sorbus californica	22·2	12·3	10·2	4·1	7·2
Rubus parviflorus	11·3	37·2	37·2	4·3	
Quercus sadleriana		37·4	33·3	4·5	22·3
Paxistema myrsinites		17·2		13·3	
Ribes lobbii	7·2	33·2	19·2	13·3	4·2

Lonicera conjugialis	15·2	4·3	10·2	17·2	7·3
Ribes viscosissimum	15·2	4·2	19·2	4·3	15·3
Chrysolepis sempervirens	22·3	25·3	19·2	76·4	22·5
Acer glabrum[3]	7·4	33·3	10·3	17·3	7·2
Amelanchier pallida	19·3	33·3	5·2	30·3	59·4
Arctostaphylos nevadensis	4·3	17·2	14·3	69·4	44·4
Arctostaphylos patula	4·5	4·2		74·3	100·5
Ceanothus velutinus	4·2	4·3	5·3	26·4	70·4
Quercus vaccinifolia	4·2	25·3	5·3	74·5	70·5
Holodiscus microphyllus	7·2	17·3		22·3	48·3
Prunus emarginata		4·2	5·2	26·3	33·4
Garrya fremontii				9·3	37·3
Juniperus communis[4]					19·3
Haplopappus greenii					15·2
Quercus garryana[5]					22·4
Herbs					
Listera convallarioides	26·2				
Mitella pentandra	30·3				
Streptopus amplexifolius[6]	22·3				
Senecio triangularis	48·3				
Athyrium filix-femina[7]	26·3				
Clintonia uniflora	63·3	42·3			
Trientalis latifolia	55·3	29·3			
Trillium ovatum[8]	48·2	29·2			
Linnaea borealis[9]	11·4	29·3			
Anemone quinquefolia[10]	22·2	17·3			
Viola glabella	33·3	12·2			

Smilacina racemosa[11]	11·2	29·3			
Osmorhiza chilensis	22·3	25·3			
Smilacina stellata[12]	48·3	12·3			
Osmorhiza occidentalis		21·2			
Phacelia hastata		25·3			
Vicia americana[13]		21·3			
Anemone deltoidea	48·3	58·3	10·3		
Pyrola secunda	11·3	54·2	48·3		
Arnica cordifolia[14]	26·3	29·4	14·3		
Adenocaulon bicolor	11·3	37·3	10·2		
Goodyera oblongifolia	33·2	25·3	14·2		
Galium triflorum	15·3	46·3	10·2		
Penstemon anguineus		17·3	24·2		
Disporum hookeri[15]		21·3	14·3		
Pteridium aquilinum[16]	52·4	54·3	33·3	22·3	
Pyrola picta[17]	37·2	42·2	33·2	35·2	
Chimaphila umbellata[18]	70·3	71·3	57·3	65·3	
Chimaphila menziesii	22·3	37·2	52·2	35·2	
Hieracium albiflorum	30·2	33·3	29·3	17·2	
Hieracium gracile	11·3				26·3
Apocynum pumila		21·3	19·2	61·3	22·2
Kelloggia galioides		12·3		35·3	22·3
Monardella odoratissima[19]			10·2	48·3	37·3
Senecio integerrimus[20]				17·3	26·3
Arenaria congesta[21]				13·4	26·3
Castilleja appelgatei				17·3	52·3
Penstemon newberryi[22]				35·3	63·3
Sedum obtusatum[23]				17·3	41·3

Phlox diffusa	13·3	41·3
Cheilanthes gracillima	17·2	56·3
Achillea lanulosa		22·3
Penstemon procerus[24]		37·3
Onychium densum		22·3
Eriogonum umbellatum[25]		37·4
Smilacina racemonsa[26]		41·3
Calyptridium umbellatum		33·2

a 1 = one individual, 2 = rare, 3 = < 10%, 4 = 10-25%, 5 = 25-50%, 6 = 50-75%, 7 = > 75%.

b Shrubs with < 10% presence: RF/Leda; *Ribes nevadensis*, *Vaccinium occidentale*, *Sambucus microbotrys*, *Ribes binominatum*, *Cornus stolonifera*. RF/Libo; *Corylus cornuta*, *Ribes sanguineum*. RF/Quva; *Ceanothus prostratus*, *Sambucus melanocarpa*. Quva/Arpa; *Quercus kelloggii* var. *cibata*, *Ceanothus cordulatus*.

c RF/Leda = *Abies magnifica*/*Leucothoë davisiae*, RF/Libo = *Abies magnifica*/*Linnaea borealis*, RF/Ptaq = *Abies magnifica*/*Pteridium aquilinum*, RF/Quva = *Abies magnifica*/*Quercus vaccinifolia*, Quva/Arpa = *Quercus vaccinifolia*-*Arctostaphylos patula*.

