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VEGETATION OF OREGON & WASHINGTON

by Jerry F. Franklin and C.T. Dyrness

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Jerry F. Franklin and C. T. Dyrness

Pacific Northwest Forest and Range Experiment Station

U. S. Department of Agriculture, Portland, Oregon

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INTRODUCTION

The Pacific Northwest is among the more diverse regions of North America in environment and vegetation. Oregon and Washington, the heart of this region, encompass wet coastal and dry interior mountain ranges, miles of coastline, interior valleys and basins, and high desert plateau (fig. 1). Moisture, temperature, and substrate vary greatly. Natural vegetation types range from dense coastal forests of towering conifers through woodland and savanna to shrub steppe.

The ecology and plant geography of the region have been studied by scientists for over half a century. Major contributors have included W. S. Cooper, R. Daubenmire, H. P. Hansen, L. A. Isaac, V. J. Krajina, D. B. Lawrence, T. T. Munger, M. E. Peck, C. V. Piper, E. H. Reid, and G. B. Rigg. Unfortunately, most of the knowledge which has been gathered is fragmented — dispersed through journals, books, theses, and unpublished files of data.

We present here a generalized account of the major vegetation types within the States of Oregon and Washington, an integration of the scattered information into a regional account. Published articles, theses, and personal data files are the source materials. The unevenness of coverage is unfortunate but unavoidable; some plant formations have been studied in great detail, and other communities or locales have received cursory or no study.

The purpose is threefold: (1) to outline major phytogeographic units and suggest how they fit together and relate to environmental factors; (2) to direct the interested reader to sources of detailed information on the environment and vegetation of the Pacific Northwest, since such information cannot be provided in an account of this size; and (3) to illustrate the major plant communities with photographs.

We hope this outline will enable the scientist or student new to the Pacific Northwest to better understand what he is seeing and how his various observations are related. Per-

haps it will also provide some new insights to readers more familiar with the region.

DEFINITIONS

Ecology is fraught with specialized and ambiguous terminology. We have followed Daubenmire's (1968a)¹ definitions in most cases, especially when dealing with synecological terminology, such as climax, association, etc. The reader unfamiliar with such terms might particularly consider pages 27 to 32, 229 to 237, and 259 to 262 of this text for orientation. The glossaries of Carpenter (1956), Hanson (1962), and Habeck and Hartley (1968) are also helpful.

NOMENCLATURE

Plant nomenclature in this paper generally follows these sources: trees, Little (1953); other vascular plants, Hitchcock et al. (1955, 1959, 1961, 1964) or Peck (1961) for taxa not covered in the former; mosses, Lawton (1965); and lichens, Howard (1950). Whenever possible, nomenclature from older ecological studies cited has been updated. In an appendix are listed the complete scientific names for taxa mentioned along with common names locally applied to many of the plants.

PALEOBOTANY, PALEOECOLOGY, AND FLORISTIC EVOLUTION

The evolution of the flora and plant formations of Oregon and Washington is not within the scope of this paper. We recommend readers interested in these subjects consult the following: Chaney (1938, 1948) and Axelrod (1958) on paleobotany, Hansen (1947) and Heusser (1960) on postglacial vegetation changes and development, and Daubenmire (1947), Mason (1947), and Detling (1968) on evolution of plant formations and floras.

¹ Names and dates in parentheses refer to literature listed in References, beginning on p. 182.

Figure 1. — Major topographic features and some cities and towns in Oregon and Washington.

Figure 2. — Physiographic and geological provinces of Oregon and Washington.

ENVIRONMENTAL SETTING

PHYSIOGRAPHY, GEOLOGY, AND SOILS

Since geology, physiography, and at least some aspects of soils are interrelated, we will consider these three environmental features together. In Oregon and Washington, all three present highly varied and complex patterns. Landforms vary from level river valleys and lava plains to precipitous mountain slopes. Elevations range from sea level to over 4,450 meters. The geologic complexity is bewildering in many areas with formations dating from the Paleozoic era (over 400 million years old) to Recent. Vulcanism has dominated the shaping of much of the landscape, but sedimentary and metamorphic rocks also abound.

Since climate and vegetation are added to landform and geology as factors in soil formation, the tremendous variety of soils is not surprising. For example, zonal great soil groups range from Desert soils in arid southeastern Oregon to Podzol soils in the cool, humid climate of the northern Cascade Range. The most striking soil changes within short distances are found on eastern slopes of the Cascade Range. Here Podzol and Chestnut soils are separated by only a few kilometers because of abrupt changes in precipitation and concomitant changes from forest to grass-shrub vegetation.

The great relief in extensive mountainous areas within Oregon and Washington perpetuates many soils in a state of profile immaturity. Soils on steep slopes are constantly influenced by gravitational instability expressed as soil creep or landslides, often severely limiting profile development. Consequently, many mountain soils are Regosols or Lithosols lacking genetic horizons, except for a thin A. In these areas, effects of the parent rock on soil properties are major and those of climate and vegetation are minimal. Areas of these azonal soils are typically characterized by extensive rock outcroppings.

Volcanic activity along the crest of the Cascade Range during Pleistocene and Recent times has extensively influenced regional soils. Large tracts at higher elevations in the Cascades are mantled with deposits of pumice and volcanic ash which, because of their youth, generally exhibit little genetic development. In many areas, such as the southern Cascade Range of Washington, there have been several depositions of volcanic ejecta; soil profiles often have three or four buried horizon sequences.

Pumice and volcanic ash soils also occur well beyond the Cascade Range. Distance from their source and orientation of these deposits are largely functions of wind direction and velocity during eruptions. Recently, it has become apparent that many, if not most, of the soils of the Pacific Northwest have had some influence from aerially deposited volcanic ejecta. Amounts of incorporated ash and pumice are often small, however, and detectable only through detailed soil mineralogic or micromorphological investigations.

For descriptive purposes, the two-State area has been separated into 15 physiographic provinces (fig. 2). The divisions used are largely those outlined by Baldwin (1964) and Fenneman (1931). Naturally, in many instances, boundaries separating provinces are arbitrary and gradual transitions exist. However, the provinces are broad stratifications of relatively homogenous areas and reduce complexity to more manageable proportions.

Geologic information for this section is from several primary sources: for Oregon, Baldwin (1964) and "Geologic Map of Western Oregon West of the 121st Meridian" (Wells and Peck 1961); for Washington, Campbell (1953) and "Geologic Map of Washington" (Hunting et al. 1961). Other pertinent references included Williams (1942), Danner (1955), Foster (1960), Snavely and Wagner (1963), Fiske, Hopson, and Waters

(1963), Peck, Griggs, Schlicker et al. (1964), and Mackin and Cary (1965).

Soils information, particularly naming and distribution of great soil groups, is based largely on "Soils of the Western United States" (Western Land Grant Universities et

al. 1964). Other references consulted include Knox (1962), Youngberg (1963), and numerous soil survey reports for localized areas.

Table 1 shows the relative importance of various great soil groups within the 15 physiographic provinces.

Table 1. — Principal great soil groups within the 15 physiographic provinces of Oregon and Washington

Province	Widespread great soil groups ¹	Less abundant great soil groups
Olympic Peninsula	Sols Bruns Acides Reddish Brown Lateritic Lithosol	Podzol Brown Podzolic Alpine Turf Alpine Meadow Humic Gley Alluvial Regosol Rockland ²
Coast Ranges	Reddish Brown Lateritic Sols Bruns Acides Regosol Lithosol	Noncalcic Brown Prairie Grumusol Humic Gley Alluvial
Klamath Mountains	Reddish Brown Lateritic	Sols Bruns Acides Noncalcic Brown Western Brown Forest Podzol Prairie Grumusol Humic Gley Alluvial Lithosol Rockland ²
Willamette Valley	Prairie Planosol Alluvial	Gray-Brown Podzolic Chernozem Reddish Brown Lateritic Grumusol Humic Gley
Puget Trough	Brown Podzolic Regosol Alluvial Reddish Brown Lateritic	Gray Wooded Prairie Sols Bruns Acides Humic Gley Lithosol
Northern Cascades	Podzol Brown Podzolic Lithosol	Western Brown Forest Gray Wooded Chestnut Alpine Turf Alpine Meadow Regosol Rockland ²
Southern Washington Cascades	Brown Podzolic Podzol Lithosol Regosol	Reddish Brown Lateritic Gray-Brown Podzolic Sols Bruns Acides Western Brown Forest Chestnut Humic Gley Alluvial Rockland ²

Table 1. — Continued

Province	Widespread great soil groups ¹	Less abundant great soil groups
Western Cascades	Brown Podzolic Regosol Reddish Brown Lateritic	Podzol Sols Bruns Acides Noncalcic Brown Prairie Humic Gley Alluvial Lithosol Rockland ²
High Cascades	Regosol Brown Podzolic	Podzol Western Brown Forest Lithosol Rockland ²
Okanogan Highlands	Brown Podzolic Gray Wooded Lithosol	Western Brown Forest Chernozem Brown Humic Gley Alluvial Regosol Rockland ²
Blue Mountains	Western Brown Forest Regosol Lithosol	Brown Podzolic Reddish Brown Lateritic Chernozem Chestnut Prairie Alpine Turf Alpine Meadow Humic Gley Alluvial Rockland ²
Columbia Basin	Brown Chestnut Chernozem Prairie Sierozem Regosol	Planosol Humic Gley Solonetz Solonchak Alluvial Lithosol Rockland ²
High Lava Plains	Brown Chestnut Lithosol Regosol (pumice)	Solonetz Solonchak Humic Gley Alluvial Regosol Rockland ²
Basin and Range	Brown Chestnut Lithosol Regosol (pumice) Western Brown Forest	Chernozem Prairie Reddish Brown Lateritic Sierozem Desert Humic Gley Solonetz Solonchak Alluvial Regosol Rockland ²
Owyhee Upland	Brown Chestnut Lithosol	Sierozem Desert Solonetz Humic Gley Alluvial Regosol Rockland ²

¹ Listed in approximate order of importance.

² A miscellaneous land type in which rock outcrops or rock rubble dominate the landscape.

Figure 3. — The rugged Olympic Mountains viewed from Hurricane Ridge (south of Port Angeles, Washington); the glacially carved valley contains the Elwha River (*photo courtesy of Olympic National Park*).

Olympic Peninsula Province

The Olympic Peninsula province is made up of a central core of the rugged Olympic Mountains surrounded by almost level lowlands. On the east, the lowland strip is 3 to 16 kilometers wide and is part of the Puget Trough. The lowland strips are very narrow on the north, but 16 to 32 kilometers wide on the west, and 48 kilometers wide along the south side of the peninsula. Most ridges in the Olympic Mountains are 1,200 to 1,500 meters in elevation with some higher peaks attaining elevations of 2,100 to 2,420 meters. Glaciation has strongly influenced landforms. All main river valleys are broad and U-shaped,

and all major peaks are ringed with cirques, many containing active glaciers. The extremely high precipitation (perhaps as high as 6,350 millimeters per year in the interior) has caused rapid down-cutting by streams, resulting in many precipitous mountain slopes (fig. 3).

Geologically, the mountainous portion of the Olympic Peninsula province is made up of two volcanic belts encircling a large interior area containing sedimentary rocks. The volcanic belts bound the peninsula on the north and east sides, and as far west as Lake Quinault on the south. The outer belt, by far the thickest, is comprised of basalt flows and breccias of Eocene age. Between the two vol-

canic belts lies a generally thin band of argillite and graywacke, also Eocene. The inner volcanic belt is very thin and discontinuous and consists of altered basalt, "pillow" lava, and flow breccia deposited late in the Mesozoic era or perhaps during the Paleocene epoch. The rugged interior of the peninsula is almost exclusively comprised of sedimentary rocks deposited late in the Mesozoic or very early in the Tertiary period. These rocks are largely graywacke, with some interbedded slate, argillite, and volcanic rocks.

The less mountainous area along the north edge of the peninsula is a complex of Oligocene and Miocene sandstones, some interbedded with siltstone and conglomerates. In addition, glacial drift occurs in fairly large deposits near Sequim and Port Angeles and west of Ozette Lake. The broad, level areas along the western and southern margins of the peninsula have been interpreted as marine terraces or glacial outwash fans.

Because of wide ranges in climate and parent materials, the soil pattern on the Olympic Peninsula province is unusually complex. Soils derived from basalt are uniformly reddish brown and moderately high in clay content. Depths vary from extremely shallow to deep. Soils from graywacke and sandstone are generally moderately shallow and stony, especially in the interior where steep topography greatly restricts profile development. Where moderate soil development has occurred, textures are most often loams to clay loams, and colors are generally brown. Large varieties of soils have formed in glacial till and outwash, depending on such factors as particle size and degree of compaction in parent materials. Fine-textured till often gives rise to poorly drained clay soils with high organic matter contents in surface layers. Well-drained soils derived from coarser till frequently have brown, loam-textured surface horizons underlain by a gravelly sandy clay subsoil.

The most common great soil groups² in the northeastern portion of the province are Podzols, Brown Podzolics, and Lithosols. Upland portions of more gentle terrain to the

west and south are generally occupied by Reddish Brown Lateritic, Sols Bruns Acides, and Lithosolic soils. In low-lying areas and along major streams, the principal great soil groups are Alluvial and Humic Gley. Soils in the mountainous central core range from Podzols, Brown Podzolics, Lithosols, and Regosols at low to moderate elevations to Alpine Turf, Rockland, and Alpine Meadow soils at highest elevations.

Coast Ranges Province

The Coast Ranges province extends from the middle fork of the Coquille River in Oregon northward into southwestern Washington where it includes the area known as the Willapa Hills. The entire southern section of the province is topographically mature — i.e., steep mountain slopes with ridges that are often extremely sharp (fig. 4). Excepting the area drained by the Wilson and Trask Rivers, the proportion of steep slopes decreases in the northern section of the Coast Ranges. Mountain passes are generally located on the eastern border of the range due to faster rates of headward erosion by the numerous westward-flowing streams. Elevations of main ridge summits in the province range from about 450 to 750 meters. Scattered peaks, often capped with intrusive igneous rocks, rise well above surrounding ridges. Marys Peak, 1,249 meters high, is the highest peak in the Coast Ranges.

Figure 4. — The Oregon Coast Ranges west of Eugene, Oregon; note accordant ridge crests and extensive stream dissection. The highest peak in the background is Roman Nose Mountain (elevation, 870 m.).

²Great soil groups mentioned in the text are briefly described in the Appendix.

Geology south of the Salmon and Yamhill Rivers differs substantially from that to the north. Geologic history of the southern Coast Ranges began during early Eocene times with deposition of "pillow" basalts near the present town of Alsea. Later in the Eocene, the vast sedimentary beds of the Tyee formation, which make up by far the largest portion of this section of the Coast Ranges, were deposited under marine conditions. The Tyee formation, largely composed of rhythmically bedded, tuffaceous and micaceous sandstone, occurs throughout the southern Coast Ranges and is virtually the only rock present in the central portion. Also during the Eocene, other smaller marine sedimentary formations were laid down, mostly to the south and along the coast. Scattered igneous intrusions, largely gabbro, occurred during the Oligocene and cap many of the most prominent peaks (e.g., Marys Peak, Prairie Peak, and Grass Mountain). During the Miocene, localized depositions of both sedimentary and volcanic rocks occurred which are now exposed near Newport and Coos Bay. The Pliocene epoch saw no new depositions, the principal activity at this time apparently being the rapid erosion of the tremendously thick beds of sediments. Pleistocene deposits, generally sandy in nature, were laid down along the coast during a period of rising sea level. This general rise of sea level, following the melting of glacial ice, also drowned the mouths of coastal rivers.

As in the southern section, all rock formations in the northern Coast Ranges are Tertiary. Eocene formations are widespread and include both volcanic and sedimentary rocks. Eocene siltstone and sandstone are found along and to the south of the Yamhill River near Vernonia, Oregon, and in the Willapa Hills of southwestern Washington. Eocene volcanic rocks, largely basalt with some tuffs and breccias, occupy extensive areas northeast of Tillamook and in the Willapa Hills. Oligocene sedimentary formations, including siltstone, shale, and sandstone, are found near Vernonia, along the Nehalem River, and, to a limited extent, in the Willapa Hills. During the Miocene epoch, extensive basalt flows occurred in the most northerly section of the Oregon Coast Ranges and in the Willapa Hills.

Near the Columbia River in Oregon, these flows are classified with the extremely widespread Columbia River Basalt. The Pliocene-Pleistocene was largely a period of erosion, with streams excavating their valleys as the ranges were slowly uplifted.

Soils developing in the very extensive deposits of sandstone exhibit a wide range of characteristics. On steep, smooth mountain slopes they tend to be shallow, stony, loam textured, and brown or yellowish brown. Soils derived from sandstone colluvium occupy uneven, benchy slopes that generally exhibit some degree of continuing instability. On broad ridgetops, soils tend to be deep, with some clay accumulation in the B horizon and, generally, a thick surface horizon of high organic matter content.

Soils developed from siltstone or shale parent materials resemble those derived from sandstone in some respects, but generally they are finer textured. Typically, they have a clay-textured B horizon and either a clay loam or clay surface horizon.

Soils from basalt are dark brown to reddish brown, and soil texture varies with soil depth; deeper soils are finer textured. On all parent materials, soils near the coast tend to have thicker, darker A horizons, indicating greater amounts of incorporated organic material.

The most common great soil groups in upland positions within the Coast Ranges province are Reddish Brown Lateritic, Sols Bruns Acides, Lithosol, and Regosol. In low-lying areas, principally along streams, soils are generally classified within the Humic Gley or Alluvial great soil groups. In the eastern foothills of the Coast Ranges, Noncalcic Brown, Prairie, and Grumusol soils are encountered.

Klamath Mountains Province

The Klamath Mountains province encompasses a complex of ranges in southwestern Oregon and northern California. The northernmost range in Oregon is commonly identified as the Siskiyou Mountains. This region is logically set apart from the remainder of southern Oregon by the boundary separating its pre-Tertiary rocks from Tertiary rock formations outside the area. The pre-Tertiary

rocks of this province probably include the oldest in Oregon.

The Klamath Mountains province is largely a region of rugged, deeply dissected terrain (fig. 5). Mountain crests, comprised of steeply folded and faulted pre-Tertiary strata, vary in elevation from 600 meters near the coast to approximately 1,200 meters in the east. Ridge accordance suggests an ancient and now greatly dissected peneplain. Many peaks rise above this summit peneplain. The highest of these monadnocks in Oregon is 2,280-meter Mount Ashland which rises 1,060 meters above the general level of its surroundings.

The geologic history of the Klamath Mountains began during the Paleozoic era with deposition of volcanic tuffs and sedimentary rocks which were subsequently metamorphosed, largely into schists. A period of erosion and folding followed until late in the Triassic period when a large series of volcanic and sedimentary rocks were deposited near Medford and Grants Pass. These rocks have all undergone extensive metamorphism into various types of schists, gneisses, marbles, and other metavolcanic or metasedimentary rocks. These rock types outcrop east of Gold Beach and at other scattered locations throughout the province. During the Jurassic period, sandstones, siltstones, and shales were laid down along the coast and in a belt extending from the southwestern corner of Oregon across the province in a generally northeasterly direction. Most of these deposits have undergone very little alteration. These rock strata were intruded with ultramafic rocks such as peridotite and dunite during late Jurassic or very early Cretaceous times. The intrusions have largely been altered to serpentine which now appears in elongated, stringerlike outcrops, generally associated with fault zones. Other rocks which were intruded at approximately the same time include a variety of granitics — diorite, quartz diorite, granodiorite, and granite. The largest areas of these rocks are found north and south of Grants Pass, east of Oregon Caves, south of Ashland, southwest of Tiller, and between Grants Pass and Gold Beach in the Pearsoll Peak area. The early Cretaceous period saw additional depositions of sedi-

Figure 5. — The Klamath Mountains in Oregon showing characteristic, deep dissection and knifelike ridges.

ments — rocks which now appear as grayish-green arkosic sandstone and siltstone.

Rock strata within the province were greatly modified by folding and deformation during the middle Cretaceous period. Apparently, the Klamath Mountains were truncated and underwent peneplanation during the Miocene and Pliocene epochs. Subsequent erosion and stream dissection have given rise to the mature topography which characterizes the area today.

The highly variable soil pattern follows the complex geology of the Klamath Mountains. The most widely distributed parent materials are sandstone and siltstone which give rise to soils ranging from shallow and stony to deep and well developed. Surface textures are generally silt loam; and B horizons, when present, are usually silty clay loam or silty clay. Soils derived from schists and gneisses tend to be deep and unstable and at least moderately fine textured. Soils formed in peridotite and serpentine are invariably bright red and fine textured. Despite the presence of clay-textured B horizons, the soils are seldom deeper than 1 meter. Soils derived from granitic parent materials are generally of sandy texture and low fertility. In many areas, weathered material is deep and soil formation, generally podzolization, is well advanced. Metavolcanic and metasedimentary rocks give

rise to a wide variety of soils. Well-developed soils are generally brown with loamy surface horizons and clay loam subsoils.

The most widely distributed great soil group is the Reddish Brown Lateritic. These soils occupy low to moderate elevations throughout the province. Less common soils in drier locations include Sols Bruns Acides, Noncalcic Brown, and Western Brown Forest soils. On the higher peaks, Lithosol, Rockland, and Podzol soils predominate. At lower elevations, soils formed under grassland vegetation fall within the Grumusol and Prairie great soil groups. These soils are extensive in central Jackson County. Alluvial and Humic Gley soils occupy low-lying depressions and scattered areas along principal streams.

Willamette Valley Province

The Willamette Valley is a broad structural depression oriented north-south and situated in Oregon between the Coast Ranges on the west and the Cascade Range on the east. The valley is approximately 200 kilometers long, extending from the Columbia River to Cottage Grove where the two mountain ranges

converge. Valley width generally ranges from 30 to 50 kilometers. Topographically, the valley is characterized by broad alluvial flats separated by groups of low hills (e.g., Portland, Chehalem, Eola, Salem, and Coburg Hills) (fig. 6). The valley floor has a very gentle, north-facing slope; elevation increases from 50 meters at Salem to only 129 meters at Eugene, 130 kilometers to the south. As a result, the Willamette River is a sluggish stream with many meanders, especially from Oregon City southward.

The Willamette Valley is bordered on the west by a variety of sedimentary and volcanic rocks of Eocene age. They include submarine pillow basalts, conglomerates, and tuffaceous sandstones and siltstones which are actually eastward extensions of Coast Ranges formations. In the southern portion of the valley, these Eocene rock formations probably extend under valley fill materials to the western margin of the Cascade Range. Marine sedimentary rocks of Oligocene and Miocene age outcrop along the eastern margin of the valley. Columbia River Basalt (Miocene) is found as far south as the Salem area and caps the Portland, Salem, and Eola Hills. Similar early

Figure 6. — The Willamette Valley in Oregon is characterized by broad, almost level alluvial terrain interrupted by low basalt hills.

Miocene basalt flows occur in the Eugene area where, for example, they are found in the Coburg Hills. A westward extension of the Cascade Andesites of Plio-Pleistocene age outcrops near Gresham and caps many of the hills near Oregon City.

The floor of the northern Willamette Valley is underlain by thick, nonmarine sedimentary deposits of Plio-Pleistocene age. These deposits are present but not as thick in the southern part of the valley. Following the Illinoian glaciation late in the Pleistocene epoch, the entire valley as far south as Eugene was drowned by water and partially filled with silt to a depth of about 30 meters. Later, near the close of Wisconsin glaciation (10,000 to 15,000 years ago), the valley was again flooded because of an ice dam on the Columbia River. Evidences of this flooding include ice-carried erratics as far south as Harrisburg and a thin covering of silt to a maximum elevation of 122 meters. Recent alluvial deposits occur along the Willamette River in areas where it has cut into Pleistocene lake beds.

Soils on the valley floor, derived from silty alluvial and lacustrine deposits, were formed under dominantly grassland vegetation. Soil morphology largely reflects effects of soil drainage, which ranges from well to very poorly drained. Well-drained soils are moderately dark in color and, typically, silt loams. Most of the more poorly drained soils are darker colored with higher clay contents. Terrace soils usually have horizons of clay accumulation, whereas flood-plain soils do not. Soils derived from igneous and sedimentary rocks situated along the edges of the valley and in low hills are similar to those found in the adjacent Coast Ranges and Western Cascades provinces.

Over most of the Willamette Valley province, Prairie soils are dominant, intermixed with lesser amounts of Planosol and Alluvial soils. Soils of more limited occurrence include Humic Gley, Gray-Brown Podzolic, Chernozem, Reddish Brown Lateritic, and Grumusol.

Puget Trough Province

The Puget Trough province extends the entire length of Washington from the Canadian border to Oregon where the Willamette

Valley is its physiographic and geological continuation. The northern half of the province includes Puget Sound, and the southern half is largely the Cowlitz River Valley and upper basin of the Chehalis River. Relief is moderate, and elevations of the trough floor seldom exceed 160 meters.

The northern, or Puget Sound basin, portion of the province is a depressed, glaciated area which is now partially submerged. The geology and topography resulted almost entirely from a lobe of the cordilleran ice cap which pushed into the area from the north during the Pleistocene epoch. There were apparently several glacial epochs, the Vashon glaciation being most recent. The terminal moraine of the Vashon glacier is located approximately 16 to 24 kilometers south of Olympia. Inside the moraine is a large area, sloping gently toward Puget Sound and containing many lakes and poorly drained depressions underlain by glacial drift. Glacial deposits range from very porous gravels and sands to a hard till in which substantial clay and silt are mixed with coarser particles. For approximately 50 kilometers south of the terminal moraine (as far south as Toledo), the area is largely covered by outwash sands and gravels which were sluiced southward by the melting Vashon glacier.

Tertiary rock formations are exposed in the southern portion of the province (south of Toledo). Topographic characteristics, however, are similar to those further north. The majority of the area is made up of Eocene basalt flows and flow breccia. Smaller areas of Miocene and Pliocene nonmarine sedimentary rocks are found south of Toledo and east of LaCenter. Immediately north of the Columbia River is a substantial area of Pleistocene lacustrine deposits, similar to those found in the Willamette Valley.

The majority of soils in the Puget Sound basin portion of the province are formed in glacial materials under the influence of coniferous forest vegetation. Brown Podzolic soils are most common. They generally have at least a moderately thick forest floor with some development of an H layer. A thin, weakly developed A2 horizon is typical beneath the humus layer. The iron- and humus-enriched B horizon is usually reddish-

brown, with textures reflecting the parent material. Associated soils include Gray Wooded, Regosols, and Lithosols. At several locations, notably east of Olympia, soils formed under grassland vegetation are common. In well-drained situations, Prairie soils predominate, with Alluvial and Humic Gley soils in streamside or depressional locations.

In the southern portion of the province, Reddish Brown Lateritic soils are the most widely distributed. They have reddish-brown, well-aggregated loam to clay loam surface horizons underlain by B horizons generally showing evidence of clay accumulation. Associated upland soils are Sols Bruns Acides and Lithosols. Alluvial and Humic Gley soils are common in low-lying areas.

Northern Cascades Province

The Northern Cascades province extends north from Snoqualmie Pass to the Canadian border. Unlike the Southern Cascades, these mountains are to a large extent comprised of ancient sedimentary rocks, most of which are folded and at least partially metamorphosed. Intrusions of large granitic batholiths are also common.

The province is a topographically mature area of great relief. Valleys are uniformly very deep and steep sided (fig. 7). An outstanding

Figure 7. — The Northern Cascades province of Washington is characterized by unusually deep dissection and maximum relief; the steep-sided, U-shaped, main valleys are the result of glaciation.

feature of the main eastward- and westward-flowing streams is their low gradient to within 6 or 7 kilometers of the main divide. On this basis, it may be concluded that the Northern Cascades are as deeply dissected as is possible with their present elevation and that their relief within the current erosion cycle is at a maximum. Another striking topographic feature is the approximately uniform elevation of the main ridgetops. Near the middle of the range, this level varies from 1,800 to 2,600 meters. Towering above this relatively even crest are two dormant volcanoes — Mount Baker and Glacier Peak. In addition to the volcanoes, there are several granitic peaks of exceptional height.

Many ridges and peaks have glacial features. There are literally hundreds of cirques; some peaks, ringed by cirques, have been eroded to matterhorns. In addition, main east-west valleys probably owe their very low gradients to glaciation. Today this portion of the Cascades contains more active glaciers than any other area within the continental United States (fig. 8).

The geologic history of the area began late in the Paleozoic era with deposition of clastic marine sediments in a constantly falling geosyncline. These were metamorphosed during a period of compression and folding when the sea withdrew during the Jurassic period. Products of this metamorphism include argillite, slate, phyllite, schist, greenschist, and greenstone — rock types widely distributed throughout the Northern Cascades province. Gneisses, which occupy a large portion of the central section of the province, are also products of this same period of metamorphism. During early Cretaceous times, another geosynclinal trough was formed and the area reinvaded by the sea. Resulting rocks include mainly graywacke, siltstone, slate, phyllite, and argillite. These rocks, perhaps not as widespread as the older deposits, are located (1) north of Mount Baker, (2) between the Skykomish and Stillaguamish Rivers, (3) north of the town of North Bend, and (4) in the northeastern portion of the province (fig. 9). Sometime during the late Cretaceous period the sea withdrew. Sediment deposition continued on the west, however, where there was

Figure 8. — Extensive glaciers and snowfields are significant alpine features in the Northern Cascades province; view of Mount Shuksan (2,781 m.) with Mount Baker (3,285 m.) in the background.

a broad plain with meandering rivers. Here, continental sedimentary formations were laid down during late Cretaceous and early Paleocene times.

The Cascade Range was gradually uplifted during the Pliocene epoch. However, prior to this time large quantities of granitic rocks intruded the preexisting strata. Large masses of these rocks, including granite, granodiorite, and quartz diorite of Tertiary age, outcrop near the crest of the range in both the southern and northern portions of the province. In addition, older, Mesozoic granite rocks occupy large areas to the east.

The volcanic peaks of Mount Baker and Glacier Peak were built up during the Pleistocene epoch, chiefly of andesite flows. At the same time, glacial till was deposited in virtually every major valley. These deposits are highly variable and may range from fine to coarse texture. Generally, the fine material is glaciolacustrine in origin.

Extreme variability of parent materials combines with effects of extensive glaciation to produce a soil pattern in the Northern Cascades province bewildering in complexity. Residual rock is either frequently covered by or intimately mixed with glacial materials.

Figure 9. — An area of Cretaceous sedimentary rock (Swauk sandstone) northwest of Wenatchee, Washington; the steeply tilted beds of sandstone are clearly visible in this area of highly erodible soils.

Soils developed from glacial materials differ considerably, depending on whether they are derived from indurated till, loose outwash, and morainal materials or from fine-textured lacustrine deposits. Another important factor is the rapid pace of geologic erosion on steep slopes, which in many areas restricts soil formation to the extent that Lithosols and Rocklands are common.

Very little specific soils information is available for the province. However, a soil survey of a limited area (Gilkeson et al. 1961) identified several Podzol soil series derived from basalt and andesite colluvium and glacial drift. These soils have a 3- to 8-centimeter-thick, grayish, A2 horizon of sandy loam or loamy sand texture. The underlying soil is brown to reddish brown as a result of iron staining and is generally gravelly silt loam in texture. With the exception of soils formed on indurated glacial till which were classed as imperfectly drained Podzols, all soils in the area were well drained.

The most widely distributed great soil groups in the Northern Cascades province are Podzol, Brown Podzolic, and Lithosol. Other, less abundant soils include Rocklands and Regosols. In subalpine areas, the most common soils are Alpine Turf, Rockland, and Alpine Meadow. In the drier, southeastern por-

tion of the province, Western Brown Forest, Gray Wooded, Chestnut, and Lithosol soils replace the podzolic soils found in higher rainfall areas.

Southern Washington Cascades Province

The Southern Washington Cascades province extends south from Snoqualmie Pass to the Columbia River. Unlike the Northern Cascades, andesite and basalt flows dominate with only minor amounts of igneous intrusive, sedimentary, and metamorphic rocks.

The area is characterized by generally accordant ridge crests separated by steep, deeply dissected valleys. The general ridge elevation is approximately 2,000 meters in the northern section and 1,200 meters in the southern. An extensive area around Mount Adams is composed mainly of recent lava flows; it comprises a gently sloping plateau at 900- to 1,500-meter elevation, differing markedly from the rest of the province. Three dormant volcanoes dominate the surrounding landscape: Mount Rainier (4,392 m.), Mount Adams (3,801 m.), and Mount St. Helens (2,948 m.) (fig. 10).

At least 90 percent of the Southern Washington Cascades province is made up of andesite and basalt flows with their associated breccias and tuffs. These lava extrusions have been classified into four rather generalized age classes: (1) Eocene to lower Oligocene, (2) upper Oligocene to lower Miocene, (3) middle Miocene, and (4) Pleistocene to Recent. The Eocene-Oligocene volcanic rocks are described as bedded andesitic breccias with interbedded andesite and basalt which have been considerably altered by faulting and folding. These rocks are widely distributed from Mount Rainier southward, largely west of the Cascade Range crest. The Oligocene-Miocene volcanic rocks are mainly andesite flows and flow breccias which, to a large extent, retain a fresh look and are in a horizontal position. These rocks outcrop in a large area north of Mount Rainier and at scattered locations to the south. The Miocene deposits are Columbia River Basalt which extends into the province from the east. Pleistocene to Recent deposits include the andesite flows and pyroclastics

which comprise the slopes of Mount Rainier, Mount Adams, and Mount St. Helens. Pleistocene to Recent vesicular basalt lavas are especially widespread in the vicinity of Mount Adams.

Tertiary granitic rocks are found only at scattered locations. The largest outcroppings are north and east of Mount Rainier. Another area of granodiorite is southwest of Randle. Small deposits of sedimentary rocks are located southwest of Mount Rainier and in the northeastern corner of the province. These include Eocene and Miocene sandstone, siltstone, and shale.

Areas adjacent to the three volcanic peaks are generally mantled with pumice deposits of variable age, origin, and thickness. Deposits near Mount St. Helens sometimes exceed 200 or 300 centimeters. The most recent pumice deposit in the vicinity of Mount Rainier is thought to have been laid down 100 to 150 years ago during the volcano's last eruption.

Pleistocene glacial activity was widespread in the Southern Cascades, although most were small alpine glaciers. At its maximum extension, the Puget Glacier pushed into the flanks of the Cascades, impounding long lakes in several mountain valleys. Today deep glaciolacus-

Figure 10. — Mount St. Helens in the southern Washington Cascades province; the Kalama River valley in the foreground contains an extensive mudflow deposit which can be traced in this photograph to its origin on the slopes of the mountain.

trine deposits mark the limits of these lakes.

Fewer soils in the Southern Washington Cascades province are developed in glacial materials and, because of generally less rugged topography, there are smaller areas of Rocklands and Lithosols than in the Northern Cascades. Soils developed in andesite and basalt range widely in profile characteristics varying from stony Lithosols to deep, well-developed Reddish Brown Lateritic soils. Soils with at least moderate development commonly have brown to reddish-brown loam or silt loam surface horizons underlain by B horizons of clay loam or silty clay loam texture. In many locations, the surface soil is mixed with or entirely composed of pumice particles. Glacial or

glaciofluvial materials often give rise to moderately well drained to imperfectly drained Brown Podzolic or Gray-Brown Podzolic soils. These soils are characteristically sandy loam in texture, and B horizons are iron stained and often contain iron concretions. Soils in areas of deep pumice deposits are most often Podzols or Brown Podzolics. Podzolic soils on pumice typically have gray sandy A2 horizons over a reddish gravelly coarse sand B2ir horizon.

The most common soils are Podzols in the northern and Brown Podzolic soils in the southern portion of the province. These are accompanied by substantial areas of Rockland, Lithosolic, and Regosolic soils, especial-

Figure 11. — The western Cascades of Oregon are deeply dissected with the higher ridges generally composed of thick flows of andesite; this view shows Twin Buttes in the foreground and the Three Sisters, located in the High Cascades province, in the background.

ly on steep terrain. Along the western boundary of the province, Reddish Brown Lateritic and Lithosolic soils are most abundant. Other less important soils in the west include Sols Bruns Acides, Regosol, Alluvial, and Humic Gley. On the eastern slopes of the Southern Washington Cascades province, the major groups include Western Brown Forest, Lithosol, and Chestnut soils.

Western Cascades Province

The Cascade Range in Oregon is divisible into two distinct physiographic provinces. The High Cascades province, on the east, includes all major peaks of the range (e.g., Mount Hood, Mount Jefferson, Three Sisters) and originated during late Pliocene and Pleistocene epochs. The Western Cascades province consists of older volcanic flows and pyroclastics laid down during the Oligocene and Miocene.

The relief of the Western Cascades province is generally rugged in the eastern portions (fig. 11), but slopes are more gentle in the west. Over much of the area there is a striking accordance of main ridge crests at an average elevation of about 1,500 meters. Elevations higher than 1,500 meters are uncommon, and only a few peaks exceed 1,800 meters.

During the Oligocene and Miocene epochs, numerous volcanic eruptions and effusions produced deposits of basalts, andesites, and pyroclastic rocks, frequently in a complex pattern. Pyroclastic rocks in this area include tuffs, breccias, and agglomerates. Besides these extrusive igneous rocks, a small amount of granite outcrops in several places, notably along the McKenzie River. Subsequent alteration by alpine glaciation occurred during the Pleistocene epoch. Glaciation is evidenced by widely spaced deposits of glacial drift and the characteristic U-shape of the major valley drainages.

Pyroclastics are abundant in the central portion of the Western Cascades province. Between the McKenzie and South Umpqua Rivers, approximately three-fourths of the total area is made up of pyroclastic rocks. To the north, breccias are almost entirely absent except in the Collowash and certain sections

of the Santiam River drainages. South of the Umpqua basin, pyroclastics remain common to the Rogue River which marks their southernmost boundary.

Basalt and andesite are the most common bedrock materials in the Western Cascades province. A large proportion of the province is made up of andesite from the North Fork of the Willamette River northward to the Clackamas River. Also, south of the South Umpqua River, andesite is again the most common rock. Basalt has a more scattered occurrence and is generally found along the western margin of the Western Cascade province.

Glacial deposits are widely distributed throughout the Western Cascades province, with the majority concentrated in the valleys of major streams. Tracing the exact extent of mountain glaciation in this area is very difficult because many morainal features have been obliterated by subsequent stream dissection.

Most of the soils of the Western Cascades province can be placed into two major groups — soils developed from pyroclastic parent materials (largely tuffs and breccias) and those derived from basic igneous rocks (mainly basalt and andesite). These parent material groupings produce strongly contrasting soil types. Since tuffs and breccias are readily weatherable, soils from these materials tend to be deep and fine textured, especially on gentler slopes. Pyroclastic soils are frequently imperfectly drained, and mass soil movements (e.g., slumps and earth flows) are common. Well-developed soils from tuffs and breccias typically possess moderately thick, dark-brown clay loam A horizons and olive-brown to reddish-brown silty clay or silty clay loam B horizons. On steep slopes regosolic gravelly clay loam soils are most common.

Soils derived from basalt and andesite are generally well drained and stonier and coarser textured than those from pyroclastic parent materials. These soils are more stable and not as subject to mass erosion. Most often, soils from basalt and andesite are relatively poorly developed, consisting of dark-brown gravelly loam or sandy loam surface horizons. Especially at higher elevations, surface layers often contain noticeable amounts of aerially deposited volcanic ash and pumice.

Most middle to high elevational soils in the central and eastern portions of the province are classed as Brown Podzolic or Regosols. Other less important soils in this zone include Podzol, Rockland, Lithosol, and Reddish Brown Lateritic soils. At lower elevations along the western margin of the province, Reddish Brown Lateritic soils are most abundant. Other groups represented here include Sols Bruns Acides, Noncalcic Brown, Prairie, Alluvial, and Humic Gley soils.

High Cascades Province

The High Cascades province is essentially an area of rolling terrain interrupted at intervals by glaciated channels, some quite deep, carrying westward-flowing streams. The area is dotted with volcanic peaks and cones rising to 50 to 1,600 meters above the surrounding area (fig. 12). The major peaks are, from north to south, Mount Hood (3,427 m.), Mount Jefferson (3,199 m.), and the Three

Figure 12. — The High Cascades province of Oregon is essentially a gently sloping, high plateau area containing scattered volcanic peaks composed of andesite and smaller “cinder cones”; peaks on the skyline are Mount Jefferson (3,250 m.) on the left and Three-Fingered Jack (2,389 m.) on the right and the cratered cinder cones in the foreground comprise Sand Mountain.

Sisters (3,062-3,157 m.). The general elevation of the sometimes broad, gently sloping portion is approximately 1,500 to 1,800 meters.

The High Cascades province is geologically young; some flows of lava (scoriaceous basalt) are only several hundred years old. The most extensive depositions were extruded from volcanic vents during the late Pliocene and Pleistocene epochs. These flows are of gray olivine basalts and olivine-bearing andesites with subordinate amounts of dense porphyritic pyroxene andesites. Scattered over the area are younger flows comprised of andesites and basalts which are dated as upper Pleistocene and Recent epochs. Most major peaks in the area are made up of olivine-bearing andesite and originated during the upper Pleistocene epoch. The smaller cones, commonly called cinder cones, are generally comprised of gray to red basaltic and andesitic pyroclastic rocks.

Bedrock in the High Cascades province is frequently obscured by a mantle of pumice and ash from several volcanic eruptions. The most extensive deposition of these materials resulted from the explosive culminating eruption of Mount Mazama, which occurred about 6,600 years ago.

Glacial deposits are also locally abundant, especially adjacent to some of the higher peaks. For example, the flanks of Mount Hood are typically mantled with deep deposits of glacial till.

Very little specific soils information is available for the High Cascades province except for a limited area west of Mount Hood. There, parent materials are largely glacial till producing Podzol and Brown Podzolic soils. Surface horizons range from black to gray with textures of sandy loam or silt loam. Subsoils are dark-brown to dark reddish-brown gravelly or stony clay loam. Till deposits are deep, and the soils are well drained.

In the central portion of the province, extensive areas are mantled with deposits of volcanic ejecta such as pumice, cinder, and ash. Soils in these materials generally exhibit little profile development and are classed as Regosols. Typically, a thin A1 horizon of sandy loam or loamy sand texture is underlain by a transitional AC horizon which grades into the

unaltered coarse sand or gravelly sand parent material.

Throughout most of the province, Regosol and Brown Podzolic soils are most abundant. Other soils of more limited occurrence include Podzol, Rockland, and Lithosol. In the Columbia Gorge area to the north and in the southern extremity of the province, Western Brown Forest, Regosol, and Lithosol soils predominate.

Okanogan Highlands Province

The Okanogan Highlands province is characterized by moderate slopes and broad, rounded summits. In this respect, it differs markedly from the rugged North Cascades province on the west. Excepting the main river valleys, much of the province lies above 1,200 meters. There is a scattering of peaks which attain elevations of over 2,400 meters. The province is made up of several upland areas separated by a series of broad, north-south river valleys. These south-flowing rivers are, from west to east, the Okanogan, Sanpoil, Columbia, Colville, and Pend Oreille (Clark Fork) Rivers.

Virtually the entire province was repeatedly covered by glacial ice during the Pleistocene epoch. As a result, deposits of glacial drift are found throughout the area. Although many of these deposits occur only intermittently in stream valleys, they are widespread in the eastern portion of the province, especially north of Spokane. In some of the main valleys, glaciolacustrine sediments form a series of terraces on valley walls.

The Okanogan Highlands province is, in many respects, geologically similar to the North Cascades province. There is an almost bewildering variety of rock types present, ranging in age from Precambrian to late Tertiary. The Precambrian rocks, consisting largely of phyllite, are restricted to the eastern portion of the province. Lying above these deposits are rocks of the Cambrian, Ordovician, Devonian, and Mississippian periods of the Paleozoic era. Rock types represented in these formations include quartzite, graywacke, slate, argillite, phyllite, greenstone, and some limestone. The most abundant rock types in

the province are granitics, which were deposited during the Mesozoic era. These rocks, which include granite, quartz monzonite, quartz diorite, and granodiorite, occupy most of the area in the western section of the province and are interspersed with the Paleozoic rocks to the east. Tertiary depositions are largely confined to areas adjacent to main river valleys. Bedded Tertiary sediments are found near the Okanogan, Sanpoil, Columbia, and Pend Oreille Rivers. Later in the Tertiary period these same areas were influenced by eruptions of andesite and basalt lavas. Columbia River Basalt (Miocene) extends across the Columbia River into the province in an area south of Okanogan.

In the Okanogan Highlands province, the soil pattern is closely tied to elevation. In the mountainous areas away from the major river valleys, soils tend to be cold, acid, stony, and are often shallow to bedrock. In many areas, soil profiles are poorly developed and exhibit little horizonation. In other locations, especially at higher elevations, soils often show some effects of podzolization and possess a thin or intermittent A2 horizon underlain by a B2 horizon of high iron content.

At lower elevations along river valleys and the southern boundary of the province, soils

reflect the drier climate and transitional forest-grassland vegetation. These soils typically have a dark, moderately thick, A1 horizon underlain by a B horizon which shows little increase in clay content and is distinguished largely by changes in color and structure. Soil textures are commonly sandy loam to loam.

Mountain soils are generally classed as Brown Podzolic, Gray Wooded, or Lithosols. Other less extensive soils include Humic Gley, Regosol, and Rockland. Soils in the forest-grassland transition at lower elevations are Western Brown Forest, Gray Wooded, and Lithosols. Soils formed under grass or grass-shrub communities are scattered throughout the province. These include Chernozem, Brown, Lithosol, and Alluvial soils.

Blue Mountains Province

The Blue Mountains province is made up of several ranges of mountains separated by faulted valleys and synclinal basins. The mountainous areas include the Ochoco, Blue, and Wallowa Mountains, as well as the Strawberry, Greenhorn, and Elkhorn Ranges. Relief within the various mountain ranges is highly variable. Moderate slopes are common within the Blue and Ochoco Mountains, whereas the heavily glaciated Wallowa Mountains exhibit the greatest relief (fig. 13). Maximum elevations range from about 2,100 meters in the Ochoco Mountains to 2,900 meters at Eagle Cap in the Wallowa Mountains. Valley elevations are about 750 meters in the vicinity of the Ochocos and 900 meters in the broad basin between the Blue and Wallowa Mountains (near LaGrande and Baker, Oregon). Spectacular Hells Canyon comprises the eastern boundary of the province. This canyon, occupied by the Snake River, ranges up to 1,660 meters in depth and is 24 kilometers wide at its broadest point.

Geologically, the Blue Mountains province may be conveniently separated into eastern and western units, with the dividing line a short distance east of John Day, Oregon. The western Blue Mountains contain outcrops of some of the oldest rocks in Oregon. These are Paleozoic formations (Mississippian and Penn-

Figure 13. — The Wallowa Mountains of Oregon are more deeply dissected and have steeper slopes than other sections of the Blue Mountains province; snowcapped peaks in the background include Eagle Cap, the highest in the range.

sylvanian) of limestone, mudstone, and sandstone which outcrop along tributaries of the upper Crooked River. Ultramafic intrusions, some altered to serpentine, occur in the Strawberry Range. Triassic and Jurassic formations are located near the communities of Suplee and Izee and consist of a wide range of rocks such as conglomerate, sandstone, siltstone, shale, and limestone. The Clarno (Eocene) and John Day (Oligocene) are two formations widely known because of their abundant vertebrate fossils. Located along the lower John Day River, these formations are composed largely of breccia and varicolored tuffs. Columbia River Basalt, a thick formation extruded in many sheets during the Miocene epoch, occupies large areas within the western Blue Mountains. Late Miocene and Pliocene formations are also present and consist of bedded tuffs and silts.

The eastern portion of the Blue Mountain province spans a large part of the geologic time scale. Paleozoic formations of the Permian period are widespread near Baker and Sumpter and consist of schists, limestone, slate, argillite, tuff, and chert. As in the western section, these formations often have ultramafic and mafic intrusions ranging from peridotite to gabbro. Triassic sedimentary formations (sandstone, siltstone, shale, and limestone) are common but are not continuous because of erosion and subsequent burial by Tertiary rocks. Triassic limestone and argillaceous beds are especially prominent in the Wallowa Mountains where they outcrop on many ridge crests. Granitic stocks, perhaps extensions of the great Idaho Batholith, are found in the Wallowa Mountains, near Baker and Sumpter and along the John Day River. Columbia River Basalt is widespread along the north slope of the Blue Mountains, forms the mass of the range between Pendleton and LaGrande, and is also found to the south. Thus it is inferred that uplift of the Blue Mountains occurred after the deposition of these lavas during the Miocene epoch. Alluvial deposits of sand and gravel, dating from the Pliocene and Pleistocene, cover the floors of many basins. Also during the Pleistocene, glaciation was widespread in both the Blue and Wallowa Mountains, as shown by numerous cirques, glacial lakes, and moraines.