[1]*K. p.* var *microphylla*, [2]*L. g.* var *californicum*, [3]*A. g.* var *torreyi*, [4]*J. c.* var *saxatilis*, [5]*Q. g.* var *breweri*, [6]*S. a.* var *denticulatus*, [7]*A. f.* var *californicum*, [8]including *T. o.* ssp *ottingeri* which replaces sp at higher elevations, [9]*L. b.* ssp *longiflora*, [10]*A. q.* var *minor* and *A. q.* var *oregona*, [11]*S. r.* var *amplexicaulis*, [12]including *S. s.* var *sessifolia*, [13]*V. a.* var *oregona*, [14]including *A. c.* var *alata* and *A. c.* var *pumila*, [15]*D. h.* var *trachyandrum*, [16]*P. a.* var *lanuginosum*,

[17]including *P*. *p*. forma *aphylla* and *P*. *p*. ssp *dentata*, [18]*C*. *u*. var *occidentalis*, [19]*M*. *o*. var *glauca*, [20]*S*. *i*. var *major*, [21]including *A*. *c*. var *suffrutescens*, [22]*P*. *n*. ssp *berryi*, [23]*S*. *o*. ssp *boreale*, [24]*P*. *p*. ssp *brachyanthus*, [25]including *E*. *u*. var *polyanthum* and *E*. *u*. *stellatum*, [26]*S*. *r*. var *glauca* in Quva-Arpa.

Table 6. Presence (Prs %) and modal cover/abundance (C/A)[a] for shrubs with > 10% presence[b] and herbs with > 20% presence in the Mountain Hemlock and Whitebark Pine Zone types.

Forest types[c]	MH/Phem	MH/Quva	MH/Pypi	RF/Pypi	WP/Homi	WB/Homi
No. relevés	29	18	21	18	23	21
Species	Prs·C/A	Prs·C/A	Prs·C/A	Prs·C/A	Prs·C/A	Prs·C/A
Shrubs						
Cassiope mertensiana	14·3					
Ledum glandulosum[1]	17·3					
Kalmia polifolia[2]	24·3					
Sambucus melanocarpa	14·3	6·3				
Alnus sinuata	28·4	6·5				
Phyllodoce empetriformis	58·4	6·3				
Sorbus californica	34·2	17·2				
Salix commutata	24·3	17·3				
Vaccinium membranacium	10·2	11·3				
Ribes lacustre	31·3	17·4				
Acer glabrum[3]	7·4	22·4				
Vaccinium scoparium	34·4	11·3	11·3			
Leucothoë davisiae	37·3	6·1	6·3			
Vaccinium arbuscula	86·4	22·3			4·3	
Quercus vaccinifolia	14·2	56·4	6·2		65·4	5·4
Ribes viscosissimum	21·2	33·3	6·3	14·3	13·3	10·2
Arctostaphylos nevadensis	24·3	67·4	28·3	24·3	91·5	52·4
Chrysolepis sempervirens	7·3	44·4	11·2	14·2	22·2	43·3
Arctostaphylos patula	7·2	39·3	17·2	19·2	74·3	62·4

Quercus sadleriana	3·5	1·4		10·2	25·3	
Holodiscus microphyllus	10·2	17·4		5·2	61·3	86·3
Prunus emarginata	7·4	22·3		5·2	26·3	19·3
Amelanchier pallida	24·2	33·3			30·3	10·3
Lonicera conjugialis	38·3	11·3			13·3	5·2
Juniperus communis[4]	10·3				13·3	14·3
Haplopappus greenii					13·3	29·4
Cercocarpus ledifolius						14·4
Herbs						
Ligusticum grayi	24·3					
Senecio triangularis	38·3					
Veratrum californicum	58·3					
Potentilla flabellifolia	28·3					
Epilobium angustifolium	24·3	22·3				
Cystopteris fragilis	24·2	11·3				
Dodecatheon jeffreyi	65·3	17·2				
Arnica latifolia	31·2	28·3				
Clintonia uniflora		22·3				
Penstemon duestus		28·3				
Montia parvifolia		22·3				
Castilleja applegatei		22·3				
Aster occidentalis		22·3				
Collinsia torreyi[5]		22·3				
Apocynum pumila		28·2				
Pteridium aquilinum[6]		22·5				
Hieracium albiflorum		28·3		14·2	13·3	
Pyrola picta	14·3	11·3	28·2	38·2		

Chimaphila umbellata[7]	14·2	33·3	33·2	19·2	13·3	
Polygonum davisiae	31·3		17·2	17·2	30·3	29·3
Penstemon newberryi[8]	14·2	39·3	44·2	14·2	82·3	67·3
Monardella odoratissima[9]	17·2	28·3		14·2		14·3
Antennaria rosea	14·3	22·3			17·3	
Saxifraga ferruginea	24·3	11·2			11·2	
Sedum obtusatum[10]	31·3	44·3			69·3	
Cryptogramma acrostichoides	28·2	22·3			35·2	
Senecio integerrimus[11]		28·3			17·3	
Penstemon procerus[12]		11·2			26·3	
Selaginella densa[13]					22·3	
Lewisia leana					22·2	
Hieracium gracile					22·3	
Boschniakia strobilacea					22·2	
Lewisia cotyledon					43·3	
Juncus parryi					48·3	
Cheilanthes gracillima	14·3	17·3			56·2	38·2
Arenaria congesta	14·2	28·3			62·3	24·3
Phlox diffusa	21·2	28·3			43·3	67·3
Eriogonum umbellatum[14]		11·2			17·3	33·3
Achillea lanulosa		28·3			22·3	29·3
Calyptridium umbellatum					39·3	14·3
Aster ledifolius					17·3	19·3
Angelica arguta	31·3	33·3				19·2
Draba howellii						20·2
Polemonium pulcherrimum						33·2

a 1 = one individual, 2 = rare, 3 = < 10%, 4 = 10-25%, 5 = 25-50%, 6 = 50-75%, 7 = > 75%.

b Shrubs with < 10% presence: MH/Phem; Ribes nevadensis, Alnus tenuifolia, Vaccinium occidentale, Ribes binominatum, Rubus parviflorus, Gaultheria humifusa, Spiraea douglassii, Spiraea densiflora, Rosa gymnocarpa. MH/Quva; Paxistema myrsinites, Corylus cornuta, Rhamnus californica. WP/Homi; Garrya fremontii. WB/Homi; Populus tremulioides.

c MH/Phem = Tsuga mertensiana/Phyllodoce empetriformis, MH/Quva = Tsuga mertensiana/Quercus vaccinifolia, MH/Pypi = Tsuga mertensiana/Pyrola picta, RF/Pypi = Abies magnifica/Pyrola picta, WP/Homi = Pinus monticola/Holodiscus microphyllus, WB/Homi = Pinus albicaulis/Holodiscus microphyllus.

[1]L. g. var californicum, [2]K. p. var microphylla. [3]A. g. var torreyi, [4]J. c. var saxatilis, [5]including C. t. var latifolia and C. t. var wrightii, [6]P. a. var lanuginosum, [7]C. u. var occidentalis, [8]P. n. ssp berryi, [9]M. c. var glauca, [10]S. c. ssp boreale, [11]S. i. var major, [12]P. p. ssp brachyanthus, [13]S. d. var scopulorum, [14]including E. u. var polyanthum and E. u. var stellatum.

FIG. 1. Latitudinal ranges of Klamath Region conifers. Redwood (*Sequoia sempervirens*), western red-cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Port-Orford-cedar (*Chamaecyparis lawsoniana*), noble fir (*Abies procera*), Alaska-yellow-cedar (*Chamaecyparis nootkatensis*), Douglas-fir (*Pseudotsuga menziesii*), western white pine (*Pinus monticola*), weeping spruce (*Picea breweriana*), western yew (*Taxus brevifolia*), mountain hemlock (*Tsuga mertensiana*), white fir (*Abies concolor*), Jeffrey pine (*Pinus jeffreyi*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), incense-cedar (*Calocedrus decurrens*), knobcone pine (*Pinus attenuata*), digger pine (*Pinus sabiniana*), silver fir (*Abies amabilis*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), Siskiyou cypress (*Cupressus bakeri* ssp. *matthewsii*), red fir including the Shasta fir variety found here (*Abies magnifica* var. *shastensis*), lodgepole pine (*Pinus contorta* var. *murrayana*), whitebark pine (*Pinus albicaulis*), common juniper (*Juniperus communis* var. *saxatilis*), foxtail pine (*Pinus balfouriana*), and western juniper (*Juniperus occidentalis*).