Following deposition of the most recent lava flows, much of the area within the central and northern portions of the Blue Mountains was covered by a layer of aerially deposited volcanic ash and fine pumice. Subsequent erosion has largely removed the ash from south-facing slopes; however, other locations are typically mantled by the material.

At the present time, considerably more soils information is available for the western portion of the province (Ochoco and Blue Mountains) than for the Wallowa Mountains. Soils in the western section include those derived from basic igneous flow rocks, acid igneous rocks and pyroclastics, and volcanic ash. Many of the soils developed on basalt and andesite tend to be shallow and lithosolic and at least moderately fine textured. Surface horizons are generally comprised of dark-brown loam or silt loam, and subsoil textures range from clay loam to clay. Soils derived from rhyolite and tuff also are commonly shallow and lithosolic; however, they are considerably more coarse textured. Most often, the soil material is a dark-brown sandy loam of very weak structure. Soils derived from volcanic ash may occur over either bedrock or buried soil material. Thickness of the ash mantle varies, but most often it is in the range of 1/2 to 1 meter. Volcanic ash gives rise to soils characteristically dark brown in color and fine sandy loam in texture.

Most of the soils in the mountainous, central portion of the province which have formed under forest vegetation are classed as Western Brown Forest, Regosol, or Lithosol soils. Other forest soils of more limited extent include Brown Podzolics and Reddish Brown Lateritics. In the eastern portion of the province, there are several upland areas possessing soils formed under grassland or shrub-grassland vegetation. Principal great soil groups represented in these areas include Chernozem, Chestnut, Prairie, and Lithosol. At lowest elevations, especially along the boundaries of the province, Chestnut and Lithosol soils predominate. Alpine Turf, Rockland, and Alpine Meadow soils are found on some of the higher peaks within the Wallowa Mountains. At the other extreme, Alluvial and Humic Gley soils are common in low-lying depressions and along major streams.

Figure 14. — Canyons cut in basalt by the Deschutes and Crooked Rivers in the southern portion of the Columbia Basin province; west of Madras, Oregon.

Columbia Basin Province

The Columbia Basin is the largest single province; it occupies an extensive area south of the Columbia River between the Cascade Range and Blue Mountains in Oregon and roughly two-thirds of the area east of the Cascades in Washington. Topography varies from very gently undulating to moderately hilly. Steep slopes are of limited occurrence and restricted to isolated basaltic buttes or canyons cut by some of the major rivers; for example, the Deschutes River in Oregon (fig. 14). Over most of the area, elevations range from 300 to

600 meters, although they are less than 150 meters adjacent to the Columbia River.

Although early Tertiary rocks are found at scattered locations in Oregon, the important geologic events in the Columbia Basin province began during the Miocene epoch with the vast outpouring of lavas making up the Columbia River Basalt formation. This huge basalt layer covers over 500,000 square kilometers in Washington, Oregon, and Idaho and underlies virtually the entire province. The Columbia River Basalt formation, ranging in total thickness from 600 to over 1,500 meters, is made up of numerous individual flows about 8 to

30 meters thick. Bottom portions of individual flows are dense, dark-gray basalt, but near upper margins the basalt becomes scoriaceous. In some areas, deformation of the Columbia River Basalt produced ridges and hills during the Pleistocene epoch.

In the central portion of eastern Washington's Columbia Basin province is a unique geologic feature — the Channeled Scablands. This is a gigantic series of dry, deeply cut channels in Columbia River Basalt (fig. 15) which form an extensive and complex drainage network. Many of the deeply entrenched drainageways diverge upstream only to converge again further downstream. Perhaps the best known feature in the Channeled Scablands is Grand Coulee with its spectacular Dry Falls. Although the origin of these puzzling features is still debated, Bretz (1959) probably offered the most satisfactory theory. He suggests that flood waters, pouring from glacial Lake Missoula (western Montana) as a result of dam failure during the Pleistocene epoch, were responsible for cutting the channels.

Plio-Pleistocene deposits cover the Columbia River Basalt over extensive areas. The most widespread deposit is the Palouse loess which mantles an elliptical area 160 kilome-

Figure 15. — General view of channeled scabland in the Columbia Basin of central Washington; this area is characterized by numerous dry channels cut in Columbia River basalt and generally shallow, stony soils (photo courtesy of H. W. Smith).

ters long in southeastern Washington. This material, deposited during the Pleistocene epoch, is made up of massive, tan-colored silt which may be over 45 meters thick. The Palouse area is characterized by smoothly rolling hills (fig. 16) and soils of high fertility which are generally used for wheat and pea

Figure 16. — Rolling Palouse Hills, composed of deep loess deposits, near Pullman, Washington, Columbia Basin province (photo courtesy of H. W. Smith).

production. Similar buff-colored, structureless silt deposits are found in Oregon near Moro and in Grass Valley. In addition, a large area near Boardman, Oregon, is underlain by unconsolidated sand of apparently Pleistocene age. Similar deposits, probably glaciolacustrine in origin, are located west of Walla Walla and near Toppenish, Washington.

Although virtually all soils in the Columbia Basin province have been formed under grassland or shrub-grassland vegetation, a wide variety of soils is present. Most of the broad soil differences correlate with annual precipitation. In general, precipitation is heaviest along the margins of the basin and gradually decreases toward the central portion. As a result, four distinct soil regions, forming a roughly concentric circular pattern, may be identified within the province.

The first soil region is located along all province boundaries with the exception of the west but is best expressed in the Palouse Hills near the Washington-Idaho border. The climate is subhumid, with annual precipitation ranging from 400 to 600 millimeters. In this area, Prairie and Chernozem soils predominate. A typical Prairie soil derived from Palouse loess possesses a thick, dark-colored A1 horizon of silt loam texture overlying a clay loam or silty clay loam B2 horizon having well-defined prismatic structure. Typically, calcium carbonate has been leached to levels well below the base of the solum. Chernozem soils developed from similar materials generally have shallower profiles, less clay accumulation, and weaker prismatic structure in the B horizon and a zone of calcium carbonate in the B3, usually within 1 meter of the soil surface. Other soils encountered in this region include Chestnut, Alluvial, Lithosol, Regosol, and Planosol great soil groups.

The second region is adjacent but generally at lower elevations and more arid, receiving 230 to 400 millimeters of annual precipitation. The principal soils are Chestnut derived from loess. Typical Chestnut soils have moderately thick, brown silt loam A1 horizons over light-brown silt loam B horizons with incipient prismatic structure. A zone of calcium carbonate accumulation is present in the B3 horizon. Other soils present in smaller

amounts include Chernozem, Brown, Lithosol, Alluvial, and Rockland.

The third soil region roughly encircles the central portion of the basin and also is semi-arid with 230 to 400 millimeters of annual precipitation. Parent materials are principally loess and sandier windblown materials. Brown soils comprise the major zonal great group. They possess a moderately thick, dark grayish-brown, loam-textured A horizon which is low in organic matter content. B horizons show little clay accumulation and a B3ca is generally present. Lithosols are also common in this region since it encompasses a large portion of the channeled scablands. Other soils of some importance include Chestnut, Sierozem, Alluvial, Regosol, and Rockland.

The fourth soil region includes desertic soils of the lower bowl-like center of the Columbia Basin province. This is an area of arid climatic conditions receiving 100 to 230 millimeters of precipitation annually. Here the dominant great soil group is the Sierozem. These soils have thin, light-colored A horizons over B horizons which may be darker than the A and usually contain larger amounts of clay. A carbonate-enriched horizon, that may be cemented, occurs in the lower part of the B horizon. Other soils present include Regosol, Lithosol, Alluvial, Solonchak, Brown, Rockland, Solonetz, and Humic Gley groups.

High Lava Plains Province

The High Lava Plains province of central Oregon is characterized by young lava flows of moderate relief interrupted by scattered cinder cones and lava buttes. As a result of porous bedrock and scanty rainfall, many streams are seasonal. Undrained basins containing playa lakes, some dry and others with fluctuating levels, are common. Several basins, now dry, contained extensive lakes during the Pleistocene epoch (e.g., Fort Rock valley and Christmas and Fossil Lakes). Most of the province has a base elevation of about 1,200 meters above sea level.

Geologic formations in the high lava plains consist largely of Pliocene and Pleistocene lavas, tuffs, and alluvium. In many areas,

Figure 17. — Lava Butte south of Bend, Oregon — an outstanding example of a Recent volcanic cone and associated lava flows located in the western portion of the High Lava Plains province.

Quaternary valley fill deposits overlie the older volcanic flows. These are comprised of alluvium and lake deposits plus eolian sediments, all of which were derived from the volcanic rocks of the uplands.

Evidences of extensive volcanic activity during Pleistocene and Recent times are abundant, especially in the western portion of the province. The largest volcanic peak is the Paulina Peak shield volcano which contains Newberry Crater. Pumice, resulting from an eruption of this volcano about 4,000 years ago, mantles an extensive area to the north

and east of the crater. Deposits of Mount Mazama pumice are also widespread in the same general area, as well as to the south in the Basin and Range province. Broad areas of Pleistocene lava flows are a notable feature in the vicinity of Bend. In addition, several outstanding examples of Recent lava flows are situated south of Bend at Lava Butte (fig. 17) and east of Fort Rock.

Soils of the High Lava Plains province are similar to those occurring in the Basin and Range and Owyhee Upland provinces to the south and east. The central and eastern por-

Basin and Range and Owyhee Upland Provinces

Figure 18. — Hart Mountain, a typical fault-block mountain in the Basin and Range province of southeastern Oregon; note the internally drained depressions containing shallow, saline lakes.

tions, supporting shrub-grassland vegetation, are mantled mainly with Brown, Chestnut, and Lithosol soils. These soils are derived from alluvial and lacustrine sediments, as well as from residual basalt, andesite, and tuffs. Typical Chestnut soils within the province have moderately thick, very dark-brown loam A1 horizons and dark yellowish-brown clay or clay loam B2 horizons with some calcareous deposits on ped surfaces. Brown soils differ from the Chestnut in having shallower profiles, generally less clay accumulation in the B2 horizon, and a higher concentration of calcium carbonate in the lower section of the B. More restricted soils in this section of the province include Regosol, Alluvial, Solonetz, Solonchak, and Humic Gley.

In the western portion of the province, adjacent to the High Cascades province, regosolic soils developed on pumice support open coniferous forest vegetation. These are most extensive east of Newberry Crater where the younger Newberry pumice frequently overlies preexisting pumice deposits from Mount Mazama. These pumiceous Regosols are briefly described in the section covering the Basin and Range province.

Southeastern Oregon has been divided into two physiographic provinces: Basin and Range and Owyhee Upland. Although topography differs, the two provinces are similar geologically.

The Basin and Range province is characterized by fault-block mountains enclosing basins with internal drainage (fig. 18). The Owyhee Upland province exhibits considerably less faulting and in general may be described as a north-facing basin which is drained by the Owyhee River. Elevations in both provinces range from about 1,200 meters to 2,930 meters atop Steens Mountain. Except for slopes of the fault-block mountains, much of the area is rolling with low relief. Since annual precipitation in the area averages only 180 to 300 millimeters, most streams are intermittent and numerous undrained basins contain shallow, saline lakes.

Excepting small amounts of Paleozoic and Mesozoic formations which outcrop in the Pueblo and Trout Creek Mountains, virtually all rocks date from Miocene to Recent epochs. The western Basin and Range province is largely made up of Miocene to Recent flows of basalt, pyroclastics, and alluvial sediments. Further east two rock assemblages are prominent: (1) Miocene flows of rhyolite, dacite, and andesite near Abert Rim and Paisley; and (2) altered basalt and andesite flows and tuffs overlain by tuffaceous sedimentary rocks in an area just east of Lakeview. Principal fault-blocks in the area (Winter Ridge, Abert Rim, and Steens Mountain) are capped with Miocene flows of basalt. At the base of the Steens Mountain fault scarp are tuffaceous sedimentary rocks as well as flows of rhyolites, andesites, and dacites. Steens Mountain is also of interest because of evidences of extensive glaciation — glacial carved channels and cirque basins at the head of virtually every drainage (fig. 19).

To the east, near the Owyhee River, are Miocene and Pliocene beds of tuffaceous sedimentary rocks capped by flows of rhyolite and basalt. In addition, thick beds of quartzose sandstone, siltstone, and conglomerate

outcrop near the mouth of the Owyhee River. The most recent volcanic activity in the area occurred during the Pleistocene epoch and resulted in basalt flows of limited extent at Diamond (fig. 20) and Cow Lakes Craters.

Soils of these provinces may conveniently be divided into two main groups — those in the west which developed under forest vegeta-

tion and those in the east associated with grassland-shrub vegetation. A tree-covered high plateau area in the northwestern corner of the Basin and Range province is mantled with extensive deposits of Mount Mazama pumice. Although most was aurally deposited originally, the pumice has been reworked by water in some areas, or was deposited in glow-

Figure 19. — Kiger Gorge, a glacially carved valley penetrating Steens Mountain, eastern Basin and Range province, Oregon.

Figure 20. — Diamond Craters, source of Pleistocene basalt flows in the Owyhee Upland province of southeastern Oregon.

ing avalanches which swept down slopes near the volcano during the eruption. Soils derived from pumice have immature, regosolic profiles consisting of a moderately thick surface layer with some organic matter accumulation overlying nearly fresh, yellow- and buff-colored pumice gravel and sand. They are slightly acid and, due to the high porosity of the pumice particles, have water-holding and cation-exchange capacities far greater than generally expected in such coarse material.

South and east of the pumice plateau is open forest interspersed with shrub-grassland. Dominant soils in this area are Western Brown Forest, Regosols, and Lithosols. Soils of lesser importance include Chestnut, Chernozem, Prairie, and Reddish Brown Lateritics. Southeast of Klamath Lake, Humic Gley, Alluvial,

and Chestnut soils are the most common.

In the eastern section of the Basin and Range province and in the Owyhee Upland province, Brown, Chestnut, and Lithosol soils are by far most abundant. A typical Brown soil profile developed from basalt possesses a dark-brown silty clay loam A1 horizon of medium thickness over a dark yellowish-brown clay B2 horizon having prismatic structure. A calcium carbonate cemented pan is generally present at a depth of approximately 60 centimeters.

Sierozem, Desert, and Alluvial soils are present in a drier area situated east of Steens Mountain. Other soils scattered throughout the southeastern section of Oregon include Solonetz, Solonchek, Regosol, Humic Gley, and Rockland.

CLIMATE

The varied climates of Oregon and Washington result from complex interplay between maritime and continental airmasses and the mountain ranges, particularly the Cascade Range that divides the States into eastern and western parts. Climatic data for representative stations in both areas are provided in table 2; this table, the isohyetal map (fig. 21), and the isoline maps for January mean minimum and July mean maximum temperatures (figs. 22 and 23) can be consulted during the following discussion.

Western Oregon and Washington have a maritime climate, characterized by:

1. mild temperatures with prolonged cloudy periods, muted extremes, and narrow diurnal fluctuations (6° to 10° C.);
2. wet, mild winters, cool, relatively dry summers, and a long, frost-free season; and
3. heavy precipitation (typically 1,700 to 3,000 millimeters or more on the coast and 800 to 1,200 millimeters in the Puget-Willamette trough), 75 to 85 percent of which occurs between October 1 and March 31, mostly as rain.

Most precipitation is cyclonic, the result of low-pressure systems that approach from the Pacific Ocean on the dominant westerlies. During summers, storm tracks are shifted to the north, and high-pressure systems bring fair, dry weather for extended periods.

There are some important variations in the climate of the western lowlands as a result of the coastal mountains and of latitude. Coastal mountains are responsible for the drier and less muted climate of the Willamette Valley, Puget Trough, and interior valleys of southwestern Oregon. The maritime airmasses are blocked from these areas to varying degrees, and precipitation declines markedly in resultant rain shadows (table 2). At the same time, there is a general latitudinal increase in precipitation from south to north. Consequently,

the interior valleys of southwestern Oregon typically have hot, dry climates (see Medford in table 2).

Eastern Oregon and Washington combine features 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. Still, temperatures fluctuate more widely than west of the Cascades, diurnal fluctuations of 10° to 16° C. being typical. Winters are colder, summers are hotter, and frost-free seasons are shorter. Precipitation is still primarily cyclonic in origin, but is considerably less than to the west since the area lies in the rain shadow of the Cascade Range; annual precipitation is typically 250 to 500 millimeters. Precipitation is not quite as seasonal, only 55 to 75 percent of it occurring between October 1 and March 31, but summers (June through August) are very dry (30 to 70 millimeters). A high proportion of the annual precipitation falls as snow, which is relatively uncommon in the coastal areas.

Mountain masses have profound effects on the climatic regime. As mentioned, the Cascade Range is an extremely important barrier to the movement of maritime and continental airmasses. Within the Cascade Range, elevation has a primary effect on local climate. Precipitation and snowfall increase and temperatures decrease rapidly with elevation on both western and eastern slopes of the range (fig. 24). Similar phenomena occur more locally with smaller mountain masses. For example, precipitation is very high on the western slopes of the coastal ranges (Olympic Mountains, Coast Ranges, and Siskiyou Mountains) and rain shadows occur to the east. In eastern Oregon and Washington increases in precipitation and decreases in temperature are associated with mountain masses such as the Blue Mountains and Okanogan Highlands.

Some details of climate associated with individual vegetation types will be included in later sections. The reader should keep in mind (1) the basically mild, summer-dry regional climate, and (2) the blocking effects of mountain masses on westerly winds of maritime and northeasterly winds of continental airmasses.

Table 2. — Climatic data from some representative weather stations in Oregon and Washington

Area and Station	Elevation	Latitude	Longitude	Temperature					Precipitation		
				Average annual	Average January	Average January minimum	Average July	Average July maximum	Average annual	June through August	Average annual snowfall
	Meters								Millimeters		Centimeters
West of Cascade Range:											
Quinalt, Wash. ¹	72	47°28'	123°51'	10.6	3.8	1.2	17.3	23.8	3,371	244	30
Otis, Oreg. ¹	49	45°02'	123°56'	10.3	5.3	2.00	15.3	20.1	2,496	163	--
Bellingham, Wash. ²	34	48°47'	122°29'	9.5	2.7	-1.4	16.1	23.3	853	102	25
Seattle, Wash. ²	34	47°39'	122°18'	11.6	4.5	1.1	18.7	24.1	888	79	29
Portland, Oreg. ²	9	45°32'	122°40'	12.6	4.6	1.4	20.3	25.8	1,076	70	31
Medford, Oreg. ²	400	42°22'	122°52'	11.4	1.9	-1.2	22.2	31.8	502	36	19
East of Cascade Range:											
Spokane, Wash.	718	47°37'	117°31'	8.8	-3.7	-7.8	23.9	28.7	437	58	147
Yakima, Wash.	323	46°34'	120°32'	9.9	-2.5	-8.9	21.7	31.3	200	29	64
Pendleton, Oreg.	455	45°41'	118°51'	11.6	.1	-4.3	23.1	31.2	314	42	47
Klamath Falls, Oreg.	1,249	45°12'	121°47'	9.1	-1.4	-6.4	20.4	29.6	357	40	104

¹ Coastal station.

² Station in lee of Coast Ranges.

Source: U. S. Weather Bureau (1965a, 1965b).

Figure 21. — Mean annual precipitation in Oregon and Washington (U.S. Weather Bureau 1960a, b).

Figure 23. — July mean maximum temperatures in Oregon and Washington (U.S. Weather Bureau 1960a, b).

Figure 24. — Climatic cross section of the Cascade Range in the vicinity of Snoqualmie Pass, Washington ($47^{\circ}25'$ N. lat.); distance from Seattle to Ellensburg approximately 152 km. (data from U.S. Weather Bureau 1956).

MAJOR VEGETATIONAL AREAS

Broadly classifying areas as (1) forest, (2) grass or shrub-grass (hereafter called steppe and shrub-steppe), and (3) subalpine parkland and alpine communities results in a major geographic separation (fig. 25). The forested communities are seen to be characteristic of western Washington and Oregon and mountainous areas to the east, and shrub-steppe or steppe lies almost entirely in the rain shadow east of the Cascade Range. The forests may be further subdivided into those found in (1) western Washington and coastal and northwestern Oregon, (2) interior southwestern Oregon and the Willamette Valley, and (3) eastern Oregon and Washington (east of the Cascade Range crest).

We have used zones as basic organizational units for the communities within the subdivisions just outlined. Zones of various types have been used for many years in biogeography, particularly in mountain regions. They have been defined by many criteria, such as climate, existing vegetation, and potential (climax) vegetation (Daubenmire 1946). Perhaps a zone is most usefully defined as the area in which one plant association is the climatic climax (Daubenmire 1968a). This delineates an area of essentially uniform macroclimate since the climax community on deep, loamy soils and undulating topography³ is primarily a product of macroclimate. Such zones tend to occur sequentially along moisture and temperature gradients which extend through broad regions or up mountain slopes.

Vegetational zones based on climax vegetation are the organizational basis for much of this paper. Our scheme is imperfect, however, for many reasons. In some areas, data are insufficient for construction of such a system and a more typological approach must be

used (e.g., in southwestern Oregon). In other cases, zonal or modal habitats (loamy soils and undulating topography) are rare or absent, such as in most of the mountainous areas and the major part of eastern Oregon. Consequently, our forested zones are based not on climatic climax communities but rather on areas in which a single tree species is the major climax dominant; e.g., *Pinus ponderosa* or *Tsuga heterophylla*.⁴ These areas do tend to occur as zonal sequences. Typological systems are inadequate since they depend on existing vegetation and frequently emphasize widespread seral types that span widely varying environments or economically valuable species rather than biologic features.

Someday, northwestern communities might be organized along the lines of climax series as recently carried out by Daubenmire and Daubenmire (1968) in the forests of eastern Washington and northern Idaho, but available data are inadequate. In such a system, phytogeographic data are organized by dominants in climax communities, e.g., *Tsuga heterophylla*, *Abies lasiocarpa* and *Pinus ponderosa* without reference to zones, thereby avoiding the many difficulties posed by rugged mountain topography (Daubenmire 1968a).

Since we have elected to use zones, the reader should consider some attributes of the zonal scheme as he views the landscape:

1. Zones may occur as sequential belts on mountain slopes, but more often they interfinger, with each attaining its lower elevational limits in valleys and its highest limits on ridges; as a consequence, the zones along the slopes of a narrow valley can be reversed from their otherwise normal altitudinal relationship (Daubenmire 1946) (fig. 26).

³By definition, deep loamy soils and undulating topography constitute the zonal or modal habitat. In essence, neither soils nor topography significantly modify the macroclimatic factor in development of plant communities on these sites.

⁴In two cases we have named zones after major seral species characteristic of only that zone — *Picea sitchensis* and *Tsuga mertensiana*.

Figure 25. — Generalized vegetation map of Oregon and Washington (based partially on Hayes (1959), Küchler (1964), and Poulton (1962)).

LEGEND

FORESTED REGIONS

Picea sitchensis Zone

Tsuga heterophylla Zone

Puget Sound area

Mixed Conifer and Mixed Evergreen Zones

Interior Valley Zone

Pinus ponderosa Zone (broad sense)

Pumice region

Abies grandis and *Pseudotsuga menziesii* Zones

Subalpine forests (including *Abies amabilis*,
A. lasiocarpa, *A. magnifica shastensis*
and *Tsuga mertensiana* Zones)

STEPPE REGIONS

STEPPE (without shrubs)

SHRUB-STEPPE (*Artemisia* dominated)

DESERT SHRUB

Juniperus occidentalis Zone

TIMBERLINE AND ALPINE AREAS

Figure 26. — Schematic diagram illustrating interfingering of zones in mountainous topography.

2. Related to this phenomenon is the tendency for species or associations, occupying modal sites in one zone, to occur on moist, cool habitats in the adjacent warmer and drier zone and on warm, dry habitats in the adjacent cooler and moister zone. For example, east of the Cascade crest, *Pseudotsuga menziesii* can occur as a climax species on relatively moist habitats in the *Pinus ponderosa* Zone or on relatively dry ridges within the *Abies grandis* Zone. In the Washington steppe, the zonal *Agropyron-Festuca* association may occur as a topographic climax on steep north slopes in the drier *Artemisia/Festuca* or on steep south slopes in the moister *Festuca/Symphoricarpos* Zone.
3. Disturbance and the resulting seral vegetation may obscure zonal sequences. Pioneer species often range through several vegetational zones. Many of the seral dominants in a given zone tend to be climax species in adjacent warmer and drier zones. Hence, *Pinus ponderosa* and *Pseudotsuga menziesii* are common pioneers on disturbed sites in the *Abies grandis* Zone. The relative abundance of understory and reproducing tree species often indicates trends in such areas.
4. Zonal schemes reflect plant responses to strong macroclimatic gradients in temperature and moisture. Unusual physical or chemical soil properties sometimes override climatic factors to severely modify zonation patterns. Serpentine areas and the pumice region east of Crater Lake, Oregon, are examples.

FORESTED REGIONS

In Oregon and Washington, forests dominate the landscapes west of the Cascade Range and the mountain slopes to the east (fig. 25). A great many tree species are endemic, but with rare exception the dominants are conifers. In fact, the finest coniferous forests in the world occur in this region and adjacent parts of California and British Columbia.

Some of the major tree species are listed in table 3 along with data on their growth and longevity. The absence of major hardwood dominants in this region has often been noted (e.g., Küchler 1946); the dry summer climate has frequently been offered as an explanation. Their absence contrasts the forests of this region sharply with the mixed temperate forests of eastern United States.

The primarily forested areas can be divided into three major subregions: (1) western Washington and the Cascade and Coast Ranges of northern Oregon; (2) interior southwestern Oregon and the Willamette Valley, a relatively dry subregion with many Californian relationships; and (3) eastern Washington and Oregon (including the eastern slopes of the Cascade Range), an even drier and more continental subregion with affinities to the Rocky Mountain forests.

The zones in the three subregions can be related in terms of the factor primarily responsible for a given part of the zonal sequence (table 4). In the xerophytic zones, moisture is limiting for many species; each step up the zonal sequence indicates a more favorable moisture regime. Communities are very responsive to small differences in environment affecting plant moisture stresses (e.g., in exposure and soil depth). Within the temperate zones, neither moisture nor temperature conditions are severely limiting for the forest species. Forests grow and develop best in these zones, and species composition does not shift so markedly in response to local differences in site conditions. Temperature is the major factor separating subalpine types from temperate, with the related phenomenon of snowpack also profoundly influencing variation in community mosaics. Both factors appear limiting for many lower elevation species.

Western Washington and Northwestern Oregon

Western Washington and northwestern Oregon comprise the most densely forested region in the United States. At the time of the first settlers, conifer stands clothed almost the entire area from ocean shore to timberline.

Table 3. — Ages and dimensions typically attained by forest trees on better sites in the Pacific Northwest and their relative tolerances¹

Species	Age	Diameter	Height	Tolerance ²
	Years	Centimeters	Meters	
<i>Abies amabilis</i>	400+	90-110	45-55	VTOL
<i>Abies concolor</i>	300+	100-150	40-55	TOL
<i>Abies grandis</i>	300+	75-125	40-60	TOL
<i>Abies lasiocarpa</i>	250+	50-60	25-35	TOL
<i>Abies magnifica</i>	300+	100-125	40-50	INTER
<i>Abies procera</i>	400+	100-150	45-70	INTOL
<i>Chamaecyparis lawsoniana</i>	500+	120-180	60	TOL
<i>Chamaecyparis nootkatensis</i>	1,000+	100-150	30-40	TOL
<i>Larix occidentalis</i>	700+	140	50	INTOL
<i>Libocedrus decurrens</i>	500+	90-120	45	INTER
<i>Picea engelmannii</i>	500+	100+	45-50	TOL
<i>Picea sitchensis</i>	800+	180-230	70-75	TOL
<i>Pinus contorta</i>	250+	50	25-35	INTOL
<i>Pinus lambertiana</i>	400+	100-125	45-55	INTER
<i>Pinus monticola</i>	400+	110	60	INTER
<i>Pinus ponderosa</i>	600+	75-125	30-50	INTOL
<i>Pseudotsuga menziesii</i>	750+	150-220	70-80	INTOL
<i>Sequoia sempervirens</i>	1,000+	150-380	75-100	TOL
<i>Thuja plicata</i>	1,000+	150-300	60+	TOL
<i>Tsuga heterophylla</i>	400+	90-120	50-65	VTOL
<i>Tsuga mertensiana</i>	400+	75-100	25-35	TOL
 <i>Acer macrophyllum</i>	 300+	 50	 15	 TOL
<i>Alnus rubra</i>	100	55-75	30-40	INTOL
<i>Lithocarpus densiflorus</i>	180	25-125	15-30	TOL
<i>Populus trichocarpa</i>	200+	75-90	25-35	INTOL
<i>Quercus garryana</i>	500	60-90	15-25	INTOL

¹ Developed from a variety of sources, the most important being Fowells (1965). Maximum ages and sizes for species are generally much greater than those indicated here.

² Tolerance scale: VTOL = very tolerant of shade, TOL = tolerant, INTER = intermediate shade tolerance (greater in youth, lesser at maturity), and INTOL = intolerant.

Table 4. — Forested zones in different parts of Oregon and Washington

Zonal groups	Interior southwestern Oregon	Eastern Washington and Oregon	Western Washington
Xerophytic	Interior Valley	<i>Juniperus occidentalis</i> <i>Pinus ponderosa</i> <i>Pseudotsuga menziesii</i>	(¹)
	Mixed Evergreen		
Temperate	Mixed Conifer <i>Abies concolor</i>	<i>Abies grandis</i> <i>Tsuga heterophylla</i>	<i>Tsuga heterophylla</i> <i>Picea sitchensis</i> <i>Abies amabilis</i>
Subalpine	<i>Abies magnifica shastensis</i> <i>Tsuga mertensiana</i>	<i>Abies lasiocarpa</i>	<i>Tsuga mertensiana</i>

¹ There are xerophytic areas in the Puget Trough.

Presently, 82 percent of western Washington and Oregon is classed as forest land (Barrett 1962), a total of about 11,764,000 hectares.

Forests grow rapidly in this region; the size, density, and longevity of virgin old-growth stands are impressive (fig. 27). Dominant tree species typically reach heights of 50 to 75 meters at maturity (table 3). Many species often live beyond 500 years, a significant ecological feature. For example, in this area *Pseudotsuga menziesii* is mainly a pioneer or seral species that reproduces after fire or other disturbances. Its long life span enables it to persist during extended periods of stability and to reseed an area following the next disturbance.

Much forest land in western Washington and Oregon is occupied today by relatively young seral stands that have followed clearing, logging, and wildfire. Such stands are typically referred to as "second growth" regardless of origin. Clearing away the obstructing forest was, of course, the first order of business for settlers. Much of this cleared

acreage has since been covered by towns, cities, and farms. The lumbering industry began almost simultaneously and grew rapidly in importance around the turn of the century. Activity was initially most intense in the lowlands of western Washington, but slowly shifted southward and higher into the mountains as the virgin forests were cut over. Carelessness, often associated with clearing and logging, has resulted in extensive fires during the dry warm summers and falls (fig. 28). Single burns usually reforest well from individual and/or grouped trees left by the fast-moving fires (fig. 29); repeatedly burned areas often remain treeless for many years (fig. 30).

At present, logging in the subregion is generally by clearcutting (Barrett 1962), partly for economic and partly for silvicultural reasons. *Pseudotsuga menziesii*, the preferred species, normally requires relatively open conditions for reproduction and rapid juvenile growth. In some areas, clearcuts are made as staggered patches (fig. 31), and in others, continuous clearcutting is practiced. Logging

Figure 27. — Old-growth *Pseudotsuga menziesii* stand, with abundant *Tsuga heterophylla* reproduction, typical of the dense coniferous forests clothing the Cascade and Coast Ranges in western Washington and northwestern Oregon.

Figure 28. — Wildfires of both natural and human origin have been responsible for the extensive seral forests of *Pseudotsuga menziesii*.

Figure 29. — Single wildfires typically leave individual trees or groups of trees which reforest the burned area quickly.

Figure 30. — Repeated wildfires can produce extensive tracts which remain deforested for decades without human intervention; Tillamook Burn, Oregon, first burned in 1933 and since reburned several times.

Figure 31. — Old-growth forests in western Washington and Oregon are typically logged in “staggered-setting” clearcuts of 15 to 30 hectares (Santiam River drainage, Willamette National Forest, Oregon).

slash is typically broadcast-burned after cutting and the site is seeded or planted, usually to *Pseudotsuga*.

Four vegetation zones can be recognized in western Washington and the Cascade and Coastal Ranges of northern Oregon: the coastal *Picea sitchensis* Zone, the very widespread *Tsuga heterophylla* Zone, *Abies amabilis* Zone, and the subalpine *Tsuga mertensiana* Zone. Typical tree species and their zonal occurrence in western Washington are listed in table 5.

“PICEA SITCHENSIS” ZONE

Picea sitchensis characterizes this long narrow zone which stretches the length of Washington and Oregon’s coast. It is, in fact, just part of a coastal forest zone which extends

north to Alaska and grades into *Sequoia sempervirens* forests in extreme southwestern Oregon. The *Picea sitchensis* Zone is generally only a few kilometers in width, except where it extends up river valleys. On the west side of the Olympic Peninsula, where an extensive coastal plain exists, it is much broader. Although the zone is generally found below elevations of 150 meters, it goes to 600 meters when mountain masses are immediately adjacent to the ocean. This zone could be considered a variant of the *Tsuga heterophylla* Zone distinguished by *P. sitchensis*, frequent summer fogs, and proximity to the ocean. Perhaps for this reason Krajina (1965) has not recognized a similar zone in British Columbia; our *Picea sitchensis* Zone is comparable to the Coastal Subzone of the Humid Transition Life Zone recognized by D. R. M. Scott (Barrett 1962).

Table 5. — Representative tree species and their relative importance in both seral and climax communities in forested zones of western Washington¹

Species	Zones			
	<i>Picea sitchensis</i>	<i>Tsuga heterophylla</i>	<i>Abies amabilis</i>	<i>Tsuga mertensiana</i>
<i>Abies amabilis</i>	m	m	M	M
<i>Abies grandis</i>	m	m	m	—
<i>Abies lasiocarpa</i>	—	—	m	M
<i>Abies procera</i>	—	—	M	m
<i>Chamaecyparis nootkatensis</i>	—	—	m	M
<i>Picea sitchensis</i>	M	m	—	—
<i>Pinus monticola</i>	—	² m	m	m
<i>Pinus contorta</i>	m	² m	m	m
<i>Pseudotsuga menziesii</i>	M	M	M	m
<i>Tsuga heterophylla</i>	M	M	M	m
<i>Acer macrophyllum</i>	m	m	—	—
<i>Alnus rubra</i>	M	M	—	—
<i>Thuja plicata</i>	M	M	m	—

¹ M = major species, m = minor species.

² Except major species in the Puget Trough province.

Environmental Features

The *Picea sitchensis* Zone has what could be considered the mildest climate of any northwestern vegetation zone (table 6). Extremes in moisture and temperature regimes are minimal; the climate is uniformly wet and mild. Precipitation averages 2,000 to 3,000 millimeters, but frequent fog and low clouds during the relatively drier summer months are probably as important in ensuring minimal moisture stresses. Fog drip adds as much as 26 percent to annual precipitation (Ruth 1954). This is the consequence of condensation in tree crowns.

Some of the finest forest soils in the region are found in this zone — deep, relatively rich, and fine textured. Major great soil groups on

upland forest sites are Brown Lateritics, Reddish Brown Lateritics, and Sols Bruns Acides. Surface soils are typically strongly acid (e.g., pH 5.0 to 5.5), high in organic matter (e.g., 15 to 20 percent) and total nitrogen (e.g., 0.50 percent), and low in base saturation (e.g., 10 percent).

Forest Composition

The coniferous forest stands in this zone are typically dense, tall, and productive (fig. 32). Constituent tree species are *Picea sitchensis*, *Tsuga heterophylla*, *Thuja plicata*, *Pseudotsuga menziesii*, *Abies grandis*, and *A. amabilis* (in Washington). The first three are by far the most common. *Alnus rubra* is one of the most abundant trees on recently disturbed sites,

Table 6. — Climatic data from representative weather stations within the *Picea sitchensis* Zone

Station	Eleva- tion	Lati- tude	Longi- tude	Temperature					Precipitation		
				Average annual	Average January	Average January minimum	Average July	Average July maximum	Average annual	June through August	Average annual snowfall
	Meters			-----	-----	Degrees C.	-----	-----	Millimeters		Centi- meters
Quinalt, Wash.	72	47° 28'	123° 51'	10.6	3.8	1.2	17.3	23.8	3,371	244	30
Astoria, Oreg.	66	46° 11'	123° 50'	10.6	4.7	2.1	16.0	20.6	1,967	140	--
Otis, Oreg.	49	45° 02'	123° 56'	10.3	5.3	2.2	15.3	20.9	2,496	163	--
Port Orford, Oreg.	96	42° 44'	124° 31'	11.3	7.9	4.3	14.9	19.2	1,780	81	--

Source: U. S. Weather Bureau (1956, 1965a, 1965b).

Figure 32. — A young, even-aged *Tsuga heterophylla* stand typical of the dense, productive forests found in the *Picea sitchensis* Zone.

Figure 33. — *Polystichum munitum* and *Oxalis oregana* dominate the understory of this *Picea sitchensis* stand; note the "prop" roots of the *Picea* which has developed on a rotting log (Neskowin Crest Research Natural Area, Siuslaw National Forest, Oregon).

and *Pinus contorta* is common along the ocean. *Sequoia sempervirens*, *Umbellularia californica*, and *Chamaecyparis lawsoniana* are found in this zone in southwestern Oregon.

Mature forests have lush understories with dense growths of shrubs, dicotyledonous herbs, ferns, and cryptogams (fig. 33). On sites modal in environmental conditions, *Polystichum munitum*, *Oxalis oregana*, *Maianthemum bifolium* var. *kamschaticum*, *Montia sibirica*, *Tiarella trifoliata*, *Viola sempervirens*, *V. glabella*, *Disporum smithii*, *Vaccinium parvifolium*, and *Menziesia ferruginea* are common understory species. On less favorable sites, e.g., old sand dunes and steep slopes facing the ocean, dense understories dominated by ericads such as *Gaultheria shallon*, *Rhododendron macrophyllum*, and *Vaccinium ovatum* are common. Wetter forested sites also have dense understories where *Oplopanax horridum*, *Athyrium filix-femina*, *Struthiopteris spicant*, *Dryopteris dilatata*, *Sambucus racemosa* var. *melanocarpa*, etc., are typical along with the "modal" site species mentioned earlier.

Cryptogams are extremely abundant and varied in the *Picea sitchensis* Zone — the so-called Olympic rain forest, noted for its mosses and liverworts (Sharpe 1956; Coleman et al. 1956; Harthill 1964), lies within this zone (fig. 34). Some common ground cryptogams are *Eurhynchium oreganum*, *Hylocomium splendens*, *Hypnum circinale*, *Rhytidiadelphus loreus*, *Mnium menziesii*, and *M. insigne*. *Isoetecium spiculiferum*, *Ptilidium californicum*, *Porella navicularis*, and *Scapania bolanderi* are a small sample of the abundant epiphytes. *Alnus rubra* is an especially favorable host for epiphytic development (Pechanec and Franklin 1968; Coleman et al. 1956).

Successional Patterns

Early successional trends following fire or logging in the *Picea sitchensis* Zone are similar to those encountered in the *Tsuga heterophylla* Zone (see next section). There is a stronger tendency, however, toward development of dense shrub communities dominated by *Rubus spectabilis*, *Sambucus racemosa* var.

Figure 34. — Mosses and liverworts are abundant and varied in the forests of the wet *Picea sitchensis* Zone; epiphytes cover trees and shrubs in this Olympic “rain forest” (photo courtesy Olympic National Park).

melanocarpa, *Vaccinium* spp., etc., because of the favorable growing conditions.

There are two major kinds of seral forest stands in the zone: (1) conifer forest containing varying mixtures of *Picea*, *Tsuga*, and *Pseudotsuga*, and (2) *Alnus rubra* stands. *Alnus rubra* reproduces abundantly and grows extremely fast on disturbed forest land within the zone. In many cases, it overtops conifer regeneration, resulting in pure or nearly pure *Alnus* forest (fig. 35). Replacement of *A. rubra* by other tree species is often very slow, even though it is a relatively short-lived spe-

cies. Successional sequences have not been thoroughly studied, although it appears that *Alnus rubra* can variously be replaced by semipermanent brushfields (Newton et al. 1968), by *Picea sitchensis* released from a suppressed state (Franklin and Pechanec 1968), or by *Thuja plicata* or *Tsuga heterophylla*, the latter often invading via down logs. *Alnus rubra* is noteworthy for its soil-improving properties; this species fixes significant amounts of nitrogen in this region (Tarrant 1968) and can have other effects on soil chemistry and microbiology as well (Franklin et al. 1968; Lu et al. 1968).

Figure 35. — The prolific and fast-growing *Alnus rubra* often pioneers on logged or burned lands in the *Picea sitchensis* Zone, offering severe competition for conifers; this typical 50-year-old *Alnus rubra* stand has an understory dominated by *Rubus spectabilis* (Siuslaw National Forest, Oregon).

Succession in most mature conifer forest types is toward replacement of mixed *Picea*, *Thuja*, *Tsuga*, and *Pseudotsuga* forests by *Tsuga heterophylla*. This species is apparently more tolerant than the *Picea sitchensis* and dominates the reproduction in old-growth forests. Since *P. sitchensis*, *Thuja plicata*, and *Pseudotsuga menziesii* are all long-lived species, even very old stands usually retain at least some of the original representation of these species. On moist to wet sites, it appears *T. plicata* and, in some cases, *P. sitchensis* will be at least a part of the climax along with *T. heterophylla*.

Much of the forest regeneration in conifer stands takes place on rotting logs, "nurse logs," which often support hundreds of *Tsuga*, *Picea*, and *Thuja* seedlings (fig. 36) (Sharpe 1956). Some of these survive, and their roots eventually reach mineral soil. The consequences are often readily visible in forests as lines of mature trees growing along the remains of the original nurse logs.

Special Types

Including, as it does, the ocean strand, headland, and coastal plain environments, the *Picea sitchensis* Zone is the locale of a rich variety of specialized communities.

Sand dune and strand communities. — Sand dunes are the major locale where ocean-facing vegetation types have been studied by ecologists. In Oregon and Washington, there are extensive areas of such dunes — on 225 kilometers of 500 kilometers of shoreline in Oregon alone (Wiedemann 1966) (fig. 37). The greatest development is the Coos Bay dune sheet covering 86 kilometers of continuous coastline and a major site of Cooper's (1958) monumental study of dune origin and form.

Some features of shoreline vegetation are immediately obvious — e.g., communities of sand colonizers and stabilizers, the often impenetrable, bordering belts of shrubs and forests of *Pinus contorta* and *Picea sitchensis*. Strong, seashore winds greatly influence composition and form of the vegetation by desiccating foliage, transporting salt spray, and abrading the plants with sand. As a conse-

Figure 36. — *Tsuga*, *Picea*, and *Thuja* seedlings developing on a rotting nurse log, a typical phenomenon in forests of the *Picea sitchensis* Zone (Quinault Research Natural Area, Olympic National Forest, Washington); the range pole in this and other photos, unless otherwise noted, is 1 m. in height and marked in dm. segments.

Figure 37. — Sand dunes are very extensive along the Oregon coast, occupying nearly half the 500 kilometers of shoreline; pictured is the north end of the Coos Bay dune sheet, the most extensive single area of dune development in the Northwest (photo courtesy Siuslaw National Forest).

quence, the stands of *Pinus contorta* and *Picea sitchensis* are frequently deformed on the oceanside and increase in height to the lee (fig. 38). Also obvious in some localities are the plant communities, even whole forest stands, being engulfed by moving sand dunes (fig. 39).

Dune and strand vegetation of the Oregon coast has been studied by many scientists, including Egier (1934), Green (1965), Byrd (1950), Hanneson (1962), Kumler (1963), and Wiedemann (1966). Any discussion should probably begin with the early plant colonizers which begin sand stabilization. Some of the more important species are *Glehnia leiocarpa*, *Carex macrocephala*, *Franseria chamissonis*, *Abronia latifolia*, *Convolvulus soldanella*, *Lupinus littoralis*, *Poa macrantha*, *Polygonum paronychia*, *Juncus lesueurii* and *falcatus*, *Potentilla anserina*, *Calamagrostis nutkaensis*, *Elymus mollis*, *Plantago maritima*, and *Cotula coronopifolia* (Heusser 1960, Kumler 1963). *Ammophila arenaria* is an important pioneer deserving special mention. It was first introduced in the late 1800's for use in dune control planting on the Oregon coast

Figure 38. — Ocean winds and spray strongly influence form and composition of beach-bordering communities; *Picea sitchensis* at Cape Perpetua, Oregon (photo courtesy Siuslaw National Forest).

Figure 39. — Active or moving sand dune burying a coastal stand of *Pinus contorta* (Siuslaw National Forest, Oregon).

(Green 1965). Since that time, it has become naturalized and occurs widely, especially along the immediate shoreline (next to the high tide line). In fact, *Ammophila arenaria* is responsible for development of foredunes along portions of the coast, a dune type relatively uncommon prior to 1930 (Wiedemann 1966).

The shrub communities are often extremely dense and 1 to 3 meters in height. The most constant element is apparently *Gaultheria shallon* (Heusser 1960, Kumler 1963, Wiedemann 1966). Other species typically present are *Vaccinium ovatum*, *Myrica californica*, *Rhododendron macrophyllum*, *Arctostaphylos uva-ursi*, *Rubus spectabilis*, and *Arctostaphylos columbiana*. Shrub stands on wetter sites (e.g., deflation plains) may include *Salix hookeriana*, *Alnus rubra*, *Ledum glandulosum* var. *columbianum*, *Spiraea douglasii* and *Lonicera involucrata* (Wiedemann 1966).

Pinus contorta and *Picea sitchensis* seedlings are frequently present.

The forest stands on sand dunes are typically composed of *Pinus contorta* or *Picea sitchensis* or both. *Pseudotsuga menziesii*, *Thuja plicata*, or even *Tsuga heterophylla* (in later stages of development) may occasionally be present but are not typical. In southern Oregon, *Chamaecyparis lawsoniana* can be a pioneer forest species. It appears that *Pinus contorta* is seral on most (but not all) sand dune sites (Wiedemann 1966).

Wiedemann (1966) conducted the most comprehensive study of succession on Oregon sand dunes. He concentrated on deflation plains, areas where moist sand near the water table has been exposed, effectively stopping sand movement. Earliest stages in succession are herbaceous communities which differ compositionally, depending on moisture conditions: dry meadow, meadow, rush meadow,

BARE SAND

Figure 40. — Plant succession on Oregon coastal sand dunes (from Wiedemann (1966) with later modifications by Wiedemann).

and marsh. Major species in these communities are:

Community	Species
Dry Meadow	<i>Lupinus littoralis</i> , <i>Ammophila arenaria</i> , <i>Poa macrantha</i> , <i>Festuca rubra</i>
Meadow	<i>Festuca rubra</i> , <i>Lupinus littoralis</i> , <i>Aira praecox</i> , <i>Hypochaeris radicata</i> , <i>Fragaria chiloensis</i>
Rush Meadow	<i>Trifolium wilddenovii</i> , <i>Juncus phaeocephalus</i> and <i>falcatus</i> , <i>Aster subspicatus</i> , <i>Sisyrinchium californicum</i>
Marsh	<i>Carex obnupta</i> , <i>Potentilla anserina</i> , <i>Hypericum anagaloides</i> , <i>Ranunculus flammula</i> , <i>Lilaeopsis occidentalis</i>

A wet shrub community can develop directly from any of the last three communities and is

followed, in turn, by forests of *Pinus contorta* and *Picea sitchensis*. Some exceptions to this general outline include: open *Pinus contorta*/*Carex obnupta* forests and forest bogs of *Pinus contorta*, *Thuja plicata*, *Ledum groenlandicum*, *Darlingtonia californica*, *Lysichitum americanum*, and *Struthiopteris spicant*. Successional sequences on deflation plains and areas of dry active and inactive sand are schematically illustrated in fig. 40.

On the southern Oregon coast (from Coquille south), the coastline vegetation differs significantly (Heusser 1960, Peck 1961). The shrub and forest stands of *Gaultheria shallon*, *Pinus contorta*, and *Picea sitchensis* are absent. In their place (above the beach) are communities of herbs and low shrubs grading into a zone of taller shrubs. Typical species on the exposed seaward slopes are *Juniperus communis*, *Zygadenus fremontii*, *Mesembryanthemum chilense*, *Eriogonum latifolium*, *Sidalcea malvaeflora*, *Plantago subnuda*, *Agoseris hir-*

Figure 41. — Herbaceous communities occupy exposed portions of many headlands along the Oregon coast as shown here at Heceta Head (photo courtesy Siuslaw National Forest).

suta, *Scirpus setaceus*, *Brodiaea coronaria* var. *macropoda*, and *Iris douglasiana* var. *oregonensis*. The shrub zone is dominated by *Ceanothus thyrsiflorus*, *Garrya elliptica*, *Rhododendron occidentale*, *Alnus sinuata*, *Ribes menziesii*, and *Arctostaphylos columbiana* (Heusser 1960, Peck 1961, Gratkowski 1961a). *Ulex europaeus*, an introduced shrub, is an important weed species along the southern coast where it creates impenetrable thickets and a serious fire hazard (Wiedemann 1966, Gratkowski 1961a).

Tidal marshes. — The marsh communities on tidal flats are relatively unknown. Peck (1961) lists the following species as those most characteristic along Oregon's northern coast: *Triglochin maritima*, *Distichlis spicata*, *Puccinellia pumila*, *Scirpus americanus*, *S. pacificus*, *Juncus effusus*, *J. balticus*, *Salicornia pacifica*, *Glaux maritima*, *Cuscuta salina*, *Grindelia stricta*, and *Jaumea carnosa*. Heusser (1960) mentions that *Distichlis spicata* and *Salicornia pacifica* are codominants on tidal flats on the east side of the Olympic Peninsula. Johannessen (1964) studied prograding tidal marsh at Nehalem Bay in Oregon. He found *Triglochin maritima* was typical of the lowest habitats, near deep river channels. Higher and broader expanses of mud flats were dominated by *Scirpus pacificus* and *Carex lyngbyei* and those farther inland, by *Deschampsia caespitosa* and *Juncus balticus*. Muenscher (1941) has provided species lists for salt marshes and tidal flats along Puget Sound in Whatcom County, Washington.

Prairies. — Prairies, treeless areas in an otherwise heavily forested locale, are scattered through the *Picea sitchensis* Zone (fig. 41). These have been studied in only two locales: a fern-dominated prairie on the coastal plain of the western Olympic Peninsula (Lotspeich et al. 1961) and a grassy headland prairie on the Oregon coast (Davidson 1967). Fortunately, both are representative of widespread prairie "types." Both of these prairies are surrounded by *Picea sitchensis* and *Tsuga heterophylla* forest.

The Quillayute Prairie (Lotspeich et al. 1961) is dominated by *Pteridium aquilinum* var. *pubescens*; other common species are *Achillea millefolium*, *Anthoxanthum odoratum*, *Eriophyllum lanatum*, *Fragaria vesca* var. *bracteata*, *Holcus lanatus*, *Hypericum perforatum*, *Prunella vulgaris* var. *lanceolata*, and *Spiraea douglasii* var. *menziesii*. Encroachment of the forest on this prairie was believed to be extremely slow prior to human disturbance. Rapid invasion of the prairie by *Picea sitchensis* has followed plowing, burning, or grazing of the original vegetation.

Davidson (1967) recognized five communities on a 10-acre headland prairie. The *Polystichum munitum*-*Rubus parviflorus*, *Artemisia suksdorfii*-*Solidago canadensis*, and *Solidago canadensis* communities were most important. *Pteridium aquilinum* was present in most stands, but not a dominant. Notable species in one or more communities besides the aforementioned were: *Equisetum maximum*, *Ranunculus occidentalis*, *Heracleum lanatum*, *Stachys mexicana*, *Galium aparine*, *Marah oregana*, *Rubus spectabilis*, *Angelica lucida*, *Carex obnupta*, *Lupinus littoralis*, *Achillea millefolium*, *Plantago lanceolata*, *Holcus lanatus*, *Agrostis tenuis*, *Elymus glaucus*, *Anthoxanthum odoratum*, *Festuca rubra*, *Dactylis glomerata*, *Bromus sitchensis*, and *Rosa nutkana*. Gradual invasion of the prairie by *Picea sitchensis* appears to be taking place, primarily along trees which have fallen into the prairie and become nurse logs.

Forested swamps. — Cedar and alder swamps are another specialized series of communities which are probably more common in the *Picea sitchensis* Zone than in any other. Swamps of this type are found in the *Tsuga*

heterophylla Zone as well, and even, occasionally, in the *Abies amabilis* Zone. However, they are most common on the coastal plains and portions of glacial drift adjacent to Puget Sound. The constant habitat characteristic is a high water table, or even standing surface water, for all or a portion of the year.

The chief tree species on these sites are *Thuja plicata* or *Alnus rubra* or both. In fact, it is in some of these swamp communities that *A. rubra* appears to be a climax species. *Picea sitchensis*, *Pinus contorta*, and *Tsuga heterophylla* may also be present. Although the understory is often dominated by only one or two species, such as *Lysichitum americanum* or *Carex obnupta*, a great variety of shrubby or herbaceous species may be present. Some of the more characteristic are *Struthiopteris spicant*, *Athyrium filix-femina*, *Oenanthe sarmentosa*, *Stachys mexicana*, *Mitella* spp., *Tolmiea menziesii*, *Spiraea douglasii*, *Salix hookeriana*, and *Rubus spectabilis*.

"TSUGA HETEROPHYLLA" ZONE

The *Tsuga heterophylla* Zone is the most extensive vegetation zone in western Washington and Oregon and the most important in terms of timber production. This is the region famous for subclimax *Pseudotsuga menziesii* and climax *Tsuga heterophylla*-*Thuja plicata* formations (Weaver and Clements 1938; Oosting 1956; Cooper 1957). The *Tsuga heterophylla* Zone extends south from British Columbia through the Olympic Peninsula, Coast Ranges, Puget Trough, and both Cascade physiographic provinces in western Washington (fig. 25). In Oregon, it is split into two major segments — located in the Coast Ranges and in the Western and High Cascades provinces — by the Willamette and other dry interior valleys. The southern limits are the Klamath Mountains on the coast (except for a narrow coastal strip) and the divide between the North and South Umpqua Rivers in the Cascade Range (about 43° 15' N. lat.). Elevational range in the Cascade Range varies from essentially sea level to 600 or 700 meters at 49° north latitude and from 150 to 1,000 meters at 45° north latitude. In the Olympic Mountains, the *Tsuga heterophylla* Zone occurs between 150 and 550 meters on the western

Figure 42. — *Pseudotsuga menziesii* is often the sole dominant tree in forests of the *Tsuga heterophylla* Zone, even in old-growth stands, although it is almost invariably seral (along Cave Creek, Gifford Pinchot National Forest, Washington).

slopes and from nearly sea level to 1,125 meters on the drier eastern slopes (Fonda 1967). Where conditions are favorable, elements of this zone appear on the east side of the Cascade Range (discussed later in this paper) and in the northern Rocky Mountains (Daubenmire 1952; Daubenmire and Daubenmire 1968).

The *Tsuga heterophylla* Zone as recognized here is analagous to Krajina's (1965) Coastal Western Hemlock Zone, except for our separation of the coastal *Picea sitchensis* Zone. In western Washington, it is essentially in agreement with Scott's definition of Merriam's Humid Transition Zone (Barrett 1962); however, in southwestern Oregon, the *Tsuga het-*

erophylla Zone does not include much of the area considered Humid Transition Zone.

It is emphasized that although this is called the *Tsuga heterophylla* Zone, based on the potential climax species, large areas are dominated by forests of *Pseudotsuga menziesii*. Much of the zone has been logged or burned, or both, during the last 150 years, and *Pseudotsuga* is usually a dominant (often a sole dominant) in the seral stands which have developed (Munger 1930, 1940). Even old-growth stands (typically 400 to 600 years old) frequently retain a major component of *Pseudotsuga* (fig. 42).

Environmental Features

The *Tsuga heterophylla* Zone has a wet, mild, maritime climate (table 7). Since the zone lies farther from the ocean, moisture and temperature extremes are greater than in the *Picea sitchensis* Zone. Also, there is a great deal of climatic variation in this widespread zone associated with latitude, elevation, and location in relation to mountain massifs. Precipitation averages 1,500 to 3,000 millimeters and occurs mainly during the winter; Orloci (1965) has suggested 1,650 centimeters precipitation is the lower limit of the Coastal Western Hemlock Zone in British Columbia. Summers are relatively dry with only 6 to 9 percent of the total precipitation. Moisture stresses are sufficient to result in distinctive community spectra along moisture gradients (McMinn 1960). Mean annual temperatures average 8° to 9° C., and neither January nor July temperatures are extreme (table 7).

Despite the fact soils in the *Tsuga heterophylla* Zone are derived from a wide variety of parent rocks, they tend to have some general features in common. Soil profiles are generally at least moderately deep and of medium acidity. Surface horizons are well aggregated and porous. Organic matter content ranges from moderate in the Cascades to high in portions of the Coast Ranges and Olympic Peninsula, where thick, very dark A1 horizons are especially common. Forest floor depths are generally less than 7 centimeters, except at higher elevations where they may reach 15 centimeters in thickness. Depending on degree of profile development, amounts of clay ac-

cumulation in the B horizon vary from low to medium. Most soils in the zone are of medium texture, ranging from sandy loam to clay loam. In many areas, zonal soils are limited to moderate slope positions, but on the steeper slopes poorly developed Regosols and Lithosols are encountered most often. Great soil groups, characteristic of the *Tsuga heterophylla* Zone, include Sols Bruns Acides and Reddish Brown Lateritic soils in the Coast Ranges and Olympic Peninsula provinces, and Brown Podzolic soils as well as Reddish Brown Lateritic in the Cascade Range.

Forest Composition

Major forest tree species in this zone are *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata*. *Abies grandis*, *Picea sitchensis* (near the coast), and *Pinus monticola* occur sporadically. Both *Pinus monticola* and *Pinus contorta* are common on glacial drift in the Puget Sound area. In Oregon, especially near the southern limits of the zone, *Libocedrus decurrens*, *Pinus lambertiana*, or even *Pinus ponderosa*, may be encountered. *Abies amabilis* is common near the upper altitudinal limits or even well within the *Tsuga heterophylla* Zone in the northern Cascade Range and Olympic Mountains. *Chamaecyparis lawsoniana* is a major element of the forests in a portion of the southern Oregon Coast Ranges. *Taxus brevifolia* is found throughout the zone, but always as a subdominant tree.

Hardwoods are not common in forests of the *Tsuga heterophylla* Zone and, except on recently disturbed sites or specialized habitats (e.g., riparian sites), are almost always subdominant. *Alnus rubra*, *Acer macrophyllum*, and *Castanopsis chrysophylla* are the most widespread. *Populus trichocarpa* and *Fraxinus latifolia* with *Acer macrophyllum* and *Alnus rubra* are found along major water courses. *Arbutus menziesii* and *Quercus garryana* may be found on drier, lower elevation sites anywhere in the zone, but are not characteristic. *Umbellularia californica* and *Lithocarpus densiflorus* are found in the southern Oregon Coast Ranges.

The forest communities of the *Tsuga heterophylla* Zone have been studied in detail at many locations. Excluding strictly succession-

Table 7. — Climatic data from representative stations within the *Tsuga heterophylla* Zone

Station	Elevation	Latitude	Longitude	Temperature					Precipitation		
				Average annual	Average January	Average January minimum	Average July	Average July maximum	Average annual	June through August	Average annual snowfall
	Meters								Millimeters		Centimeters
Darrington, Wash.	168	48°15'	121°36'	9.7	1.0	-3.3	17.4	25.7	2,045	154	120
Greenwater, Wash.	521	47°09'	121°39'	7.4	-1.2	-3.7	15.8	22.6	1,487	138	198
Castle Rock, Wash.	36	46°17'	122°54'	10.4	2.9	-2	17.6	26.7	1,453	109	27
Wind River, Wash.	351	45°48'	121°56'	8.8	0	-3.7	17.5	26.9	2,528	119	233
Detroit, Oreg.	485	44°44'	122°09'	9.3	.9	-3.2	17.9	27.5	1,929	110	156
McKenzie Bridge, Oreg.	419	44°10'	122°10'	10.1	1.6	-2.6	18.9	29.4	1,789	106	--
Valsetz, Oreg.	346	44°50'	123°40'	9.6	2.4	-7	16.6	25.6	3,207	144	38

Source: U. S. Weather Bureau (1956, 1965a, 1965b).

Table 8. — Abundance of selected species in three associations found in the *Tsuga heterophylla* Zone of the western Oregon Cascade Range

Species	Association		
	<i>Pseudotsuga</i> <i>/Holodiscus</i>	<i>Tsuga</i> / <i>Berberis</i>	<i>Tsuga</i> / <i>Polystichum</i>
<u>Trees</u>			
<i>Pseudotsuga menziesii</i>	Abundant	Common	Occasional
<i>Tsuga heterophylla</i>	Rare	Common	Common
<i>Thuja plicata</i>	--	Occasional	Common
<i>Acer macrophyllum</i>	Occasional	--	Rare
<i>Libocedrus decurrens</i>	Occasional	--	--
<i>Pinus lambertiana</i>	Occasional	--	--
<i>Arbutus menziesii</i>	Rare	--	--
<i>Taxus brevifolia</i>	Common	Common	Occasional
<u>Shrubs</u>			
<i>Acer circinatum</i>	Common	Common	Occasional
<i>Holodiscus discolor</i>	Common	--	--
<i>Gaultheria shallon</i>	Abundant	Occasional	Rare
<i>Corylus cornuta californica</i>	Common	--	Rare
<i>Vaccinium parvifolium</i>	Common	Common	Common
<i>Rhododendron macrophyllum</i>	Rare	Common	Rare
<i>Symphoricarpos mollis</i>	Common	Rare	Rare
<i>Berberis nervosa</i>	Common	Common	Common
<i>Rubus ursinus</i>	Common	Common	Common
<u>Herbs</u>			
<i>Linnaea borealis</i>	Common	Common	Occasional
<i>Whipplea modesta</i>	Common	Rare	--
<i>Synthyris reniformis</i>	Common	Rare	--
<i>Polystichum munitum</i>	Rare	Occasional	Abundant
<i>Coptis laciniata</i>	Rare	Common	Occasional
<i>Viola sempervirens</i>	Occasional	Common	Occasional
<i>Vancouveria hexandra</i>	Rare	Rare	Common
<i>Tiarella trifoliata</i>	--	Rare	Common
<i>Disporum smithii</i>	--	--	Occasional
<i>Trillium ovatum</i>	Occasional	Occasional	Occasional
<i>Hieracium albiflorum</i>	Common	Rare	--
<i>Galium triflorum</i>	--	Occasional	Common
<i>Oxalis oregana</i>	--	Rare	Common
<i>Struthiopteris spicant</i>	--	--	Occasional
<i>Asarum caudatum</i>	--	--	Occasional
<i>Festuca occidentalis</i>	Common	--	--
<i>Iris tenax</i>	Common	--	--
<u>Mosses, Liverworts and Lichens</u>			
<i>Eurhynchium oreganum</i>	Occasional	Abundant	Common
<i>Homalothecium megaptitum</i>	Occasional	Occasional	Rare
<i>Hylcomium splendens</i>	Occasional	Rare	Occasional
<i>Rhytidiadelphus loreus</i>	Common	Occasional	Occasional
<i>Rhacomitrium canescens</i>	Occasional	--	--
<i>Mnium insigne</i>	--	--	Common
<i>Peltigera aphthosa</i>	Common	--	--
<i>Dicranum fuscescens</i>	Common	Common	Occasional
<i>Hypnum circinale</i>	Common	Common	Common
<i>Cladonia</i> spp.	Occasional	Rare	--
<i>Scapania</i> spp.	--	Rare	Occasional

Source: Unpublished data on file at Forestry Sciences Laboratory, Pacific Northwest Forest & Range Exp. Sta., Forest Serv., U. S. Dep. Agr., Corvallis, Oregon.

al studies, these include (1) community classifications of seral *Pseudotsuga menziesii* stands (Spilsbury and Smith 1947; Becking 1954, 1956), (2) community descriptions for limited areas (Dirks-Edmunds 1947; Macnab 1958; Neiland 1958; Merkle 1951; Anderson 1967), and (3) investigations of the entire spectrum of forest communities (Bailey 1966; Orloci 1965; Corliss and Dyrness 1965; Rothacher et al. 1967; and Fonda 1967). Bailey and Poulton (1968) and Mueller-Dombois (1965) concentrated upon seral communities, McMinn (1960) upon community-moisture relationships, and Eis (1962) upon community correlations with environment and productivity. Cryptogamic components of forests in the *Tsuga heterophylla* Zone have been reported by Pechanec (1961), Higinbotham and Higinbotham (1954), Spilsbury and Smith (1947), Orloci (1965), and Becking (1954).

Significantly, the more comprehensive studies have shown a similar spectrum of communities arranged along moisture gradients. For example, on dry sites, understories are characterized by *Holodiscus discolor* or *Gaultheria shallon*, or both. On mesic sites, *Berberis nervosa* and *Acer circinatum* are often used as character species. *Polystichum munitum* and *Oxalis oregana* are typical of moister sites. *Lysichitum americanum* typifies the wettest forested sites. Although the details of community composition and nomenclature vary with the investigator and the locale, this same basic pattern — *Gaultheria-Berberis-Polystichum* — is repeated throughout the *Tsuga heterophylla* Zone.

Three old-growth community types are representative of this spectrum on the western slopes of Oregon's Cascade Range (about 45° N. lat.).⁵ These community types are tentatively designated the *Pseudotsuga menziesii*/*Holodiscus discolor*, *Tsuga heterophylla*/*Berberis nervosa*, and *Tsuga heterophylla*/*Polystichum munitum* associations. Some compositional data for these associations are listed in table 8. Although these data are from old-growth communities, the same types of

Figure 43. — A *Pseudotsuga menziesii*/*Holodiscus discolor* community typical of dry forest sites in the *Tsuga heterophylla* Zone; note the open nature of the stand and reproduction of *Pseudotsuga*, which is climax here (H. J. Andrews Experimental Forest, Oregon).

understories are found in much younger forests, including seral stands dominated completely by *Pseudotsuga menziesii* (see, e.g., Spilsbury and Smith 1947).

The *Pseudotsuga menziesii*/*Holodiscus discolor* association typifies the driest forested sites. The overstory is relatively open (fig. 43) and consists primarily of *Pseudotsuga menziesii*, although species such as *Libocedrus decurrens*, *Arbutus menziesii*, and *Acer macrophyllum* are often present. All age classes of *Pseudotsuga* from seedlings to veterans are present in these stands (fig. 43), indicating it appears as the major climax species. *Holodiscus discolor*, *Corylus cornuta* var. *californica*, *Symphoricarpos mollis*, and *Gaultheria shallon* typify the shrub layer. A number of herbs not common on mesic sites find their forest optimum here; e.g., *Synthyris reniformis*, *Whipplea modesta*, *Hieracium albiflorum*, *Festuca occidentalis*, and *Iris tenax*. Similar communities are much more common outside the *Tsuga heterophylla* Zone; e.g., in southwestern Oregon.

⁵ Source materials for this discussion are unpublished data on file at Forestry Sciences Laboratory, Pacific Northwest Forest & Range Exp. Sta., Forest Serv., U. S. Dep. Agr., Corvallis, Oregon.

Figure 44. — An understory characterized by *Berberis nervosa* typifies modal sites in the *Tsuga heterophylla* Zone; a *Pseudotsuga menziesii*-*Tsuga heterophylla*/*Berberis nervosa* community in western Oregon (H. J. Andrews Experimental Forest).

The *Tsuga heterophylla*/*Berberis nervosa* association and its relatives typify the climatic climax for the *Tsuga heterophylla* Zone (fig. 44). Old-growth stands consist primarily of *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata*. *Tsuga heterophylla* is, theoretically, the sole climax species based on size-class analyses. However, long-lived *Pseudotsuga menziesii* and *Thuja plicata* are often present in stands undisturbed for 500 years or more.

The understory is generally balanced between layers in the *Tsuga*/*Berberis* association. Major shrubs are *Berberis nervosa*, *Acer circinatum*, *Vaccinium parvifolium*, *Rubus ursinus*, and *Rhododendron macrophyllum*. Typical herbs are *Linnaea borealis*, *Viola sempervirens*, *Coptis laciniata*, and *Goodyera oblongifolia*. The most common moss is *Eurhynchium oreganum*. *Polystichum munitum* and *Gaultheria shallon* are often present, but not as understory dominants.

The *Tsuga heterophylla*/*Polystichum munitum* association characterizes the herb-rich communities found on moister habitats. The overstory usually includes *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata*. Very large *Pseudotsuga* are encountered in old-growth stands, as growth conditions are near optimum for the species. Size-class analyses indicate *Tsuga heterophylla* will be the major climax species, but *Thuja plicata* also reproduces in sufficient quantity to perpetuate itself. The understory is dominated by a lush growth of herbs (fig. 45), including *Poly-*

Figure 45. — *Polystichum munitum* dominates the lush herbaceous understory on moist sites in the *Tsuga heterophylla* Zone (H. J. Andrews Experimental Forest, Oregon).

stichum munitum, *Oxalis oregana*, *Tiarella trifoliata*, *Dryopteris* spp., *Galium triflorum*, *Disporum smithii*, *Struthiopteris spicant*, *Asarum caudatum*, and *Vancouveria hexandra*. Mosses and liverworts are also common, including *Eurhynchium oreganum*, *Mnium* spp., and *Scapania* spp.

Communities typifying the wet to very wet end of the moisture scale are not common in the Oregon Cascade Range. They are frequently encountered in the *Tsuga heterophylla* Zone in western Washington. One typical community found on lower slopes and stream terraces has extremely lush understory shrubs, dicotyledonous herbs, and ferns (fig. 46). *Pseudotsuga menziesii* and *Tsuga heterophylla* may be present, but *Thuja plicata* is invariably the conspicuous tree (fig. 46). Dominants include *Oplopanax horridum*, *Athyrium filix-femina*, *Struthiopteris spicant*, *Vaccinium* spp., *Dryopteris linnaeana* and *D. spinulosa* var. *dilatata*, *Trautvetteria caroliniensis*, *Anemone deltoidea*, *Viola glabella*, *Streptopus* spp., *Smilacina* spp., *Tiarella trifoliata*, and *Achlys triphylla*. Another community, found on swampy sites, is typified by *Thuja plicata* and *Lysichitum americanum* plus a wide variety of semiaquatic species.

There are many variations of this general community spectrum throughout the *Tsuga heterophylla* Zone. There is a general response to decreasing moisture (or, conversely, increasing moisture stress) from north to south, for example. In Washington, sites sufficiently dry to develop the *Pseudotsuga*/*Holodiscus*

community are relatively rare. Instead, *Pseudotsuga menziesii*/*Gaultheria shallon* community, in which *Tsuga heterophylla* is the probable climax, is usually found on the poorest quality sites. Similarly, communities with *Polystichum*-type understories are more widespread in Washington. There is a rather regular increase of *Pseudotsuga* importance from north to south within the zone, given stands of similar age. A notable difference between communities described in Oregon and in Washington is in the importance of *Rhododendron macrophyllum*. In many *Tsuga*-zone communities in Oregon, *Rhododendron macrophyllum* is a dominant; in Washington, it occurs sporadically.

Figure 46. — *Thuja plicata* and dense understories of shrubs and herbs, such as *Oplopanax horridum* and *Athyrium filix-femina*, are typical of old-growth stands on wet benches and stream terraces in the *Tsuga heterophylla* Zone (Mount Baker National Forest, Washington).

Successional Patterns

The early stages of secondary succession following logging and burning in this zone have been the subject of a number of studies. Unfortunately, however, much of this research has been limited to the first 5 to 8 years after complete tree removal, and, therefore, detailed successional patterns for the entire period of forest reestablishment have not been worked out. Timber harvesting operations in the *Tsuga heterophylla* Zone generally involve clearcut logging, followed by controlled burning of the logging slash to reduce wildfire hazard. During the first growing season after burning, the sparse plant cover is made up of residual species from the original stand, plus small amounts of invading herbaceous species such as *Senecio sylvaticus*, *Epilobium angustifolium*, and *E. paniculatum* (fig. 47) (Dyrness 1965). A moss-liverwort stage has also been noted during the first year (Isaac 1940; Ingram 1931).

Vegetation the second year is dominated by invading annual herbaceous species, species which produce large numbers of small, wind-borne seeds (fig. 47). Over much of the zone, a very high proportion of the second-year cover is made up of *Senecio sylvaticus*, a species which is present in only very small amounts in subsequent years (Brown 1963; Isaac 1940). West and Chilcote (1968) have shown this short-term dominance is related to high nutrient requirements which are generally satisfied only on recently burned sites. Perennial invading herbaceous species, such as *Epilobium angustifolium*, *Cirsium vulgare*, and *Pteridium aquilinum*, rapidly build up their populations until the fourth or fifth year when their rate of increase slackens (fig. 47) (Ingram 1931; Isaac 1940; Yerkes 1960).

This successional stage, sometimes called the weed stage, gradually gives way to a shrub-dominated period (fig. 48). These shrubs, including residual species such as *Acer circinatum*, *Rubus ursinus*, *Berberis nervosa*, *Rhododendron macrophyllum*, and *Gaultheria shallon*, as well as invaders such as *Ceanothus velutinus* and *Salix* spp., then dominate the site until they are overtopped by tree saplings, generally *Pseudotsuga menziesii* (Kienholz 1929; Ingram 1931; Isaac 1940).

Figure 47. — Herbaceous stages in secondary succession in the *Tsuga heterophylla* Zone; range pole is 4 feet tall and marked in 6-inch segments.

A. Virtually bare condition during the first growing season following slash burning.

C. During the third year, *Epilobium angustifolium* replaces *Senecio*, which has almost completely dropped out of the stand.

B. The second year after slash burning, invading *Senecio sylvaticus* dominates the site.

D. By the fifth growing season after slash burning, the invading shrub, *Ceanothus velutinus*, is beginning to gain dominance over the herbaceous invaders (here, mainly *Epilobium angustifolium* and *E. paniculatum*). (H. J. Andrews Experimental Forest, Oregon)

Herbaceous species surviving from the original forest stand (e.g., *Polystichum munitum*, *Trientalis latifolia*, and *Oxalis oregana*) are reported to be of only minor importance in early successional stages in the Cascade Range (Kienholz 1929; Isaac 1940; Yerkes 1960). However, in the Coast Ranges of Oregon, re-

sidual species, especially *Polystichum munitum*, often constitute an important component of the seral vegetation following logging. In addition, both shrub and total plant cover tend to be substantially greater on Coast Ranges cutting units than in the Cascades (Morris 1958). Typical shrub species near the

Figure 48. — A stage of shrub dominance typically follows herbaceous stage in *Tsuga heterophylla* Zone secondary successions; *Rhododendron macrophyllum*, residual from the original forest stand, dominates this 10-year-old clearcut (Santiam River drainage, Willamette National Forest, Oregon).

coast include *Rubus spectabilis*, *Rubus parviflorus*, and *Gaultheria shallon*.

The vegetation in early stages of succession following logging and burning is characteristically very heterogeneous. Much of this variability is attributable to site differences caused by a wide range of types of logging disturbance and degrees of burning severity (Dyrness 1965). The effects of burning in control of species composition are perhaps the most notable. For example, annual invading herbaceous species, such as *Senecio sylvaticus* and *Epilobium paniculatum*, show a marked preference for burned areas; whereas residual species such as *Polystichum munitum* and *Trientalis latifolia* occur more frequently on unburned sites. Of the shrubs, *Ceanothus* spp. are often almost entirely restricted to burned areas, and residual species (e.g., *Rhododendron macrophyllum* and *Vaccinium parvifolium*) generally are much more common on unburned sites (Morris 1958; Steen 1966).

Later successional stages in the *Tsuga heterophylla* Zone have received little study. However, Bailey and Poulton (1968) attempted a classification of the vegetation of a portion of the Tillamook Burn in the Coast Ranges of Oregon approximately 20 years after its most recent fire. They found the seral vegetation to be classifiable into six associates

which showed consistent relationships to environmental factors. These associates ranged from *Vaccinium parvifolium*/*Gaultheria shallon* on relatively xeric sites to *Alnus rubra*/*Polystichum munitum* on mesic sites. They also described an *Acer circinatum*/*Polystichum munitum* associates which closely resembles a similar community widely distributed in the Coast Ranges under 100-year-old stands of *Pseudotsuga menziesii*.

The relationships between early stages of secondary succession and plant communities, present in the original *Pseudotsuga menziesii*-*Tsuga heterophylla* stands, have been studied on Vancouver Island by Mueller-Dombois (1965) and in the southern Oregon Coast Ranges by Bailey (1966). Both workers found that in these coastal areas the characteristic forest plants were present in sufficient quantities after logging and burning to permit successful identification of the preexisting communities. Mueller-Dombois concluded that the cutover vegetation is denser than that found under the original stand due to spreading forest weeds, semitolerant of shade, and invading shade-intolerant weeds. Both weed groups compete for the same vacant spaces, but in general, the intolerant weeds appear to be more successful in burned areas and the semitolerant forest weeds in unburned localities.

The composition and density of the seral forest stands is dependent on the type of disturbance, available seed source, and environmental conditions. A very common occurrence is the development of dense, nearly pure, essentially even-aged stands of *Pseudotsuga menziesii* (fig. 49). This tendency is encouraged by the extensive planting and seeding of this species after logging or wildfires. These stands are often dense enough to eliminate most of the understory vegetation (fig. 50). Reestablishment of the characteristic understory species and invasion of western hemlock then takes place as mortality begins to open up the stand at 100 to 150 years of age. On the other hand, stands of *Pseudotsuga* may be relatively open, resulting in persistent understories dominated by *Gaultheria shallon* or *Acer circinatum*. Other common types of young stands in the zone are (1) those dominated by *Alnus rubra*, particularly on *Polystichum munitum*-characterized habitats (Bailey and Poulton 1968), and (2) stands in which *Tsuga heterophylla* or *Thuja plicata* are major components right from the beginning of secondary forest development. The latter two situations are most commonly found in wetter parts of the *Tsuga heterophylla* Zone; i.e., the northern Washington Cascade Range, the west side of the Olympic Mountains, and in the Coast Ranges.

Figure 49. — Dense, nearly pure, essentially even-aged *Pseudotsuga menziesii* stands typically develop on cutover areas in western Washington and northwestern Oregon by natural seeding or planting.

Truly climax forests are rare, but examples of old-growth forests which have been undisturbed for 400 to 600 years are relatively common. From these, we can draw some conclusion about the potential climax species. The eventual replacement of *Pseudotsuga* by *Tsuga heterophylla* in the absence of disturbance has been described by many authors (e.g., by Munger 1940, Hansen 1947, Cooper 1957, and Barrett 1962, in general terms, and by Bailey 1966, Fonda 1967, and Orloci 1965 for specific areas). As mentioned, *Tsuga heterophylla* may appear with the *Pseudotsuga* and a mixed stand develop. On other sites, significant *Tsuga* invasion may not occur for 50 or 100 years after disturbance. The point is that on most sites in the zone, *Tsuga heterophylla* is able to reproduce itself beneath the forest canopy and the relatively intolerant *Pseudotsuga* is not (fig. 51). Numerous examples can be found of mixed old-growth *Pseudotsuga*-*Tsuga* forest in which abundant seedlings, saplings, and poles of *Tsuga heterophylla* are present and those of *Pseudotsuga* are completely lacking.

However, there is some variation within the zone regarding the climax tree species. On environmentally median sites, *Tsuga heterophylla* appears to be essentially the sole climax species. On very dry sites, *Tsuga heterophylla* is absent and, consequently, *Pseudo-*

Figure 50. — Young conifer stands in the *Tsuga heterophylla* Zone are often dense enough to completely eliminate most of the understory; dense 66-year-old *Pseudotsuga menziesii* stand near Cottage Grove, Oregon.

Figure 51. — The shade-tolerant, climax *Tsuga heterophylla* is capable of reproducing under a forest canopy, but the intolerant *Pseudotsuga menziesii* is not; *Tsuga* saplings developing under a *Pseudotsuga* overstory (Santiam River drainage, Willamette National Forest, Oregon).

tsuga menziesii attains a climax role. On the wet to very wet sites, *Thuja plicata* will certainly be a part of any climax forest; size-class analyses do not support climax status for this species on modal or dry sites, however, even though many ecologists have hypothesized a *Tsuga-Thuja* climax for most of the region. The tendency for *Thuja plicata* to be a part of the mixed stands, successionally intermediate between the pioneer *Pseudotsuga* forests and the climax *Tsuga heterophylla* forests, has perhaps misled some ecologists in interpreting its successional role.

Special Types

Puget Sound area. — Here, large areas differ from the surrounding *Tsuga heterophylla* Zone in community types. Prairie, oak woodland, and pine forest are encountered, for ex-

ample. Climate and soil are both major factors in these differences. The area lies in the rain shadow of the Olympic Mountains. Precipitation is typically between 800 and 900 millimeters in the Puget lowlands, although it drops as low as 460 millimeters on the northeastern side of the Olympic Peninsula and in the San Juan Islands (U. S. Weather Bureau 1960b). And, as pointed out earlier, a continental ice sheet covered the Puget Trough during the Pleistocene epoch (Vashon glaciation). Consequently, most soils are developed in glacial drift and outwash. Such soils are often coarse textured, poor in nutrients, and excessively drained.

Although plant communities around Puget Sound are similar to others in the *Tsuga heterophylla* Zone, there are many notable features which are not common elsewhere: (1) stands with *Pinus contorta*, *Pinus monticola*, and even *Pinus ponderosa* as major constituents along with *Pseudotsuga menziesii*, and with *Gaultheria shallon* as an extremely common understory species; (2) *Quercus garryana* groves — many being actively invaded by *Pseudotsuga menziesii*; (3) extensive prairies often being invaded by *Pseudotsuga menziesii* and associated with groves of *Quercus*; (4) abundant poorly drained sites with swamp or bog communities; and (5) occurrence of species rarely or never found elsewhere in western Washington or northwestern Oregon, e.g., *Juniperus scopulorum*, *Populus tremuloides*, *Pinus ponderosa*, and *Betula papyrifera*. None of these communities or community mosaics, excepting the bogs (Rigg 1917, 1919, 1922a, 1922c, 1958; Fitzgerald 1966), have been studied in detail, although generalized accounts of one or more may be found in Barrett (1962), Hansen (1947), and Rigg (1913).

Many of these features are found on the Tacoma Prairies (Hansen 1947) near Olympia, Washington. *Quercus garryana*, *Pseudotsuga menziesii*, some *Pinus contorta*, and occasional *Pinus ponderosa* are associated with extensive open areas or prairies. The development of prairie (grassland) soil profiles in some openings indicates they have been free of forest for many years; possibly they were periodically burned by Indians to aid in hunting and to maintain the lileaceous *Camassia* roots,

Figure 52. — Mima Prairie near Olympia, Washington, showing (1) distribution of the mima mounds, which average 12 meters in diameter and 2 meters in height, and (2) invasion of a prairie area by *Pseudotsuga menziesii* (photo courtesy V. B. Scheffer).

which they used for food. Hansen (1947) has noted that *Tsuga heterophylla* pollen was never as abundant in local pollen profiles as in other parts of the Puget Trough. *Pseudotsuga* is now rapidly invading the prairies as well as *Quercus* groves (fig. 52).

“Mima mounds” are found on some of these prairies (fig. 52). These mounds range from swellings on the prairie surface to a maximum of about 2.1 meters in height and average about 12.2 meters in diameter. Several different theories of origin have been proposed, two of which are seriously considered. Dalquest and Scheffer (1942) attributed them to gopher activity (*Thomomys talpoides*). Newcomb (1952) related them to the glacial climate by proposing the mounds were due to thrusting action of ground ice wedges.

Eventually, the Puget lowlands may be recognized as a separate vegetative zone similar to the Coastal Douglas-fir Zone found in British Columbia (Krajina 1965). Its close relations with this zone are obvious. Many of the

Figure 53. — Talus communities dominated by *Acer macrophyllum* (background) or *Acer circinatum* (foreground) are widespread in the *Tsuga heterophylla* Zone (Lake Twentytwo Research Natural Area, Mount Baker National Forest, Washington).

Puget lowland communities also appear related to those found in the Willamette Valley; possibly some ecologists would group them together. However, both coastal British Columbia and the Puget Sound areas were glaciated and do involve large bodies of ocean water which significantly affect the local climate. Neither of these circumstances applies to the Willamette and other interior valleys of western Oregon.

Talus communities. — Nonforested talus or scree slopes occur in many parts of the *Tsuga heterophylla* Zone. Very often the communities on these sites are dominated by the shrub *Acer circinatum*. These should probably be described as a series of communities because of the great variety in stand composition and structure, depending on substrate (size, arrangement, and chemistry of rocks, moisture conditions), elevation, exposure, etc. Some typical associates of *Acer circinatum* on more xeric talus include *Cryptogramma acrostichoides*, *Festuca occidentalis*, *Holodiscus discolor*, *Symphoricarpos mollis*, *Corylus cornuta* var. *californica*, *Cheilanthes gracillima*,

Figure 54. — *Chamaecyparis lawsoniana* is found in the southern part of the *Tsuga heterophylla* Zone and attains optimal development there; note the dense understory of evergreen shrubs (Siskiyou National Forest, Oregon).

Selaginella wallacei, *Xerophyllum tenax*, *Synthyris reniformis*, *Rhacomitrium canescens* var. *ericoides*, *Aira caryophylla*, and *Ceanothus sanguineus*. *Acer circinatum*-dominated talus communities may be found well into the *Abies amabilis* Zone and be intergraded with the *Alnus sinuata* communities described later in this paper.

Talus communities dominated by *Acer macrophyllum* occur in the Oregon Coast

Figure 55. — Old-growth *Chamaecyparis lawsoniana* are quite fire resistant, and vigorous specimens frequently have deep basal fire scars (Coquille River Falls Research Natural Area, Siskiyou National Forest, Oregon).

Ranges (Bailey and Poulton 1968). Similar communities have been noted in northern Washington (fig. 53).

Port-Orford-cedar variant — Near its southern edge in the Oregon Coast Ranges, *Chamaecyparis lawsoniana* is added to *Tsuga heterophylla* Zone forests. In these forests, *Chamaecyparis* is associated with species such as *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Abies grandis*, *Thuja plicata* (only on wetter sites), *Lithocarpus densiflorus*, *Rhododendron macrophyllum*, *Arbutus menziesii*, and *Pinus lambertiana* (fig. 54). It appears to have the same ecological role as *Pseudotsuga menziesii*, a long-lived but seral dominant. Old-growth specimens of *Chamaecyparis lawsoniana* develop thick bark and are quite resistant to fire. Old but vigorous specimens frequently have numerous fire scars (fig. 55). Structural analyses of old-growth stands indicate it is not capable of reproducing under closed forest conditions and is replaced by more tolerant associates — *Abies grandis* and *Tsuga heterophylla*.⁶

Chamaecyparis lawsoniana is considered in this discussion of the *Tsuga heterophylla* Zone because it attains optimum development there. In fact, it grows in several different zones and on a wide variety of sites in south-

⁶ Data on file at Forestry Sciences Laboratory, Pacific Northwest Forest & Range Exp. Sta., Forest Serv., U. S. Dep. Agr., Corvallis, Oregon.

Figure 56. — Mixed stands are typical of the *Abies amabilis* Zone; overstory dominants in this stand are *Abies procera*, *Pseudotsuga menziesii*, and *Tsuga heterophylla* (background), but poles (foreground) and reproduction are the climax *Abies amabilis* (Wildcat Mountain Research Natural Area, Willamette National Forest, Oregon).

western Oregon — from sand dunes along the coastal strip to over 1,500 meters in the Siskiyou Mountains and down into the interior valleys; from swampy sites to dry, rocky ridges; and even on serpentine soils (Whittaker 1960; Fowells 1965). Indeed, it is difficult to understand why the natural range of the species is so restricted geographically. *Chamaecyparis lawsoniana* is seriously threatened by a killing root disease, *Phytophthora lateralis*, which was recently introduced into its natural range. This disease has already decimated *Chamaecyparis lawsoniana* in the coastal region and could possibly eliminate it from most of its natural range.

“ABIES AMABILIS” ZONE

The *Abies amabilis* Zone lies between the temperate mesophytic *Tsuga heterophylla* Zone of the lowlands and the subalpine *Tsuga*

mertensiana Zone. It occurs on the western slopes of the Cascade Range from British Columbia south to about 44° north latitude, generally at elevations from 1,000 to 1,500 meters in Oregon and 600 to 1,300 meters in northern Washington. The *Abies amabilis* Zone is also conspicuous in the Olympic Mountains, except in the rain shadow on the northeastern slopes of the peninsula (Fonda 1967). Where local conditions are favorable, comparable communities are found (1) on eastern slopes of Washington's Cascade Range, (2) south to 43° north latitude in Oregon's Western Cascades Province, and (3) on wet, cool sites (streamsides and benches) in the *Tsuga heterophylla* Zone. Our *Abies amabilis* Zone is analogous to the Wet Subzone, Coastal Western Hemlock Zone of Krajina (1965); it includes all of the poorly defined Canadian Life Zone (Barrett 1962).

Environmental Features

The *Abies amabilis* Zone is wetter and cooler than the adjacent *Tsuga heterophylla* Zone and receives considerably more precipitation in the form of snow (table 9), much of which accumulates in winter snowpacks as deep as 1 to 3 meters. The complex of soil-forming processes leads toward podzolization. This trend is less pronounced in the south where Brown Podzolic soils are the rule, and most pronounced in the north where true Podzols are typical. Organic matter accumulations are of a mor or duff-mull type. These generally average only 5 to 10 centimeters thick, except in northern Washington where accumulations up to 30 centimeters or more in thickness are encountered along with well-developed bleicherde (A2) and ortstein (B2ir) mineral horizons.

Forest Composition

Forest composition in the *Abies amabilis* Zone varies widely, depending upon stand age, history, and locale (Franklin 1965a, b). Typical tree species are *Abies amabilis*, *Tsuga heterophylla*, *Abies procera*, *Pseudotsuga menziesii*, *Thuja plicata*, and *Pinus monticola* (fig. 56). Around Mount Adams and in Oregon, *Abies lasiocarpa*, *Abies grandis*, *Picea engelmannii*, *Pinus contorta*, and *Larix occidentalis* may also occur in the zone. At its upper margin, *Tsuga mertensiana* and *Chamaecyparis nootkatensis* appear. Understories

Table 9. — Climatic data from representative weather stations within the *Abies amabilis* Zone

Station	Elevation	Latitude	Longitude	Temperature					Precipitation		
				Average annual	Average January	Average January minimum	Average July	Average July maximum	Average annual	June through August	Average annual snowfall
	Meters			-----	-----	Degrees C.	-----	-----	Millimeters		Centimeters
Snoqualmie Pass, Wash.	991	47° 25'	121° 25'	5.5	-3.2	-6.6	14.4	21.1	2,656	227	982
Spirit Lake, Wash.	1,063	46° 16'	122° 09'	5.6	-2.0	-4.4	14.9	22.3	2,253	140	718
Government Camp, Oreg.	1,280	45° 18'	121° 45'	5.6	-1.7	-4.9	14.0	20.8	2,190	190	792

Source: U. S. Weather Bureau (1956, 1965a).

are usually dominated by ericaceous genera, such as *Vaccinium*, *Menziesia*, *Gaultheria*, *Chimaphila*, *Rhododendron*, and *Pyrola*. *Cornus canadensis*, *Clintonia uniflora*, *Rubus lasiococcus*, *R. pedatus*, *Linnaea borealis*, *Xerophyllum tenax*, and *Viola sempervirens* are also common species. *Rhytidiopsis robusta* is the most constant and conspicuous bryophyte.

Forested communities vary markedly in composition from very dry to very moist sites. In southern Washington (Franklin 1966) the *Abies amabilis*/*Vaccinium alaskaense* association is the zonal climax. It is characterized by well-developed shrub, herb, and moss layers (fig. 57). *Vaccinium alaskaense*, *V. ovalifolium*, *Cornus canadensis*, *Clintonia uniflora*, *Linnaea borealis*, and *Rhytidiopsis robusta* typify these modal communities. On drier sites are associations with depauperate understories dominated by low shrubs such as *Berberis nervosa* and *Gaultheria shallon* or, on lithosolic sites, by the coarse liliaceous *Xerophyllum tenax*. More mesic sites have communities with herb-rich understories dominated by species such as *Tiarella unifoliata*, *Streptopus curvipes*, *Achlys triphylla*, *Dryopteris linnaeana*, *Vancouveria hexandra*, *Oxalis oregana*, *Struthiopteris spicant* and *Smilacina sessilifolia* (figs. 58 and 59). Communities on the wettest forested sites have dense, rich understories typified by *Athyrium filix-femina* and *Oplopanax horridum*.

Figure 57. — Understory in an *Abies amabilis*/*Vaccinium alaskaense* community, the zonal climax in the southern Washington Cascade Range; *Vaccinium alaskaense*, *Xerophyllum tenax*, *Cornus canadensis*, *Clintonia uniflora*, and *Rhytidiopsis robusta* are notable species (Wind River Research Natural Area, Gifford Pinchot National Forest, Washington).

Figure 58. — *Abies procera* attains maximum development on mesic sites in the *Abies amabilis* Zone; these sites are characterized by herb-rich understories (near Mount St. Helens, Gifford Pinchot National Forest, Washington).

There is considerable geographic variation in *Abies amabilis* communities. Thornburgh (1969) found it more useful to consider *Abies amabilis* Zone communities near Mount Rainier as a continuum. In the Olympic Mountains (Fonda 1967) and Northern Cascade Range, herb-rich communities characterized by species such as *Oxalis oregana* or *Struthiopteris spicant* are more common than in the southern Washington Cascades. In Oregon, changes include: (1) reduced importance of *Vaccinium alaskaense*-*Cornus canadensis* communities, (2) increased importance of communities with herbaceous and *Vaccinium membranaceum*-*Xerophyllum tenax* understories, and (3) addition of *Rhododendron macrophyllum* as an understory dominant on some sites. A community dominated by *Picea engelmannii* and *Abies amabilis* with a rich herbaceous understory is found on wet, frosty habitats in Oregon's western Cascade Range.

Successional Patterns

The major climax species throughout the zone is *Abies amabilis* (Thornburgh 1969; Fonda 1967; Franklin 1966); size and age class analyses of many stands illustrate this clearly (fig. 60). A typical successional sequence begins with invasion of the site by *Pseudotsuga menziesii* or *Abies procera*, or both. Western hemlock may be established simultaneously or develop later under a forest canopy, or both. In any case, *Pseudotsuga* and *Abies procera* fail to reproduce. The heavy-seeded, fire-sensitive *Abies amabilis* is usually last to invade the site (Schmidt 1957), coming in under the mixed canopy of *Pseudotsuga menziesii*, *Abies procera*, and *Tsuga heterophylla*; if seed sources are available, *Abies amabilis* can also function as a pioneer species, however.

Four hundred to 500 years after disturbance, a typical mixed stand includes scattered, large (100- to 150-cm. d.b.h.) *Pseudotsuga menziesii*, more abundant but somewhat smaller (70- to 100-cm. d.b.h.) *Tsuga heterophylla*, and abundant seedlings, saplings, and poles of *Abies amabilis*. Many stands with this or a similar structure are encountered in the Cascade Range.

Figure 59. — Lush herbaceous understories typify forest understories on moist sites in the *Abies amabilis* Zone; *Achlys triphylla*, *Vancouveria hexandra*, *Dryopteris linnaeana*, and *Streptopus curvipes* on *Abies amabilis*/*Streptopus* habitat type (Gifford Pinchot National Forest, Washington).

Replacement of the shade-tolerant *Tsuga heterophylla* by *Abies amabilis* on most sites is probably a consequence of mechanical factors (Thornburgh 1969). Fragile *Tsuga* seedlings are unable to survive winter accumulations of litter and snow characteristic of forest floors in the zone, whereas those of *Abies amabilis* are (Thornburgh 1969). Surviving *Tsuga heterophylla* reproduction is invariably confined to down logs and mounds of rotten wood. *Tsuga heterophylla* seedlings do conduct photosynthesis more efficiently at low light intensities, and reportedly they grow faster than those of *Abies amabilis* (Thornburgh 1969). However, their successional relationship reverses itself at the lower edge of the zone.

Stand structure analyses indicate *Tsuga heterophylla* is a minor climax species along with *Abies amabilis*, especially at lower elevations within the zone. Climax species on wet sites are not easily predicted since seedlings and saplings of all species are relatively scarce. It does appear that both *Tsuga heterophylla* and *Thuja plicata* are at least minor climax species.

Early stages in forest succession (from disturbance through development of a closed forest canopy) have not been studied in de-

Figure 60. — *Abies amabilis* is the major climax species in this zone dominating the reproduction in old-growth stands; *Abies amabilis* saplings in an *Abies procera* stand (Wildcat Mountain Research Natural Area, Willamette National Forest, Oregon).