FIG. 2. Major physiographic features of the Klamath Region in California. Trends of the mountain ranges shown by name locations.

FIG. 3. The Russian Peak area looking west from the Scott Valley 10 km south of Etna on State Route 3. Localized glaciation seen on Eaton Peak, 2,322m (center) as well as in the Sugar Creek (to the left) and Duck Lake Creek (to the right) drainages.

FIG 4. Lithic patterns, showing subprovinces and major granitic intrusions, of the Klamath Region in California. Study areas: (1) north Siskiyou Mountains, (2) Bear Peak area, (3) south Siskiyou Mountains, (4) North Trinity Mountain area, (5) western Marble Mountains, (6) English Peak area, (7) Russian Peak area, (8) central Trinity Alps, (9) Boulder Creek area, (10) Eagle Peak area, (11) Granite Peak area, (12) Weaver Bally, (13) Shasta Bally, (14) Ammon Ridge.

FIG. 5. Direct ordination of individual conifers. Samples plotted by elevation and moisture (Table 2) outline the environmental space (5A). Isorithms for species dominance (5B-5R) form nomograms of population levels based on canopy cover. L- low dominance, <10%; M- moderate dominance, 10-25%; H- high dominance, 25-50%; V- very high dominance, >50%.

FIG. 6. Ordination of midelevation forests based on canopy composition of 68 samples. Lines group samples of similar canopy composition. A- forests of typical mixed, midelevation composition (white fir, Douglas-fir, sugar pine, ponderosa pine, incense-cedar). I- ponderosa pine-dominated forests with other species absent or in reduced influence. II- ponderosa pine-dominated mixed forests, white fir, Douglas-fir, and incense-cedar secondarily important. III- mixed forests; the five species with equal dominance, or with white fir and/or Douglas-fir dominance. B- forests with mixed composition enriched by typically higher elevation species (Shasta fir, lodgepole pine, western white pine, mountain hemlock, Engelmann spruce, weeping spruce). The presence of any of these in the canopy is needed for inclusion. IV- Engelmann spruce-dominated forests. V- Enriched mixed forests with no species dominance. VI- Enriched mixed forests with a high dominance of white fir and/or Douglas-fir.

FIG. 7. Distribution of forest potential based on tree reproduction in relation to moisture (Table 2) and elevation gradients. Criteria for classification into III and V as in Fig. 6. No samples were classified into I, II, IV, VI using those criteria.

FIG. 8. Indirect ordination of 221 stands in the Russian Peak area using methods described in text. Boxes around type symbols indicate extent of vegetation unit(s). When type symbols are not separated, they cannot be segregated in the x,y-ordination. Segregation occurs along the gradient (z) of increasing canopy coverage. WF/Bene, Abies concolor/Berberis nervosa; WF/Cepr, Abies concolor/Ceanothus prostratus; RF/Leda, Abies magnifica/Leucothoë davisiae; RF/Libo, Abies magnifica/Linnaea borealis; RF/Quva, Abies magnifica/Quercus vaccinifolia; Quva-Arpa, Quercus vaccinifolia-Arctostaphylos patula; MH/Phem, Tsuga mertensiana/Phyllodoce empetriformis; MH/Pypi, Tsuga mertensiana/Pyrola picta; RF/Pypi, Abies magnifica/Pyrola picta; WP/Homi, Pinus monticola/Holodiscus microphyllus; WB/Homi, Pinus albicaulis/Holodiscus microphyllus.

FIG. 9. Direct ordination of Russian Peak vegetation types. Elevation and soil moisture (Table 2) outline the environmental space as in Fig. 5.

FIG. 10.. Known locations of subalpine fir in the Russian Peak area. Extent of localized populations in seeps behind Little Duck Lake and on Grizzly Peak exaggerated.

FIG. 11. Known locations of Engelmann spruce in the Russian Peak area. Isolated trees grow at lower elevations along Sugar and Duck Lake Creeks.