Figure 61. — *Alnus sinuata* communities are on sites subject to heavy snow accumulations and snow creep or avalanching; hence, the 3- to 5-meter-tall *Alnus* have strongly bowed stems (H. J. Andrews Experimental Forest, Oregon).

tail. However, major dominants during the preforest stage of succession are generally species present in the forest stands before disturbance. Some examples are all the *Vaccinium* spp., *Xerophyllum tenax*, and *Sorbus* spp. *Pteridium aquilinum* is often a major invader not present before disturbance. An exception to these generalizations is on wet sites where disturbance may produce dense shrub communities of *Sambucus*, *Rubus spectabilis*, and *Ribes* spp.

Special Types

Alnus sinuata communities. — *Alnus sinuata* characterizes a community type found most often in this zone. These shrub communities occupy sites subject to deep winter snow accumulations and extensive snow creep; they often suffer recurrent snow avalanches as well. Consequently, *Alnus sinuata* individuals, 3 to 5 meters tall, have strongly

Figure 62. — *Alnus sinuata* communities are permanently maintained on some sites by recurrent snow avalanches (Mount Rainier National Park, Washington).

bowed stems (fig. 61). In the Washington Cascade Range, repeated avalanching is at least partially responsible for creation and maintenance of these communities (fig. 62). In Oregon, *Alnus sinuata* communities appear on sites that are not avalanche tracks but do have heavy snow accumulations and abundant seepage water. High water tables have been ascribed to a nearly impervious subsoil in some areas,⁷ but in others there appears to be no difference in substrate between forest and shrub communities (Daubenmire and Daubenmire 1968; Aller 1956). *Alnus sinuata* communities are to all appearances a stable community type or are only very slowly encroached upon by forest vegetation. The only conifer capable of surviving and reproducing

⁷ Unpublished soil survey data from the H. J. Andrews Experimental Forest on file with Forestry Sciences Laboratory, Pacific Northwest Forest & Range Exp. Sta., Forest Serv., U. S. Dep. Agr., Corvallis, Oregon.

on sites with recurrent avalanches is *Chamaecyparis nootkatensis*. Since the sites occupied by *Alnus sinuata* communities are normally very wet, the understory is typically rich in dicotyledonous herbs, such as *Montia* spp., ferns, and Carices and usually includes *Oplopanax horridum*. Similar communities occur in higher forested zones on the east slopes of the Cascade Range, in the northern Rocky Mountains (Daubenmire and Daubenmire 1968), and in the Blue Mountains where *Alnus tenuifolia* dominates.⁸

Meadow communities. — There are many types of mountain meadow and other nonforested communities associated with the *Abies amabilis* Zone. A mesic meadow type, dominated by *Pteridium aquilinum* and *Rubus parviflorus*, is extremely widespread and is often contiguous with *Alnus sinuata* communities and may intergrade with subalpine meadow types at higher elevations.⁹ Hickman (1968) categorized and listed constituent species for the different vegetation types found in forest openings along the ridges and peaks of Oregon's Western Cascades province; the majority of these are associated with the *Abies amabilis* Zone. Included in Hickman's lists are three different meadow types, and seep, talus, and outcrop communities.

"TSUGA MERTENSIANA" ZONE

The *Tsuga mertensiana* Zone is the highest forested zone along the western slopes and crest of the Cascade Range and in the Olympic and Klamath Mountains. Elevational limits of the *Tsuga mertensiana* Zone are generally between 1,300 and 1,700 meters in northern Washington and 1,700 and 2,000 meters in the southern Oregon Cascades. The zone extends varying distances east of the Cascade crest until it is gradually replaced by the *Abies lasiocarpa* Zone more typical of interior subalpine environments. A similar replacement of *Tsuga mertensiana* forests by those of *Abies lasiocarpa* occurs in the rain shadow portion of the Olympic Mountains (Fonda 1967). *Tsuga mertensiana*-dominated forests

reappear in portions of the northern Rocky Mountains in association with those of *Abies lasiocarpa* and *Picea engelmannii* (Daubenmire 1952; Daubenmire and Daubenmire 1968; Habeck 1967).

The *Tsuga mertensiana* Zone can be divided into major subzones — a lower subzone of closed forest and an upper parkland subzone. In the lower subzone, there is essentially continuous forest cover of *Tsuga mertensiana* and its associates. The upper subzone is a mosaic of forest patches and tree groups interspersed with shrubby or herbaceous subalpine communities. In this section, we will be concerned only with the lower subzone; the subalpine meadow-forest mosaic will be considered during the discussion of timberline and alpine regions.

As defined here, the *Tsuga mertensiana* Zone is comparable to the Mountain Hemlock Zone of Krajina (1965). It also includes most of the Hudsonian Life Zone (Barrett 1962) and, perhaps, the upper part of the Canadian Life Zone as well.

Environmental Features

The *Tsuga mertensiana* Zone is wet and the coolest of the forested zones in western Oregon and Washington (table 10). Annual precipitation ranges from about 1,600 to 2,800 millimeters. This includes 400 to 1,400 centimeters of snowfall which accumulates in snowpacks up to 7.5 meters deep.

Soils within the zone are podzolic, although the degree of podzolization varies greatly. In the north, Podzols and Gley Podzolic soils are common, with well-developed mor humus layers. In central and southern Oregon, true Podzols are rare and weakly developed Brown Podzolic soils with a relatively thin, but densely matted, mor humus layer are the rule.

Forest Composition

Forest composition within the zone varies considerably with locale (table 11). Relatively few species are found as dominants — *Tsuga mertensiana* in old-growth forests throughout

⁸ Personal communication, Dr. F. C. Hall.

⁹ Personal communication, Mr. G. W. Douglas.

Table 10. - Climatic data from representative weather stations within the *Tsuga mertensiana* Zone

Station	Eleva- tion	Lati- tude	Longi- tude	Temperature					Precipitation		
				Average annual	Average January	Average January minimum	Average July	Average July maximum	Average annual	June through August	Average annual snowfall
	Meters			-----	-----	Degrees C.	-----	-----	Millimeters	Millimeters	Centi- meters
Mount Baker Lodge, Wash.	1,362	48° 52'	121° 40'	4.5	-2.6	-5.7	12.1	17.5	2,821	313	1,398
Paradise Ranger Station, Wash.	1,821	46° 47'	121° 44'	3.4	-3.4	-7.0	11.6	17.4	2,635	226	1,362
Crater Lake National Park Headquarters, Oreg.	2,124	42° 54'	122° 08'	3.8	-3.7	-8.4	13.4	21.9	1,643	99	1,324

Source: U. S. Weather Bureau (1956, 1965a, 1965b).

Table 11. — Relative importance of tree species in the closed-forest subzone of the *Tsuga mertensiana* Zone

Species	Washington		Oregon	
	Western Cascades	Eastern Cascades	Northern Cascades	Southern Cascades
<i>Abies amabilis</i>	¹ M	m	M	—
<i>Abies lasiocarpa</i>	m	M	M	—
<i>Abies magnifica</i> var. <i>shastensis</i>	—	—	—	M
<i>Abies procera</i>	m	—	m	—
<i>Chamaecyparis nootkatensis</i>	M	m	m	—
<i>Picea engelmannii</i>	—	m	m	m
<i>Pinus albicaulis</i>	—	m	m	m
<i>Pinus contorta</i>	m	M	M	M
<i>Pinus monticola</i>	m	m	m	m
<i>Pseudotsuga menziesii</i>	m	m	m	—
<i>Thuja plicata</i>	m	—	—	—
<i>Tsuga heterophylla</i>	m	m	m	—
<i>Tsuga mertensiana</i>	M	M	M	M

¹ M indicates a species is a major constituent of either seral or climax forests or both; m indicates a species is a minor component.

Figure 63. — Pure, old-growth stands of *Tsuga mertensiana* are common throughout the *Tsuga mertensiana* Zone; note the clumping tendency of the trees in this stand near timberline (Gifford Pinchot National Forest, Washington).

the zone (fig. 63), and *Abies lasiocarpa* or *Pinus contorta*, or both, in seral stands in drier portions of the zone. *Abies amabilis* is conspicuous in the zone in Washington and northern Oregon, but it drops out completely in the southern Oregon High Cascades. There are a wide variety of understory species of which many are Ericaceae, Rosaceae, and Compositae.

The spectrum of communities found within the *Tsuga mertensiana* Zone varies locally with gradients in temperature, moisture, and accumulation and duration of snow, as well as geographically. In southern Washington the *Tsuga mertensiana*-*Abies amabilis*/*Vaccinium membranaceum* community is typical of modal sites. It has a depauperate understory composed of *Vaccinium membranaceum*, *Xerophyllum tenax*, *Pyrola secunda*, *Rubus lasiococcus*, and perhaps a few additional species. A variant of this community, in which the understory is completely dominated by a dense cover of *Xerophyllum tenax*, is common in the southern Washington and northern Oregon Cascade Range (fig. 64).

On wetter, cooler habitats, e.g., north slopes and along drainages, communities have dense shrub understories 1 to 1-1/2 meters in height. The most extreme example in southern Washington is a *Chamaecyparis nootkensis*/*Rhododendron albiflorum*/Gley Podzol association (Franklin 1966). A tangle of *Vaccinium ovalifolium*, *V. membranaceum*, *Rhododendron albiflorum*, *Menziesia ferruginea*, and *Sorbus* spp. is characteristic of this shrub layer. Typical herbs include *Rubus pedatus*, *R. lasiococcus*, *Valeriana sitchensis*, *Viola sempervirens*, *Listera caurina*, and *Erythronium montanum*.

In southern Oregon, the extensive *Tsuga mertensiana* communities found along the crest of the Cascade Range are much simpler structurally and floristically. The sparse understories are usually dominated by *Vaccinium membranaceum* or *V. scoparium* along with minor amounts of other species such as *Chimaphila umbellata* and *Arctostaphylos nevadensis*.

Successional Patterns

Large acreages of the *Tsuga mertensiana* Zone have been burned over during the last 150 years in southern Washington and Oregon. Consequently, seral communities are often conspicuous. Early stages in succession have not been studied, but they often involve domination of the site by fire-resistant species conspicuous in the understory — *Vaccinium membranaceum* and *Xerophyllum tenax*, for example.

Forest development on burned areas is often very slow, as would be expected in the severe environment of this zone. In some cases, semipermanent communities of *Vaccinium* spp., *Xerophyllum*, *Sorbus* spp., and *Spiraea* have been created by repeated burning (fig. 65). Indians used this method to perpetuate fields of *Vaccinium membranaceum* from which they collected berries for food.

Successional sequences of tree species vary geographically. On moist sites, *Tsuga mertensiana* and *Abies amabilis* can function as pioneer species. On dry sites, and particularly in Oregon's High Cascades province, seral forests of *Pinus contorta* or *Abies lasiocarpa* are often the first to develop (fig. 66). These are gradually replaced by *Tsuga mertensiana* and, except in southern Oregon, by *Abies amabilis*.

In Washington and northern Oregon, *Abies amabilis* appears to be the major climax species in closed-forest portions of the *Tsuga mertensiana* Zone (Franklin 1966; Thornburgh 1969). Although nearly all old-growth stands do contain mature *Tsuga mertensiana*, reproduction is often nearly absent; a full range of *Abies amabilis* size classes is usually present. *Tsuga mertensiana* and *Chamaecyparis nootkatensis* may be minor climax species on some habitats. In southern Oregon, more tolerant arborescent associates are absent from *Tsuga mertensiana* stands and *Tsuga* is the climax species. Apparently, regeneration develops after the old-growth stands begin to break up, since significant *Tsuga mertensiana* regeneration is not common under closed-forest canopies.

Southwestern Oregon

Southwestern Oregon is an extremely interesting and complex region environmentally, floristically, and synecologically. Climate ranges from cool and moist in the coastal regions to hot and dry in the interior valleys, which are the driest locales west of the Cascade Range. The geology and, consequently, soils are extremely varied. Floristically the region combines elements of the Californian, north coast, and eastern Oregon floras, with a large number of species indigenous only to the Klamath Mountains region (Whittaker

Figure 64. — Communities with understories dominated by *Xerophyllum tenax* and *Vaccinium membranaceum* are very widespread on poorer sites in the *Tsuga mertensiana* Zone; a *Tsuga mertensiana*-*Abies amabilis*/*Xerophyllum tenax* community on a ridgetop with shallow soil (Wildcat Mountain Research Natural Area, Willamette National Forest, Oregon).

Figure 65. — Fields of *Vaccinium membranaceum* and other shrubs have been created and maintained by repeated burning in the *Tsuga mertensiana* and *Abies amabilis* Zones (near Mount Adams, Washington; photo courtesy Gifford Pinchot National Forest).

Figure 66. — *Pinus contorta* is a major pioneer species in High Cascades portions of the *Tsuga mertensiana* Zone; here, *Tsuga mertensiana* is developing in a stand of dead and dying *Pinus contorta* (near Olallie Butte, Mount Hood National Forest, Oregon).

1960, 1961). This environmental and floristic diversity combines with a long history of prehistoric and historic disturbances, primarily by fire, to produce an extremely varied array of communities.

This section deals with portions of southwestern Oregon lying outside the *Tsuga heterophylla* and *Picea sitchensis* Zones. It includes the main body of the Siskiyou Mountains,¹⁰ interior valleys, and western slopes of the Cascade Range. Most of the region is potentially occupied by forest communities of some kind.

¹⁰ The Siskiyou Mountains are the northernmost range in the Klamath Mountains group (Irwin 1966). Since this is the only range in this group encountered in Oregon, we will use the term "Siskiyou Mountains."

The major southwestern Oregon tree species can be arrayed in relation to tolerance of moisture stress:

Species	Tolerance
<i>Quercus garryana</i>	High
<i>Quercus kelloggii</i>	
<i>Pinus ponderosa</i>	
<i>Arbutus menziesii</i>	
<i>Libocedrus decurrens</i>	
<i>Pseudotsuga menziesii</i>	
<i>Pinus lambertiana</i>	
<i>Pinus monticola</i>	
<i>Abies concolor</i>	
<i>Chamaecyparis lawsoniana</i>	
<i>Abies magnifica</i> var. <i>shastensis</i>	
<i>Tsuga mertensiana</i>	
<i>Tsuga heterophylla</i>	Very low

We might expect a systematic sequence of zones along the moisture and temperature gradients (which are broadly correlated with elevation) based on this array and the relative shade tolerance of the species:

Species	Tolerance
<i>Tsuga heterophylla</i>	High
<i>Abies concolor</i>	
<i>Tsuga mertensiana</i>	
<i>Chamaecyparis lawsoniana</i>	
<i>Pseudotsuga menziesii</i>	
<i>Libocedrus decurrens</i>	
<i>Abies magnifica</i> var. <i>shastensis</i>	
<i>Pinus lambertiana</i>	
<i>Pinus monticola</i>	
<i>Pinus ponderosa</i>	
<i>Arbutus menziesii</i>	
<i>Quercus garryana</i>	
<i>Quercus kelloggii</i>	Low

In fact, history and environmental complexity often make it impossible to distinguish zones, particularly in the heavily disturbed valley regions. Furthermore, very few data on plant communities are available for the interior valleys and western slopes of the Cascade Range. Therefore, we have taken a more typological approach. The "zonal" outline is as follows

(no climax implication is intended in naming the first three zones):

Interior Valley Zone (*Pinus-Quercus-Pseudotsuga*)

Mixed-Evergreen Zone (*Pseudotsuga/sclerophyll*)

Mixed-Conifer Zone (*Pseudotsuga-Pinus-Libocedrus-Abies*)

Abies concolor Zone

Abies magnifica shastensis Zone

The *Abies magnifica shastensis* Zone is bounded at its upper limits by the *Tsuga mertensiana* Zone (discussed earlier) wherever elevations are sufficiently great (Siskiyou Mountains and Cascade Range).

The arrangement of these zones in the Cascade Range and eastern and western Siskiyou Mountains is illustrated in figure 67. The only major difference is the replacement of the Mixed-Conifer Zone by a Mixed-Evergreen

Zone in the western Siskiyou Mountains. It will be obvious that most of the major formations found in southwestern Oregon are actually the northern extensions of formations which are considered typical of the California Coast Ranges and Sierra Nevada.

Fire has played an extremely important role in southwestern Oregon. Fire danger can reach very high levels during the long, hot, dry summers. Fires, both naturally caused and Indian-set, were common prior to the arrival of the white man. Early settlers were responsible for additional burning, but formal fire control activities have been in effect since the early 1900's. As will be seen, many of the communities are created and perpetuated by fires; e.g., some sclerophyllous shrub (chaparral) types and *Pinus attenuata* forests. Fire and fire control activities are having a profound influence on the shape of the future landscape.

Figure 67. — Arrangement of vegetation zones in the Cascade Range and western Siskiyou Mountains of southwestern Oregon.

INTERIOR VALLEY ("PINUS-QUERCUS-PSEUDOTSUGA") ZONE

"Interior" valleys refer to the valley bottoms and lowlands enclosed by the Cascade Range on the east and the Coast Ranges or Siskiyou Mountains on the west. The major units of this type are the Umpqua, Rogue River, and Willamette valleys. These valley bottoms and adjacent foothills constitute the Interior Valley or *Pinus-Quercus-Pseudotsuga* Zone. Cities, farmlands, and other human developments are a dominant landscape feature. The natural vegetational mosaic includes grasslands, *Quercus* woodlands, coniferous forests, sclerophyllous shrub communities, and riparian types.

The reader should recognize that even though these three major interior valleys share many features in common, there are significant differences between them. Further, this treatment is heavily weighted toward the most mesic, the Willamette valley, because of the near absence of data for the Rogue River and Umpqua valleys. Detling (1968) has taken a different approach typifying vegetation of the Willamette valley as "Pine-oak Forest" and that of the main Umpqua and Rogue valleys as "Chaparral" with a peripheral belt of Pine-oak Forest in the latter.

Environmental Features

The interior valleys of western Oregon are the warmest and driest regions west of the Cascade Range (table 12). This is primarily because they are in the rain shadow of the Coast Ranges or Siskiyou Mountains. This effect is accentuated by their location at the dry end of the general north to south decrease in precipitation and increase in temperature found in western Oregon and Washington. Summers are hot and dry, potential evapotranspiration far exceeding the moisture buildup during the mild, wet winters. There is, of course, a climatic gradient across these valleys; precipitation gradually decreases moving east and down the eastern slopes of the Coast Ranges to a minimum within the valleys, and increases again ascending the western foothills of the Cascade Range. Also, the

valleys become increasingly hot and dry from north to south. For example, the Willamette valley is the wettest and the upper Rogue River valley (around Medford, Oregon) is the driest. More locally, the Willamette valley is hotter and drier in the upper valley (around Eugene) than it is 100 miles to the north at its mouth (Portland).

Soils in the Interior Valley Zone include many types found infrequently elsewhere in the Pacific Northwest. Some of the more important great soil groups are the Prairie, Planosol, Alluvial, Reddish Brown Lateritic, and Sols Bruns Acides. Grumusols, swelling, clayey soils dominated by montmorillonite clay, are found in these interior valleys. Lithosolic soils are common on many of the valley foothills, particularly in the Umpqua and upper Rogue River valleys. These shallow rocky soils accentuate the difficulties for vegetation during the droughty summer months.

Community Composition

As mentioned, there is a wide variety of natural and seminatural community types in the Interior Valley Zone. The term "seminatural" is used because the majority have been subjected to major human influences such as logging, clearing, grazing, or burning (or a combination of these). We will consider community composition by individual types (or type groups): *Quercus* woodland, conifer forest, grassland, sclerophyllous shrub, and riparian forest.

***Quercus* woodland.** — Forest stands, groves, and savannas dominated by the deciduous oaks, *Quercus garryana* and *Quercus kelloggii*, and by the evergreen *Arbutus menziesii* are a conspicuous feature of the Interior Valley Zone (fig. 68). Thilenius (1964) indicates there are over 400,000 hectares of oak woodlands in northwestern Oregon alone. *Quercus garryana* is often the sole dominant in the Willamette valley, although *Acer macrophyllum*, *Pseudotsuga menziesii*, or *Arbutus menziesii* may be present. *Quercus kelloggii* is found from the southern Willamette valley south. In the Umpqua valley, mixed stands of both *Quercus* spp. and *Arbutus menziesii* are com-

Table 12. — Climatic data from representative stations within the Interior Valley Zone

Area and Station	Elevation	Latitude	Longitude	Temperature					Precipitation			
				Average annual	Average January	Average January minimum	Average July	Average July maximum	Average annual	June through August	Average annual snowfall	
	Meters			-----	-----	Degrees C.	-----	-----	--- Millimeters ---	--- meters ---	Centi-	meters
Salem, Oreg.	60	44°55'	123°01'	11.4	3.6	-0.1	19.2	28.0	1,038	55	20	
Corvallis, Oreg.	62	44°38'	123°12'	11.3	4.0	.6	18.9	27.1	1,004	47	--	
Eugene, Oreg.	110	44°07'	123°13'	11.2	3.7	.1	19.1	27.9	1,040	53	18	
Roseburg, Oreg.	154	43°14'	123°22'	12.1	5.2	1.6	19.9	28.0	830	47	17	
Grants Pass, Oreg.	282	42°26'	123°19'	12.1	3.9	-.3	21.2	32.3	767	31	17	
Medford, Oreg.	400	42°22'	122°52'	12.2	3.0	-1.2	22.3	31.8	497	35	19	

Source: U. S. Weather Bureau (1965a).

Figure 68. — Woodlands of *Quercus garryana* and *Q. kelloggii* are typical of the Interior Valley Zone; mosaic of *Quercus* woodland and grassland near Ashland, Oregon, at the head of the Rogue River valley.

Figure 69.—Mixed stands of *Quercus garryana* and *Arbutus menziesii* with scattered *Pseudotsuga menziesii* are typical of many low hills in the Umpqua valley; note the *Rosa eglanteria* and *Rhus diversiloba* in the foreground pasture.

mon, often with scattered *Pseudotsuga menziesii* (Gratkowski 1961a) (fig. 69). In the Rogue River valley, *Quercus garryana* appears to be more important than *Quercus kelloggii* on the most xeric habitats.

Quercus communities have been studied in detail only in the Willamette valley. Thilenius (1964, 1968) recognized four major *Quercus garryana* communities in the central valley area and named them after understory dominants: *Corylus cornuta*-*Polystichum munitum*, *Amelanchier alnifolia*-*Symphoricarpos albus*, *Prunus avium*-*Symphoricarpos albus*, and *Rhus diversiloba*. Characteristic understory species for these communities are listed in table 13. The *Corylus cornuta*-*Polystichum munitum* and *Amelanchier alnifolia*-*Symphoricarpos albus* are types found on the least disturbed sites. *Prunus avium*, an extremely tolerant introduced shrub or tree, dominates the understory in the third community type. *Prunus avium* saplings often produce nearly impenetrable thickets.

Table 13. — Characteristic species of major *Quercus garryana* communities in the central Willamette valley

Layer	<i>Corylus cornuta</i> / <i>Polystichum munitum</i>	<i>Amelanchier alnifolia</i> / <i>Symphoricarpos albus</i>	<i>Prunus avium</i> / <i>Symphoricarpos albus</i>	<i>Rhus</i> <i>diversiloba</i>
Tree	<i>Quercus garryana</i> <i>Acer macrophyllum</i> <i>Pseudotsuga menziesii</i> <i>Abies grandis</i>	<i>Quercus garryana</i> <i>Pseudotsuga menziesii</i> <i>Acer macrophyllum</i>	<i>Quercus garryana</i> <i>Pseudotsuga menziesii</i> <i>Acer macrophyllum</i>	<i>Quercus garryana</i> <i>Pseudotsuga menziesii</i> <i>Acer macrophyllum</i>
Tall Shrub	<i>Corylus cornuta</i> <i>Prunus avium</i> ¹ <i>Amelanchier alnifolia</i> <i>Holodiscus discolor</i> <i>Osmaronia cerasiformis</i> <i>Crataegus douglasii</i>	<i>Amelanchier alnifolia</i> <i>Osmaronia cerasiformis</i> <i>Prunus avium</i> ¹	<i>Prunus avium</i> ¹ <i>Corylus cornuta</i> <i>Amelanchier alnifolia</i>	
Low Shrub	<i>Polystichum munitum</i> <i>Symphoricarpos albus</i> <i>Rubus parviflorus</i> <i>Rhus diversiloba</i> <i>Pteridium aquilinum</i> <i>Rubus ursinus</i> <i>Rosa eglanteria</i> ¹ <i>Rosa gymnocarpa</i>	<i>Symphoricarpos albus</i> <i>Rhus diversiloba</i> <i>Polystichum munitum</i> <i>Rosa nutkana</i> <i>Rosa eglanteria</i> ¹	<i>Symphoricarpos albus</i> <i>Rhus diversiloba</i> <i>Polystichum munitum</i> <i>Rubus ursinus</i>	<i>Rhus diversiloba</i> <i>Rosa eglanteria</i> ¹ <i>Symphoricarpos albus</i> <i>Rubus ursinus</i>
Herb	<i>Tellima grandiflora</i> <i>Galium</i> spp.	<i>Galium</i> spp.	<i>Galium</i> spp.	<i>Poa pratensis</i> ¹ <i>Torilis arvensis</i> ¹ <i>Galium</i> spp. <i>Osmorhiza chilensis</i> <i>Satureja douglasii</i> <i>Fragaria virginiana</i> var. <i>platypetala</i> <i>Elymus glaucus</i>

Source: Thilenius (1964).

¹ Exotic species.

Figure 70. — *Quercus garryana* communities with grass-*Rhus diversiloba* understories are widespread in the Willamette valley; *Corylus cornuta* var. *californica* (left foreground) is more common than *Rhus* in this 80-year-old stand near Albany, Oregon.

The *Quercus garryana*/*Rhus diversiloba* community is most widespread and occupies the most xeric habitats (Thilenius 1964, 1968). It is also found on sites which have been or are heavily grazed and can be the consequence of this grazing. *Rhus diversiloba* occurs in two growth forms — a ground cover and a liana — which are generally connected by a dense, shallow root system. It is generally less palatable to livestock than any of its associates. Thilenius (1964) hypothesized that even if the ground-cover *Rhus diversiloba* is grazed, it can draw on liana *Rhus*, which is

out of reach of grazing animals, for photosynthate. He further suggests that once *Rhus diversiloba* has replaced its associates, it maintains dominance even when grazing is stopped.

Thilenius (1964) recognized a *Rhus*-Gramineae variant of the *Rhus diversiloba* community which includes an abundance of herbs (fig. 70) (introduced species are indicated by an asterisk): *Poa pratensis**, *Dactylis glomerata**, *Agrostis tenuis*, *Festuca rubra*, *Torilis arvensis**, *Holcus lanatus**, *Elymus glaucus*, *Danthonia californica*, *Plantago lanceolata**,

*Bromus rigidus**, *Hypericum perforatum**, and *Sanicula crassicaulis*.

Hall (1956) also provides some data on composition of a *Quercus garryana* woodland. Typical species in a relatively undisturbed stand were *Rhus diversiloba*, *Amelanchier alnifolia*, *Ligusticum apiifolium*, *Elymus glaucus*, *Bromus laevipes*, *Osmorhiza chilensis*, *Vicia americana* and *Trisetum cernuum*. Thinning the *Quercus* resulted in an increase in most of these species as well as addition of *Sanicula crassicaulis* and *Fragaria* sp. as important species. Clearing resulted in abundant *Quercus* coppice but increases in only *Rhus diversiloba* and *Elymus glaucus*.

Whittaker (1960) described Oak Woodland as the driest forested formation in his transect across the Siskiyou Mountains. In his driest exemplary locale (adjacent to but not in the Rogue River valley), oak woodlands dominated by an overstory of *Quercus kelloggii* and *garryana* and an understory of grasses occupied east and southeast slopes; *Arbutus menziesii* was absent, but *Ceanothus integerimus*, *Arctostaphylos viscida*, and *Cercocarpus betuloides* were important high shrubs. Northeastern slopes (more mesic sites) were occupied by open stands of *Pseudotsuga menziesii*, *Pinus ponderosa*, and *Libocedrus decurrens* over a well-developed lower canopy of *Quercus garryana*. *Quercus* coverage decreased and grass coverage increased on increasingly xeric sites, and south or southwest slopes were grassland with only widely scattered *Quercus* spp. or none at all.

Waring (1969) described a Black Oak Type (*Quercus kelloggii*) in the foothills of the eastern Siskiyou Mountains which commonly included *Pseudotsuga menziesii*, *Pinus ponderosa*, *Arbutus menziesii*, and occasional *Quercus garryana*. Typical understory species were *Rhus diversiloba*, *Apocynum pumilum*, *Lonicera hispidula* var. *vacillans*, *Balsamorhiza deltoidea*, *Arctostaphylos viscida*, *Festuca californica*, *Lupinus albifrons*, *Brodiaea multiflora*, *Boschniakia strobilacea*, *Castilleja* spp., *Gilia capitata* and *Plectritis macrocera*.

Obviously, a number of diverse entities are here lumped under "Quercus Woodland." They range from very open savannas with grass understories to dense forest stands and from pure *Quercus* types to communities with

an abundance of conifer associates, particularly *Pseudotsuga menziesii* and *Pinus ponderosa*. Obviously included are communities both seral and climax. Some of these successional relationships will be considered later in this paper.

Conifer forest. — Coniferous forests occupy large areas of the foothill regions in and around the interior valleys. In the Willamette valley, such stands are widespread and composed mainly of *Pseudotsuga menziesii* (Hansen 1947, Sprague and Hansen 1946, Habeck 1961, Anderson 1967). *Abies grandis* and *Acer macrophyllum* are also widespread components of these stands. *Quercus garryana* and *Arbutus menziesii* may be present, especially as remnants of pioneer stands which prepared the way for the conifers; the intergradation possible between the previously discussed *Quercus*-dominated communities and coniferous-dominated communities should be obvious. Occasionally, *Pinus ponderosa* or *Libocedrus decurrens* may be encountered, the former generally on specialized habitats (coarse alluvial deposits along the river channels) and the latter at the southern end of the valley. *Thuja plicata* is sometimes conspicuous at the northern end of the Willamette valley around Portland.

Further south in the Umpqua valley, *Pseudotsuga menziesii* forest is common on hill crests and more mesic slopes where it is often associated with *Pinus ponderosa* and *Libocedrus decurrens* (Gratkowski 1961a).

The Rogue River valley has perhaps the most diverse valley coniferous forests. *Pseudotsuga menziesii* is still one of the most important species but *Pinus ponderosa*, *Pinus lambertiana*, and *Libocedrus decurrens* are also common (Gratkowski 1961a). *Pinus jeffreyi* woodlands, characteristic of serpentine areas, are also notable, but these will be discussed in a separate section of this paper.

The total community composition of the valley coniferous forests has not been studied in many locations. Those found in the Willamette valley are best known (Sprague and Hansen 1946; Anderson 1967). Anderson (1967) recognized at least two community types which typify some of the foothill coniferous forests: the *Corylus californica*/*Bromus vul-*

garis and *Acer circinatum*/*Gaultheria shallon* (*Corylus californica*-*Holodiscus* subtype) communities. Compositional data for these communities are provided in table 14. It is apparent from a comparison of Anderson (1967) and Thilenius (1964) that most of the understory dominants can be found under both *Quercus garryana* and *Pseudotsuga menziesii* canopies. Some additional comments on understory composition in Willamette valley conifer stands can be found in Sprague and Hansen (1946) and Sabhasri and Ferrell (1960).

The only other coniferous forest data are from the foothills around the Rogue River valley (Whittaker 1960; Waring 1969). Whittaker's (1960) data are hard to interpret, but it appears that he classes low-elevation conifer forests in the western Siskiyou Mountains with the "Mixed Evergreen Formation," *Pseudotsuga*-*Sclerophyll* in this case. These forests varied greatly with moisture regime but appeared to include: (1) a tree layer of *Pseudotsuga menziesii* (sometimes with *Pinus ponderosa* or *lambertiana* or both); (2) smaller trees of *Castanopsis chrysophylla*, *Lithocar-*

Table 14. — Characteristic species in two coniferous forest communities found in the foothills of the Willamette valley

Layer	<i>Corylus californica</i> / <i>Bromus vulgaris</i>	<i>Acer circinatum</i> - <i>Gaultheria shallon</i> — <i>Corylus californica</i> - <i>Holodiscus</i> subtype
Tree	Dominant — <i>Pseudotsuga menziesii</i> , <i>Abies grandis</i> , <i>Acer macrophyllum</i> Occasional — <i>Quercus garryana</i>	Dominant — <i>Pseudotsuga menziesii</i> Occasional — <i>Abies grandis</i> , <i>Acer macrophyllum</i> , <i>Cornus nuttallii</i>
Shrub	<i>Corylus cornuta</i> var. <i>californica</i> , <i>Holodiscus discolor</i> , <i>Rosa gymnocarpa</i> , <i>Symphoricarpos albus</i> , <i>Rhus diversiloba</i>	<i>Acer circinatum</i> , <i>Corylus cornuta</i> var. <i>californica</i> , <i>Holodiscus discolor</i> , <i>Rosa gymnocarpa</i>
Herb	<i>Bromus vulgaris</i> , <i>Aster radulinus</i> , <i>Fragaria vesca</i> var. <i>bracteata</i> , <i>Satureja douglasii</i> , <i>Vicia americana</i> var. <i>truncata</i> , <i>Berberis nervosa</i> , <i>Synthyris reniformis</i> , <i>Madia madioides</i> , <i>Osmorhiza chilensis</i>	<i>Gaultheria shallon</i> , <i>Berberis nervosa</i> , <i>Adenocaulon bicolor</i> , <i>Polystichum munitum</i> , <i>Anemone deltoidea</i> , <i>Galium triflorum</i> , <i>Festuca occidentalis</i>

Source: Anderson (1967).

pus densiflora, *Arbutus menziesii*, and *Quercus kelloggii*; and (3) understory shrubs such as *Quercus chrysolepis*, *Berberis nervosa*, *Rhus diversiloba*, and *Rosa gymnocarpa*. *Ceanothus integerrimus* and *Arctostaphylos viscida* characterized the understory on driest sites. Gratkowski¹¹ indicates the major conifers on the valley floor in this area are *Pinus ponderosa* and *Libocedrus decurrens* with *Arctostaphylos viscida* and *Ceanothus cuneatus* as understory dominants.

In the floristically poorer eastern Siskiyou Mountains, Waring (1969) recognized a Ponderosa Pine Type as the most xeric of his coniferous types. *Pseudotsuga menziesii*, *Arbutus menziesii*, and, sometimes, *Abies concolor* were associated with the *Pinus ponderosa*. *Arctostaphylos patula*, *A. viscida*, *A. nevadensis*, *Achillea millefolium* var. *lanulosum*, *Solidago canadensis*, *Apocynum pumilum*, and *Lupinus* spp. typified the understory.

Grasslands. — There are extensive areas of grassland in the Interior Valley Zone. Some of these were created by settlers and latter-day farmers through clearing or burning or both (fig. 71). Other grasslands occupy sites that appear incapable of supporting tree growth, e.g., grass balds associated with Grumusols or lithosolic, extremely xeric, southerly exposed slopes. Almost all grassland areas (and *Quercus savanna*) have been heavily grazed by domestic livestock — cattle, sheep, or angora goats — and are extensively used as unimproved pastureland today (fig. 72).

The nature of the original grassland communities is strictly conjectural, since grazing and introduction of alien species have altered all stands to some degree. Turner (1969) has suggested these grasslands probably looked similar to parts of the "California annual-type grassland" with *Danthonia californica* and *Stipa* spp. typical dominant species. Habeck (1961) provided a list of grasses which may have been characteristic of dry and moist sites in the Willamette valley. Species on well-drained sites included *Agrostis hallii*, *Agropyron pauciflorum*, *Bromus carinatus*, *B. vulgaris*, *Danthonia californica*, *Elymus glaucus*, *Festuca octoflora*, *F. californica*, *F. rubra*, *F.*

Figure 71. — Many of the grasslands in the Interior Valley Zone were created by clearing or burning (or both) of forest lands; burning hill pasture in the Umpqua valley, Oregon.

Figure 72. — Grassland areas in the Interior Valley Zone are heavily grazed. Typically low-lying pasturelands are improved (foreground), and hill grasslands and oak woodland (background) are used as unimproved pasture (near Corvallis, Oregon; photo courtesy Range Management, Oregon State University).

¹¹ Personal communication.

occidentalis, *F. subulata*, *Poa scabrella*, *Sitanion jubatum*, and *Stipa lemmonii*. Habeck (1961) suggests a large number of forbs were probably also present on the native prairies.

There are very few descriptive data even for existing valley grasslands, and these are all confined to the vicinity of Corvallis in the Willamette valley (Livingston 1953; Turner 1969; Valassis 1955; Owen 1953), although the general patterns probably have much wider relevance. Typical constituent species are (introduced species are indicated by an asterisk):

Perennial Grasses — *Danthonia californica*, *Festuca rubra*, *F. elatior* var. *arundinacea**, *Agrostis hallii*, *A. tenuis*, *Poa pratensis**, *P. compressa**, *Elymus glaucus*, *Danthonia intermedia*, *Holcus lanatus**, *Stipa columbiana*, *Sitanion hystrix*, *Carex* spp., *Lolium perenne**, *Dactylis glomerata*, *Koeleria cristata*, and *Arrhenatherum elatius**.

Annual Grasses — *Bromus rigidus**, *B. commutatus**, *B. mollis**, *Elymus caput-medusae**, *Cynosurus echinatus**, *Festuca dertonensis**, *F. myuros**, *Avena fatua**, *Aira caryophyllaea**, *Briza minor**, and *Gastridium ventricosum**.

Forbs — *Torilis nodosa**, *Daucus carota**, *Ranunculus occidentalis*, *Lactuca serriola**, *Sherardia arvensis**, *Vicia americana*, *V. tetrasperma**, *Erodium cicutarium**, *Hypericum perforatum**, *Taraxacum officinale**, *Fragaria chiloensis*, *Plantago lanceolata**, *Galium divaricatum**, *Veronica peregrina*, *Lathyrus sphaericus**, *Eriophyllum lanatum*, *Hypochaeris radicata**, *Achillea millefolium* var. *lanulosa*, *Sanicula bipinnatifida*.

There is obviously a very high proportion of introduced species in the existing communities; they include all the annual grass dominants. One of these, *Elymus caput-medusae*, is an extremely undesirable species which dominates many stands (Turner et al. 1963; Turner 1969).

Turner (1969) was the only investigator who examined community composition on several sites. *Elymus caput-medusae* and *Danthonia californica* were generally the domi-

nants on his study sites. At one location, Turner thought there might be three grassland types: *Festuca rubra*-dominated on the most mesic habitat, *Stipa columbiana*-dominated on the most xeric, and *Danthonia californica*-dominated on the intermediate habitat. From his descriptions, we would judge that several of the native perennial grasses have considerable ability to resist grazing pressure and persist even though alien annuals are the most widespread dominants.

Livingston (1953) provided a short list of grasses for *Quercus* savanna used as unimproved pasture: *Melica geyeri*, *Dactylis glomerata*, *Poa compressa*, *Lolium perenne*, *Bromus mollis*, *Festuca myuros*, and *Cynosurus echinatus*.

The successional status of valley grasslands hasn't been studied. Scattered bushes of *Rosa eglanteria* and *Rhus diversiloba* are found in many grasslands (fig. 73) and these can become dominant over parts of pasture tract. Some grasslands are readily invaded by *Quercus* spp. (Sprague and Hansen 1946). Other habitats appear to be climax grassland sites, and these include some with relatively deep fine-textured soils as well as Grumusols and xeric lithosolic sites.

Sclerophyllous shrub communities. — Communities of sclerophyllous shrubs are conspicuous in southern interior valleys, especially the Rogue River valley (Gratkowski 1961a) (fig. 74). Very little is known about these communities. Gratkowski (1961a) lists *Ceanothus cuneatus* (especially on the most xeric sites) and *Arctostaphylos viscida* as

Figure 73. — Grasslands are sometimes invaded by *Rosa eglanteria* or *Rhus diversiloba* in the Interior Valley Zone; *Rosa eglanteria* is common in this annual grassland dominated by *Bromus mollis*, *Cynosurus echinatus*, *Lolium perenne*, and *Daucus carota* (photo courtesy Range Management, Oregon State University).

Figure 74. — Chaparral is conspicuous in southern interior valleys; *Ceanothus cuneatus* (left) and *Arctostaphylos viscida* (right), on the background slope, are typical in the Rogue River valley and are mixed with *Quercus* spp. in this area.

major brushfield dominants in the valley bottoms. Other characteristic or abundant brushfield species listed by Gratkowski (1961a) are: *Ceanothus integerrimus*, *C. cordulatus*, *Rhus diversiloba*, *R. trilobata*, and *Lithocarpus densiflorus* with *Cornus glabrata* and *Quercus chrysolepis* on moister sites.

Detling (1961, 1968) views at least some of these shrub communities as southern Oregon chaparral, a northern extension of Californian chaparral types. He lists *Ceanothus cuneatus*, *Arctostaphylos viscida*, and *A. canescens*, as chief constituents of Oregon chaparral, *Ceanothus cuneatus* occupying the most xeric sites. Other chaparral species are *Cercocarpus betuloides*, *Eriodictyon californicum*, *Garrya fremontii*, *Rhamnus californica* var. *occidentalis*, *Rhus trilobata*, *Amelanchier pallida*, and *Chrysothamnus nauseosus* var. *albicaulis*. Detling (1961) indicates some chaparral communities are climax (e.g., *Ceanothus cuneatus* on the Rogue River valley floor), whereas others depend on fire for continuance. He found a *Pinus ponderosa*/*Arctostaphylos canescens* community in the Illinois valley in which *Pinus ponderosa* was believed climax, but indicates none of the chaparral communities (as he defined them) were normally associated with *Pseudotsuga menziesii*.

Riparian communities. — Hardwood forests are typical of riparian habitats and other

poorly drained sites subject to annual flooding; however, these plant communities have not been studied. In the Willamette valley, they are typified by *Fraxinus latifolia*, *Populus trichocarpa*, *Acer macrophyllum*, and *Alnus rubra*, with an understory of *Salix* spp. (figs. 75 and 76). Similar forests are found elsewhere in the Interior Valley Zone, although *Alnus rhombifolia* tends to replace *Alnus rubra* in more southerly valleys. Extensive, nearly pure stands of *Populus trichocarpa* occupy many of the islands and line the shores along the broad lower Columbia River. In fact, a *Populus trichocarpa* plantation was the first artificially established forest stand in the Pacific Northwest; this stand, planted on an island on the lower Willamette River, has since been harvested for pulpwood.

Successional Relationships

Successional relationships of the communities within the Interior Valley Zone are essentially unknown except in the Willamette valley. Before the Willamette valley was settled, much of it was occupied by prairies and oak savannas (Smith 1949; Habeck 1961). Dense forests were confined primarily to the mountain foothills and flood plains. Indians were probably responsible for most of the fires which created and maintained these open conditions (Kirkwood 1902; Morris 1934).

Figure 75. — *Populus trichocarpa* is typical of riparian sites in the Interior Valley and *Tsuga heterophylla* Zones, often forming pure stands on islands in the Willamette and lower Columbia Rivers (near Wind River, Washington, Gifford Pinchot National Forest).

The most notable change since the settlement of the Willamette valley has been the replacement of prairie and *Quercus* savanna by closed *Quercus* forest. Habeck (1961, 1962) has documented this change using land survey records from the 1850's. Thilenius' (1964, 1968) detailed analyses of *Quercus garryana* stands confirm the fact that most closed canopy *Quercus* forests have originated since 1850. He found scattered large trees of open-grown form and averaging 237 years old which were surrounded by smaller *Quercus* of

Figure 76. — *Acer macrophyllum* is a common hardwood on both riparian and upland sites in the Interior Valley Zone; this 100-year-old stand is located along the Santiam River near Jefferson, Oregon.

forest-grown form, averaging 74 to 105 years of age.

Fire control activities instituted by the settlers are believed responsible for this major successional change. The hypothesis that open *Quercus* savannas were maintained by fire is strengthened by the fire resistance displayed by large, isolated trees during fall field burnings.

There are various opinions regarding the species which will succeed *Quercus garryana* and constitute the forest climax of the Willam-

ette valley (fig. 77). *Quercus garryana* provides a favorable environment for establishment of *Pseudotsuga menziesii* seedlings (Sprague and Hansen 1946; Collins 1947; Owen 1953). Large *Quercus* often shelter abundant conifer reproduction. Old *Quercus* snags of open-grown form can be found in many foothill *Pseudotsuga menziesii* stands, victims of the conifer seedlings they sheltered (fig. 78). Consequently, Sprague and Hansen (1946) felt *Quercus garryana* stands would be replaced by *Pseudotsuga menziesii* and that these stands might, in turn, be replaced by climax forests of *Abies grandis* or *Abies grandis* and *Pseudotsuga menziesii*. Habeck (1962) agreed that *Pseudotsuga menziesii* was increasing in importance, and *Quercus garryana* was not reproducing under its own canopy. However, he felt that the significance of *Acer macrophyllum* had been overlooked and concluded *Quercus garryana* would be succeeded by *Pseudotsuga menziesii* or *Acer macrophyllum* or both.

Thilenius (1964) concluded that several successional sequences are likely, depending on local conditions. These include replacement of *Quercus garryana* forest by: (1) *Pseudotsuga menziesii* and *Acer macrophyllum*, the former more abundant on drier and the latter on moister sites; (2) *Abies grandis*, either directly or with an interceding stand of *Pseudotsuga*; and (3) *Quercus garryana*, reproduction being sufficient in some communities (especially *Rhus diversiloba*) for it to qualify as climax. Thilenius (1964) also wondered whether the exotic *Prunus avium* might sometimes replace *Quercus* forest; the ability of *Pseudotsuga menziesii* seedlings to develop in understory *Prunus* thickets will be critical.

Successional sequences in the interior valleys to the south (e.g., Umpqua and Rogue River) have not been studied. Some which have been observed are replacement of (1) *Quercus* spp.-*Arbutus menziesii* stands by conifers, (2) *Pinus ponderosa* stands by *Pseudotsuga*, and (3) *Pseudotsuga menziesii* stands by *Abies grandis*. As to the climatic climax species in the Interior Valley Zone, there is evidence for *Abies grandis* in the Willamette valley and *Pseudotsuga menziesii* in the Umpqua valley. In various parts of the Rogue

Figure 77. — Successional sequences suggested for upland sites in the central Willamette valley; any of the community types are possible climaxes on selected sites except, perhaps, for *Quercus garryana* savanna (interpreted from Sprague and Hansen 1946; Habeck 1961, 1962; Thilenius 1964).

Figure 78. — Old *Quercus* snags of open-grown form can be found in many Willamette valley *Pseudotsuga menziesii* stands, overtopped and killed by the *Pseudotsuga* reproduction they sheltered (photo courtesy, Range Management, Oregon State University).

Figure 79. — Mixed-evergreen forest includes upper stratum of conifers and a lower stratum of sclerophyllous hardwoods; this stand is dominated by *Pseudotsuga menziesii* and *Arbutus menziesii* with an understory of *Lithocarpus densiflorus* (near Oregon Caves, Siskiyou National Forest, Oregon).

River valley, *Pseudotsuga*, *Pinus ponderosa*-*Quercus* spp. and chaparral may be the potential climatic climax.

MIXED-EVERGREEN ("PSEUDOTSUGA"-SCLEROPHYLL) ZONE

In the western Siskiyou Mountains, modal sites are generally occupied by a mixed forest of evergreen needle-leaved trees (upper strata) and sclerophyllous broad-leaved trees (lower strata) (fig. 79). Whittaker (1960, 1961), who has conducted the only significant work in this zone, felt Mixed-Evergreen Forest should be recognized as a major community type of North America.

Environmental Features

Environmentally, this zone is almost unknown. It is relatively warm and wet during

the winter months and hot and dry during the summer. Annual precipitation would appear to be between 600 and 1,700 millimeters or more, depending on elevation and distance from the coast. Less than 20 percent falls during the growing season (Gratkowski 1961a). Average annual temperatures of about 47° to 49° F., average July temperatures of 62° to 66° F., and average January temperatures of 32° to 36° F. are likely.

Soils have not been studied, but they are certainly diverse since there is a very wide variety of parent material. Differences in soils have important phytosociologic implications, as shown by Whittaker's (1960) contrasting of vegetation on diorite, gabbro, and serpentine in this area. Major great soil groups present in this zone probably include Reddish Brown Lateritic, Western Brown Forest, and Noncalic Brown, as well as numerous Lithosols.

Forest Composition

For community descriptions within the Mixed-Evergreen Zone, we are almost entirely dependent upon Whittaker (1960); we will use his description of vegetation growing on diorite, with average moisture conditions as modal for the zone. The upper canopy level is dominated by *Pseudotsuga menziesii*, although *Pinus lambertiana* is frequently present. The lower tree canopy of sclerophyllous trees is dominated by *Lithocarpus densiflorus*, associated with *Quercus chrysolepis*, *Arbutus menziesii*, and *Castanopsis chrysophylla*. The shrub layer averages about 30-percent coverage and is typically composed of *Quercus chrysolepis*, *Berberis nervosa*, *B. pumila*, *Rubus ursinus*, *Rosa gymnocarpa*, *Rhus diversiloba*, and *Gaultheria shallon*. The herbaceous layer is not well developed (6.5-percent coverage) but includes *Whipplea modesta*, *Achlys triphylla*, *Trientalis latifolia*, *Goodyera oblongifolia*, *Pteridium aquilinum*, *Apocynum pumilum*, *Disporum hookeri*, *Lonicera hispidula*, *Festuca occidentalis*, and *Melica harfordii*.

Whittaker (1960) described a *Chamaecyparis lawsoniana*-*Pseudotsuga menziesii* forest on more mesic sites in which these species are dominants. Small sclerophyllous trees are present but not dominant. *Taxus brevifolia*, *Acer circinatum*, *Corylus cornuta* var. *californica*, and *Cornus nuttallii* are typical understory species along with *Gaultheria shallon*, *Berberis nervosa*, *Rubus ursinus*, *Linnaea borealis*, *Polystichum munitum*, and *Achlys triphylla*.

Whittaker (1960) refers to communities on more xeric dioritic sites as "Sclerophyll-*Pseudotsuga*" as they are characterized by an overgrowth (with less than 50-percent coverage) of *Pseudotsuga menziesii* and a closed canopy of sclerophylls. *Lithocarpus densiflorus* is characteristically the dominant sclerophyll, but *Arbutus menziesii* and *Quercus chrysolepis* are also abundant. Typical shrubs are *Rosa gymnocarpa*, *Rhus diversiloba*, and *Rubus ursinus*; *Pteridium aquilinum* is the only major herb. Whittaker (1960) indicates he found similar stands without *Pseudotsuga menziesii* or *Pinus lambertiana* on south

slopes (*Lithocarpus-Arbutus-Quercus chrysolepis* communities); he felt these were the result of more severe fires since *Pseudotsuga menziesii* seedlings were present. Gratkowski (1961a, b) also mentions extensive tracts of *Lithocarpus-Arbutus* communities in the Siskiyou Uplands and indicates excellent conifer reproduction is often present where a seed source exists.

Vegetation on gabbro was intermediate between that on diorite and on serpentine. The canopy levels were more open. *Umbellularia californica* and *Arctostaphylos cinerea* were added to the sclerophyllous species and *Pinus ponderosa*, *Libocedrus decurrens* and *Pinus lambertiana* were more important than on diorite.

Special Types

Excepting the unique vegetation found on serpentine sites (discussed later), brushfields are the most conspicuous "special communities" found within the Mixed-Evergreen Zone (fig. 80). Many of the large and abundant brushfields found in the Siskiyou Uplands

Figure 80. — Chaparral, forming fields of sclerophyllous shrubs, is very abundant in the Mixed-Evergreen Zone; this typical community is composed of *Arctostaphylos* spp., *Quercus chrysolepis*, and *Ceanothus* spp. (Siskiyou Mountains, Oregon).

(Gratkowski 1961) lie within this zone. Gratkowski (1961a) describes these communities as "... dense evergreen chaparral [which] is part of the Chaparral Association of the Broad Sclerophyll Formation" Typical constituent species are: *Arctostaphylos canescens*, *A. patula*, *Lithocarpus densiflorus*, *Quercus chrysolepis*, *Q. vaccinifolia*, *Q. sadleriana*, *Castanopsis chrysophylla* var. *minor*, *Garrya fremontii*, *G. buxifolia*, *Rhamnus californica*, *Ribes marshallii*, *Ceanothus cordulatus*, and *Berberis pumila*. Gratkowski (1961b) indicates that communities dominated by *Arctostaphylos patula*, *Ceanothus cordulatus* and *Quercus chrysolepis* are particularly abundant.

The chaparral and forest communities appear to be successional related in many cases; that is, they are often fire-induced seral types, especially in moist areas (e.g., nearer the coast). Since most shrub dominants sprout after fire, successive burns can eliminate conifers and increase shrub density. On the other hand, chaparral is probably climax on many sites (Gratkowski 1961a): e.g., dry eastern slopes of the Siskiyou Mountains and sites with severe southerly exposures and shallow soils further west. Gratkowski (1961a) feels soil moisture during the dry summer season may be inadequate for tree growth on many of these sites.

MIXED-CONIFER ("PINUS-PSEUDOTSUGA-LIBOCEDRUS-ABIES") ZONE

Mixed forests of *Pseudotsuga menziesii*, *Pinus lambertiana*, *P. ponderosa*, *Libocedrus decurrens*, and *Abies concolor* (or *A. grandis*) typify midelevations in the southwestern Oregon Cascade Range and eastern Siskiyou Mountains. They are northern extensions of the well-known Sierran montane or mixed-conifer forest (Oosting 1956; Küchler 1964). The Mixed-Conifer Zone occurs from about 43° north latitude south along the western flanks of the Cascade Range at elevations of about 750 to 1,400 meters. It is also found in the eastern Siskiyou Mountains, but generally at slightly higher elevations (Waring 1969; Dennis 1959). The Mixed-Conifer Zone is generally bounded by the Interior Valley and

the *Abies concolor* Zone at its lower and upper limits, respectively; to the north it grades into the *Tsuga heterophylla* Zone.

Environmental Features

Very few environmental data are available for the Mixed-Conifer Zone except for the eastern Siskiyou Mountains (Waring 1969). Precipitation varies from about 900 to 1,300 millimeters, with very little occurring during the summer months (table 15). Mean temperatures are about the same as in the *Tsuga heterophylla* Zone, but summers are distinctly warmer and drier. Waring (1969) has demonstrated that the moisture regime in mixed-conifer forests is more favorable than in the Ponderosa Pine and Black Oak types discussed earlier.

Forest soils in the Mixed-Conifer Zone of southwestern Oregon are extremely varied due to the complex geological history and topography. Soils typically belong to the Reddish Brown Lateritic, Gray-Brown Podzolic, Western Brown Forest, and Lithosolic great soil groups. Representative Reddish Brown Lateritics have thin organic layers (2 to 5 cm.), dark reddish-brown, slightly acid surface soils and red to dark-red strongly acid subsoils. Organic matter averages only 4 to 5 percent in the surface soil.

Forest Composition

The major forest tree species in the Mixed-Conifer Zone are *Pseudotsuga menziesii*, *Pinus lambertiana*, *P. ponderosa*, *Libocedrus decurrens*, and *Abies concolor*.^{1 2} These species occur in many combinations and degrees of mixture (Hayes 1959) (fig. 81). *Pseudotsuga menziesii* is probably the most abundant species, but it tends to decrease and *Pinus* spp. tends

^{1 2}The *Abies* under discussion here is part of the *Abies grandis*-*A. concolor* species complex, widespread in southwestern and eastern Oregon. Southwestern Oregon populations approach *Abies grandis* most closely morphologically; others approach *Abies concolor* morphologically and ecologically (Hamrick 1966). For convenience, we will refer to all of the morphologically variable populations in the Mixed-Conifer and *Abies concolor* Zones as *Abies concolor*.

Table 15. — Climatic data from representative stations within the Mixed-Conifer Zone

Station	Elevation	Latitude	Longitude	Temperature					Precipitation		
				Average annual	Average January	Average January minimum	Average July	Average July maximum	Average annual	June through August	Average annual snowfall
	Meters			-----	-----	Degrees C.	-----	-----	Millimeters		Centimeters
Butte Falls, Oreg.	635	42° 32'	122° 33'	--	--	--	--	--	931	64	--
Prospect, Oreg.	630	42° 44'	122° 31'	9.9	1.9	-3.2	19.0	31.1	1,059	62	162
Siskiyou Station, Oreg.	1,295	42° 03'	122° 36'	9.1	1.3	-3.2	18.4	24.5	863	53	--
Toketee Falls, Oreg.	617	43° 16'	122° 26'	10.5	1.9	-1.4	20.4	30.4	1,219	85	114

Source: U. S. Weather Bureau (1965a); Johnsgard (1963).

Figure 81. — Major forest trees in the Mixed-Conifer Zone are *Pseudotsuga menziesii*, *Pinus lambertiana*, *Libocedrus decurrens*, *Pinus ponderosa*, and *Abies concolor*; the first three of these are readily identifiable in this typical southwestern Oregon mixed-conifer stand.

to increase in importance from north to south within the zone. *Pinus lambertiana* and *P. ponderosa* usually occur as scattered individuals (Hayes and Hallin 1962) but give the forests much of their character. The proportion of *Libocedrus decurrens* tends to be greatest on relatively xeric sites in this zone. *Abies concolor* is often represented mainly by seedlings and saplings in existing mixed-conifer stands (fig. 82). Other typical tree species include *Acer macrophyllum*, *Arbutus menziesii*, and *Pinus monticola*. *Tsuga heterophylla* and *Thuja plicata* are frequently encountered on

more mesic habitats in the northern parts of the Mixed-Conifer Zone. *Castanopsis chrysophylla* may occur as either a shrub or small tree.

Understory communities have not been described within the Mixed-Conifer Zone in the Cascade Range. Reconnaissance data^{1 3} sug-

^{1 3} Unpublished data from studies of the South Umpqua drainage and Abbott Creek Research Natural Area on file with Forestry Sciences Laboratory, Pacific Northwest Forest & Range Exp. Sta., Forest Serv., U. S. Dep. Agr., Corvallis, Oregon.

gest major understory on modal sites is similar to those found on drier sites within the *Tsuga heterophylla* Zone:

Shrub layer – *Rhododendron macrophyllum*, *Corylus cornuta* var. *californica*, *Castanopsis chrysophylla*, *Holodiscus discolor*, *Berberis nervosa*, *B. aquifolium*, *Gaultheria shallon*, *Pachistima myrsinites*, *Rosa gymnocarpa*, *Rhus diversiloba*, and *Vaccinium membranaceum*.

Herb layer – *Rubus ursinus*, *Achlys triphylla*, *Chimaphila umbellata*, *Linnaea borealis*, *Viola sempervirens*, *Trientalis latifolia*, *Synthyris reniformis*, *Whipplea modesta*, *Adenocaulon bicolor*, *Hieracium albiflorum*, *Pyrola picta*, *Pyrola asarifolia*, and *Iris chrysophylla*.

On more mesic sites (e.g., protected draws and north slopes) *Tsuga heterophylla* seedlings, *Taxus brevifolia*, *Cornus nuttallii*, and

Figure 82. – *Abies concolor* is often represented only by seedlings and saplings in existing mixed-conifer stands, such as this *Pinus ponderosa* forest (Rogue River National Forest, Oregon).

Figure 83. — Forests of *Pseudotsuga menziesii* and *Libocedrus decurrens* often occupy more xeric sites in the Mixed-Conifer Zone; *Libocedrus-Pseudotsuga* stand on steep, south-exposed slopes in the Abbott Creek Research Natural Area (Rogue River National Forest, Oregon).

Figure 84. — *Arctostaphylos nevadensis* and *Ceanothus prostratus* are typical of the many rocky openings found in the Mixed-Conifer Zone (Abbott Creek Natural Area, Rogue River National Forest, Oregon).

Acer circinatum are typically added. The number and coverage of herbaceous species also increases on more mesic sites. Forests of *Pseudotsuga menziesii* and *Libocedrus decurrens* often occupy more xeric sites (fig. 83). *Arctostaphylos nevadensis* and *Ceanothus prostratus* are characteristic understory species on these habitats and in the rocky openings often associated with the xeric forest types (fig. 84).

The Mixed-Conifer forests have been studied in more detail in the eastern Siskiyou Mountains (Waring 1969; Dennis 1959). The same tree species occur there, although *Libocedrus decurrens* appears to be less common than in the Cascade Range. Characteristic understory species are *Corylus cornuta* var. *californica*, *Holodiscus discolor*, *Castanopsis chrysophylla*, *Symphoricarpos mollis*, *Rubus ursinus*, *Rosa gymnocarpa*, *Adenocaulon bicolor*, *Hieracium albiflorum*, and *Senecio integerrimus*.

Successional Patterns

Successional relationships have not been studied in the Mixed-Conifer Zone. It is known that brushfields frequently develop on burned- or logged-over forest lands within the zone (Gratkowski 1961a; Hayes 1959) (fig. 85). Dominants in such communities include *Ceanothus velutinus*, *C. sanguineus*, *C. inte-*

Figure 85. — Brushfields often develop on burned or logged-over lands within the Mixed-Conifer Zone; the Cat Hill brushfield, partially shown here, probably originated after a fire in the 1850's and has since been reburned (near Blue Rock, Rogue River National Forest, Oregon).

gerrimus, *C. prostratus*, *C. cordulatus*, *Castanopsis chrysophylla*, *Quercus chrysolepis*, *Amelanchier alnifolia*, *Arctostaphylos canescens*, and *Lithocarpus densiflorus* (Gratkowski 1961a). These brushfield communities can significantly slow the rate of forest succession or, with repeated fire, become semipermanent communities.

Ceanothus velutinus is important as a brushfield dominant or invader following logging or fire in the Mixed-Conifer Zone as well as many other zones: e.g., in parts of the *Tsuga heterophylla* (Morris 1958; Zavitkovski 1966), *Abies concolor*, and *A. magnifica shastensis* Zones, and in many of the forest types of eastern Oregon and Washington (Dyrness and Youngberg 1966; Mueggler 1965). In western Oregon, *Ceanothus velutinus* var. *laevigatus* and var. *velutinus* are generally found below and above 800 meters, respectively (Gratkowski 1961a; Zavitkovski 1966). In this area, *Ceanothus velutinus* is generally absent from understories of older stands lacking recent disturbance, but it often appears in abundance following logging and slash burning (Morris 1958) (fig. 86). This reproduction is from seed stored in the forest floor (Gratkowski 1962); heat from fires and increased insolation breaks the seedcoat dormancy. The relationship of *Ceanothus velutinus* to establishment and growth of coniferous reproduction has been hotly debated for 50 years (Zavitkovski and Newton 1968). It can fix nitrogen (Wollum 1962, 1965; Wollum et al. 1968), and may provide a favorable microenvironment for establishment of conifer seedlings under some conditions (Gratkowski 1962; Zavitkovski and Newton 1968). On other sites, it may seriously hinder establishment of coniferous stands.

Successional relationships among the tree species are not completely known. Many stands are relatively young and/or have been subjected to one or more fires since their establishment. *Pinus lambertiana* is seral, but long-lived; reproduction occurs sporadically in stands and small openings (fig. 87). *Pinus ponderosa* is also seral, although it may achieve climax status on poorly drained sites (Stephens 1965) and on extremely xeric sites. *Pseudotsuga menziesii*, the major forest dominant, is normally seral except on xeric sites,

Figure 86. — After forest lands have been logged and burned, *Ceanothus velutinus* reproduces from seed stored in the soil, despite its general absence from understories of older stands; it frequently hinders establishment and growth of conifer seedlings in the Mixed-Conifer Zone.

Figure 87. — Small openings are typical of mature mixed-conifer forests and provide opportunities for regeneration of less tolerant species; *Pseudotsuga menziesii*, *Pinus lambertiana*, *Abies concolor*, and *Lithocarpus densiflorus* seedlings are present in this opening (Abbott Creek Research Natural Area, Rogue River National Forest, Oregon).

where it may join *Libocedrus decurrens* in maintaining self-perpetuating populations. *Abies concolor* (or *A. grandis*) appears to be the major climax species within the Mixed-Conifer Zone; it is the most tolerant species normally present and dominates the conifer reproduction (fig. 82).

Unfortunately, we cannot outline further the diversity of forest and other communities found within the Mixed-Conifer Zone due to lack of data. Future research will doubtless illustrate the varied and complex plant communities within this zone.

Figure 88. — *Abies concolor* forests are especially extensive and well developed along the southern and southwestern flanks of the Oregon Cascade Range; this pure *Abies concolor* forest is typical of those found near Mount McLoughlin (Rogue River National Forest, Oregon).

"ABIES CONCOLOR" ZONE

Forests dominated by *Abies concolor* are the major feature of the *Abies concolor* Zone. This zone grades into the Mixed-Conifer and *Abies magnifica shastensis* Zones at its lower and upper limits, respectively. It occupies a relatively narrow elevational band, occurring at about 1,400 to 1,600 meters in the Cascade Range and 1,650 to 1,800 meters and 1,400 to 1,800 meters in the eastern and western Siskiyou Mountains, respectively (Waring 1969; Whittaker 1960). However, around Lake of the Woods and along the southwestern flank of the southern Oregon Cascade Range, there are extensive tracts at the appropriate elevations, and consequently, *Abies concolor* forests are widespread and well developed there (fig. 88). The *Abies concolor* Zone of southwestern Oregon extends around the southern end of the Cascade Range into southeastern Oregon, an area discussed later. It correlates with the "White Fir Phase" of the Mixed-Conifer Forest in northern California (Griffin 1967) and is considered an element of Merriam's Canadian Life Zone (Den- nis 1959).

Environmental Features

Climatic and edaphic data for the *Abies concolor* Zone are not available. The zone does experience lower temperatures, less plant moisture stress (Waring 1969), and less soil drought (Griffin 1967) than the adjacent Mixed-Conifer Zone. It is the lowest zone where significant winter snow accumulations occur; Waring (1969) mentioned that heavy snowfalls are damaging to brittle-limbed species such as *Pinus ponderosa* and *Arbutus menziesii*. Major soil types include Gray-Brown and Brown Podzols.

Forest Composition

Abies concolor is the major tree species within the *Abies concolor* Zone, often forming pure or nearly pure stands (fig. 88). The most common associate is *Pseudotsuga menziesii*. *Pinus lambertiana*, *P. ponderosa*, and *P. monticola* may be present in small numbers. *Libocedrus decurrens* is often associated on

mesic sites. *Abies magnifica* var. *shastensis* is increasingly common toward the upper limits of the *Abies concolor* Zone. *Pinus contorta* is encountered as a pioneer species in the Cascade Range.

Characteristic understory species in *Abies concolor* forests are (Whittaker 1960; Waring 1969; Dennis 1959):

Shrubs — *Holodiscus discolor*, *Rosa gymnocarpa*, *Berberis nervosa*, *Corylus cornuta* var. *californica*, *Acer glabrum* var. *douglasii*, *Rubus ursinus*, *R. nivalis*, *Amelanchier alnifolia*, and *Castanopsis chrysophylla*.

Herbs — *Campanula scouleri*, *Lathyrus polyphyllus*, *Anemone deltoidea*, *Achlys triphylla*, *Trientalis latifolia*, *Tiarella unifoliata*, *Galium triflorum*, *Adenocaulon bicolor*, *Vancouveria hexandra*, *Clintonia uniflora*, *Trillium ovatum*, *Hieracium albiflorum*, *Arenaria macrophyllum*, *Phacelia heterophylla*, and *Fragaria vesca* var. *bracteata*.

Successional Patterns

Abies concolor appears to be the sole climax species on modal habitats (fig. 89). *Libocedrus decurrens* may be a climax associate on more mesic habitats and *Pseudotsuga menziesii* or *Libocedrus decurrens* or both on xeric habitats.

Special Types

A variety of nonforested communities is found in the *Abies concolor* Zone. Brushfields similar to those found in the Mixed-Conifer Zone are encountered. *Ceanothus velutinus* remains a typical dominant, and *Ribes* spp. appear increasingly in the Cascade Range. *Arctostaphylos patula* is a major shrubby associate in the eastern Siskiyou Mountains (Dennis 1959).

Many different kinds of mountain meadows and barren openings are also found within the *Abies concolor* and adjacent *Abies magnifica shastensis* Zones. The compositions of these various meadow communities are not known. There is extensive evidence of invasion of many of these meadows by tree species. *Libocedrus decurrens* is conspicuous as a pioneer tree in many areas (fig. 90); e.g.,

Figure 89. — *Abies concolor* appears to be the sole climax species on modal sites in the *A. concolor* Zone; *Abies concolor* regeneration completely dominates under this mixed stand of *A. concolor*, *A. magnifica* var. *shastensis*, and *Libocedrus decurrens*.

Figure 90. — Invasion of meadows by *Libocedrus decurrens* is common within the *Abies concolor* Zone (Abbott Creek Research Natural Area, Rogue River National Forest, Oregon).

along the divide between the Rogue and Umpqua Rivers and on the high ridges within the Umpqua River drainage.

"ABIES MAGNIFICA SHASTENSIS" ZONE

Abies magnifica var. *shastensis*^{1 4} dominates the forests between the subalpine *Tsuga mertensiana* Zone and the *Abies concolor* Zone (fig. 91). The *Abies magnifica shastensis* Zone is generally found at elevations between 1,600 and 2,000 meters in the Cascade Range and 1,800 and 2,200 meters in the Siskiyou Mountains (Dennis 1959; Whittaker 1960). It is well developed on the western slopes of the Cascade Range; e.g., in the vicinity of Crater Lake National Park. The forests of this zone are closely allied with *Abies magnifica* or Red Fir forests of the California Cascade Range and Sierra Nevada (Oosting and Billings 1943; Kchler 1964; Griffin 1967). They are generally considered a part of Merriam's Canadian Life Zone (Bailey 1936; Dennis 1959).

Environmental Features

Environmental data are lacking for the *Abies magnifica shastensis* Zone. The Crater Lake climatic station (table 10) is near its boundary with the *Tsuga mertensiana* Zone. Two major climatic features are known: (1) much of the annual precipitation falls as snow, which accumulates in winter snowpacks with maximum depths of 2 meters or more; (2) critical plant moisture stresses do not occur during the short summers (Waring 1969; Griffin 1967). Soils tend towards Brown Pod-

zolic types with well-developed mor humus layers; podzolic A2 horizons are not encountered, however.

Forest Composition

Abies magnifica var. *shastensis* is the major tree species within the *Abies magnifica shastensis* Zone (fig. 91). *Abies concolor*, *Pinus monticola*, *P. contorta*, and *Tsuga mertensiana* are the most common associates. Many other species are not common but may be present, especially on specialized habitats, including *Pseudotsuga menziesii*, *Pinus ponderosa*, *Libocedrus decurrens*, *Picea engelmannii*, *Abies amabilis*, and *A. lasiocarpa*.

The understory in *Abies magnifica* var. *shastensis* stands is highly variable in density. Under dense forest stands, it may be nearly absent and include only Oosting and Billings' (1943) ericaceous and saprophytic "Pirola-Corallorrhiza union": *Chimaphila umbellata*, *C. menziesii*, *Pyrola secunda*, *P. picta*, *Corallorrhiza maculata*, *Pterospora andromeda*,

Figure 91. — Pure, even-aged stands of *Abies magnifica* var. *shastensis* are common within the *A. magnifica shastensis* Zone of southwestern Oregon (Rogue River National Forest, Oregon).

^{1 4} Taxonomic controversy surrounds this southern Oregon *Abies* (Franklin 1964). It has been referred to as both *Abies procera* and *A. magnifica* var. *shastensis*. Populations in southwestern Oregon appear to be part of a species complex involving *Abies procera* and *A. magnifica*; it has been suggested these constitute hybrid populations between these species. For convenience, we will refer to these populations as *Abies magnifica* var. *shastensis* which they resemble ecologically. Although Whittaker (1960) referred to his populations as *Abies nobilis* (synonym for *A. procera*), he stated (personal communication) that elements of *Abies magnifica*, *A. magnifica* var. *shastensis*, and *A. procera* were all present.

and *Sarcodes sanguinea*. In other cases, the understory is relatively rich, especially in herbs; typical species are (Waring 1969; Whitaker 1960; Dennis 1959):

Shrubs — *Vaccinium membranaceum*, *Ribes marshallii*, *R. viscosissimum*, *Arctostaphylos patula*, *A. nevadensis*, and *Castanopsis chrysophylla*.

Herbs — *Anemone deltoidea*, *A. oregana*, *Valeriana sitchensis*, *Arenaria macrophylla*, *Campanula scouleri*, *Achlys triphylla*, *Arnica latifolia*, *A. cordifolia*, *Osmorhiza chilensis*, *Hieracium albiflorum*, *Viola glabella*, *Polemonium californicum*, and *Stellaria crispa*.

Successional Patterns

Successional relationships in the *Abies magnifica shastensis* Zone are not completely understood. Any of the tree species may invade an area directly following fire or logging, but *Pinus contorta* and *P. monticola* are confined strictly to a seral role on normal forest sites. Interesting two-storied stands of scattered old *Abies magnifica* var. *shastensis* over a *Pinus contorta* lower canopy are sometimes encountered; reproduction of *Abies magnifica* var. *shastensis* is typically present within the understory.

Abies magnifica var. *shastensis* exhibits varied behavior. In many stands it appears to be climax; i.e., it is reproducing in sufficient numbers to maintain the population. In other areas, *Abies magnifica* var. *shastensis* stands are apparently succeeded by *Abies concolor* or *Tsuga mertensiana* (particularly at the lower and upper limits of the zone, respectively), or even by *Abies amabilis* (on some protected sites toward the north end of the zone). This variable behavior is interesting since *Abies magnifica* is the major climax species in the Sierran *Abietum magnificae* (Oosting and Billings 1943), whereas *Abies procera* is never climax in the northern Cascade Range (Franklin 1966; Thornburgh 1969).

Special Types

Brushfields are encountered with the *Abies magnifica shastensis* Zone. *Ribes* spp., *Vac-*

cinium membranaceum, and *Ceanothus velutinus* are typical dominants. Dennis (1959) described two shrub communities within this zone in the eastern Siskiyou Mountains — *Arctostaphylos patula/Ceanothus velutinus* and *Artemisia tridentata/Lonicera conjugialis*. Both included scattered *Abies magnifica* var. *shastensis* and *Pinus monticola*. Shrub communities dominated by *Cercocarpus ledifolius* are also encountered in the Siskiyou Mountains.

A variety of wet and dry meadow communities is associated with the *Abies magnifica* var. *shastensis* forest, as mentioned earlier. No data are available on the extent or composition of these communities.

Eastern Oregon and Washington

Conifer forests are conspicuous in the dry interior regions. They clothe the eastern slopes of the Cascade Range and extend, with only minor interruptions, around the northern edge of Washington to the northern Rocky Mountains. Forests also dominate in the Blue, Ochoco, and Wallowa Mountains of Oregon.

In this region, elements of the continental Rocky Mountain forests meld with some of those from coastal areas. In addition, forest species mix with species from steppe and shrub-steppe communities, especially near lower timberline. It is a country typified by the "western yellow pine" (*Pinus ponderosa*) forests.

Forests of the interior region have been studied by foresters and ecologists for many years. Shantz and Zon (1924) and Hansen (1947) provided generalized accounts. Notable synecological studies include those of Daubenmire (1952, 1953, 1956, 1966), Daubenmire and Daubenmire (1968), Driscoll (1962, 1964a, 1964b), Hall (1967), Berry (1963), Dyrness and Youngberg (1958, 1966), Swedberg (1961), Trappe and Harris (1958), Volland (1963), West (1964, 1969), and McMinn (1952). Weaver (1943, 1955, 1959, 1961, 1964, 1968) has written extensively about the role of fire in these forests. The intricate relationship between *Pinus ponderosa* and *Pinus contorta* in the central Ore-

gon pumice region has received special consideration by Kerr (1913); Munger (1914); Tarrant (1953); Youngberg and Dyrness (1959); and Berntsen (1967).

Through these studies, many forest associations have been identified, characterized by different climax tree species: *Juniperus occidentalis*, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Abies grandis*, *Thuja plicata*, *Tsuga heterophylla*, *Abies lasiocarpa*, *Pinus contorta*, and *Libocedrus decurrens*. *Abies concolor*¹⁵ and *Abies magnifica* var. *shastensis*¹⁶ associations, so widespread in California and southwestern Oregon, are also encountered on eastern slopes of the southern Oregon Cascade Range. At higher elevations, near the crest of the Cascade Range, occur *Tsuga mertensiana*

¹⁵ *Abies grandis* and *Abies concolor* form a continuously varying biological complex in eastern Oregon. Most of the *Abies grandis* found in northeastern Oregon (Blue Mountains and Cascade Range) intergrades with *Abies concolor*. In this area we will, for convenience, refer to the populations as *Abies grandis* since the complex resembles this species morphologically. In south-central Oregon, we will refer to the complex as *Abies concolor*. These two species and the zones they typify occupy analogous positions synecologically and environmentally in their respective "areas."

¹⁶ See footnote 14.

and sometimes *Abies amabilis* associations. These have already been discussed.

This abundance of climax forest types and the complex array of seral communities result from an abundance of coniferous species and environmental diversity. Climax associations are generally arrayed elevationally as zones, the consequence of differing responses of tree species to temperature and moisture gradients interacting with differing degrees of tolerance. Daubenmire (1966) has illustrated this phenomenon for forests of eastern Washington and northern Idaho (fig. 92). At various points along the gradient, increasingly tolerant species enter the forest communities producing a sequence of steps based on the climax tree species.

For discussion of interior forests we will group the series of climax associations into seven zones:

Juniperus occidentalis
Pinus ponderosa
Pinus contorta
Pseudotsuga menziesii (plus *Libocedrus decurrens*)
Abies grandis (plus *Abies concolor*)
Tsuga heterophylla (plus *Thuja plicata*)
Abies lasiocarpa

Figure 92. — Coniferous trees in eastern Washington and northern Idaho showing the usual order in which the species are encountered with increasing altitude; horizontal bars designate upper and lower limits of species relative to the climatic gradient, portions of a species range where it is climax in the face of intense competition indicated by heavy lines (from Daubenmire 1966).

All of these zones delineate important phyto-geographic units, but they do not occur on a single mountain slope nor do they necessarily occur as sequential belts. The *Pinus contorta* Zone does not really qualify as part of a zonal series since *P. contorta* does not occur as a climatic climax. However, since climax *Pinus contorta* forests are so conspicuous in parts of eastern Oregon, they are treated at the zonal level.

Typical zonal sequences at various locations in eastern Oregon and Washington are indicated in table 16. Obviously, a great variation is possible. Lack of a zone in a particular area can result from species absence, the consequence of macroclimate or history, or from localized edaphic conditions. For example, in northern Idaho, *Tsuga heterophylla*, *Thuja plicata*, and *Abies grandis* are all common (Daubenmire and Daubenmire 1968). To the south, along the Rocky Mountains within Idaho, *Tsuga*, *Thuja*, and finally *Abies grandis* drop out in turn, gradually altering the zonal sequence. Similarly, *Tsuga heterophylla* and *Thuja plicata* are absent from the eastern slopes of the southern Oregon Cascade Range and Blue Mountains, whereas *Juniperus occidentalis* is generally absent from eastern Washington. Examples of the influence of localized edaphic and climatic conditions include the *Pinus ponderosa*-*Pinus contorta* complex on Mazama pumice in south-central Oregon and the tendency on finer textured soils for elimination of a *Pinus ponderosa* Zone between steppe and the *Pseudotsuga menziesii* Zone (as illustrated by Brayshaw 1965).

A most important regional variation in zonal sequences involves the relative importance of the *Abies grandis* and *Pseudotsuga menziesii* Zones. The *Abies grandis* Zone (including *Abies concolor*) is probably the most extensive forested zone in eastern Oregon; the *Pseudotsuga menziesii* Zone is poorly represented or absent. Conversely, on eastern slopes of the northern Washington Cascade Range and in the Okanogan Highlands, the *Pseudotsuga menziesii* Zone becomes relatively more important than the *Abies grandis* Zone until, in adjacent British Columbia, the latter is absent (Brayshaw 1965).

Table 17 provides an overview of forest composition and successional relationships in the forested zones of eastern Oregon and Washington.

"JUNIPERUS OCCIDENTALIS" ZONE

The *Juniperus occidentalis* Zone is the northwestern representation of the Pinyon-Juniper Zone so conspicuous in the Great Basin region (Billings 1951). It is generally a savanna zone (fig. 93), occupying habitats intermediate in moisture between *Pinus ponderosa* forest and steppe or shrub-steppe (Driscoll 1964b). The *Juniperus occidentalis* Zone is found only in eastern Oregon, reaching maximum development in central Oregon around the Deschutes, Crooked, and John Day Rivers. Similar communities occur at various localities throughout southeastern Oregon; Driscoll (1964b) has suggested a physiographic subdivision of the zone into three units based on soil parent materials. Elevational range of the zone appears to be between about 760 and 1,400 meters, although most stands Driscoll (1964b) sampled were between 1,200 and 1,400 meters.

Environmental Features

The *Juniperus occidentalis* Zone is the most xeric of the tree-dominated zones in the Pacific Northwest. Annual precipitation is low. At Bend, in the *Pinus ponderosa*-*Juniperus occidentalis* transition, it averages 312 millimeters, but in the center of the zone 200 to 250 millimeters is typical (table 18). Most precipitation falls during the winter, and the hot summer months are often completely dry.

The zone includes Sierozem, Brown, and Chestnut great soil groups (Driscoll 1964b). Brown soils and associated Regosols are most common. Surface soils are typically light colored, coarse textured (sandy loams), low in organic matter (e.g., 1 to 4 percent), and slightly acid (pH 6.0) to neutral. Soils average around 76 centimeters in depth, although roots may penetrate underlying cracked bedrock. Subsoils typically have white calcareous or siliceous deposits on pedis or rocks.

Table 16. — Typical zonal forest sequences at locations in eastern Washington and Oregon adapted from the indicated sources¹

Northwestern Washington and northern Idaho (Daubenmire 1952, 1966)	Eastern slopes, Washington Cascade Range (Franklin and Trappe 1963)	Eastern slopes, central Oregon Cascade Range (Swedberg 1961; West 1964)	Eastern slopes, southern Oregon Cascade Range (Dyrness and Youngberg 1958, 1966)	Ochoco and Blue Mountains, Oregon (Hall 1967)
<i>Pinus ponderosa</i>	(<i>Pinus ponderosa</i>)	<i>Juniperus occidentalis</i>	<i>Juniperus occidentalis</i>	(<i>Juniperus occidentalis</i>)
<i>Pseudotsuga menziesii</i>	<i>Pseudotsuga menziesii</i>	<i>Pinus ponderosa</i>	<i>Pinus contorta</i>	<i>Pinus ponderosa</i>
<i>Abies grandis</i>	<i>Abies grandis</i>	<i>Abies grandis</i>	<i>Abies concolor</i>	<i>Abies grandis</i>
<i>Tsuga heterophylla</i>	(<i>Tsuga heterophylla</i> and/or <i>Abies amabilis</i>)	(<i>Abies amabilis</i>)	(<i>Abies magnifica</i> var. <i>shastensis</i>)	
<i>Abies lasiocarpa</i> or <i>Tsuga mertensiana</i>	<i>Abies lasiocarpa</i> or <i>Tsuga mertensiana</i>	<i>Tsuga mertensiana</i>	(<i>Tsuga mertensiana</i>)	(<i>Abies lasiocarpa</i>)

¹ Species names in parentheses indicate the enclosed zone may be absent or only fragmentally represented.

Table 17. — Importance and ecological role of major tree species in representative forest zones and locales in eastern Oregon and Washington¹

Species	Eastern Washington Cascade Range					Central Oregon Cascade Range					Ochoco and Blue Mountains	
	<i>Pinus ponderosa</i> Zone	<i>Pseudotsuga menziesii</i> Zone	<i>Abies grandis</i> Zone	<i>Tsuga heterophylla</i> Zone	<i>Abies lasiocarpa</i> Zone	<i>Juniperus occidentalis</i> Zone	<i>Pinus ponderosa</i> Zone	<i>Pseudotsuga menziesii</i> Zone	<i>Abies grandis</i> ² Zone	<i>Tsuga mertensiana</i> Zone	<i>Pinus ponderosa</i> Zone	<i>Abies grandis</i> ² Zone
<i>Abies amabilis</i>	—	—	—	—	C	—	—	—	—	C	—	—
<i>Abies grandis</i>	—	—	C	S	S	—	—	—	C	S	—	C
<i>Abies lasiocarpa</i>	—	—	—	S	C	—	—	—	S	C	—	—
<i>Libocedrus decurrens</i>	—	S	S	S	S	—	—	—	S	—	—	S
<i>Larix occidentalis</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Larix lyallii</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Picea engelmannii</i>	—	—	S	S	Sc	—	—	—	S	S	—	S
<i>Pinus contorta</i>	—	—	S	—	S	—	—	—	S	S	—	—
<i>Pinus lambertiana</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pinus monticola</i>	—	—	S	S	S	—	—	—	S	S	—	S
<i>Pinus ponderosa</i>	C	S	S	S	—	—	C	—	S	S	C	S
<i>Juniperus occidentalis</i>	—	—	—	—	—	C	S	—	—	—	S	—
<i>Populus tremuloides</i>	S	S	S	—	—	—	—	—	—	—	—	—
<i>Pseudotsuga menziesii</i>	—	C	S	S	S	—	—	—	S	S	—	Sc
<i>Thuja plicata</i>	—	—	—	Sc	—	—	—	—	—	—	—	—
<i>Tsuga heterophylla</i>	—	—	—	C	S	—	—	—	—	—	—	—
<i>Tsuga mertensiana</i>	—	—	—	—	C	—	—	—	S	C	—	—

¹ C = major climax species, c = minor climax species, S = major seral species, and s = minor seral species.

² *Abies grandis*-*A. concolor* complex.

Table 18. — Climatic data from representative stations within the *Juniperus occidentalis* zone

Station	Eleva- tion	Lati- tude	Longi- tude	Temperature					Precipitation		
				Average annual	Average January	Average January minimum	Average July	Average July maximum	Average annual	June through August	Average annual snowfall
	Meters			----- Degrees C. -----					Millimeters		Centi- meters
Bend, Oreg.	1,097	44° 04'	121° 19'	8.0	-0.9	-6.5	17.9	28.7	318	50	92
Redmond, Oreg.	913	44° 17'	121° 10'	9.1	-.1	-5.9	18.8	29.5	216	42	61
Prineville, Oreg.	866	44° 21'	120° 54'	8.0	-.56	-6.6	18.1	29.8	238	41	35

Source: U. S. Weather Bureau (1965a).

Figure 93. — The *Juniperus occidentalis* Zone is primarily a savanna region, ecotonal between *Pinus ponderosa* forest and *Artemisia* shrub-steppe (near Bend, Oregon).

Community Composition

Driscoll (1962, 1964a, 1964b) has provided the only comprehensive description of communities in the *Juniperus occidentalis* Zone. His general description of the vegetation of the zone is as follows (Driscoll 1964b):

Juniperus occidentalis is the dominant tree species of the area. An occasional *Pinus ponderosa* may be found in canyon bottoms or on north slopes where soil moisture is more effective. Natural wide spacing of individual junipers provides the aspect of a savanna *Artemisia tridentata* is most often the dominant shrub in the understory. Occasionally it is displaced wholly or to codominance by *Purshia tridentata*. Other shrubs characteristic of the area are *Chrysothamnus nauseosus*, *C. viscidiflorus*, *Tetradymia*

canescens, *Leptodactylon pungens*, and *Artemisia arbuscula*. *Ribes cereum*, *Grossularia velutina*, [*Ribes velutinum*], and *Grayia spinosa* occur infrequently. Suf-frutescents are represented by various species of *Eriogonum*.

Agropyron spicatum and *Festuca idahoensis* are the characteristic grasses of relatively undisturbed communities. *Poa secunda* and *Stipa thurberiana* are common. Other grasses include *Sitanion hystrix*, *Stipa comata*, *Bromus tectorum*, *Festuca octoflora*, and *Koeleria cristata*.

Forbs commonly do not constitute major components of relatively undisturbed communities. Some of the more common perennial forbs are *Agoseris* sp., *Achillea millefolium*, *Eriophyllum lanatum*, *Astragalus* spp., *Erigeron linearis*, and *Lupinus* spp.

From the 11 associations and variants described by Driscoll (1964a, 1964b), we can pick five which typify major variations in *Juniperus occidentalis* communities (table 19). The *Juniperus/Artemisia/Agropyron* association was found on well-drained loamy soils on undulating topography; hence, its climatic climax designation. *Artemisia tridentata* (average maximum height 0.6 m.) and *Agropyron spicatum* typified the shrub and herb components, both attaining maximum status here. *Chrysothamnus nauseosus* was the only other shrub. *Stipa thurberiana*, *Poa secunda*, *Lomatium triternatum*, *Bromus tectorum*, and *Festuca octoflora* were other notable species.

The *Juniperus/Festuca* association was notable for its high coverage of *Juniperus occidentalis* and *Festuca idahoensis* and low shrub cover (table 19). The shrub cover was lowest in the *Juniperus/Agropyron* association. The *Juniperus/Artemisia-Purshia* association was lowest in *Juniperus occidentalis* and highest in shrub coverage (*Artemisia tridentata* and *Purshia tridentata*). The *Juniperus/Artemisia/Agropyron-Astragalus* association (fig. 94) occupied the most xeric sites. *Festuca idahoensis* was found only in *Juniperus* shade in this association. Of the few perennial herbs, *Astragalus lectulus* was quite specific to this association.

Succession

Very little is known concerning successional relationships in the *Juniperus occidentalis* Zone. Burning can kill *Juniperus occidentalis* and temporarily produce an herb- or shrub-dominated community which is gradually reinvaded by trees. Sparsity of *Juniperus occidentalis* in some associations was explained in this way (Driscoll 1964b). The fire-sensitive *Purshia tridentata* is similarly affected. Grazing by cattle can result in a reduction of the preferred *Agropyron spicatum* and *Festuca idahoensis*; deer browsing affects primarily the *Purshia tridentata* and *Juniperus*.

"PINUS PONDEROSA" ZONE

Pinus ponderosa forests are widely distributed in eastern Oregon and Washington. They occupy: (1) a narrow band (15 to 30 km.

wide) on the eastern flanks of the entire Cascade Range (generally); (2) much of the high pumice plateau extending east from the High Cascades province; (3) large areas in the Blue Mountains province (Ochoco, Blue, and Wallowa Mountains) of northeastern Oregon and extreme southeastern Washington; and (4) extensive tracts in the Okanogan Highlands province of northeastern Washington. The band of *Pinus ponderosa* forests generally increases in elevation from north to south. Throughout much of Washington they are at approximately 600 to 1,200 meters in elevation. In the Blue Mountains province and northeastern Oregon generally, the elevational range is about 900 to 1,500 meters. Elevations in the south-central Oregon pumice area are considerably higher—about 1,450 to 2,000 meters.

At their upper limits, *Pinus ponderosa* forests may grade into forests of *Pseudotsuga menziesii*, *Abies grandis*, or *A. concolor* depending on the locale (table 16). Throughout much of Oregon, they abut *Artemisia tridentata* steppe or open *Juniperus occidentalis-Artemisia tridentata* woodland at their lower

Figure 94. — The *Juniperus occidentalis/Artemisia tridentata/Agropyron spicatum-Astragalus lectulus* association was the most xeric described by Driscoll (1964b).

Table 19. — Five associations found in the *Juniperus occidentalis* Zone and some characteristics of each

Assóciation	Climax type	Coverage		
		<i>Juniperus</i>	Shrubs ¹	Herbs ²
<i>Juniperus/Artemisia/Agropyron</i>	Climatic	10.0	9.6	14.3
<i>Juniperus/Festuca</i>	Topoedaphic	76.7	1.6	15.1
<i>Juniperus/Agropyron</i>	Topoedaphic	43.0	1.4	9.1
<i>Juniperus/Artemisia-Purshia</i>	Topoedaphic	6.6	16.2	4.6
<i>Juniperus/Artemisia/Agropyron-Astragalus</i>	Topoedaphic	27.7	9.8	9.6

Source: Driscoll (1964b).

¹ Shrubs and suffrutescents.

² Perennial herbs only.

limits. At lower elevational limits in Washington, *Pinus ponderosa* forests grade into either grassland or *Artemisia* steppe. At some locations in northern Oregon and southern Washington, there is an ecotonal belt of *Quercus garryana* between *Pinus ponderosa* forest and steppe.

The discussion of the *Pinus ponderosa* Zone which follows considers seral *Pinus ponderosa* forests as well as forests in which the *Pinus* is climax. The *Pinus ponderosa* Zone, in the strict sense, includes only the latter; in this narrower definition, the *Pinus ponderosa* Zone correlates with the Ponderosa Pine-Bunchgrass Zone of Krajina (1965) and Brayshaw (1965). It is important to realize that in many locations there is no belt of climax *Pinus ponderosa* forests between steppe and areas of *Pseudotsuga menziesii* (Brayshaw 1965; Johnson 1959) or *Abies grandis* (Hall 1967) climax. The *Pinus ponderosa* Zone, more broadly defined, correlates roughly with Merriam's Arid Transition Zone (Barrett 1962; Bailey 1936) and includes representation of Kchler's (1964) Ponderosa Shrub and Western Ponderosa Forests.

Environmental Features

The climate of the *Pinus ponderosa* Zone is characterized by a short growing season and minimal summer precipitation (table 20). Average annual precipitation ranges from about 355 to 760 millimeters, much of it falling as winter snow. Diurnal summer temperatures fluctuate widely, with hot days and cold nights. In many areas, frost may occur any night of the year. The months of July, August, and September are very dry, with rainfall averaging less than 25 millimeters. Much of this summer rain is ineffective, as it usually comes during brief, high-intensity convection storms. Winter temperatures are generally low; as a result, snow often accumulates to considerable depths.

Since *Pinus ponderosa* occupies drier sites than any other forest type (except *Juniperus occidentalis*), its distribution is closely correlated with supplies of available soil moisture. This is often reflected by a distinct relationship between occurrence of *Pinus ponderosa* and soil texture, especially at the dry end

of its range. Many studies have shown better survival and growth of *Pinus ponderosa* on coarse-textured, sandy soils than on fine-textured, clayey soils (Pearson 1923; Howell 1932; Stone and Fowells 1955; Fowells and Kirk 1945). These effects can be largely attributed to more extensive root proliferation on coarse-textured soils. On xeric sites, a mosaic of *Pinus ponderosa* communities (on coarse-textured soils) and steppe or shrub-steppe communities (on finer textured soils) is common (Hall 1967). An extreme example is a disjunct stand of *Pinus ponderosa* in central Oregon, located 64 kilometers from the nearest other *Pinus ponderosa* forest (fig. 95). Despite less than 250 millimeters annual precipitation, abundant regeneration attests that the stand is maintaining itself. Berry (1963) attributed existence of this anachronistic forest primarily to the uniformly sandy soils it occupies.

Intensity of soil profile development varies with elevation and parent material. At lower elevations within the zone, soils tend to be coarse textured and generally have weakly differentiated A, B, and C horizons. Western Brown Forest is the most common zonal soil group. They have moderately dark-colored and thick A horizons grading into B horizons distinguished by color, and sometimes by structure, since clay eluviation is not characteristic. Surface soils are generally slightly acid, and reaction often becomes more neutral with depth. Soils on moister, cooler sites

Figure 95. — Coarse-textured soils favor development of *Pinus ponderosa* in forest-steppe ecotonal areas; this disjunct stand, the Lost Forest, is an extreme example, occupying sandy soils located 64 kilometers within the central Oregon shrub-steppe.

Table 20. — Climatic data from representative stations in the vicinity of the *Pinus ponderosa* Zone

Station	Eleva- tion	Lati- tude	Longi- tude	Temperature					Precipitation		
				Average annual	Average January	Average January minimum	Average July	Average July maximum	Average annual	June through August	Average annual snowfall
	Meters			-----	-----	Degrees C.	-----	-----	Millimeters		Centi- meters
Chiloquin, Oreg.	1,280	42°35'	121°47'	6.3	-3.1	-9.4	16.3	28.4	441	43	--
Joseph, Oreg.	1,341	45°21'	117°15'	6.4	-5.3	-10.6	17.5	26.6	411	94	--
Starkey, Oreg.	1,036	45°14'	118°23'	6.3	-3.6	-10.0	16.2	28.0	457	89	--
Cle Elum, Wash.	579	47°11'	120°55'	7.4	-3.2	-7.7	18.1	27.8	537	41	219
Leavenworth, Wash.	344	47°34'	120°40'	8.4	-5.1	-9.9	20.4	30.8	590	44	252
Northport, Wash.	411	48°55'	117°47'	8.3	-4.5	-8.2	20.6	31.4	477	96	141

Source: U. S. Weather Bureau (1956, 1965a, 1965b) and Johnsgard (1963).

generally show some evidence of podzolization — e.g., they may have moderately thick accumulations of duff and litter and thin A1 horizons underlain by distinct, light-colored A2 (bleicherde) horizons. Soil reaction ranges from slight to medium acidity. The most representative great soil group is the Gray Wooded.

The *Pinus ponderosa* Zone includes large areas of immature regosolic soils, particularly the 5,000,000-hectares pumice plateau of south-central Oregon. These pumice soils are developed in deposits of dacitic and rhyolitic pumice erupted from Mount Mazama (Crater Lake) and Newberry Crater, respectively. Thin A horizons have moderate to low organic matter content and grade into relatively unweathered pumice sand and gravel. A finer textured buried soil is generally encountered at 1/2 to 3 meters. These coarse-textured pumice soils apparently enable *Pinus ponderosa* to extend its range east into areas where the vegetation would otherwise be *Artemisia* steppe. The frequent coincidence of eastern boundaries of *Pinus ponderosa* forest and pumice soil areas provides evidence for this.

Forest Composition

Pinus ponderosa is associated with a rich variety of tree species. Only four of these — *Juniperus occidentalis*, *Populus tremuloides*, *Pinus contorta*, and *Quercus garryana* — are generally associates in climax *Pinus ponderosa* stands (the narrowly defined *Pinus ponderosa* Zone). Even these associates are restricted to specific habitats in the zone or geographically. *Juniperus occidentalis* occurs as a minor component of xeric *Pinus ponderosa* stands in much of southeastern Oregon (Dealy 1969; Swedberg 1961; West 1964). Groves of *Populus tremuloides* occur on riparian and poorly drained wet areas throughout the *Pinus ponderosa* Zone and adjacent forest and steppe zones as well (fig. 96) (Johnson 1961; Dealy 1969; Daubenmire 1952). *Quercus garryana* is associated only on the east slopes of the Cascades in northern Oregon and southern and central Washington. *Pinus contorta* and *P. ponderosa*, frequent seral associates in more mesic zones (e.g., *Pseudotsuga menziesii* Zone), are the sole constituents of extensive

Figure 96. — Groves of *Populus tremuloides* are common on riparian and poorly drained habitats within the *Pinus ponderosa* Zone (Colville Indian Reservation, Washington).

forests in the pumice region of south-central Oregon (Dyrness and Youngberg 1966).

The remaining tree species found in *Pinus ponderosa* stands are generally present only on sites where *Pinus ponderosa* is seral; e.g., more mesic zones such as the *Abies grandis* or *Pseudotsuga menziesii*. Any of these may occur as accidentals within climax *Pinus ponderosa* stands, however. *Abies grandis*, *Pseudotsuga menziesii*, *Larix occidentalis*, and *Pinus monticola* are associated with *Pinus ponderosa* essentially throughout northeastern Oregon and eastern Washington (including eastern slopes of the Cascade Range) (Swedberg 1961; Hall 1967; Daubenmire and Daubenmire 1968). *Libocedrus decurrens* occurs only along the eastern slopes of the central and northern Oregon Cascades (Swedberg 1961; West 1969; Sherman 1969). *Abies concolor* is a major constituent of some seral *Pinus pon-*

Figure 97. — The open nature of many mature *Pinus ponderosa* stands provides niches for sciophytic species, including many typical of steppe and shrub-steppe communities (eastern slopes of the Cascade Range near Sisters, Oregon).

derosa stands of the southern and central Oregon Cascade Range and pumice region (Volland 1963; Dyrness and Youngberg 1966).

Community composition in *Pinus ponderosa* stands varies widely with geographic location, soils, elevation and aspect, and successional status. The history of stand disturbances, such as by fire and logging, influence overstory density which, in turn, can have profound effects on understory composition and density (Moir 1966; Robinson 1967; Sherman 1966). The open nature of typical mature *Pinus ponderosa* stands (fig. 97) provides abundant niches for sciophytic species, including many typical of steppe and shrub-steppe communities.

Pinus ponderosa community types or associations have been identified in many localities: (1) south-central Oregon (Volland 1963; Dyrness 1960; Dyrness and Youngberg 1966;

Dealy 1969), (2) the Blue Mountains of northeastern Oregon,¹⁷ and (3) eastern Washington (Daubenmire 1952; Daubenmire and Daubenmire 1968). West (1964) and Swedberg (1961) found a continuum viewpoint useful in interpreting *Pinus ponderosa* communities along environmental gradients on the eastern slopes of Oregon's Cascade Range. All of these studies show that some characteristic understory dominants, such as *Festuca idahoensis* and *Purshia tridentata*, occur throughout the entire zone — from northeastern Washington to south-central Oregon. However, many others have more restricted distributions, so that the character of the understory tends to vary with locale. Consequently, communities will be considered by geographic location.

¹⁷ F. C. Hall (1967) and personal communications.

Figure 98. — Grassy *Pinus ponderosa* communities often consist of a mosaic of arborescent and herbaceous patches, the latter developing well only in treeless openings; a *Pinus ponderosa*/*Agropyron spicatum* community in eastern Oregon.

In eastern Washington, six *Pinus ponderosa* associations have been recognized (Daubenmire and Daubenmire 1968):

Pinus ponderosa/*Symphoricarpos albus*,
Pinus ponderosa/*Physocarpus malvaceus*,
Pinus ponderosa/*Festuca idahoensis*,
Pinus ponderosa/*Agropyron spicatum*,
Pinus ponderosa/*Stipa comata*, and
Pinus ponderosa/*Purshia tridentata*.

The first two associations comprise a shrubby group found on deep, fine-textured, fertile soils. *Pinus* reproduction is sparse, but sufficient to produce an all-aged forest. The *Pinus ponderosa*/*Symphoricarpos albus* association is considered a climatic climax (Daubenmire 1952), since it occurs on loamy soils and undulating topography. The understory is dominated by a nearly continuous, 0.5- to 1-meter-tall cover of low, deciduous shrubs, mainly *Symphoricarpos albus*, *Spiraea betulifolia* var. *lucida*, *Rosa woodsii*, and *R. nutkana*. There is a rich variety of herbaceous, mainly peren-

nial, associates, of which several grasses (e.g., *Calamagrostis rubescens*, rhizomatous *Agropyron spicatum*) have the highest constancies. The *Pinus ponderosa*/*Physocarpus malvaceus* association occupies slightly more mesic sites and adds a taller shrub layer (2 m.) of *Physocarpus malvaceus*, *Holodiscus discolor*, and *Ceanothus sanguineus* to the *Symphoricarpos* understory discussed above.

The other four *Pinus ponderosa* associations — *Festuca idahoensis*, *Agropyron spicatum*, *Stipa comata*, and *Purshia tridentata* — Daubenmire and Daubenmire (1968) refer to as a grassy group (fig. 98). Understories are dominated by xerophytic grasses; soils are stony, coarse textured, or shallow; and reproduction of *Pinus* is episodic. The first three associations were grouped in a *Pinus ponderosa*/*Agropyron spicatum* association in an earlier study (Daubenmire 1952). Each has an understory dominated almost exclusively by a single large perennial bunchgrass — *Festuca*

idahoensis, caespitose *Agropyron spicatum*, or *Stipa comata*. The *Pinus ponderosa*/*Purshia tridentata* association has a *Purshia*-dominated shrub layer superimposed on a variety of perennial grasses including *Festuca idahoensis*, caespitose *Agropyron spicatum*, *Stipa comata*, and *Aristida longiseta*. In some stands, forbs such as *Balsamorhiza sagittata* and *Erigeron compositus* are abundant.

Cooke (1955) has provided data on occurrence of fungi, mosses, and lichens in *Pinus ponderosa*/*Agropyron spicatum* and *Pinus ponderosa*/*Symphoricarpos albus* stands in eastern Washington and adjacent Idaho.

Studies have indicated that soil moisture regime is the most important single factor influencing the distribution of these climax vegetation types (McMinn 1952; Daubenmire 1968b). Supplies of available soil moisture are exhausted early in the growing season in areas of the more xeric habitat types; e.g., *Pinus ponderosa*/*Agropyron spicatum*. Mesic associations are characterized by a delayed onset of soil drought.

Six climax *Pinus ponderosa* associations have been identified in the Blue Mountains province.¹⁸ The *Pinus ponderosa*/*Agropyron spicatum* and *Pinus ponderosa*/*Purshia tridentata*/*Agropyron spicatum* associations are often found in areas transitional between steppe or shrub-steppe and forest. In the extreme southern Blue Mountains, a *Pinus ponderosa*/*Purshia tridentata*/*Carex rossii* association is found on some coarse-textured soils. *Sitanion hystrix* and *Stipa occidentalis* are common associates in the herb-poor understory. *Pinus ponderosa*/*Elymus glaucus* communities are limited to areas adjacent to dry meadows. The *Pinus ponderosa*/*Festuca idahoensis* associations are characterized by an abundance of other grasses and sedges in the understory, including *Agropyron spicatum*, *Sitanion hystrix*, *Calamagrostis rubescens*, *Carex rossii*, and *C. geyeri*. At higher elevations, adjacent to *Abies grandis* forests, the *Pinus ponderosa*/*Carex geyeri* association occurs. Constituent species include *Cercocarpus ledifolius* and *Poa nervosa*.

Apparently, many *Pinus ponderosa* stands on the eastern slopes of Washington's Cascade Range (Rummell 1951; Weaver 1961) and in the Blue Mountains (Hall 1967) have an understory dominated by *Calamagrostis rubescens* or mixed *Calamagrostis* and *Carex geyeri*. Hall¹⁹ identified two communities of this type in the Blue Mountains, one with herbaceous associates (e.g., *Arnica cordifolia*, *Hieracium albiflorum*, and *Carex concinnoides*), the other with herbs and a shrubby layer of *Symphoricarpos albus*, *Spiraea*, and *Rosa*. However, *Pinus ponderosa* is seral to *Pseudotsuga menziesii* or *Abies grandis* in these Blue Mountains communities and, perhaps, in most *Pinus*/*Calamagrostis* communities in the Washington Cascades as well.

Understory vegetation found in *Pinus ponderosa* stands on pumice soils in south-central Oregon differs considerably from that found on nearby residual soils. Total plant cover tends to be lower, especially in the more xeric communities, and the herbaceous flora is more depauperate on pumice soils. Sclerophyllous shrubs such as *Arctostaphylos patula*²⁰ and *Ceanothus velutinus* assume much more importance in these areas (fig. 99).

Communities occurring on pumice soils, in order of increasing effective moisture, are (Dyrness and Youngberg 1966):

Pinus ponderosa/*Purshia tridentata*,
Pinus ponderosa/*Purshia tridentata*/*Festuca idahoensis*,
Pinus ponderosa/*Purshia tridentata*-
Arctostaphylos patula,
Pinus ponderosa/*Ceanothus velutinus*-
Purshia tridentata, and
Pinus ponderosa/*Ceanothus velutinus*.

With the exception of the seral *Pinus*/*Ceanothus*, these communities are considered to be

¹⁹ F. C. Hall, personal communication.

²⁰ This taxon has been variously identified as *Arctostaphylos patula* Greene, *A. parryana* var. *pinetorum* (Rollins) Wiesel. & Schr., *A. patula* ssp. *Platphylla* (Gray) P. V. Wells, and *A. obtusifolia* Piper. These revisions were made to distinguish the nonsprouting types prevalent in eastern Oregon from the crown-sprouting *Arctostaphylos patula*. For convenience, we will refer to this entire group as *Arctostaphylos patula* Greene.

¹⁸ F. C. Hall (1967) and personal communication.

Figure 99. — Sclerophyllous shrubs such as *Ceanothus velutinus* are important understory species in *Pinus ponderosa* stands on pumice soils in south-central Oregon; a *Pinus ponderosa*/*Ceanothus velutinus* community.

Figure 100. — *Pinus ponderosa*/*Purshia tridentata* communities in the central Oregon pumice region are characterized by open stands with little *Pinus* regeneration.

edaphic climaxes because of the immaturity of the pumice soils. The *Pinus/Purshia* community is situated at lowest elevations and is characterized by open stands having little advance pine regeneration (fig. 100). Grass and herbaceous cover is sparse; characteristic species are *Stipa occidentalis*, *Sitanion hystrix*, *Gayophytum diffusum*, and *Cryptantha affinis*. The *Pinus/Purshia/Festuca* community occurs on finer textured soils derived from water-lain pumice deposits. Numerous dense stands of *Pinus ponderosa* seedlings and saplings are present in the understory. Characteristic species include *Stipa occidentalis*, *Carex rossii*, *Achillea millefolium* var. *lanulosa*, *Paeonia brownii*, and *Eriophyllum lanatum*.

The *Pinus/Purshia-Arctostaphylos* community is situated at slightly higher elevations than the *Pinus/Purshia* and is accompanied by greater amounts of tree reproduction and seral *Pinus contorta*. This community shares many species with the *Pinus/Purshia*, but has additional herbs such as *Phacelia heterophylla*, *Fragaria cuneifolia*, and *Epilobium angustifolium*. In the *Pinus/Ceanothus-Purshia* community, *Ceanothus velutinus* replaces *Arctostaphylos patula* in the shrub layer. More abundant tree reproduction and occasional patches of *Salix* sp. indicate more mesic conditions. Characteristic grasses and herbs are *Stipa occidentalis*, *Carex rossii*, *Sitanion hystrix*, *Apocynum androsaemifolium*, and *Hieracium cynoglossoides*. In the *Pinus/Ceanothus* community *Abies concolor* generally dominates the tree reproduction (fig. 99) and is, therefore, assumed to be climax (Volland 1963; Dyrness and Youngberg 1966). The *Pinus/Ceanothus* type is restricted to higher elevations, and characteristic species include *Chimaphila umbellata* and *Pyrola picta*.

On residual soils in south-central Oregon, *Festuca idahoensis* is much more widespread, generally dominating the herbaceous layer under *Pinus ponderosa* stands (Dealy 1969). Apparently, the climatic climax in this area is represented by the *Pinus ponderosa/Purshia tridentata/Festuca idahoensis* association. On residual soils, this association is characterized by herbaceous species such as *Balsamorhiza sagittata* and *Hieracium cynoglossoides*, which are absent in pumice soil areas.

Successional Patterns

The importance of fire in shaping the vegetation within the *Pinus ponderosa* Zone is stressed by virtually every ecologist who worked there. Fire scars at the base of almost every large tree offer abundant evidence of repeated fires. Before fire control was initiated about 1900, fires burned through *Pinus ponderosa* stands at intervals variously reported as 8 to 20 years (Weaver 1955, 1959; Soeriaatmadja 1966; Hall 1967). Generally, these were ground fires which consumed only surface organic debris, including branches and down trees, a portion of the understory vegetation, and many of the young tree seedlings.

Because *Pinus ponderosa* is more fire resistant than most associated tree species, past fires have had a profound effect on its distribution. Although young *Pinus ponderosa* seedlings are readily killed by fire, older trees possess thick bark which offers effective protection from fire damage. Competing tree species, such as *Abies grandis* and *Pseudotsuga menziesii*, are considerably less fire tolerant, especially in the sapling and pole size classes. As a result, periodic fires in the past served to maintain *Pinus ponderosa* in ecotonal areas where, without fire disturbance, the climax tree species would have attained dominance (Weaver 1955, 1959, 1961). Fire control activities during the past 60 to 70 years have, on the moister sites, resulted in gradual replacement of *Pinus ponderosa* by such species as *Abies concolor*, *A. grandis*, *Libocedrus decurrens*, and *Pseudotsuga menziesii* (Swedberg 1961; Johnson 1961; West 1969).

Fire has also influenced the understory vegetation. Several workers reported that burning substantially reduces shrub cover and increases grass cover, especially on more xeric sites (Brayshaw 1965; Hall 1967; Daubenmire and Daubenmire 1968). *Purshia tridentata* is probably most readily eliminated of the common shrubs, although on some sites fire reduction and consequent competition from increases in canopy density may have the same effect (Sherman 1966). On the other hand, the shrubs *Arctostaphylos patula* and *Ceanothus velutinus* may increase in importance following severe fires (fig. 101) since heat gener-

Figure 101. — Fires in *Pinus ponderosa* forests on the east slope of Oregon's Cascade Range may give rise to communities dominated by sclerophyllous shrubs such as *Arctostaphylos patula* and *Ceanothus velutinus*.

Figure 102. — Dense, stagnated thickets of *Pinus ponderosa* saplings are common on shallow, stony soils in the *Pinus ponderosa* Zone; these are frequently attributed to the exclusion of periodic, natural wildfires during the last 50 years.

ated by burning aids in germination of seeds of these species (Gratkowski 1962; Johnson 1961). In the absence of fire, these species apparently perpetuate themselves, at least in pumice soil areas, by vegetative regeneration (Dyrness 1960).

Dense, stagnated stands of *Pinus ponderosa* saplings are common throughout the zone (fig. 102), especially on shallow, stony soils of low productivity. These stands have been attributed to fire exclusion during the past half century (Weaver 1955, 1959, 1961). It is claimed that, previously, periodic fires regulated amounts of advance regeneration and resulted in the open, grassy, parklike stands that early settlers described. However, Daubenmire and Daubenmire (1968) feel that the dense, patchy, episodic reproduction in their grassy *Pinus ponderosa* associations cannot be completely attributed to fire control since a patchy structure is absent in *Pinus/Symphoricarpos* and *Pinus/Physocarpus* stands. Furthermore, it is possible that many *Pinus ponderosa* thickets actually originated with fires. Brayshaw (1965) observed that burning immediately preceding a heavy seed year assisted establishment of unusually numerous pine seedlings by greatly reducing competition from other vegetation. West (1968) reported that at least 15 percent of *Pinus ponderosa* seedlings develop from unrecovered rodent caches in central Oregon (fig. 103).

In many areas, there is a strong tendency for climax *Pinus ponderosa* forests to be even aged by small groups rather than to be truly uneven aged. Daubenmire and Daubenmire (1968) commented that grassy *Pinus ponderosa* stands consist of "... a mosaic of dense patches of trees, each tending to be distinctive in height and age."

Heavy livestock grazing has, in some respects, effects on understory vegetation opposite to those of burning. That is, heavy grazing pressures often favor shrubs at the expense of grass cover. For example, Brayshaw (1965) reports that heavy grazing may extend the *Symphoricarpos* type into areas formerly dominated by *Agropyron*. On the other hand, grazing in *Pinus/Symphoricarpos* stands may eliminate all native shrubs and herbs, resulting in a sward of *Poa pratensis* and *P. compressa* (Daubenmire and Daubenmire 1968). Changes

Figure 103. — *Pinus ponderosa* seedlings often develop from unrecovered seed caches of rodents in the Oregon Cascade Range.

in grass species may also occur as a result of grazing pressure. Understories in the *Pinus ponderosa*/*Festuca idahoensis* association in northeastern Washington can be shifted, apparently irreversibly, to domination by *Bromus tectorum*, *Linaria dalmatica*, and *Hypericum perforatum* (Daubenmire and Daubenmire 1968).

Logging in the *Pinus ponderosa* Zone is usually carried out on a single-tree selection basis. Most often, older trees, which are more susceptible to attack by the western pine beetle (*Dendroctonus brevicomis*) are removed first, leaving the younger, more vigorous trees in the stand as growing stock (fig. 104). Selective logging of *Pinus ponderosa* in areas transitional to *Abies grandis* or *A. concolor* substantially accelerates the successional trend towards dominance by these climax tree species. Some forest managers attempt to reserve these sites for the growth of *Pinus ponderosa* through the removal of *Abies* seed sources wherever practical (Volland 1963).

Logging also affects the understory vegetation and reproduction of *Pinus ponderosa*. In one study (Garrison and Rummell 1951; Garrison 1961, 1965), selective logging by tractors reduced herb and shrub coverage by 33 percent, denuding some areas and burying others in slash. The understory required about 14 years to recover to near its original condition. Deforestation generally results in dominance by those understory species present before logging, with invading species playing only a very minor role in the postdisturbance period (Daubenmire 1952); a notable exception is *Crataegus douglasii* on *Pinus*/*Symphoricarpos* sites (Daubenmire and Daubenmire 1968).

Figure 104. — Logging in the *Pinus ponderosa* Zone is usually carried out on a selective basis to eliminate overmature, low-vigor trees (of which several are visible here) susceptible to attack by the western pine beetle (Pringle Falls Research Natural Area, Deschutes National Forest, Oregon).

Figure 105. — *Pinus ponderosa* forest and steppe or shrub-steppe often form an intricate mosaic in ecotonal areas with the communities on coarser and finer textured soils, respectively (near Tonasket, Okanogan National Forest, Washington).

Nonforested Communities

Pinus ponderosa forests form a mosaic with shrub-steppe or steppe communities in many locales (fig. 105). For example, in eastern Washington, *Pinus ponderosa* stands first appear within a matrix of steppe, and increase in extent in more mesic areas until steppe or shrub-steppe communities constitute islands within a matrix of *Pinus ponderosa* forest (Daubenmire and Daubenmire 1968). Many of the nonforest communities in the *Pinus ponderosa* Zone are identical with those found within the steppe zones, e.g., the *Purshia tridentata*/*Festuca idahoensis* association (Daubenmire 1969); others occur only in forest zones.

One of the best described *Pinus ponderosa*-steppe mosaics is that encountered in the Ochoco Mountains of eastern Oregon (Hall 1967). Hall described three associations which occur in natural forest openings:

Artemisia rigida/*Poa secunda* with *Sitanion hystrix* and *Trifolium macrocephalum* as major associates;

Artemisia arbuscula/*Agropyron spicatum* with *Poa secunda* and *Purshia tridentata* as major associates; and

Artemisia arbuscula/*Festuca idahoensis* with *Phlox douglasii*, *Balsamorhiza serrata*, and *Poa secunda* as associates.

Hall (1967) attributed the presence of these nonforested communities to soil conditions, specifically to periodic moisture saturation, heavy soils which impede tree root penetration, and soil drought during the summer. He also mentioned a *Purshia tridentata*-*Cercocarpus ledifolius*-dominated community, characteristic of rock outcrops in the lower part of the *Pinus ponderosa* Zone.

Daubenmire (1969) mentioned two communities, encountered as edaphic climaxes within the forested zones of eastern Washington. The *Artemisia rigida*/*Poa secunda* association is widely distributed on Lithosols from steppe through the *Pseudotsuga menziesii* Zone. The *Festuca idahoensis*-*Eriogonum heracleoides* association is found only in forest "parks" and includes *Antennaria rosea* and *Castilleja miniata* as characteristic species.

Severe fires or destructive logging practices can eliminate *Pinus ponderosa* and give rise to shrub-dominated communities, as mentioned earlier. Reestablishment of trees in such communities may be very slow.

"PINUS CONTORTA" ZONE

Pure, or nearly pure, stands of *Pinus contorta* are widely distributed throughout forested areas of eastern Oregon and Washington. The majority are seral, having developed after fire or logging. However, *Pinus contorta* is considered an edaphic or topoedaphic climax on many sites in the pumice plateau of south-central Oregon. Since other areas where *Pinus contorta* may be a climax tree species are small and very scattered, our *Pinus contorta* Zone will be limited to the pumice plateau. It is interesting that Moir (1969) has recently provided experimental evidence for a *Pinus contorta* Zone in the Rocky Mountains.

Pinus contorta is well known for rapid invasion of severely disturbed sites, justifying its designation as a pioneer species. Pollen analyses indicate it was one of the first trees to occupy the infertile materials deposited at the close of the last glacial period in the southern Oregon Cascades (Hansen 1946). After gradual replacement by *Pinus ponderosa* during the succeeding 25 centuries, *Pinus contorta* quickly regained dominance with the widespread deposition of Mount Mazama pumice 6,600 years ago. It has retained dominance on pumice and ash soils at several other locations in the Oregon and Central Washington Cascades (Roach 1952; Herring 1968). *Pinus contorta* forests are extensive on volcanic ash and pumice in the Blue Mountains of northeastern Oregon (Trappe and Harris 1958), but are rarely found on south slopes where this material is thin or absent. These forests are apparently fire created and generally seral to *Abies grandis*.

Pinus contorta has unusually wide ecologic amplitude — thriving on wet, poorly drained sites, as well as coarse-textured, droughty soils. After fires, prolific seeding allows it to quickly invade and establish dominance, especially on more extreme sites where competitors are absent. For this reason, pure stands of

Pinus contorta are often found only on very wet or dry soils, and the more productive, medium-textured soils support other tree species (Stephens 1966).

Environmental Features

The climate of the *Pinus contorta* Zone is characterized by (1) low summer rainfall, (2) wide diurnal temperature fluctuations, especially in the summer, and (3) a relatively short growing season (table 21). Since elevations within the zone range from approximately 1,200 to 1,525 meters, growing-season frosts are not uncommon, and much of the precipitation occurs as snow. Average annual precipitation ranges from about 350 to 700 millimeters.

Topographically, the pumice plateau includes broad, level areas in enclosed depressions, gently rolling terrain, and numerous small volcanic cones. *Pinus contorta* stands are generally on nearly level terrain in depressions locally known as lodgepole flats. Temperature measurements show that cold-air drainage from surrounding slopes often produces substantially lower nighttime temperatures in these low-lying areas. For example, Berntsen (1967) found minimum spring temperatures were as much as 4.5° C. higher on a slope supporting *Pinus ponderosa* than those registered in an adjacent *Pinus contorta* stand at the base of the slope.

Climax stands of *Pinus contorta* are found on both well and poorly drained pumice soils. All are Regosols developed in aerially deposited pumice, mostly from Mount Mazama (Crater Lake). Poorly drained soils occupy low topography in basinlike depressions or areas adjacent to intermittent streams. These soils have a dark-gray sandy loam or loam A1 horizon underlain by a light-gray to white C horizon composed of pumice gravel and sand. Depth to water table is generally 60 centimeters or less throughout the growing season. On better drained sites, the pumice soil exhibits (1) a thin, dark grayish-brown, loamy coarse sand A1 horizon underlain by (2) a yellowish-brown, gravelly, loamy coarse sand AC horizon which grades, in turn, into (3) relatively fresh, unweathered pumice gravel and sand (fig. 106).

Table 21. — Climatic data from representative stations within the *Pinus contorta* Zone

Station	Elevation	Latitude	Longitude	Temperature					Precipitation		
				Average annual	Average January	Average January minimum	Average July	Average July maximum	Average annual	June through August	Average annual snowfall
	Meters			-----	-----	Degrees C. -----			Millimeters		Centimeters
Chemult, Oreg.	1,449	43° 14'	121° 47'	5.3	-3.9	-11.1	15.3	28.2	676	66	417
Crescent, Oreg.	1,357	43° 27'	121° 42'	5.1	-3.1	-11.2	14.3	26.8	485	56	---
Lapine, Oreg.	1,336	43° 40'	121° 29'	5.6	-3.3	-10.8	15.5	29.8	361	64	---

Source: U. S. Weather Bureau (1965a) and Johnsgard (1963).

Forest Composition

Four communities have been identified in the *Pinus contorta* Zone (Youngberg and Dahms 1969):

Pinus contorta/*Arctostaphylos uva-ursi*,
Pinus contorta/*Purshia tridentata*/
Festuca idahoensis,
Pinus contorta/*Purshia tridentata*, and
Pinus contorta/*Purshia tridentata*-
Ribes cereum.

The *Pinus*/*Arctostaphylos* community grows on poorly drained soils and is rich in grasses and herbs. Characteristic species include *Ribes cereum*, *Fragaria cuneifolia*, *Trifolium longipes*, and *Festuca idahoensis*. The *Pinus*/*Purshia*/*Festuca* community occurs on seasonally wet soils and includes such species as *Ribes cereum*, *Fragaria cuneifolia*, *Sitanion hystrix*, and *Carex rossii*. Both *Pinus*/*Purshia* (fig. 107) and *Pinus*/*Purshia*-*Ribes* communities appear on well-drained sites where *Pinus contorta* is climax because of low temperatures. Understory cover in the *Pinus*/*Purshia* type is sparse with characteristic species (e.g., *Stipa occidentalis*, *Sitanion hystrix*, and *Carex rossii*) similar to those occurring in nearby *Pinus ponderosa*/*Purshia tridentata* stands.

Figure 106. — Better drained pumice soils in south-central Oregon typically have dark-colored A1 and AC horizons overlying the lighter colored gravelly C; note the abrupt boundary between Mazama pumice and buried soil.

Figure 107. — The *Pinus contorta*/*Purshia tridentata* community is widespread in the central Oregon pumice region; *Pinus contorta* achieves climax status on poorly drained sites and in frosty depressions in this area (Pringle Falls Research Natural Area, Deschutes National Forest, Oregon).

Figure 108. — *Pinus contorta* regeneration is often excessive on disturbed sites or in decadent stands, resulting in dense, stagnated patches of saplings.

Species composition of the *Pinus/Purshia-Ribes* community is similar to that of the *Pinus/Purshia* except for the addition of *Ribes cereum* and *Fragaria cuneifolia*.

Successional Patterns

Kerr (1913) first reported the interesting forest patterns in this area. Pure stands of *Pinus contorta* occupy depressions and broad, level areas at lower elevations, but on every hill and slight rise in topography it is replaced by *Pinus ponderosa*. Munger (1914) concluded that *Pinus contorta* owed its widespread distribution to frequent fires and contended that it was continually encroaching on sites previously occupied by *Pinus ponderosa*. Later, however, the effects of fire were discounted when soil investigations disclosed that many sites supporting pure stands of *Pinus contorta* were subject to permanent or fluctuating high water tables (Tarrant 1953). Further study of the area revealed many sites where climax stands of *Pinus contorta* were growing on well-drained soils. Since these

were generally located in enclosed depressions suggestive of frost pockets, it was postulated that *Pinus contorta* occupied these sites because of its greater resistance to low temperatures, especially during the early growing season (Youngberg and Dyrness 1959). Berntsen (1967) confirmed this hypothesis and indicated selection for *Pinus contorta* occurs during seed germination. Emerging *Pinus contorta* seedlings were appreciably more resistant to low temperatures than *Pinus ponderosa* seedlings.

Consequently, two types of climax *Pinus contorta* stands have been recognized: (1) an edaphic climax in poorly drained soil areas, and (2) a topoedaphic climax in frost pocket depressions where the soil is often well drained. The transition between nearly pure stands of *Pinus contorta* and those of *Pinus ponderosa* on adjacent slopes is often strikingly abrupt, although there frequently is a narrow band where the two species intermingle. Climax *Pinus contorta* stands are generally even aged and nearly pure, except for occasional clumps of *Populus tremuloides* in poorly drained areas. As stands reach old age and

begin to break up, they are quickly replaced by abundant *Pinus contorta* seedlings (fig. 108). Cones in these populations are nonserotinous; therefore, seed fall occurs virtually every year (Mowat 1960).

Nonforested Communities

Numerous wet meadows are interspersed with *Pinus contorta* stands at lowest elevations within the zone (fig. 109). These meadows are on very poorly drained pumice soils and exhibit a mesic flora as a result of the shallow water table. Principal grasses are *Poa* spp., *Deschampsia caespitosa*, and *Sitanion hystrix*. In addition, *Juncus* spp. and sedges such as *Carex praeegracilis* and *Carex nebrascensis* are common. Herbaceous species vary appreciably depending on grazing pressure; however, two of the more common are *Trifolium longipes* and *Ranunculus occidentalis* (Dyrness 1960).

"PSEUDOTSUGA MENZIESII" ZONE

Associations in which *Pseudotsuga menziesii* is climax are the next zonal step in some areas. In most of eastern Washington and adjacent British Columbia, a *Pseudotsuga menziesii* Zone is apparently well developed (Daubenmire 1952, 1966; Daubenmire and Daubenmire 1968; Brayshaw 1965). In eastern Oregon, it is conjectural (West 1964, 1969; Swedberg 1961) or absent (Dyrness and Youngberg 1966; Hall 1967), except in parts of the Wallowa Mountains (Johnson 1959; Head 1959). A typical elevational range for the zone is 600 to 1,300 meters in northeastern Washington. The *Pseudotsuga menziesii* Zone correlates with the Interior Douglas-fir Zone in British Columbia (Krajina 1965) and the lower part of the Canadian Life Zone (Barrett 1962).

The *Pseudotsuga menziesii* Zone normally abuts the *Abies grandis* and *Pinus ponderosa* Zones at its upper and lower limits, respectively (table 16). In places, climax *Pinus ponderosa* forests may be absent and the *Pseudotsuga menziesii* Zone borders shrub steppe; this is particularly common on fine-textured soils in north-central Washington. In other locations, *Abies grandis* forests are ab-

sent and *Abies lasiocarpa* abuts the upper limits of the *Pseudotsuga menziesii* Zone.

Environmental Features

The *Pseudotsuga menziesii* Zone is more mesic than the *Pinus ponderosa* Zone. Temperatures undoubtedly average cooler and annual precipitation higher (Krajina 1965), although Daubenmire (1956) could not identify climatic criteria distinguishing the zones at their ecotone. It is known that soil moisture conditions are more favorable in the *Pseudotsuga menziesii* Zone (Daubenmire 1968b; McMinn 1952; Brayshaw 1965).

Forest Composition

Pseudotsuga menziesii, *Pinus ponderosa*, *P. contorta*, and *Larix occidentalis* are the major tree species in the *Pseudotsuga menziesii* Zone (fig. 110). *Quercus garryana* may be present along the flanks of the Cascade Range from about 45° to 47° north latitude. *Libocedrus decurrens* also occurs from Mount Hood south. *Populus tremuloides* and *Juniperus occidentalis* are minor associates.

Pseudotsuga menziesii associations have been identified only in eastern Washington and the Wallowa Mountains (Daubenmire

Figure 109. — Numerous wet meadows dominated by grasses and sedges are interspersed with *Pinus contorta* stands at lower elevations in the *Pinus contorta* Zone (Bear Flat between Chemult and Silver Lake, Oregon).

Figure 110. — Mixed stands of *Pseudotsuga menziesii* and *Larix occidentalis* are common in parts of the *Pseudotsuga menziesii* Zone; note reproduction of the climax *Pseudotsuga* (Colville National Forest, Washington).

Figure 111. — *Pseudotsuga menziesii* replacing *Pinus ponderosa* (Meeks Table Research Natural Area, Snoqualmie National Forest, Washington).

1952; Daubenmire and Daubenmire 1968; Johnson 1959; Head 1959). Daubenmire recognized two associations with shrubby understories in his study area. The *Pseudotsuga menziesii*/*Symphoricarpos albus* association has an understory dominated by low shrubs: *Symphoricarpos albus*, *Spiraea betulifolia*, var. *lucida*, *Rosa woodsii*, and *R. nutkana*. Taller shrubs belonging to the *Physocarpus* union (Daubenmire 1952) are absent. Similar communities were noted by Johnson (1959). The *Pseudotsuga menziesii*/*Physocarpus malvaceus* association includes the aforementioned shrubs as understory constituents and *Physocarpus malvaceus* and *Holodiscus discolor*.

The *Pseudotsuga menziesii*/*Calamagrostis rubescens* association is probably the most widespread, existing in the Wallowa Mountains (Head 1959) as well as in eastern Washington (Daubenmire and Daubenmire 1968). It has a nearly shrub-free understory, dominated by *Calamagrostis rubescens* along with other herbs such as *Carex concinnoides*, *C. geyeri*, and *Arnica latifolia*. Daubenmire and Daubenmire (1968) have recognized a phase of this type in which *Arctostaphylos uva-ursi* is an understory dominant. Similar forest communities occur in adjacent British Columbia (Brayshaw 1965).

Successional Patterns

Any of the four major tree species — *Pseudotsuga menziesii*, *Pinus ponderosa*, *P. contorta*, and *Larix occidentalis* — may dominate forest stands in the *Pseudotsuga menziesii* Zone. *Pseudotsuga menziesii* is climax (fig. 111), but the other three are better adapted to fires, which were common prior to 1900. Hence, any of these species may form pure or nearly pure stands, depending upon fire history and available seed source. This is one of the zones in which fire protection and selective logging of *Pinus ponderosa* are accelerating natural trends toward elimination of the pine.

As mentioned, a zone of climax *Pseudotsuga menziesii* forest is largely conjectural on the eastern slopes of the central Oregon Cascade Range. There are *Pinus ponderosa* forests with *Pseudotsuga menziesii* and *Libocedrus decurrens* reproduction (West 1964, 1969;

Swedberg 1961; Sherman 1969) suggesting either one or both are climax. However, at least small numbers of *Abies grandis* seedlings are normally present whenever significant numbers of *Pseudotsuga* are encountered. The question thus remains whether habitats with potential climax communities of *Pseudotsuga menziesii* exist in this area or whether the zonal sequence is *Pinus ponderosa*-*Abies grandis*. A better case can be made for climax *Libocedrus decurrens* habitats in at least some areas [see West's (1964, 1969) Warm Springs transect and Sherman (1969)]. *Libocedrus* appears tolerant of more xeric habitats than *Pseudotsuga menziesii* and is more shade tolerant than *Pinus ponderosa*.

The *Pseudotsuga menziesii* Zone definitely seems to be absent in south-central Oregon and the Ochoco and Blue Mountains (Hall 1967). Hall recognized no association in which *Pseudotsuga menziesii* was a major climax dominant.

"ABIES GRANDIS" ZONE

The *Abies grandis* Zone is the most extensive midslope forest zone in the Oregon and southern Washington Cascade Range and Blue Mountains of eastern Oregon. The *Abies grandis* Zone typically occurs at 1,100 to 1,500 meters in the central Oregon Cascade Range, 1,500 to 2,000 meters in the Ochoco and Blue Mountains (Hall 1967), and 1,650 to 2,000 meters (*Abies concolor* Zone) in south-central Oregon (Dyrness and Youngberg 1966). The *Abies grandis* Zone has no counterpart in British Columbia, and climax *Abies grandis* forests are included in the *Tsuga heterophylla* series in the northern Rocky Mountains (Daubenmire and Daubenmire 1968). This zone is analagous to the upper part of Merriam's Canadian Life Zone (Barrett 1962) and the forests within Kuchler's (1964) Grand Fir-Douglas-Fir type.

The *Abies grandis* Zone is typically bounded by the *Abies lasiocarpa* Zone at its upper limits and the *Pseudotsuga menziesii* or *Pinus ponderosa* Zones at its lower limits. However, locally at higher elevations or on more mesic sites in the Cascade Range, it may abut forests in which *Abies amabilis*, *Tsuga heterophylla*,

Thuja plicata, or *Tsuga mertensiana* are climax. At its lower limits, it may be adjacent to *Artemisia* steppe without an intervening belt of climax *Pseudotsuga menziesii* or *Pinus ponderosa* (Hall 1967).

Environmental Features

The *Abies grandis* Zone provides the most moderate environmental regime of any of the east-side forest zones (except for the areas where *Tsuga* or *Thuja* are present) (table 22). Neither moisture nor temperature conditions are extreme. Precipitation is generally higher and temperatures lower than in lower forested zones. Daubenmire (1956, 1968b) concluded that differences in summer dryness and soil drouth differentiate the *Abies grandis* and *Tsuga heterophylla* from the *Pseudotsuga menziesii* associations. Soil drouth is of minor ecologic significance in the *Abies grandis* Zone (Daubenmire 1968b, McMinn 1952). The *Abies grandis* Zone is distinguished climatically from subalpine forests by its higher temperatures (Daubenmire 1956) and lesser accumulations of snow.

Soils generally exhibit minimal development in the *Abies grandis* Zone but are relatively deep largely due to accumulations of volcanic ash throughout much of the zone's range. The dominant soil processes are podzolic, and typical great soil groups are Gray Wooded, Brown Podzolic, and Western Brown Forest. Regosolic soils with A-C profile sequences in pumice or ash parent materials are also common. Thin (2 to 5 cm.), mull-type humus layers are typical along with relatively thin, brown or dark-brown, weakly to moderately acid A1 horizons. Continuous bleached A2 horizons (bleicherde) are not common. Clay eluviation is minimal in B horizons which are distinguished primarily by color. *Abies concolor* sites in the pumice region are distinguished by A1-AC-C sequences. A horizons average only 30 centimeters thick; they are generally slightly acid (pH 6.2) with 8 to 9 percent of organic matter.

Forest Composition

Major tree species in the *Abies grandis* Zone are *Abies grandis* (or *A. concolor*), *Pinus*

Table 22. — Climatic data from representative stations in the vicinity of the *Abies grandis* Zone

Station	Eleva- tion	Lati- tude	Longi- tude	Temperature					Precipitation		
				Average annual	Average January	Average January minimum	Average July	Average July maximum	Average annual	June through August	Average annual snowfall
	Meters			----- Degrees C. -----					Millimeters		Centi- meters
Parkdale, Oreg.	530	45°31'	121°36'	8.4	-1.3	5.1	17.6	26.9	1,064	43	231
Meacham, Oreg.	1,234	45°30'	118°24'	6.4	-3.6	-7.1	17.6	25.4	835	115	396
Minam, Oreg.	1,092	45°41'	117°36'	--	--	--	--	--	632	82	--
Mount Adams Ranger Station, Wash.	597	46°00'	121°32'	8.1	-2.1	-6.1	18.4	28.6	1,157	44	309
Lake Wenatchee, Wash.	600	47°50'	120°48'	--	--	--	--	--	988	51	450
Plain, Wash.	549	47°46'	120°40'	7.2	-4.6	-9.7	18.3	28.2	632	43	--

Source: U. S. Weather Bureau (1965a, b).

ponderosa, *P. contorta*, *Larix occidentalis*, and *Pseudotsuga menziesii*. Any of the four associates listed here may dominate seral forest stands. Many other species are present in limited numbers or in localized areas such as *Picea engelmannii*, *Abies lasiocarpa*, *Libocedrus decurrens*, *Pinus lambertiana*, *P. monticola*, *Tsuga mertensiana*, and *Abies magnifica* var. *shastensis*.

Composition of *Abies grandis* (or *A. concolor*) associations has been studied in eastern Washington (Daubenmire 1952; Daubenmire and Daubenmire 1968), the central Oregon Cascade Range (Swedberg 1961; Sherman 1969; West 1964), the Ochoco and Blue Mountains (Hall 1967), the Wallowa Mountains (Johnson 1959; Head 1959), and south-central Oregon (Dyrness and Youngberg 1966). Most *Abies grandis* associations can be related to two major groups: (1) *Abies grandis*/*Pachistima myrsinites* and *Abies grandis*/*Vaccinium membranaceum*²¹ (Daubenmire 1952; Daubenmire and Daubenmire 1968; Head 1959; Swedberg 1961; Hall 1967) and (2) the *Abies grandis*/*Calamagrostis rubescens* (Hall 1967; Johnson 1959).

The *Abies grandis*/*Pachistima myrsinites* and */Vaccinium membranaceum* associations have well-developed herbaceous understories. Characteristic species include:

Shrubs — *Rosa gymnocarpa*, *Pachistima myrsinites*, *Ribes lacustre*; and

Herbs — *Bromus vulgaris*, *Galium triflorum*, *Smilacina stellata*, *Thalictrum occidentale*, *Arnica cordifolia*, *Mitella stauropetala*, *Arenaria macrophylla*, *Hieracium albiflorum*, *Linnaea borealis*, *Adenocaulon bicolor*, *Anemone piperi*, *A. lyallii*, *Viola glabella*, *Trillium ovatum*, *Clintonia uniflora*, *Asarum caudatum*, *Lupinus latifolius*, and *Rubus lasiococcus*.

Under very dense canopies, a group of sciophytes forms a sparse understory (fig. 112)

²¹ F. C. Hall (personal communication) has described three related *Abies grandis* associations in the Blue Mountains province to which we have referred by the collective term, "the *Abies grandis*/*Vaccinium membranaceum* type." These are: *Abies grandis*/*Vaccinium membranaceum* (by far the most widespread), *Abies grandis*/*Bromus vulgaris* (southern Blue Mountains), and *Abies grandis*/*Linnaea borealis* (northern Blue Mountains).

[the *Pirola*-*Corallorrhiza* union of Oosting and Billings (1943) again]; typical species are *Chimaphila umbellata*, *C. menziesii*, *Corallorrhiza maculata*, *Pyrola asarifolia*, *P. secunda*, *P. picta*, *Monotropa hypopitys*, and *Listera convallarioides*.

The *Abies grandis*/*Calamagrostis rubescens* association is typically found on volcanic ash soils in the Ochoco and Blue Mountains.²² It also has a herb-rich understory characterized by *Calamagrostis rubescens*, *Carex geyeri*, *C. concinnoides*, *Arnica cordifolia*, *Lupinus caudatus* and *Hieracium albiflorum*. Hall²³ and Johnson (1959) have recognized variants in which understory shrubs such as *Spiraea*, *Rosa*, *Salix*, and *Symphoricarpos albus* are typical. On upper slopes in the Ochoco and Blue Mountains, the *Abies*/*Calamagrostis* and *Abies*/*Vaccinium* associations generally occupy the south and north slopes, respectively.

The *Abies concolor*/*Ceanothus velutinus* association of south-central Oregon has much higher shrub and lower herbaceous coverage than the *Abies grandis* associations (Dyrness and Youngberg 1966). *Ceanothus velutinus*, *Arctostaphylos nevadensis*, and *A. patula* are the major shrubs. *Stipa occidentalis*, *Carex*

²² F. C. Hall (1967) and personal communication.

²³ F. C. Hall (1967) and personal communication.

Figure 112. — Understory vegetation is sparse under dense stands in the *Abies grandis* Zone; *Abies grandis*-*Pseudotsuga menziesii* forest in the Blue Mountains of Oregon (range pole is marked in 1-foot segments).

Figure 113. — *Pinus contorta* is a common seral species in the *Abies grandis* zone of eastern Oregon; *Abies grandis* and *Picea engelmannii* succeeding *Pinus contorta* in the Blue Mountains of Oregon (range pole is marked in 1-foot segments).

rossii, *Sitanion hystrix*, *Gayophytum diffusum*, *Cryptantha affinis*, *Fragaria cuneifolia*, *Epilobium angustifolium*, *Chimaphila umbellata*, and *Apocynum androsaemifolium* make up most of the sparse herbaceous layer.

Successional Patterns

Data on early successional stages following logging or burning on *Abies grandis* habitats are scarce. *Cirsium vulgare* was a major species on a clearcut and burned area in the Wallowa Mountains (Pettit 1968); *Ceanothus sanguineus*, *Physocarpus malvaceus*, *Spiraea betulifolia*, var. *lucida*, *Astragalus* sp., *Fragaria* spp., *Carex rossii*, *Epilobium paniculatum*, *Bromus tectorum*, and *Rumex acetosella* were also noted. Later in preforest succession, shrub communities are encountered in the *Abies grandis* Zone, at least in eastern Washington and northern Idaho (Daubenmire 1952; Mueggler 1965). Typical shrub invaders (Daubenmire and Daubenmire 1968) are *Salix scouleriana*, *Spiraea betulifolia* var. *lucida*, *Ceanothus velutinus*, *C. sanguineus*, *Amelanchier alnifolia*, *Sambucus cerulea*, and *S. racemosa*

var. *melanocarpa*. Mueggler (1965) related the composition of these shrub communities to type of originating disturbance and age.

Throughout much of the *Abies grandis* and *Abies concolor* Zones in the Cascade Range, *Ceanothus velutinus* is again a major brush-field dominant, often behaving ecologically as described for southwestern Oregon. *Ceanothus velutinus* and species such as *Castanopsis chrysophylla* and *Arctostaphylos patula* may form a sclerophyll scrub following wildfires in the central and southern Oregon *Abies grandis*-*A. concolor* Zones.

As mentioned, *Pinus contorta*, *P. ponderosa*, and *Pseudotsuga menziesii* often dominate seral stands in the *Abies grandis* Zone. Fires were most important in instigating these stands, although they were generally less frequent than in the more xeric *Pinus ponderosa* Zone. In the Blue Mountains, *Pinus contorta* is a common seral species on *Abies grandis*/*Vaccinium membranaceum* habitats and *Pinus ponderosa* is typically successional to *Abies grandis*/*Calamagrostis rubescens*.²⁴ Most of the *Pinus contorta* forest described by Trappe and Harris (1958) is seral to *Abies grandis* (fig. 113). Sites occupied by *Pinus contorta* forests may go through a period of dominance by *Pseudotsuga menziesii* or *Picea engelmannii* prior to development of climax *Abies grandis* forests. *Pinus ponderosa* is the typical seral species on *Abies concolor*/*Ceanothus velutinus* habitats (Dyrness and Youngberg 1966) and *Pseudotsuga menziesii* is typical on *Abies grandis*/*Pachistima myrsinites* habitats in eastern Washington (Daubenmire 1952).

Larix occidentalis is a major seral dominant in parts of the Blue Mountains (*Abies grandis*/*Vaccinium membranaceum* habitats) and eastern Washington and can form a nearly pure type following repeated fires (fig. 114). *Picea engelmannii* is not ubiquitous in the *Abies grandis* Zone, but may be common in some areas; it is replaced only gradually since reproductive vitality is often high. *Pinus monticola* is an important species in localized areas. *Libocedrus decurrens* occurs sporadically as a seral species within the zone in the Cascade Range south of Mount Hood.

²⁴ F. C. Hall, personal communication.

Figure 114. — *Larix occidentalis* forms nearly pure, seral stands in parts of the *Abies grandis* and *Pseudotsuga menziesii* Zones after fires; 30-year-old *Larix* reproduction on an old burn (near Twin Lakes, Colville National Forest, Washington).

Most of the seral species attain optimum growth in the *Abies grandis* Zone. Daubenmire (1961) found that *Pinus ponderosa* grew better on *Abies grandis*/*Pachistima myrsinites* habitats than on sites where *Pseudotsuga menziesii* or *Pinus ponderosa* were climax. In Montana, *Larix occidentalis* grew better in the *Abies grandis* than in the cooler *Abies lasiocarpa* or drier *Pseudotsuga menziesii* Zones (Roe 1967). Selective logging of *Pinus ponderosa* within the *Abies grandis* Zone has produced strong successional pressures toward its elimination since reproduction is composed of more tolerant species. Forestry practices are shifting toward clearcutting of old-growth forest, partially to eliminate rotted *Abies* and partially to favor the *Pinus*.

Abies grandis or *A. concolor* are the major climax species. In some areas, *Pseudotsuga menziesii* may play a minor climax role. There are locations where *Abies grandis*-dominated forests occur which are themselves subject to replacement by the more tolerant *Abies amabilis*, *Tsuga heterophylla*, or *Thuja plicata*; these are considered elsewhere in this paper.

Special Types

Nonforest communities are common in many parts of the *Abies grandis* Zone. Some of these (discussed earlier) are successional to forest and others are climax shrub or grassland communities which are covered in the discussions of the *Pinus ponderosa* and *Abies lasiocarpa* Zones. Mountain meadows are the most important single group of permanent nonforest communities in the *Abies grandis* Zone.

Mountain meadow communities are conspicuous, essentially permanent, herbaceous communities, typically found on relatively gentle topography along and near the heads of stream courses (fig. 115). These are not sub-alpine communities and, though associated with zones from the *Abies lasiocarpa* to *Pinus ponderosa*, they are probably most typical of the *Abies grandis* Zone.

Deschampsia caespitosa, a perennial grass, typifies the dense herbaceous cover of climax mountain meadow communities (Reid and Pickford 1946) (fig. 116). Other major species

Figure 115. — Mountain meadows are common on gentle topography along and near the heads of stream courses in the *Abies grandis* Zone; they constitute an important grazing resource.

Figure 116. — *Deschampsia caespitosa*, a perennial grass, dominates mountain meadow communities in good condition.

are *Festuca rubra*, *Carex* spp., *Juncus balticus*, *Aster occidentalis*, *Polygonum bistortoides*, *Trifolium* spp., and *Senecio* spp.

Most *Deschampsia* meadows have been overgrazed by domestic livestock (fig. 115) and have deteriorated into other kinds of communities. Reid and Pickford (1946) recognized four major steps in deterioration: (1) perennial grass or climax, (2) mixed grass and weed (fig. 117), (3) perennial weed, and (4) annual weed. Serious erosional problems are associated with these changes in community composition. Major dominants in the perennial weed stage are *Senecio* spp., *Achillea millefolium* var. *lanulosum*, *Wyethia* spp., *Potentilla* spp., *Aster occidentalis*, *Taraxacum officinale*, and *Poa pratensis*. The annual weed stage is characterized by *Bromus mollis*, *Muhlenbergia filiformis*, *Polygonum douglasii*, and *Madia* spp. Development of climax vegetation from these deteriorated communities is usually extremely slow, even if grazing is completely eliminated.

"TSUGA HETEROPHYLLA" ZONE

Habitats where *Tsuga heterophylla* or *Thuja plicata* are climax are encountered on the eastern slopes of the Cascade Range in Washington and northern Oregon. These constitute the *Tsuga heterophylla* Zone. It is essentially an eastern extension of the widespread coastal *Tsuga heterophylla* Zone, although the composition of seral forests and understory is somewhat altered. This inland *Tsuga heterophylla* Zone correlates with the Interior Western Hemlock Zone in British Columbia (Krajina 1965, Bell 1965, Smith 1965) and the *Tsuga heterophylla* series of Daubenmire and Daubenmire (1968).

Interior *Tsuga heterophylla* and *Thuja plicata* forests are most common in the eastern Washington Cascades at elevations between 800 and 1,200 meters. In Oregon, they are increasingly rare to their southern limit at about 44° 30' north latitude. Both species are absent from the Blue and Wallowa Mountains. Habitats sufficiently mesic to support *Tsuga heterophylla* or *Thuja plicata* are very often disjunct, occurring within areas of *Abies grandis* Zone.

Environmental Features

Environmental data are not available for the *Tsuga heterophylla* Zone; however, the zone occurs under what appears to be the most equitable climatic regime of all the interior forest zones. Krajina (1965) indicated a precipitation range of 560 to 1,700 millimeters and mean annual temperatures of 2.5° to 7.5° C. for the zone in British Columbia. Major great soil groups are Brown Podzolic, Podzolic, and Gray-Brown Podzolic, including some with gleyed subsoils.

Forest Composition

Forest tree species found within the *Tsuga heterophylla* Zone include most of those found in the adjacent *Abies grandis* and *Abies lasiocarpa* (or *Tsuga mertensiana*) Zones. *Pseudotsuga menziesii*, *Abies grandis* and *Pinus monticola* are the most abundant seral species (table 17). It is in this zone in northern Idaho that the well-known western white pine (*Pinus monticola*) forests are best developed (fig. 118). *Thuja plicata* and *Tsuga heterophylla* are typically present together, although *Thuja plicata* is sometimes found on sites too xeric for *Tsuga heterophylla*.

Daubenmire and Daubenmire (1968) have described four *Tsuga* or *Thuja* associations in eastern Washington and northern Idaho: *Tsuga heterophylla*/*Pachistima myrsinites*, *Thuja plicata*/*Oplopanax horridum*, *Thuja plicata*/*Pachistima myrsinites*, and *Thuja plicata*/*Athyrium filix-femina*. The *Tsuga heterophylla*/*Pachistima myrsinites* is the most important. *Thuja plicata* is usually present, but it does not reproduce well. The understory is composed of the floristically rich *Pachistima* union (Daubenmire 1952) discussed earlier, the most constant species being *Pachistima myrsinites*, *Tiarella unifoliata*, *Vaccinium membranaceum*, *Clintonia uniflora*, and *Dryopteris linnaeana*. The *Thuja plicata*/*Oplopanax horridum* association is found in low-lying situations in association with the *Tsuga*/*Pachistima* association. Stands belonging to the *Thuja*/*Oplopanax* have a dense understory including a shrub layer dominated by *Oplopanax horridum*, many members of the *Pachisti-*

Figure 117. — Most mountain meadows have been severely overgrazed by domestic livestock, resulting in major compositional changes.

ma union, *Athyrium filix-femina*, and *Dryopteris dilatata*. Successional relations in stands are unclear; reproductive vigor variously indicates *Tsuga heterophylla* and/or *Thuja plicata* may be climax. Associations comparable to both of these were recognized by Bell (1965).

The *Thuja plicata*/*Pachistima myrsinites* and *Thuja plicata*/*Athyrium filix-femina* associations constitute a comparable pair outside the range of *Tsuga heterophylla*. The *Pachistima* union typifies the understory in the first and a variety of mesic-site herbs and *Alnus sinuata* in the second. *Abies grandis* is a major long-lingering seral species in the *Thuja plicata*/*Pachistima myrsinites* association; *Thuja plicata* is the major climax species in both.

Successional Patterns

Early stages in forest succession on disturbed sites have been discussed by Daubenmire (1952), Daubenmire and Daubenmire (1968) and Mueggler (1965). Shrub communities are

Figure 118. — Many seral species, such as the *Pinus monticola* shown here, attain their best development in the mesic *Tsuga heterophylla* and *Abies grandis* Zones.

often conspicuous prior to development of a tree overstory. Most of the *Tsuga heterophylla* Zone on the eastern slopes of the Cascade Range is occupied by relatively youthful stands in which the seral *Abies grandis*, *Pseudotsuga menziesii*, *Pinus monticola*, *Larix occidentalis*, *Pinus contorta*, and *Picea engelmannii* are dominant. *Tsuga heterophylla* and *Thuja plicata* are often represented only by reproduction in these stands.

The successional relationships between *Tsuga heterophylla*, *Thuja plicata*, and *Abies grandis* are complex. Daubenmire and Daubenmire (1968) state:

Three species of trees in the *Tsuga* series [*Abies grandis*, *Tsuga heterophylla*, *Thuja plicata*] show . . . an ability to continue reproduction . . . but all have distinctive autecologies so that for the most part only one is the climax dominant in any one habitat type.

It is on this basis they recognize each as the major climax in one or more of the *Tsuga heterophylla* series of associations.

"ABIES LASIOCARPA" ZONE

Climax forests of *Abies lasiocarpa* characterize the subalpine forest zone at many locations in eastern Washington and Oregon. The *Abies lasiocarpa* Zone is best represented on the high secondary ranges extending east from the crest of the Washington Cascade Range (Franklin and Trappe 1963), in the Okanogan Highlands province of northeastern Washington, and in the Blue and Wallowa Mountains of northeastern Oregon (Daubenmire 1952; Johnson 1959; Head 1959). Its lower elevational boundary is normally 1,500 meters or more in the Cascade Range and 1,300 to 1,700 meters elsewhere. The *Abies lasiocarpa* Zone is a more continental analog of the *Tsuga mertensiana* Zone with which it merges in the Cascade Range. It is the local representative of the very widespread Rocky Mountain *Abies lasiocarpa*-*Picea engelmannii* forests (Oosting 1956) and correlates with the Englemann Spruce-Subalpine Fir Zone recognized in British Columbia (Krajina 1965), the *Abies lasiocarpa* Zone of the northern Rocky Mountains (Daubenmire and Daubenmire 1968), and Merriam's Hudsonian Life Zone (Barrett 1962).

The *Abies lasiocarpa* Zone may be bounded at its lower limits by forests in which *Tsuga heterophylla*, *Thuja plicata*, *Abies grandis*, or *Pseudotsuga menziesii* are climax, depending upon locale. Where mountain masses are sufficiently high, it extends upward to the subalpine-alpine ecotone and, in these cases, typically includes an area of forest-meadow parkland. As with the *Tsuga mertensiana* Zone, we will concern ourselves only with the closed forest portion of the *Abies lasiocarpa* Zone in this section.

Abies lasiocarpa-*Picea engelmannii* forests are often conspicuous in frost pockets and other habitats characterized by drainage and accumulation of cold air. These often occur well below the expected elevational limits for the *Abies lasiocarpa* Zone. In the Washington Cascade Range, the best developed *Abies lasiocarpa*-*Picea engelmannii* forest occur in glaciated valley bottoms and not on the mountain slopes.

Environmental Features

Environmental data are extremely scarce for the *Abies lasiocarpa* Zone. It is the coolest and moistest of the forested zones. Cool summers, cold winters, and development of deep winter snowpacks are more important factors than total precipitation in differentiating the *Abies lasiocarpa* from lower forested zones, however. Mean annual temperatures probably range from about 2.5° to 4.5° C. Climatically, the *Abies lasiocarpa* Zone is more continental than the *Tsuga mertensiana* Zone, with lower winter and higher summer temperatures and lesser precipitation and snowpack accumulations, on the average.

Zonal soils in the *Abies lasiocarpa* Zone are generally Podzols or Brown Podzols with well-developed but relatively thin mor humus layers. Regosolic and lithosolic soils are also common in some localities. Soils are more acid than in the lower forested zones — typically pH 4.5 to 5.9.

Forest Composition

Major forest tree species in the *Abies lasiocarpa* Zone are *Abies lasiocarpa*, *Picea engelmannii*, and *Pinus contorta* (fig. 119). *Pseudo-*

tsuga menziesii, *Abies grandis*, *Larix occidentalis*, and *Pinus monticola* may be conspicuous lower in the zone; *Pinus albicaulis* and, sometimes, *Larix lyallii* are abundant higher in the zone. *Pinus ponderosa* and *Populus tremuloides* are relatively uncommon. *Abies amabilis*, *A. procera*, and *Tsuga mertensiana* may be encountered as minor stand components, although locally *Tsuga mertensiana* dominates stands disjunct from the *Tsuga mertensiana* Zone.

Daubenmire and Daubenmire (1968) recognized five *Abies lasiocarpa* associations in eastern Washington and northern Idaho: *Abies lasiocarpa*/*Pachistima myrsinites*, *Abies lasiocarpa*/*Xerophyllum tenax*, *Abies lasiocarpa*/*Menziesia ferruginea*, *Abies lasiocarpa*/*Vaccinium scoparium*, and *Pinus albicaulis*-*Abies lasiocarpa*. The first three associations tend to form a topographic series within the zone: the *Abies*/*Pachistima* occupies the lowest part of the zone, *Abies*/*Xerophyllum* is typical of upper south slopes and ridgetops, and *Abies*/*Menziesia* occupies the wettest and coolest sites — north slopes and ravines. The *Abies*/*Pachistima* association has representatives of the *Pachistima* union (Daubenmire 1952) as its understory; *Clintonia uniflora* and *Galium triflorum* are especially well represented. Many species occur only in this association and nowhere else in the *Abies lasiocarpa* Zone: *Acer glabrum*, *Arnica cordifolia*, *Hieracium albiflorum*, *Amelanchier alnifolia*, *Aster conspicuus*, *Mitella stauropetala*, *Actaea rubra*, *Clintonia uniflora*, *Coptis occidentalis*, *Viola glabella*, *Adenocaulon bicolor*, *Rubus parviflorus*, *Arenaria macrophylla*, *Galium triflorum*, and *Spiraea betulifolia*. In the *Abies*/*Xerophyllum* association, the depauperate understory is dominated by *Xerophyllum tenax* and *Vaccinium membranaceum*. The *Abies*/*Menziesia* association has a well-developed shrub layer in which *Menziesia ferruginea* is sometimes combined with *Rhododendron albiflorum* or *Ledum glandulosum*. In northern Idaho, Daubenmire and Daubenmire (1968) have also recognized comparable *Menziesia ferruginea* and *Xerophyllum tenax* associations in which *Tsuga mertensiana* is the characteristic tree species.

The *Abies lasiocarpa*/*Vaccinium scoparium* association is widespread (Daubenmire and

Daubenmire 1968; Johnson 1959) and seems particularly common in drier locales. *Vaccinium scoparium* is the major understory species; typical associates are *Juniperus communis*, *Vaccinium membranaceum*, *V. caespitosum*, *Carex* spp., *Hieracium albiflorum*, *Arnica cordifolia*, and *Aster* spp. (Illingworth and Arlidge 1960).

The *Pinus albicaulis*-*Abies lasiocarpa* (Daubenmire and Daubenmire 1968) and *Abies lasiocarpa*-*Picea engelmannii* (Head 1959) associations described within the zone are relatively open forest types associated with the subalpine parkland.

Successional Patterns

Pre-forest successional developments in the *Abies lasiocarpa* Zone are poorly known. Herbaceous stages characterized by species such as *Epilobium angustifolium* may occur. Shrub communities similar to those found in lower forested zones (Daubenmire and Daubenmire 1968; Mueggler 1965) may develop on the most moderate sites; i.e., those potentially occupied by the *Abies lasiocarpa*/*Pachistima myrsinites* association. Elsewhere, disturbed areas are usually dominated by the same species that make up the forest understory — e.g., *Xerophyllum tenax*, *Vaccinium membranaceum*, and *Menziesia ferruginea*.

Successional relationships among tree species in the *Abies lasiocarpa* Zone are better understood. *Pinus contorta* is one of the most ubiquitous and conspicuous of the seral species. *Picea engelmannii* is also very important in many areas and conflicting opinions are common regarding its successional status. In the Rocky Mountains, some workers have concluded *Picea engelmannii* is a climax species (Oosting and Reed 1952), others that it is subclimax (Fowells 1965). Daubenmire and Daubenmire (1968) state that *Picea engelmannii* is a major climax species only in the *Abies lasiocarpa*/*Vaccinium scoparium* association; it is a persistent long-lived seral species in five other associations and a minor climax component in the *Abies lasiocarpa*/*Pachistima myrsinites* association. The subtle trend toward elimination of *Picea engelmannii* was not considered in an earlier treatment (Daubenmire

1952) in which *Picea engelmannii*-*Abies lasiocarpa* associations and a zone were proposed. Franklin and Mitchell (1967) concluded *Abies lasiocarpa* generally replaces *Picea engelmannii* on the eastern slopes of Washington's Cascade Range.

The relationship between *Tsuga mertensiana* and *Abies lasiocarpa* is not completely clear. Locally, *Tsuga mertensiana* is a dominant species in the northern Rocky Mountains *Abies lasiocarpa* Zone (Daubenmire and Daubenmire 1968; Habeck 1967). Sometimes it appears to be the major climax species, but in others reproduction of *Abies lasiocarpa* is also abundant. Factors differentiating sites with and without *Tsuga mertensiana* in this area have not been determined (Daubenmire and Daubenmire 1968). In some parts of Washington's eastern Cascade Range, and even as far south as central Oregon (Sherman 1969), disjunct populations of *Tsuga mertensiana* occur mixed with *Abies lasiocarpa* in which resolution of the successional question is not clear. Within the main *Tsuga mertensiana* Zone in the Cascade Range, *Abies lasiocarpa* is almost always seral, however (Franklin and Mitchell 1967).

Hence, *Abies lasiocarpa* is the major and often sole climax species within the closed forest portion of the *Abies lasiocarpa* Zone of eastern Washington and Oregon. Only occasionally do *Picea engelmannii* or *Tsuga mertensiana* challenge its dominance there.

Special Types

Permanent nonforest communities dominated by herbs or shrubs occur within the forest matrix. Many of these are clearly extensions of subalpine meadow types and will be discussed later. Two, more characteristic of the closed-forest portion of *Abies lasiocarpa* Zone, are grassy parks and *Artemisia tridentata* var. *vaseyana* communities.

Grassy parks or balds are frequently encountered on or near ridgetops in the *Abies lasiocarpa* Zone (Daubenmire and Daubenmire 1968; Secor 1960; Johnson 1959; Hall 1967) (fig. 120). These are typically dominated by grasses such as *Agropyron spicatum*, *Festuca idahoensis*, and *F. viridula*, although

Figure 119. — Mixed stands of *Abies lasiocarpa* and *Picea engelmannii* typify the subalpine forests in more continental mountain areas.

many other species may be conspicuous — e.g., *Hieracium albertinum*, *Arenaria capillaris* var. *americana*, and *Polygonum phytolaccaefolium* in northern Idaho and *Artemisia arbuscula*, *Phlox* spp., *Poa secunda*, and *Achillea millefolium* in the Ochoco Mountains. A

lower fringe of *Prunus emarginata* is sometimes present. These grasslands are associated with south-facing slopes and are more xeric than adjacent forest stands (Daubenmire 1968b). Whatever their origin, wind-transfer of moisture (snow) from these balds and soil

Figure 120. — Wind transfer of snow and soil drought are important in maintaining grassy balds or parks frequently found on south slopes near ridgetops in the *Abies lasiocarpa* Zone (photo courtesy R. Daubenmire).

drouth seem important in maintaining them as topographic climaxes.

Artemisia tridentata var. *vaseyana*, a cold-requiring diploid ancestor of *Artemisia tridentata* var. *tridentata*, characterizes another group of nonforest communities associated with the *Abies lasiocarpa* Zone (as well as lower forest zones) (Daubenmire 1969; Johnson 1959; Hall 1967). *Carex* spp., *Agropyron spicatum*, and *Festuca idahoensis* are typical associates.

STEPPE VEGETATION

In the rain shadow of the Cascade Range is a large region of steppe and shrub-steppe vegetation including most of central and southeastern Washington and much of eastern Oregon. This is the region of the bunchgrass and sagebrush communities (Shantz and Zon

1924). Typical community dominants include shrubs such as *Artemisia tridentata*, *Purshia tridentata*, *Artemisia rigida*, *A. arbuscula*, and *Atriplex confertifolia*, large perennial grasses such as *Agropyron spicatum*, *Festuca idahoensis*, *Elymus glaucus*, and *Stipa thurberiana*, and alien invaders such as *Bromus tectorum*, *Poa pratensis*, and *Elymus caput-medusae*. Forest vegetation is generally confined to mountain slopes with sufficient precipitation, either regionally (e.g., approaching the Rocky Mountains) or locally (e.g., higher elevations on interior ranges such as the Blue Mountains).

Climatically, the steppe areas can be typified as arid to semiarid with low precipitation, warm-to-hot dry summers, and relatively cold winters (table 23). Some marine influences are still felt (conditions are not so extreme as those in the Great Basin, for example), but continental-type climatic conditions prevail.

Table 23. — Climatic data from representative stations within steppe areas of eastern Washington and Oregon

Station	Eleva- tion	Lati- tude	Longi- tude	Temperature					Precipitation		
				Average annual	Average January	Average January minimum	Average July	Average July maximum	Average annual	June through August	Average annual snowfall
	Meters			-----	-----	Degrees C.	-----	-----	Millimeters		Centi- meters
Ellensburg, Wash.	526	47°02'	120°31'	8.4	-4.7	-9.3	20.6	28.9	230	33	--
Moses Lake, Wash.	368	47°07'	119°12'	9.2	-3.9	-8.3	21.3	30.7	212	35	--
Kennewick, Wash.	119	46°13'	119°08'	12.0	-2	-4.3	24.2	33.3	190	24	34
Pullman, Wash.	776	46°46'	117°12'	8.6	-2.2	-5.3	20.1	28.1	610	75	102
The Dalles, Oreg.	31	45°36'	121°12'	11.8	.1	-2.5	22.7	30.6	389	23	--
Pendleton, Oreg.	455	45°41'	118°51'	11.2	-7	-4.3	23.1	33.2	320	44	47
Burns, Oreg.	1,265	43°35'	119°03'	7.8	-4.1	-9.7	20.2	29.8	289	43	122
Ontario, Oreg.	654	44°03'	116°58'	10.6	-2.5	-7.3	24.5	35.1	236	24	--
Lakeview, Oreg.	1,455	42°11'	120°21'	7.8	-2.6	-7.9	19.2	29.2	364	41	136

Source: U. S. Weather Bureau (1956, 1965a,b).

A great variety of soils occurs in the steppe region. The zonal sequence from the hottest, driest sites to the wettest of the steppe habitats would run through Sierozem, Brown, Chestnut, Chernozem and Prairie great soil groups. From soils with light-colored, thin A horizons poor in organic matter and calcium accumulations high in the profile (Sierozem), the soils grade to thick, very dark-brown to black A horizons rich in organic matter in which calcium carbonate accumulations may be deep in the profile or absent (Prairie). At the same time, the wide variety of intrazonal soils includes most notably those having accumulations of salts (Solonchak) and large amounts of exchangeable sodium (Solonetz).

Fire and grazing were apparently of limited importance in steppe vegetation before arrival of Europeans and their livestock (Daubenmire 1969, Heady 1968). Large herds of ungulates were never an integral part of the steppe communities in the Northwest as they were in the Great Plains. The limited grazing was confined to deer, wapiti, and antelope until arrival of the horse in the early 1700's. Cattle were introduced in the steppe vegetation in the early 19th century and sheep about 1860, and the latter were generally more abundant until about 1940.²⁵ Aboriginal man had little need to use fire in the steppes in contrast to forested regions or areas where he used fire as an adjunct in hunting.

Man has wrought massive changes in the steppe vegetation of the Northwest by the cultivation, animals, and plants he introduced. The best lands are cultivated almost entirely for wheat, peas, and similar crops. Some of the poorer lands, cropped for a time, have since been abandoned. Additional lands lacking sufficient natural moisture have been "reclaimed" through irrigation, most notably in the Columbia Basin province. Remaining lands have been subjected to various degrees of grazing and often overgrazed by domestic and feral livestock. Overgrazing was considered a serious problem more than 60 years ago (Griffiths 1902, 1903; Cotton 1904). Man-caused range fires were common in many steppe areas and still occur occasionally.

²⁵ Gerald S. Strickler, personal communication.

To appreciate how grazing and wildfire can affect the natural vegetation, one should consider features of some of the major climax dominants and alien invaders (Daubenmire 1969). These features are central to any consideration of succession and successional status in the steppes.

1. Some of the major shrub species, notably *Artemisia* spp. and *Purshia tridentata*, are fire sensitive and can be temporarily eliminated from a site by burning.²⁶
2. Most of the major large perennial grasses, e.g., *Agropyron spicatum* and *Festuca idahoensis*, are not adapted to heavy grazing by ungulates. They evolved in an environment in which such animals were sparsely represented. They rarely recover to their former status after severe overgrazing, but are relatively insensitive to fire.
3. Two alien species, *Bromus tectorum* and *Poa pratensis*, are well adapted to parts of the steppe region. They will invade or increase under heavy grazing pressure (in their respective areas) and relinquish occupied sites to native vegetation either very slowly or not at all when grazing pressures are lifted. Hence, shifts to these species are generally only reversed by human intervention. Recently, another alien species, *Elymus caput-medusae* subsp. *asper*, has entered parts of the steppe region and threatens to further alter the ecology of the region.

The vegetation of the Northwestern steppes has been studied by many scientists. Early generalized accounts include those of Colville (1896), Griffiths (1902, 1903), Cotton (1904), Weaver (1917), Shantz and Zon (1924), and Aldhous and Shantz (1924). In recent years, more detailed reports cover synecological aspects of steppe and shrub-steppe vegetation in eastern Washington (Daubenmire 1940, 1942, 1956, 1966; McMinn

²⁶ Steppe shrub dominants are generally nonsprouting; *Purshia tridentata* exhibits widely varying sprouting behavior, depending on environmental conditions (Blaisdell 1953; Blaisdell and Mueggler 1956; Driscoll 1963).

1952; Cooke 1955; Daubenmire and Colwell 1942) and portions of eastern Oregon (Poulton 1955; Eckert 1957; McKell 1956; Tueller 1962). Anderson (1956) has divided eastern Oregon into ecological provinces; Humphrey (1945) has considered major range types in both States; and Billings (1951) constructed a general zonal approach to the Great Basin which is relevant to a part of southeastern Oregon.

From these accounts, it is possible to recognize numerous diverse community types, including many which would qualify as climatic climaxes (zonal associations) within a part of their range. In general, no single sequence of zonal belts of vegetation applies throughout the steppe region. Consequently, we focus attention on the steppes of Washington's Columbia Basin province, where the entire vegetational mosaic is most fully understood. Here a cross section of the communities encountered in the steppe regions of the Pacific Northwest can be illustrated and related; some similarities and differences between this region and the other major steppe region in central and southeastern Oregon will be suggested.

Columbia Basin Province of Eastern Washington

The Columbia Basin province of eastern Washington is a large, contiguous area of steppe and shrub-steppe vegetation — over 6,000,000 hectares. The vegetational mosaic of this area has been thoroughly studied (see earlier citations), and except as noted, this discussion is abstracted from the most recent regional account (Daubenmire 1969).

ZONAL ASSOCIATIONS

Nine zonal associations, communities which can occur as climatic climaxes, have been recognized in the steppe region of the Columbia Basin province. These are the:

Artemisia tridentata/*Agropyron spicatum*,
Artemisia tridentata/*Festuca idahoensis*,
Agropyron spicatum-*Poa secunda*,
Agropyron spicatum-*Festuca idahoensis*,
Festuca idahoensis/*Symphoricarpos albus*,

Festuca idahoensis/*Rosa nutkana*,
Artemisia tripartita/*Festuca idahoensis*,
Festuca idahoensis-*Hieracium*
cynoglossoides, and
Purshia tridentata/*Festuca idahoensis*
 associations.

The last five associations are found on the periphery of the steppe region near its contact with forest vegetation. These tend to be lush, meadowlike communities with conspicuous amounts of large perennial grasses and broad-leaved forbs. The term "meadow steppe" has often been applied to these types. The other four zonal associations lie in the more arid interior of the Columbia Basin province. Vegetation is more open and forbs are less conspicuous in these communities.

The nine zonal associations have differentiated in response to differences in temperature and total and seasonal distribution of precipitation. Where they occur on modal sites, as climatic climaxes, they characterize or distinguish regional units or zones of steppe vegetation. Four of these zones — the *Artemisia*/*Agropyron*, *Artemisia*/*Festuca*, *Agropyron*-*Festuca*, and *Festuca*/*Symphoricarpos* Zones — are encountered along a transect beginning in the driest part of the Columbia Basin province and extending eastward up the gentle slope of the Columbia plateau to foothills of the Rocky Mountains. They provide an exemplary cross section of the zonal associations. The composition of some stands found along this transect belonging to the zonal associations is shown in table 24. This tabulation includes only pristine stands found on zonal habitats (sites with gently undulating topography and deep, well-drained silt loam soils). The following association descriptions amplify this tabulation and encompass all stands belonging to the association under consideration, since any of these zonal associations may occur as a topographic climax in one or more adjacent zones.

Artemisia tridentata/*Agropyron* *spicatum* Association

The driest of the zones has as a climatic climax the *Artemisia*/*Agropyron* association (fig. 121). Four layers are found in this association: (1) a shrub layer composed principally

Figure 121. — The *Artemisia tridentata*/*Agropyron spicatum* association is the climatic climax in driest parts of the Columbia basin steppe region; the range pole is 4 feet tall and marked in 6-inch segments (photo courtesy Range Management, Oregon State University).

of *Artemisia tridentata* var. *tridentata* and 1 to 2 meters in height — very small amounts of other shrubs such as *Chrysothamnus viscidiflorus*, *C. nauseosus* var. *albicaulis*, *Artemisia tripartita* or *Grayia spinosa* may be present; (2) a layer of caespitose perennial grasses dominated by *Agropyron spicatum* — variable amounts of *Stipa comata*, *S. thurberiana*, *Poa cusickii*, or *Sitanion hystrix* may be present; (3) a layer of plants within 1 decimeter of the soil surface, including species such as *Poa secunda*, *Bromus tectorum*, and *Lappula redowskii*; (4) a surface crust typically composed of crustose lichens and acrocarpous mosses (e.g., *Tortula brevipes*, *T. princeps*, and *Aloida rigida*). Variation of *Artemisia tridentata* coverage in this association is from 5 to 26 percent, and this variation is not believed related to past grazing. Seasonal sequences in phenology are marked with mosses, small perennials, and annuals develop-

ing earliest and larger grasses and forbs flowering in June. Shrubs remain active all summer by tapping permanent moisture supplies in the subsoil; flowering extends from late June (*Tetradymia canescens*) to October (*Artemisia tridentata*).

This association is found on a wide variety of soils including those belonging to the Sierozem, Brown and Brown-Chestnut (intergraded) great soil groups.

Successional changes in the *Artemisia*/*Agropyron* Zone are most often associated with grazing, fire, or cultivation. Grazing most seriously affects the larger perennial grasses since they are preferred by cattle and sheep and are not adapted to withstand grazing. Heavy grazing tends, therefore, to eliminate *Agropyron spicatum*, *Festuca idahoensis*, *Poa cusickii*, etc., and to increase annual grasses, particularly *Bromus tectorum*. The smaller perennial *Poa secunda* is generally not signifi-

Figure 122. — *Artemisia tridentata* is sensitive to fire since it is a nonsprouter; the patchiness of *Artemisia* in this *Artemisia/Agropyron* community suggests the influence of past burning (photo courtesy Range Management, Oregon State University).

Figure 123. — A monotonous, herbaceous cover dominated by perennial grasses characterizes the climatic climax of the *Agropyron spicatum-Poa secunda* community (photo courtesy Range Management, Oregon State University).

cantly affected, and *Artemisia* suffers mechanical damage only if the grazing animals are cattle. *Bromus tectorum* will apparently relinquish ground only very slowly once grazing pressure is lifted. Fire seriously affects only one dominant, *Artemisia tridentata*. It is often completely killed by range fires, and although the remaining dominants can regenerate from subterranean organs, *Artemisia* must reoccupy the site by invasion and gradual expansion, a relatively slow process (fig. 122). A combination of both burning and overgrazing can result in development of an annual rangeland dominated by *Bromus tectorum* in which *Chrysothamnus nauseosus* may be the only significant shrub. Cropped and abandoned fields will also develop a community dominated by *Bromus tectorum*, but the tumbleweeds *Salsola kali* and *Sisymbrium altissimum* may dominate the old field for a year or two while the *Bromus* population builds up.

The *Artemisia/Agropyron* association is the most extensive element in the steppe mosaic of eastern Washington, and essentially identical communities are widely distributed elsewhere, including British Columbia (Tisdale 1947), central Oregon (Eckert 1957), southern Idaho, and Montana. Three other zonal associations (*Purshia/Festuca*, *Artemisia tripartita/Festuca*, and *Artemisia tridentata/Festuca*) can occur as topographic climaxes on moister sites within the *Artemisia/Agropyron* Zone. Conversely, the *Artemisia/Agropyron* association can occur as a topographic climax on drier sites in adjacent zones.

Artemisia tridentata/ Festuca idahoensis Association

East along the transect, a second large perennial grass, *Festuca idahoensis*, is added to climatic climax communities, indicating presence in a second zone typified by the *Artemisia tridentata/Festuca idahoensis* association (table 24). The significance of this addition has been discussed by Daubenmire (1966); the addition indicates the moisture balance of the macroclimate in this zone is more favorable for plant growth.

The only significant floristic difference between the *Artemisia/Festuca* and *Artemisia/Agropyron* association is the addition of *Festuca idahoensis* as a major grass (table 24).

Artemisia tridentata remains the dominant shrub. Soils associated with this association belong to the Brown or Solonetz great soils groups. Response of the *Artemisia/Festuca* community to fire or grazing is essentially the same as that of the *Artemisia/Agropyron* association.

Agropyron spicatum-Festuca idahoensis Association

Eventually a point is reached on transect where *Artemisia tridentata* drops from climax communities on zonal habitats (table 24). This leaves a monotonous herbaceous cover dominated by perennial grasses (fig. 123). Again, this change indicates an improved moisture régime (Daubenmire 1966) and a third zone, the *Agropyron spicatum-Festuca idahoensis* Zone.

The definitive *Agropyron spicatum-Festuca idahoensis* association is dominated by these two perennial grasses plus *Poa secunda*. There are few forbs; and *Artemisia tri-*

dentata, *A. tripartita*, *Symphoricarpos albus*, and *Rosa* spp. do not occur in this association (table 24). *Opuntia polyacantha* may be a minor climax species south of the Snake River. The *Agropyron-Festuca* association occurs on a wide variety of soils, including those belonging to Brown, Chestnut, Chernozem, Planosol, Solodized-Solonetz, and Prairie-Grumosol (intergraded) great soil groups. Fire has little effect on this community since neither of the dominants is seriously affected. As in the prior associations, *Bromus tectorum* is the main increaser with grazing.

Festuca idahoensis/Symphoricarpos albus Association

The fourth and moistest of the steppe zones is the *Festuca idahoensis/Symphoricarpos albus* Zone (fig. 124). Here, a whole group of species is added (table 24), producing a luxurious meadow-steppe (Daubenmire 1966). This zone has as its climax the *Festuca idahoensis/Symphoricarpos albus* association.

Figure 124. — The vegetational mosaic in the *Festuca idahoensis/Symphoricarpos albus* Zone includes herb-rich meadow steppe dominated by *Festuca* and *Agropyron spicatum*, thickets of low shrubs such as *Symphoricarpos* and *Rosa*, and taller thickets of *Crataegus douglasii* in moist draws (photo courtesy Range Management, Oregon State University).

Figure 125. — The climax grasslands of the *Festuca idahoensis*/*Symphoricarpos* Zone in the Columbia basin are sometimes referred to as meadow-steppe because of the dense cover of sod-forming grasses and the abundance of broad-leaved herbs (photo courtesy R. Daubenmire).

The *Festuca*/*Symphoricarpos* association has a dense herbaceous layer dominated by *Festuca idahoensis* and *Agropyron spicatum* (fig. 125). The *Agropyron spicatum* on this site is rhizomatous, not caespitose as is the case in drier associations. A rich assemblage of other perennial grasses and broad-leaved forbs are associated with these grasses (table 24). Some of the more conspicuous are *Hieracium albertinum*, *Lupinus sericeus*, *Castilleja lutescens*, *Balsamorhiza sagittata*, *Helianthella uniflora*, *Astragalus arrectus*, *Poa ampla*, *Iris missouriensis*, *Potentilla gracilis*, *Geranium viscosissimum* and *Koeleria cristata*. The assemblage of grasses and forbs discussed here is common to the peripheral ring of meadow-steppe associations referred to earlier. It is the shrub component (or lack of same) which dis-

tinguishes them. Dwarfed sterile *Rosa nutkana*, *R. woodsii*, and *Symphoricarpos albus* are present but inconspicuous. Associated soils belong to the Chernozem, Prairie, and Planosol great soil groups.

Within the herbaceous matrix described above are thickets of shrubs 0.5 to 3 meters in height which have been recognized as a *Symphoricarpos albus* phase of the *Festuca*/*Symphoricarpos* association. These thickets may be 4 to 25 meters in diameter and consist primarily of *Symphoricarpos albus*, a low marginal zone of *Symphoricarpos* around a core of *Rosa* spp., or even a core of *Prunus virginiana* with marginal belts of *Rosa* and *Symphoricarpos*. Herbaceous species are the same as in adjacent grassland, except highly sciophytic species may be purged and all are

reduced in stature. There is no evidence these shrub thickets are spreading; grassland and shrub thickets form a stable mosaic.

Fire has little effect on the *Festuca/Symphoricarpos* association, since all important species can regenerate from underground organs. Heavy grazing results in a major and irreversible change, however; perennial grasses, shrubs, and most forbs are eliminated, and an invader, *Poa pratensis*, becomes dominant. The *Poa pratensis* community is not replaced with the elimination of grazing and can become an essentially pure sward. This replacement of native grasses and herbs by *Poa pratensis* is characteristic of all habitats (except lithosolic sites) in the *Festuca/Symphoricarpos*, *Festuca/Rosa*, and lower forested zones.

ASSOCIATIONS ON SPECIALIZED HABITATS

Within the steppe region are a wide variety of habitats which have soils sufficiently unusual in physical or chemical properties to develop climax communities not assignable to any of the zonal associations. Some of these are associated with particular zones as defined by the nine zonal associations; many are not. Consequently, some of the associations typical of such sites are handled separately in this section.

Sandy or Gravelly Soils

Deep soils dominated by gravel or sand have low moisture-holding capacity. Associations found on such soils within the drier interior steppe zones share a dominance of *Stipa comata*. In this series of *Stipa comata* associations, a shrubby species is usually present: *Artemisia tridentata*, *A. tripartita*, or *Purshia tridentata*. These shrub dominants appear insensitive to soil differences so conspicuously reflected in the compositional shift of the herbaceous cover.

Lithosols

Lithosolic sites are those where soils are stony and extremely shallow to bedrock. These sites provide an extremely rigorous plant environment, with heat and drought in the summer and intense frost action (the

result of excess water) during the winter. The lithosolic series of associations have in common a carpet of *Poa secunda*, a crust of mosses and lichens, and a lithosolic substrate (fig. 126). Nearly all associations have a taller layer of shrubs, but the species vary — *Eriogonum niveum*, *E. sphaerocephalum*, *E. douglasii*, *E. compositum*, *E. thymoides*, *E. microthecum*, or *Artemisia rigida*. Many stands are outstandingly dominated by a single shrub species but others have dominance divided between several. Several plant groups — *Allium*, *Eriogonum*, *Lomatium*, Cruciferae — have their best steppe representation in the lithosolic associations.

The *Artemisia rigida/Poa secunda* association is the most widespread member of this series. It occurs on Lithosols from the *Artemisia/Agropyron* Zone to the *Pseudotsuga menziesii* Zone in eastern Washington, and south to central and southeastern Oregon.

Saline-Alkali Soils

A carpet of *Distichlis stricta* links the associations found on saline-alkali soils which are high in salts, sodium ion, and pH. *Distich-*

Figure 126. — Lithosolic sites in the Columbia basin steppe region are occupied by a series of associations of which the *Poa secunda-Eriogonum niveum* is one; range pole is 4 feet tall and marked in 6-inch segments (photo courtesy Range Management, Oregon State University).

lis is a low (herbage less than 20 cm. high), perennial, strongly rhizomatous grass. Superimposed on this sward may be an open stand of either *Sarcobatus vermiculatus* (a deciduous, succulent-leaved shrub) or *Elymus cinereus* (a large, coarse bunchgrass). Lack of a moss-lichen crust between the vascular plants is notable. Of the three dominants, *Elymus* appears least tolerant of high salinity and pH.

Crataegus douglasii Associations

On moister sites within the *Festuca/Symphoricarpos* and *Festuca/Rosa* Zones, the *Crataegus douglasii*-*Symphoricarpos albus* and *Crataegus douglasii*-*Heracleum lanatum* associations may occur. Both have a nearly complete woody plant cover 5 to 7 meters tall which is dominated by *Crataegus douglasii*. The *Crataegus*-*Symphoricarpos* association is typically found in moist draws and includes *Symphoricarpos albus* and many herbs common to the *Festuca/Symphoricarpos* association. Some examples are *Galium boreale*, *Geranium viscosissimum*, *Iris missouriensis*, and *Potentilla gracilis*. *Spiraea betulifolia*, *Crataegus columbiana*, *Prunus virginiana*, and *Amelanchier alnifolia* are often present.

The *Crataegus/Heracleum* association is found on aggraded valley floors. Understory dominants are *Heracleum lanatum*, *Hydrophyllum fendleri* var. *albifrons*, and *Urtica dioica*, singly or collectively. Only *Lomatium dissectum* is shared with the *Festuca/Symphoricarpos* or *Festuca/Rosa* associations. However, many elements more common in forested zones may be present, such as *Circaea alpina*, *Elymus glaucus*, *Geum macrophyllum*, and *Pteridium aquilinum*.

Most sites, potentially occupied by these associations, have been heavily grazed and replaced with a sward of *Poa pratensis* and *Poa compressa* along with exotic forbs such as *Cirsium vulgare*, *Dipsacus sylvestris*, and *Taraxacum officinale*.

Populus tremuloides may occur in either of these communities, and such stands are recognized as phases of the respective associations. In drier zones, *Populus trichocarpa*/*Cicuta douglasii* association replaces the *Crataegus douglasii/Heracleum lanatum* association in similar topographic situations.

Shrub/*Poa secunda* Associations

Within the lowest, driest part of the *Artemisia/Agropyron* Zone is a series of three associations found on reasonably deep, loamy soils which are drier than those on associated zonal habitats. These are the *Artemisia tridentata/Poa secunda*, *Grayia spinosa/Poa secunda*, and *Eurotia lanata/Poa secunda* associations. These associations lack a large perennial grass and, in fact, the species used in the names are often nearly the only vascular plants present. The *Eurotia lanata/Poa secunda* association is found on the hottest and driest sites of this series. It is associated with highly calcareous Regosols.

Colluvium, Alluvium, and Talus

A series of associations typified by *Rhus glabra* are found on colluvial or alluvial soils in canyons in the *Agropyron-Poa* and *Artemisia/Agropyron* Zones. Most *Rhus glabra* stands are heavily grazed, and *Bromus tectorum* and annuals such as *Erodium cicutarium* usually are understory dominants. When a dominant perennial grass is present, it can be *Agropyron spicatum*, *Sporobolus cryptandrus*, or *Aristida longiseta*.

A *Celtis douglasii/Bromus tectorum* association typifies colluvial cones and aprons in the *Agropyron-Poa* Zone. A *Grayia spinosa/Bromus tectorum* community can be found on talus in some areas. Shrub "garlands" of *Philadelphus lewisii*, *Prunus virginiana* var. *melanocarpa*, *Amelanchier alnifolia*, and *Rosa* spp. are typical talus margins in the interior steppe zones (fig. 127).

Sand Dunes

Sand dunes are a common phenomenon near the Columbia River in the lowest part of the Columbia Basin province. *Psoralea lanceolata* is found on active windward slopes of some of these dunes. *Elymus flavescens* can be found on high dune summits, and *Rumex venosus* or *Agropyron dasystachyum* on slip faces of active dunes. Stabilized dune surfaces can have communities of *Chrysothamnus nauseosus* and *C. viscidiflorus*, *Agropyron das-*

Figure 127. — Shrub garlands of *Philadelphus lewisii*, *Prunus virginiana*, and *Amelanchier alnifolia* are typically found around talus in the interior of the Columbia basin (photo courtesy R. Daubenmire).

ystachyum, *Oryzopsis hymenoides*, *Koeleria cristata*, *Poa secunda*, *Achillea millefolium* var. *lanulosa*, *Microsteris gracilis*, *Descurainia pinnata*, and *Holosteum umbellatum*. The *Artemisia tridentata*/*Stipa comata* association has been noted on very old dune surfaces. *Juniperus scopulorum* savanna is found on some of the sand dunes.

Oregon Steppe and Shrub-Steppe

Steppe and shrub-steppe communities are widespread in Oregon, dominating the entire southeastern quarter of the State and a strip around the northwestern and western margins of the Blue Mountains. The communities found in the latter area, near the Columbia River, are very similar to those described in the section on the Columbia Basin province (Poulton 1955; Anderson 1956). Therefore, we will confine this section to the shrub-

steppe of southeastern Oregon; i.e., the High Lava Plains, Basin and Range, and Owyhee Uplands provinces (fig. 2).

In some respects, the steppes of southeastern Oregon are similar to those of the Columbia Basin province: (1) both areas have hot, dry summers and cold winters; and (2) there are similar communities, e.g., the *Artemisia tridentata*/*Agropyron spicatum* and *Artemisia tridentata*/*Festuca idahoensis* associations. Contrasts between the two areas are notable, however: (1) southeastern Oregon shrub-steppes average much higher in elevation; (2) deep, loamy soils are not common in southeastern Oregon; (3) desert or salt desert shrub communities are common enough to appear on regional vegetation maps; (4) *Juniperus occidentalis* and *Cercocarpus ledifolius* occur in association with shrub-steppe; and (5) meadow-steppes of sod-forming grasses and dicotyledonous herbs, which ring much of the

Figure 128. — *Artemisia* communities dominate the shrub-steppe of southeastern Oregon; in this High Lava Plains province landscape, *Artemisia tridentata* communities occur on the hills, *Artemisia arbuscula* communities on the shallow soils of basalt flows, and *Artemisia cana* communities in seasonally ponded valley bottoms (photo courtesy Range Management, Oregon State University).

Columbia Basin province, are nearly absent. Hence, although the physiognomy and dominants of many communities are often similar, the environmental and community mosaics are different.

The steppe and shrub-steppe communities of southeastern Oregon have not been comprehensively treated. Nevertheless, from the generalized accounts of Poulton (1962), Anderson (1956), and Shantz and Zon (1924) and detailed but localized work by Eckert (1957), Dean (1960), Tueller (1962), Culver (1964), Dealy (1969), and McKell (1956), many of the important community types in the vegetational mosaic emerge.

“ARTEMISIA” COMMUNITIES

Artemisia communities dominate nearly every vegetational mosaic in southeastern Oregon's shrub-steppe (fig. 128). There are four major *Artemisia* species, each of which characterizes particular habitats:

Artemisia tridentata on the deeper soils,
Artemisia arbuscula on shallow, stony soils,
Artemisia rigida on very shallow
 soils (Lithosols), and
Artemisia cana on moister habitats.

Associations of *Artemisia tridentata*, *A. arbuscula*, and *A. rigida* have been described in detail (Eckert 1957; Culver 1964; Hall 1967); lists of characteristic species for six of these associations are provided in table 25.

Artemisia tridentata/ *Agropyron spicatum* Association

The *Artemisia tridentata*/*Agropyron spicatum* association is very similar to the Columbia Basin province association of the same name (fig. 129); it is the most widespread as-

Figure 129. — The *Artemisia tridentata*/*Agropyron spicatum* community is probably the most widespread single type in southeastern Oregon and contains the same dominants as in the Columbia basin; the range pole is 2-1/2 feet tall and marked in 6-inch segments (photo courtesy Range Management, Oregon State University).

Table 25. — Characteristic species for *Artemisia* associations found in the High Lava Plains (Eckert 1957), Owyhee Upland (Culver 1964), and southern Blue Mountains (Hall 1967) provinces

Association	Species group	High Lava Plains	Owyhee Uplands	Southern Blue Mountains
<i>Artemisia tridentata</i> /	Shrubs	<i>Artemisia tridentata</i>	<i>Artemisia tridentata</i>	
<i>Agropyron spicatum</i>	Grasses	<i>Agropyron spicatum</i>	<i>Agropyron spicatum</i>	
		<i>Poa secunda</i>	<i>Poa secunda</i>	
	Herbs	<i>Phlox diffusa</i>	<i>Lupinus sericeus</i>	
		<i>Aster scopulorum</i>	<i>Lomatium triternatum</i>	
		<i>A. canescens</i>	<i>L. macrocarpum</i>	
		<i>Chaenactis douglasii</i>	<i>Zygadenus paniculatus</i>	
		<i>Collinsia parviflora</i>	<i>Microseris troximoides</i>	
		<i>Phlox gracilis</i>	<i>Astragalus filipes</i>	
		<i>Lappula redowskii</i>	<i>A. lentiginosus</i>	
		<i>Gayophytum ramosissimum</i>		
<i>Artemisia tridentata</i> /	Shrubs	<i>Artemisia tridentata</i>	<i>Artemisia tridentata</i>	
<i>Festuca idahoensis</i>		<i>Chrysothamnus viscidiflorus</i>	<i>Chrysothamnus viscidiflorus</i>	
		<i>Symphoricarpos rotundifolius</i>		
		<i>Ribes cereum</i>		
		<i>Juniperus occidentalis</i>		
	Grasses	<i>Festuca idahoensis</i>	<i>Festuca idahoensis</i>	
		<i>Agropyron spicatum</i>	<i>Agropyron spicatum</i>	
		<i>Poa secunda</i>	<i>Poa secunda</i>	
		<i>Koeleria cristata</i>	<i>Sitanion hystrix</i>	
			<i>Bromus tectorum</i>	
			<i>Elymus cinereus</i>	
	Herbs	<i>Phlox diffusa</i>	<i>Balsamorhiza sagittata</i>	
		<i>Antennaria corymbosa</i>		
		<i>Calochortus nitidus</i>		

Table 25 — Continued

Association	Species group	High Lava Plains	Owyhee Uplands	Southern Blue Mountains
<i>Artemisia tridentata</i> /	Shrubs		<i>Artemisia tridentata</i>	
<i>Elymus cinereus</i>	Grasses	(mentioned but not described)	<i>Elymus cinereus</i>	
			<i>Poa secunda</i>	
			<i>Agropyron spicatum</i>	
			<i>Bromus tectorum</i>	
	Herbs		<i>Penstemon speciosus</i>	
			<i>P. cusickii</i>	
			<i>Thlaspi arvense</i>	
			<i>Eriogonum umbellatum</i>	
<i>Artemisia arbuscula</i> /	Shrubs	<i>Artemisia arbuscula</i>	<i>Artemisia arbuscula</i>	<i>Artemisia arbuscula</i>
<i>Agropyron spicatum</i>		<i>Eriogonum sphaerocephalum</i>		<i>Purshia tridentata</i>
		<i>Juniperus occidentalis</i>		
	Grasses	<i>Agropyron spicatum</i>	<i>Agropyron spicatum</i>	<i>Agropyron spicatum</i>
		<i>Poa secunda</i>	<i>Poa secunda</i>	<i>Poa secunda</i>
		<i>Festuca idahoensis</i>	<i>Sitanion hystrix</i>	<i>Sitanion hystrix</i>
			<i>Bromus tectorum</i>	
	Herbs	<i>Phlox diffusa</i>	<i>Penstemon aridus</i>	<i>Trifolium macrocephalum</i>
		<i>Erigeron linearis</i>	<i>Lagophylla ramosissima</i>	
		<i>Collinsia parviflora</i>		
<i>Artemisia arbuscula</i> /	Shrubs	<i>Artemisia arbuscula</i>	<i>Artemisia arbuscula</i>	<i>Artemisia arbuscula</i>
<i>Festuca idahoensis</i>		<i>Juniperus occidentalis</i>		
	Grasses	<i>Festuca idahoensis</i>	<i>Festuca idahoensis</i>	<i>Festuca idahoensis</i>
		<i>Agropyron spicatum</i>	<i>Agropyron spicatum</i>	<i>Agropyron spicatum</i>
		<i>Poa secunda</i>	<i>Poa secunda</i>	<i>Poa secunda</i>

Table 25 — Continued

Association	Species group	High Lava Plains	Owyhee Uplands	Southern Blue Mountains
	Herbs	<i>Phlox diffusa</i>	<i>Arabis holboellii</i>	<i>Phlox douglasii</i>
		<i>P. hoodii</i>	<i>Phlox diffusa</i>	<i>Balsamorhiza serrata</i>
		<i>P. longifolia</i>	<i>Erigeron linearis</i>	
		<i>Microseris troximoides</i>	<i>Astragalus miser</i>	
		<i>Antennaria dimorpha</i>	<i>Balsamorhiza hookeri</i>	
		<i>Astragalus stenophyllus</i>	<i>Agoseris heterophylla</i>	
		<i>Lupinus saxosus</i>	<i>Achillea millefolium</i>	
		<i>Trifolium gymnocarpon</i>	<i>Haplopappus stenophyllus</i>	
		<i>T. macrocephalum</i>		
<i>Artemisia rigida/</i>	Shrubs		<i>Artemisia rigida</i>	<i>Artemisia rigida</i>
<i>Poa secunda</i>	Grasses		<i>Poa secunda</i>	<i>Poa secunda</i>
			<i>Bromus tectorum</i>	<i>Sitanion hystrix</i>
			<i>Festuca pacifica</i>	
			<i>Agropyron spicatum</i>	
			<i>Sitanion hystrix</i>	
	Herbs		<i>Mimulus nanus</i>	<i>Phlox douglasii</i>
			<i>Zygadenus paniculatus</i>	

sociation in southeastern Oregon. Eckert (1957) and Culver (1964) recognized the *Artemisia tridentata*/*Agropyron* association as the climatic climax in their areas (High Lava Plains and Owyhee Uplands provinces, respectively). Eckert (1957) found it a highly variable community in which *Artemisia tridentata* was the only important shrub (average coverage 10 percent). *Agropyron spicatum* was the dominant grass and *Poa secunda* the typical associate in both localities. The component of

perennial and annual herbs differed considerably between the High Lava Plains and Owyhee Uplands provinces, however (table 25). Eckert (1957) noted an abundance of annual herbs. *Tortula ruralis* was a conspicuous mass in the leaf-fall area of the shrubs. *Festuca idahoensis* and *Stipa thurberiana* are typically minor elements, but *Festuca* and *Stipa* phases (as well as *Purshia tridentata* phases) of the association have been described or listed (Culver 1964; Eckert 1957). The *Festuca* phase

Figure 130. — Larger perennial grasses have been found to decrease under grazing pressure, although *Poa secunda* may increase, and *Artemisia tridentata* appears little affected; top, the area to the left of the fence (lacking *Agropyron spicatum*) has been continuously and heavily grazed, and the area to the right has been protected for 8 years; and bottom, an *Artemisia tridentata*/*Poa secunda* community which has developed under heavy cattle grazing (photos courtesy Range Management, Oregon State University).

Figure 131. — *Chrysothamnus viscidiflorus* dominates the abandoned cultivated land in the foreground; the *Artemisia tridentata* island (right background) has never been plowed (photo courtesy Range Management, Oregon State University).

occupies more mesic sites and the *Stipa* phase more xeric sites than the typical association.

Tueller (1962) compared grazed and ungrazed *Artemisia tridentata*/*Agropyron spicatum* stands along fence lines and in enclosures. The important perennial grasses — *Agropyron spicatum*, *Festuca idahoensis*, and *Stipa thurberiana* — decreased with grazing (fig. 130). *Poa secunda* and many of the herbs increased with grazing. *Artemisia tridentata* was indeterminant; significant changes in its status with grazing were not found. *Chrysothamnus* spp. varied in response, increasing in some cases and appearing indeterminant in others. *Bromus tectorum* or *Chrysothamnus* spp., or both, dominate many severely overgrazed areas as well as abandoned farmland (fig. 131).

Soils associated with the *Artemisia*/*Agropyron* association belonged to the Brown great soil group, were usually moderately deep (60 to 80 cm. to cemented layers or bedrock), and usually had well-developed, clay B horizons.

Artemisia tridentata/ *Festuca idahoensis* Association

The *Artemisia tridentata*/*Festuca idahoensis* association is a topographic or topoe-daphic climax on sites more mesic than those

Figure 132. — *Artemisia arbuscula* typically dominates communities on shallower, stonier soils than those found under *Artemisia tridentata*; this is an *Artemisia arbuscula*/*Festuca idahoensis* community on the High Lava Plains province of central Oregon (photo courtesy Range Management, Oregon State University).

Figure 133. — *Artemisia rigida* dominates the *Artemisia rigida*/*Poa secunda* association widespread on lithosolic sites throughout the steppes and drier forests of eastern Oregon and Washington (photo courtesy Range Management, Oregon State University).

occupied by the *Artemisia tridentata*/*Agropyron* association (Culver 1964; Eckert 1957). *Artemisia tridentata* is the dominant shrub, although *Chrysothamnus viscidiflorus* is an important minor component. *Festuca idahoensis*, *Poa secunda*, and *Agropyron spicatum* are dominant grasses. The grass and perennial herb associates differ in the two study areas (table 25). The more mesic nature of Eckert's stands is indicated by occurrence of rhizomatous *Agropyron spicatum*, *Symphoricarpos rotundifolius*, *Ribes cereum*, and *Juniperus occidentalis* as typical constituents.

In the Owyhee Uplands province, Culver (1964) found the *Artemisia tridentata*/*Festuca* association on Brown soils. In the High Lava Plains province (Eckert 1957), it was the only association found on Chestnut as well as Brown soils. In any case, these soils had higher moisture storage capacities than those supporting adjacent *Artemisia tridentata*/*Agropyron spicatum* communities.

Artemisia tridentata/*Elymus cinereus* Association

Culver (1964) describes and Eckert (1957) mentions an *Artemisia tridentata*/*Elymus cinereus* association which occurred primarily on moist alluvial bottom lands. Culver (1964) and Anderson (1956) mention occurrence of

such a type on uplands, as well. *Artemisia tridentata* and *Chrysothamnus viscidiflorus* are the characteristic shrubs. *Elymus cinereus* is always conspicuous and sometimes dominates the ground layer. Culver (1964) mentions several herbs which were restricted to this association in the Owyhee Uplands (table 25).

Artemisia arbuscula Associations

Artemisia arbuscula has a much lower growth form (1 to 4 dm.) than *A. tridentata* which also dominates large portions of the eastern Oregon shrub-steppe. Two major *Artemisia arbuscula* associations have been recognized: *Artemisia arbuscula*/*Agropyron spicatum* and *A. arbuscula*/*Festuca idahoensis* (fig. 132) (Eckert 1957; Culver 1964; Hall 1967). *Artemisia arbuscula*, *Agropyron spicatum*, and *Poa secunda* are the major species in the *Artemisia arbuscula*/*Agropyron spicatum* association. A variety of associates is present depending upon locale (table 25). *Artemisia arbuscula*, *Festuca idahoensis*, *Poa secunda*, *Agropyron spicatum*, and a variety of perennial herbs distinguish the *Artemisia arbuscula*/*Festuca idahoensis* association (table 25).

These associations typically occur with *Artemisia tridentata* communities as edaphic climaxes on shallow, stony phases of the zonal Brown soils. The *Agropyron* type occupies

more xeric sites than the *Festuca* type in the steppe area (Culver 1964; Eckert 1957). Where they occur within a forest mosaic (Ochoco Mountains), the *Agropyron* type is on about 35 centimeters of clayey soil derived from basic igneous rock and the *Festuca* type is on comparable soils from acid igneous rock (Hall 1967).

Tueller (1962) studied effects of grazing in habitats characterized by the *Artemisia arbuscula*/*Festuca idahoensis* association. He found the larger perennial grasses — *Festuca idahoensis*, *Sitanion hystrix*, *Agropyron spicatum*, and *Koeleria cristata* — decreased with grazing. *Chrysothamnus viscidiflorus*, *Poa secunda*, and a variety of herbs increased whereas amounts of *Artemisia arbuscula* remained constant under grazing.

Other *Artemisia* Associations

Several other *Artemisia*-dominated communities have been mentioned by various authors. These include:

<u>Community</u>	<u>Location</u>	<u>Source</u>
<i>Artemisia tridentata</i> - <i>Chrysothamnus</i> spp.	High Lava Plains province	Eckert (1957)
<i>Artemisia tridentata</i> - <i>Chrysothamnus nauseosus</i> / <i>Stipa thurberiana</i>	Sand hills; Owyhee Uplands province	Culver (1964)
<i>Artemisia tridentata</i> - <i>Grayia spinosa</i>	Steep, south-exposed talus; Owyhee Uplands province	Culver (1964) Dean (1960)
<i>Artemisia tridentata</i> - <i>Sarcobatus vermiculatus</i> / <i>Stipa thurberiana</i>	Slopes; High Lava Plains and Owyhee Uplands provinces	Eckert (1957) Dean (1960)
<i>Artemisia tridentata</i> / <i>Stipa comata</i> - <i>Carex</i> spp.	Sandy soils; High Lava Plains province	Eckert (1957)
<i>Artemisia tridentata</i> - <i>Purshia tridentata</i>	High Lava Plains, Basin and Range, Blue Mountains provinces	Eckert (1957) Tueller (1962) Dealy (1969)
<i>Artemisia tridentata</i> / <i>Stipa occidentalis</i> - <i>Lathyrus bijugatus</i>	Basin and Range province	Dealy (1969)
<i>Artemisia tridentata</i> - <i>Purshia tridentata</i> / <i>Festuca idahoensis</i>	Basin and Range province	Dealy (1969)
<i>Artemisia arbuscula</i> / <i>Danthonia unispicata</i>	Basin and Range province	Dealy (1969)
<i>Artemisia arbuscula</i> / <i>Koeleria cristata</i>	Basin and Range province	Dealy (1969)
<i>Artemisia cana</i> / <i>Muhlenbergia-Juncus</i>	Basin and Range province	Dealy (1969)

Artemisia rigida/ *Poa secunda* Association

Artemisia rigida is the shrub dominant of the *Artemisia rigida*/*Poa secunda* association (fig. 133). This association is widespread on lithosolic sites (Culver 1964; Hall 1967; Daubenmire 1969). *Artemisia rigida* is normally the only shrub present; average coverage was about 20 percent in the Owyhee area (Culver 1964). *Poa secunda* is the dominant grass (cover 40 percent). Other typical grasses and herbs are listed in table 25.

This association is always found on very shallow, stony soils. Hall (1967) reported 15 centimeters of soil as typical of *Artemisia rigida* habitats compared with 35 centimeters on *Artemisia arbuscula* habitats.

STATUS OF "JUNIPERUS OCCIDENTALIS"

Juniperus occidentalis is sometimes associated with *Artemisia tridentata* and *A. arbuscula* communities throughout much of central and southeastern Oregon. In the High Lava Plains province, its occurrence is related to more mesic microhabitats (Eckert 1957); *Juniperus* is typical of escarpments and rock outcrops, mesic northerly slopes (with *Artemisia arbuscula*/*Festuca idahoensis* communities), and intermittent drainage ways in this area. Soil depths are commonly greater under trees than under adjacent *Artemisia*. In some locales of the High Lava Plains province, *Juniperus occidentalis* is sufficiently common that *Juniperus* associations or phases of shrub-steppe associations are recognized; unique microcommunities and soil properties are associated with the trees (Eckert 1957). A *Juniperus occidentalis* belt is recognized at 1,750- to 1,950-meter elevation in the Steens Mountains (Hansen 1956); *Artemisia arbuscula* is its most typical associate there. *Juniperus* also occurs along the Owyhee River canyon (Head 1959).

DESERT OR SALT DESERT SHRUB

Communities variously designated as desert shrub, salt desert shrub, shadscale (*Atriplex confertifolia*), salt sage (*Atriplex nuttallii*), or saltbush-greasewood (*Atriplex-Sarcobatus*) have been mapped but described in only general terms (Shantz and Zon 1924; Poulton 1962; Küchler 1964; Hansen 1956). These communities are on saline soils and often intermingled with upland communities dominated by *Artemisia tridentata*. Salt desert shrub communities are most common in the Basin and Range province, where interior drainage and old lakebeds are typical.

Important shrubs in these communities can include *Grayia spinosa*, *Atriplex confertifolia*, *A. nuttallii*, *Eurotia lanata*, *Artemisia spinescens*, and *Sarcobatus vermiculatus*. Grasses sometimes associated with these shrubs include *Elymus cinereus*, *E. triticoides* (which may dominate on ancient lakebeds), and *Distichlis stricta*. An *Atriplex confertifolia*/*Sitanion hystrix* community with some *Artemisia*

spinescens, *Eurotia lanata*, *Poa secunda*, and *Oryzopsis hymenoides* is one of the most common communities. *Sarcobatus vermiculatus*/*Distichlis stricta* communities are also typical of some of the moister saline habitats.

The desert shrub communities are much better developed to the south and east where they dominate extensive areas (Shantz and Zon 1924; Billings 1949, 1951).

GRASSLAND COMMUNITIES

Steppe communities lacking a major shrub constituent, such as the grassy types so abundant in the *Agropyron-Festuca* and *Festuca/Symphoricarpos* Zones of the Columbia Basin province (Daubenmire 1969), are not common in southeastern Oregon (fig. 134). Johnson (1959) described an *Agropyron spicatum-Poa secunda* Zone on the southeastern slopes of the Wallowa Mountains in which two steppe communities were recognized:

Agropyron spicatum-Poa secunda, the most extensive community with *Balsamorhiza sagittata* and *Eriogonum heracleoides* as associates, and

Figure 134. — Steppe communities lacking a major shrub dominant are not common in southeastern Oregon; where they do occur, burning may have been responsible, as in this *Agropyron spicatum-Lygodesmia spinosa* community located near Fort Rock, Oregon (photo courtesy Range Management, Oregon State University).

Festuca idahoensis-*Agropyron spicatum*,
an uncommon community with
Balsamorhiza and *Bromus*
brizaeformis as typical constituents.

The *Agropyron*-*Poa* community also occurred on Lithosols in the adjacent *Pseudotsuga menziesii* Zone (Johnson 1959). A similar community was noted by Dean (1960) in a part of the Owyhee River canyon and by Hall²⁷ in the Blue Mountains.

Hall also described a *Poa secunda*-*Danthonia unispicata* association which occurs on Lithosols throughout much of eastern Oregon. This scabland community generally replaces the *Artemisia rigida*-*Poa secunda* type on less permeable bedrock.

"CERCOCARPUS LEDIFOLIUS" COMMUNITIES

Communities dominated by *Cercocarpus ledifolius* are often found in the ecotone between *Pinus ponderosa* and *Artemisia* shrub-steppe in central Oregon (fig. 135) (Dealy 1969); *Cercocarpus* also forms pure stands at higher elevations in some of the mountain ranges of extreme southeastern Oregon, par-

²⁷ F. C. Hall, personal communication.

Figure 135. — *Cercocarpus ledifolius* communities are common in the forest-steppe ecotone in central Oregon; *Chrysothamnus nauseosus* is the major associate in this stand (Deschutes National Forest, Oregon).

ticularly in the Mahogany Mountains. Dealy (1969) recognized two associations in central Oregon: *Cercocarpus ledifolius*/*Festuca idahoensis* and *Cercocarpus*/*Festuca*-*Agropyron spicatum*. *Pinus ponderosa*, *Juniperus occidentalis*, *Artemisia tridentata*, *Ribes cereum*, and *Chrysothamnus viscidiflorus* are typical shrub or arborescent associates in both associations, but *Cercocarpus ledifolius* is strongly dominant with 36- and 66-percent crown cover, respectively. The chief difference in herbaceous understory is codominance of *Festuca idahoensis* and *Agropyron spicatum* in the *Cercocarpus*/*Festuca*-*Agropyron* community. *Agropyron spicatum*, *Sitanion hystrix*, *Koeleria cristata*, and *Poa secunda* are minor components of the *Festuca*-dominated understory in the *Cercocarpus*/*Festuca* community. These communities are important browse types for deer which often leave browse-lines on larger *Cercocarpus* and hedge younger plants.

"PURSHIA TRIDENTATA" COMMUNITIES

Purshia tridentata is a dominant in poorly known but widespread communities, particularly near the foothills of the Cascade Range. Dealy (1969) has described two of these: *Purshia tridentata*-*Artemisia arbuscula*/*Stipa thurberiana* and *Purshia tridentata*/*Festuca idahoensis* communities which are found near the forest-steppe ecotone in central Oregon. Similar communities are also found in the southern Blue Mountains²⁸ and southeastern Wallowa Mountains (Johnson 1959). As mentioned earlier, *Purshia* is codominant with *Artemisia tridentata* on some sites within the steppe proper.

RIPARIAN COMMUNITIES

A rich variety of poorly known community types is found on riparian or other moist sites within the southeastern Oregon shrub-steppe. *Populus tremuloides* communities or colonies are common near the forest-steppe transition (Dealy 1969). *Populus tremuloides* is also extremely conspicuous between 1,950-

²⁸ F. C. Hall, personal communication.

Figure 136. — *Populus tremuloides* is conspicuous between elevations of 1,950 and 2,400 meters on Steens Mountain in southeastern Oregon; *Populus* groves are typically associated with wet meadows in this landscape mosaic.

and 2,400-meter elevation in the Steens Mountains, forming the only widespread arborescent communities there (fig. 136) (Hansen 1956). The herbaceous understory is often lush in these communities.

Other types include riparian *Salix-Crataegus*, *Salix-Prunus*, and *Elymus cinereus* communities (Dean 1960; Hansen 1956), wet *Carex* meadows (Hansen 1956), and the tule marshes of the Klamath Lake area in which *Scirpus validus* is an important dominant (Shantz and Zon 1924).

TIMBERLINE AND ALPINE VEGETATION

On the highest mountain ranges of Oregon and Washington are subalpine parklands and alpine meadows. The parklands constitute an ecotone in which tree dominance is gradually giving way under the increasingly harsh alpine

environment. Typically, the area between forest line²⁹ and scrub line is a mosaic of tree patches and meadow communities (fig. 137), the former gradually being reduced in area and in stature as elevations increase. This belt was referred to as the Hudsonian Zone by Merriam (Bailey 1936). In western Washington and British Columbia, it has been split into two units by Krajina (1965) and Franklin (1966) depending on occurrence of trees as a climatic or topographic climax. In this fashion, a part is considered the upper segment of

²⁹We recognize three types of timberline: *forest line*, the general upper limit of contiguous closed forest; *tree line*, the upper limit of erect arborescent growth; and *scrub line*, the general upper limit of krummholz (= elfinwood or wind-timber line) (Arno 1966; Habeck and Hartley 1968). Our timberline region in this discussion covers the entire area from forest line to scrub line.

Figure 137. — Timberline regions are typically mosaics of tree groups, meadows, snow patches, and rock outcrops (Jefferson Park, Willamette National Forest, Oregon).

the *Tsuga mertensiana* Zone (Parkland Subzone) and the other constitutes the lower part of the Alpine Zone.

In any case, the entire forest-meadow mosaic of the region between forest and scrub line is the major topic of this section. Alpine communities will be considered briefly; many of them or their variants are components of the timberline mosaic. However, alpine communities, *sensu* above scrub line, are neither well developed nor well known in the Pacific Northwest, as will be seen.

Occurrence of Timberline Regions

Elevations sufficient to develop true timberline conditions are encountered generally in the northern Cascade Range and Olympic Mountains in Washington and in the Wallowa

Mountains of Oregon. Further south in the Cascade Range, major peaks such as Mount Rainier, Mount Hood, and Three Sisters have sufficient elevation to develop a climatic timberline and alpine regions. Timberline environments are occasionally encountered in the Blue, Steens, and Warner Mountains of Oregon and the Okanogan Highlands and Rocky Mountain outliers of eastern Washington.

Average elevation of forest and scrub line at representative Oregon and Washington locations is listed in table 26. It can be seen that the timberline mosaics generally involve a 300- to 500-meter elevational band. Elevations of forest and scrub line vary with exposure on an order of ± 150 meters, dropping on cool, northerly exposures and rising on warmer, southerly exposures (Bailey 1936; Arno 1966). Timberline elevations decrease

Table 26. — Average elevation of forest and scrub line at selected locations in Oregon and Washington

Area	Latitude	Longitude	Forest line	Scrub line
----- Meters -----				
Mount Baker	48° 45'	121° 50'	1,400	1,750
Wenatchee Mountains	47° 30'	120° 45'	2,000	2,440
Mount Rainier	47° 10'	121° 40'	1,580	2,100
Mount St. Helens	46° 15'	122° 10'	1,340	--
Mount Hood	45° 20'	121° 45'	1,680	1,980
Three Sisters	44° 10'	121° 50'	1,980	2,290
Mount McLoughlin	42° 50'	122° 20'	2,130	2,440
Olympic Mountains (central)	47° 45'	123° 30'	1,460	1,890
Olympic Mountains (northeast)	47° 50'	123° 20'	1,680	1,980
Wallowa Mountains	45° 10'	117° 20'	--	2,700

Source: Partially from Arno (1966), Bailey (1936), and Brockman (1949)

notably with increasing latitude; Daubenmire (1954) indicates the general tendency is for timberline to drop about 110 meters per degree of increase in latitude under a given climatic regime. The forest and scrub lines are markedly lower in coastal mountain regions (dominated by a maritime climate) than they are further inland. For example, forest line is about 500 meters higher at the eastern edge of the Cascade Range than it is at the same latitude on the western edge.

Timberline Tree Species

A great many tree species occur in timberline areas, some of which are listed in table 27. *Abies lasiocarpa*, *Tsuga mertensiana*, *Pinus albicaulis*, and *Larix lyallii* are characteristic, however. *Abies lasiocarpa* is the most wide-

spread, occurring in all timberline areas except in parts of southern Oregon. Near forest line, it is usually abundant as an erect tree dominating the islands of forest (fig. 138). It is reduced to a shrubby krummholz form at higher elevations where it often forms dense mats by layering.

Tsuga mertensiana is widely distributed at timberline throughout all but the most xeric portions of the Cascade Range and Olympic Mountains. In the most maritime portions of these ranges, it is usually more important than *Abies lasiocarpa*; timberline on Mount Baker is completely dominated by *Tsuga mertensiana* and both *Abies lasiocarpa* and *Pinus albicaulis* are very rare. Its timberline growth behavior is like that of *Abies lasiocarpa* (fig. 139).

Figure 138. — *Abies lasiocarpa* is the most widespread of the timberline tree species; pictured are groups of this species near timberline in the eastern Cascade Range (Wenatchee National Forest, Washington).

Table 27. — Tree species typically found between forest line and timberline in selected parts of Washington and Oregon

Species	Cascade Range			Olympic Mountains, Washington	Wallowa Mountains, Oregon
	Northwestern Washington	Northeastern Washington	Central Oregon		
<i>Abies amabilis</i>	m	—	m	m	—
<i>Abies lasiocarpa</i>	M	M	M	M	M
<i>Abies magnifica</i> var. <i>shastensis</i>	—	—	m	—	—
<i>Chamaecyparis</i> <i>nootkatensis</i>	m	—	—	m	—
<i>Larix lyallii</i>	—	M	—	—	—
<i>Picea engelmannii</i>	—	m	—	—	m
<i>Pinus albicaulis</i>	m	M	M	m	M
<i>Pinus contorta</i>	—	m	m	m	m
<i>Tsuga mertensiana</i>	M	—	M	M	—

Note: M = major species; m = minor species.

Pinus albicaulis is present in most timberline areas. However, it is unquestionably most important in more xeric regions — eastern and southern parts of the Cascade Range and Okanogan and Wallowa Mountains, or locally, on the eastern rain-shadow slopes of the major volcanoes such as Mount Rainier and Mount Hood. *Pinus albicaulis* is able to grow erect to higher elevations than either *Abies lasiocarpa* or *Tsuga mertensiana* although it will form krummholz at its upper limits. It sometimes functions as a pioneer tree species in invasion of meadow areas (Franklin and Mitchell 1967). The wingless seeds of *Pinus albicaulis* are distributed primarily by the Clark's nutcracker (*Nucifraga columbiana*), a large jay, which consumes a portion of the seed crop and hoards the rest. Reproduction develops from the forgotten hoards (fig. 140). Their relationship is the same as that described for *Pinus cembra*-*Nucifraga caryocatactes* in the European Alps and for *Pinus pumila*-*Nucifraga caryocatactes* var. *japonicus* in Japan.

Larix lyallii is, with rare exception, limited to the eastern half of the northern Cascade Range and Okanogan Mountains in Washington. It occurs only at or near timberline in these areas and appears exceptionally well adapted to the environment (fig. 141). *Larix lyallii* typically grows to higher elevations than any of its associates and maintains an erect habit when other species are unable to grow or occur only as krummholz beneath the *Larix*. As a result, *Larix lyallii* stands often form a distinctive forest belt between forest and alpine; this belt is particularly conspicuous during the fall as a swath of brilliant orange yellow.

Many other species do occur in localized timberline areas. *Chamaecyparis nootkatensis* is a major krummholz species in parts of the Washington Cascade Range and northeastern Olympic Mountains. *Pinus contorta* is typical in more xeric timberline tracts in association with *Pinus albicaulis*. *Picea engelmannii* is occasional at timberline east of the Cascade crest. *Abies amabilis* is common below the tree line in the most maritime portions of the Cascade Range and Olympic Mountains. *Abies magnifica* var. *shastensis* and *Pinus monticola* occupy similar sites in the southern Oregon Cascade Range (e.g., at Crater Lake).

Figure 139. — *Tsuga mertensiana* is an important timberline tree species throughout most of the Cascade Range and Olympic Mountains.

Figure 140. — *Pinus albicaulis* is a major timberline tree species in drier mountain areas; reproduction of the species is largely dependent upon the hoarding habits of a large jay, *Nucifraga columbiana*, which give rise to groups of seedlings and saplings (Sunrise Ridge, Mount Rainier National Park, Washington).

Meadow Communities

The variety and richness of the meadow flora and communities make the subalpine parkland attractive to scientists and laymen alike. Many of the species (and communities in the broad sense) are circumpolar. The mosaic of meadow communities is an intricate and often sharp response to local variations in substrate, moisture conditions, and duration of winter snowpack.

Even within the Pacific Northwest, the dominant meadow communities in the parkland mosaic and lower alpine vary from area to area just as the tree species do. Many communities occur throughout and retain their same basic character over a wide geographic range, but their importance in the mosaic changes. We will consider first the meadow communities found in a cooler and moister maritime region, the western slopes of Wash-

ington, and then outline some different meadow types characteristic of southern Oregon and of the interior mountain ranges.

WESTERN WASHINGTON

The meadow communities found in the subalpine parkland of western Washington are not well known. Kuramoto's (1968) study has been the only serious effort. Much of the extensive work carried out by Krajina and his students (Krajina 1965; Brooke 1965; Peterson 1965; Archer 1963) in adjacent British Columbia is relevant, however. The following sketch is based on these sources, personal experience (Franklin and Trappe 1963), and unpublished data provided by Mr. George Douglas, University of Washington. For fuller accounts we recommend Brooke (1965), Kuramoto (1968), and Archer (1963).

Phyllodoce empetrifomis-*Cassiope mertensiana* Communities

Ericaceous communities dominated by *Phyllodoce empetrifomis* and *Cassiope mertensiana* are widespread in the Cascade Range and Olympic Mountains. *Vaccinium delicosum* is a typical associate at lower elevations and may form communities in which it is the sole dominant (fig. 142). Other typical associates are *Luetkea pectinata*, *Polygonum bistortoides*, *Deschampsia atropurpurea*, *Hieracium gracile*, *Castilleja parviflora*, *Erigeron peregrinus*, *Polytrichum piliferum* and *Rhacomitrium sudeticum*. Alpine Podzols (O-A2-B2-C horizon sequence) or alpine rankers (O-A-C horizon sequence) are typically associated with *Phyllodoce*-*Cassiope* communities.

Valeriana sitchensis Communities

One of the lushest subalpine communities occurs on well-watered, but well-drained lower and middle slopes (fig. 143). This tall (about 1 m.), forbby community is dominated by *Valeriana sitchensis* and a rich assemblage of associated plants such as *Veratrum viride*, *Polygonum bistortoides*, *Arnica latifolia*, *Lupinus latifolius*, *Carex spectabilis*, *Anemone occidentalis*, and *Potentilla flabellifolia*.

Figure 141. — Although limited in distribution, *Larix lyallii* appears exceptionally well adapted to the timberline environment, often growing to higher elevation than any arborescent associates; this *Larix* is in fall coloration (Wenatchee National Forest, Washington).

Luetkea pectinata Communities

Luetkea pectinata is characteristic of a highly variable group of communities found on stabilized talus, lithosolic slopes, and fell-fields. These may be either hydric or relatively xeric sites. Many species may be associated with the *Luetkea* such as *Carex nigricans*, *Phyllodoce empetrifolia*, *Cassiope mertensiana*, *Arnica latifolia*, *Lupinus latifolius*, *Deschampsia atropurpurea*, *Castilleja parviflora*, *Anemone occidentalis*, *Polygonum bistortoides*, *Valeriana sitchensis*, *Potentilla flabellifolia*, *Epilobium alpinum* var. *clavatum*, *Pogonatum alpinum*, and *Vaccinium deliciosum*.

Figure 142. — A *Vaccinium deliciosum*-*Phyllodoce empetrifolia* community typical of those found lower in the subalpine parklands of the Cascade Range.

Figure 143. — *Veratrum viride*, one of the major dominants in the lush *Valeriana sitchensis* communities found on well-watered parkland slopes in the northern Cascade Range.

Carex spectabilis Community

Carex spectabilis, a relatively tall (up to 1 meter) *Carex*, sometimes dominates another meadow type found on relatively mesic lithosols and rock rubble. *Lupinus latifolius* is one of the more typical associates.

Snowbed Communities

Carex nigricans communities typify sites with a short growing season due to persisting snowbanks. *Carex nigricans* forms a thick dominant cover; typical associates are *Juncus drummondii*, *Antennaria alpina*, *Epilobium alpinum* var. *clavatum*, *Polytrichum norvegicum*, and *Polytrichadelphus lyallii*. *Saxifraga tolmiei* and bryophytes dominate rudimentary communities growing on sites having an even more prolonged snow cover. Typical constituents are *Gymnomitrium varians*, *Polytrichum norvegicum*, *Pohlia nutans*, *Saxifraga tolmiei*, *Polytrichum piliferum*, and *Andreaea nivalis*.

Streamside Communities

The communities found along streams are some of the showiest and most varied meadow types (fig. 144). *Mimulus lewisii*, *M. tilingii*, *Epilobium latifolium*, *E. alpinum* var. *clavatum*, *Leptarrhena pyrolifolia*, *Parnassia fimbriata*, *Caltha biflora*, *C. leptosepala*, *Juncus drummondii*, *Petasites frigidus* var. *nivalis*, *Philonotis fontana*, *Drepanocladus aduncus*, and *Erigeron peregrinus* are some characteristic species. At various locations in the Cascade Range, *Mimulus lewisii*, *Caltha* spp., *Leptarrhena*, or *Epilobium latifolium* may function as dominants. In the Olympic Mountains, *Saussurea americana* is a dominant. An *Eriophorum angustifolium*-*Sphagnum* spp.-*Carex aquatilis* community is characteristic of sites affected by a high water table the year around.

Other Community Types

There are many other kinds of subalpine communities. Grass-dominated communities occur generally on some of the warmer, drier slopes, particularly in rain-shadow areas; these

Figure 144. — *Mimulus lewisii*-*Epilobium latifolium* community typical of the showy and varied meadow types found on riparian habitats in the subalpine parklands.

are more characteristic of interior ranges and will be considered later. Communities of cushion plants occupy the dry, exposed ridges lacking winter snow accumulations. There are unique communities associated with the small groups of trees and krummholz. *Juniperus communis* typifies the varied communities found on exposed rock outcrops. *Athyrium alpestre* is characteristic of relatively unstable talus slopes.

HIGH CASCADES OF OREGON

Subalpine parklands in the central and southern Oregon Cascade Range appear considerably sparser than the densely vegetated regions just discussed. The High Cascades are the consequence of Pleistocene vulcanism, and the resulting substrates combined with a somewhat warmer and drier climate are important factors in the sparser vegetation. Pumice and cinder fields, outwash flats, and lava fields are common in timberline areas and provide extremely rigorous environments for plant growth.

Subalpine herbaceous communities have been studied on Three Sisters (VanVechten 1960) and near Mount Jefferson (Swedberg 1961). Lower in the zone, *Lupinus latifolius* meadows appear on moister sites and include *Castilleja parviflora*, *Potentilla flabellifolia*,

Epilobium alpinum, *Aster ledophyllus*, *Senecio triangularis* and *Ligusticum grayi* as constituents. On somewhat drier sites, *Trisetum canescens*, *Carex nigricans*, *Juncus drummondii*, and *Aster alpigenus* appear as dominants. Dry, south slopes are dominated by *Lupinus latifolius* or *Festuca viridula* or both. *Phyllodoce empetrifomis*, *Cassiope mertensiana*, and *Vaccinium scoparium* are characteristic species on rockier sites and on cool north slopes, where they are joined by *Cardamine bellidifolia*, *Saxifraga tolmiei*, *Luetkea pectinata*, and *Castilleja* spp. This grouping and the *Carex nigricans*-*C. spectabilis* communities, associated with some wet meadows, are similar to subalpine communities previously discussed. *Phyllodoce* and *Cassiope* are also characteristic of ridges and slopes higher in the timberline region; VanVechten (1960) mentions *Luetkea pectinata*, *Castilleja parviflora*, *Hieracium gracile*, *Carex* spp., *Vaccinium scoparium*, and *Anemone occidentalis* among the associates.

Large, nearly barren pumice flats are conspicuous features of the subalpine parkland from Mount Jefferson south in the Cascade Range (VanVechten 1960; Swedberg 1961; Horn 1968). Typical colonizers are low compact perennials with large taproots. Characteristic species in the north are *Eriogonum marifolium*, *E. pyrolaeifolium*, *Lupinus lepidus*, *Penstemon procerus*, *Raillardella argentea*, *Spraguea umbellata*, *Polygonum newberryi*, *Juncus drummondii*, *Aster alpigenus*, *Carex breweri*, *Castilleja arachnoidea*, and *Lomatium angustatum*. VanVechten (1960) studied one area (the Cinder Desert) on which *Eriogonum pyrolaeifolium* was the only species of significance; occasional plants of *Spraguea umbellata*, *Draba aureola*, *Smelowskia calycina*, *Hulsea nana*, and *Carex breweri* were also present. Outwash flats apparently have similar poorly developed communities. VanVechten (1960) mentions *Eriogonum pyrolaeifolium*, *E. marifolium*, *Raillardella argentea*, *Senecio fremontii*, *Spraguea umbellata*, and *Aster alpigenus* as characteristic species.

Horn's (1968) study of the Pumice Desert at Crater Lake National Park illustrates the sparsity of vegetation on these pumice and cinder flats. Coverage of all vascular plants

totaled only 4.5 percent. *Eriogonum marifolium*, *Carex breweri*, *Stipa californica*, *Arenaria pumicola*, *Spraguea umbellata*, and *Polygonum newberryi* were the most important of 14 vascular species present on the desert. Horn (1968) conducted some environmental studies and concluded that a severe climatic regime (wide diurnal temperature fluctuations) and low soil fertility were responsible for the sparsity of the vegetation. Soil moisture was apparently available throughout the short, intense growing season.

INTERIOR MOUNTAINS

Grasslands are the dominant meadow types in many timberline areas of eastern Oregon and Washington (fig. 145). Included here are subalpine areas on the east side of the Washington Cascade Range and in the Wallowa and Blue Mountains.

A bunchgrass, *Festuca viridula*, characterizes pristine communities of this type (Pickford and Reid 1942) except in the Blue Mountains. Since we are considering a group of communities covering a wide geographic area, there are many associates. Some of these are:

Grasses and Grasslike: *Stipa lettermanii*, *S. columbiana*, *Agrostis rossae* (Cascade Range), *Carex geyeri*, *C. hoodii*, *Sitanion hystrix*, *Phleum alpinum*, *Agropyron* spp., *Bromus carinatus*, *Poa* spp. and *Trisetum spicatum*.

Forbs: *Eriogonum heracleoides*, *E. piperi*, *Gilia nuttallii*, *Lupinus leucophyllus*, *L. latifolius*, *Polemonium pulcherrimum*, *Penstemon rydbergii*, *Erigeron speciosus*, *E. saluginosus*, *E. peregrinus*, *Arenaria formosa*, *Hieracium gracile*, *Potentilla glandulosa*, *Phlox diffusa*, *Polygonum phytolaccaefolium*, *P. newberryi*, and *P. bistortoides*.

Shrubs: *Artemisia tridentata* var. *vaseyana*, *Potentilla fruticosa*, *Ribes* spp., *Phyllodoce empetrifomis*, and *Vaccinium scoparium* (all minor).

Most of the *Festuca viridula* grasslands have been grazed, many of them to excess, and are in some deteriorated grass-forb stage. In 1938, Pickford and Reid (1942) started a

Figure 145. — Grasslands dominate the subalpine parklands in drier mountain ranges of eastern Oregon and Washington; top, climax *Festuca viridula* grassland in virgin condition, and bottom, overgrazed *Festuca* grassland which has deteriorated into a community of weeds (e.g., *Eriogonum* spp.) and *Stipa* spp. (Wallowa Mountains, northeastern Oregon).

study of changes in composition, productivity, and soil erosion associated with grazing of these types in the Wallowa Mountains. Recently, Strickler (1961) continued this study and made interesting photographic and analytic comparisons of conditions in 1938 and 1956-57. *Festuca viridula*, *Agropyron subsecundum*, *Melica bulbosa*, *Stipa lettermanii*, *S. columbiana* and *Lupinus leucophyllus* composed the virgin communities; total plant coverage was high. "Mixed grass-and-weed" and "weed-needlegrass" (*Stipa* spp.) communities with a high proportion of bare soil characterized the overgrazed sites. *Eriogonum* spp., *Gilia nuttallii*, *Penstemon rydbergii*, *Arenaria formosa*, *Artemisia tridentata*, and *Stipa* spp. were generally higher in these communities. Eventual return of these communities to their climax state (dominance of *Festuca viridula*) appears questionable.

Festuca-dominated meadows are often found on xeric subalpine habitats in the Olympic Mountains (Kuramoto 1968) and in the wetter parts of the Cascade Range. They are especially common in the rain shadows on the east and northeast slopes of the major volcanoes. *Festuca viridula*-*Lupinus latifolius* meadows dominate the Sunrise Ridge area on Mount Rainier, for example (fig. 146); a pumiceous soil may be partially responsible for extensive *Festuca*-meadow development there. The total community composition on these sites is somewhat altered from that on inland sites, but the overall physiognomy and dominant genera are the same.

Dynamics in the Timberline Vegetation

Timberline areas are tension zones, dynamic ecotones, between tree and treeless regions. As at lower elevations, directional changes are constantly taking place in response to allogenic (e.g., long- and short-term climatic changes) and autogenic (changes in environment brought about by organisms) factors. Successional considerations are particularly complex in subalpine parkland since they involve relationships between tree species, various meadow communities, and forest and meadow communities.

Figure 146. — *Festuca viridula* meadows are also found in the rain shadows on the eastern slopes of the major volcanoes in the Cascade Range; *Festuca viridula*-*Lupinus latifolius* community on the northeastern slopes of Mount Rainier (Sunrise Ridge).

Successional status is not often considered among timberline tree species since all are climax in a sense. None are in danger of elimination from the parkland since they can migrate to other open areas if more tolerant species become too competitive. Gradual changes do take place, however, and timberline tree species are displaced from sites they colonize. Franklin and Mitchell (1967) have described one successional sequence in development of subalpine tree groups near Mount Rainier; Douglas (1969) has described others. *Pinus albicaulis* or *Abies lasiocarpa* pioneer and are replaced in turn by *Tsuga mertensiana* and *Abies amabilis*. The pioneer species form the advancing outer fringe of the group. A succession of tree species may occur even in krummholz stands. Archer (1963), for example, suggested that a sequence of *Chamaecyparis nootkatensis*, *Abies lasiocarpa*, and, finally, *Tsuga mertensiana* may occur in krummholz stands at Garibaldi Park.

Successional relationships among the various meadow communities are not understood. Classically, they should involve development of hydric, xeric, and snowpatch communities

Figure 147. — Changes in the subalpine forest-meadow ecotones have typically been gradual; however, massive invasions of meadow areas by tree species have taken place in the last 50 years all over the Cascade and Olympic Mountains (Paradise Valley, Mount Rainier National Park).

toward a modal mesic type. Such changes may be extremely slow, however. Generally, the heather (*Phyllodoce-Cassiope*) and *Vaccinium deliciosum* communities are considered the higher levels of meadow successional series.

Changes in the forest-meadow ecotone have undoubtedly been of greatest interest. Gradual expansion of tree groups appears to have been taking place for many years between the forest and scrub lines except where fires produced temporary setbacks (Swedberg 1961; Franklin and Mitchell 1967). In the last half century, however, massive invasion of meadow areas has taken place at many locations in the Northwest (fig. 147) (Brink 1959; VanVechten 1960; Fonda 1967; Franklin 1966). These invasions are probably related to a short-term climatic fluctuation.

Changes in the overall elevation of forest line or scrub line have not been reported in this region with one exception — on Mount St. Helens. Mount St. Helens is a relatively

Figure 148. — Timberline is low (1,340 m.) but advancing on Mount St. Helens, a Cascade Range volcano of very recent origin (less than 2,000 years old).

low (2,948 m.) peak in southwestern Washington. The existing cone (fig. 148) is of very recent origin (less than 2,000 years ago) and its slopes are mantled with a coarse pumice. Timberline is very low compared with other peaks in the vicinity (about 1,340 m.) and composed of species not normally found at timberline — *Pinus contorta* (dominant), *P. monticola*, *Pseudotsuga menziesii*, *Populus trichocarpa*, *Abies procera*, and *Tsuga heterophylla*, for example. Lawrence (1938) concluded that timberline is advancing at a discernible rate on Mount St. Helens after studying some photographs taken in 1897 and suggests present timberline is a consequence of edaphic conditions.

Alpine Communities

Very little is known about the communities found in true alpine environments near and above the scrub line or krummholz limits. Habitats capable of supporting developed alpine plant communities are not extensive in Oregon and Washington in contrast to the large alpine acreages in the Rocky Mountains. Most of the Alpine Zone is steep and rugged, occupied by glaciers, snowfields, bare rock, and rubble (fig. 149). And much of it occurs on only recently dormant Pleistocene volcanoes. Troll (1955) noted the narrow elevational band between timberline and permanent snowline on Mount Rainier.

Many of the meadow communities characteristic of the subalpine parkland do extend into at least the lower reaches of the Alpine Zone, although they may be somewhat modified in form and composition. *Phyllodoce empetrifolmis*-*Cassiope mertensiana*, *Valeriana sitchensis*, *Carex nigricans*, and *Luetkea pectinata* communities are examples. Krajina (1965) feels the *Phyllodoce*-*Cassiope* association is the climatic climax in the Alpine Zone of adjacent British Columbia. Scott (1962) lists Saxifrage-Heather association as climax in western Washington's Arctic-Alpine Zone; this zone is considered to lie between 2,300 and 2,600 meters with essentially no vegetation above that level.

In the absence of data on communities, the best we can do is to indicate some species typical of the Alpine Zone. On Mount Rainier

Figure 149. — The Alpine Zone is not well developed in Oregon and Washington; areas above timberline are occupied primarily by glaciers, snowfields, bare rock, and rubble (Mount Rainier from Sunrise Ridge).

these include *Eriogonum pyrolaefolium*, *Saxifraga tolmiei*, *Spraguea umbellata*, *Silene acaulis*, *Draba aureola*, *Smelowskia ovalis*, *Lupinus lepidus*, *Polemonium pulcherrimum*, *Castilleja angustifolia*, *Erigeron aureus*, *Dryas octopetala*, *Oxyria digyna*, *Salix nivalis*, and many Gramineae, *Carex*, and Juncaceae (Jones 1938). On Three Sisters, typical alpine plants are *Hulsea nana*, *Draba aureola*, *Claytonia megarhiza*, *Polemonium elegans*, *Phacelia hastata*, *Trisetum spicatum*, *Poa pringlei*, *Carex breweri*, and *Oxyria digyna* (VanVechten 1960).

SITUATIONS OF SPECIAL INTEREST

There are many habitats supporting unusual floras or communities which are of particular interest to the geneticist, ecologist, or plant geographer. These may be the result of unusual substrates (e.g., serpentine) or of unique topographic features. Sufficient data are available to consider three such areas: (1) areas of recent vulcanism, (2) serpentine tracts, and (3) the Columbia Gorge.

Table 28. — Representative species in three plant associations on lava flows near Santiam Pass, Oregon

Item	<i>Aceretum circinati lavosum</i>	<i>Pseudotsugeto-abietum lasiocarpae</i>	<i>Pseudotsugetum-abietum grandis</i>
Substrate	Block basalt	Block basalt with smaller size scoria in broken crust	Grayer, rounded block basalts with high proportion sand and ash
Trees		<i>Pseudotsuga menziesii</i> , <i>Abies lasiocarpa</i>	<i>Pseudotsuga menziesii</i> , <i>Abies grandis</i> , <i>Pinus contorta</i> , <i>P. monticola</i>
Shrubs	<i>Acer circinatum</i> , <i>Rhamnus purshiana</i> , <i>Holodiscus glabrescens</i> , <i>Arctostaphylos columbiana</i>	<i>Acer circinatum</i> , <i>Arctostaphylos nevadensis</i> , <i>A. columbiana</i> , <i>Castanopsis chrysophylla</i> , <i>Pachistima myrsinites</i>	<i>Castanopsis chrysophylla</i> , <i>Pachistima myrsinites</i> , <i>Acer circinatum</i> , <i>Rubus parviflorus</i> , <i>Ceanothus velutinus</i>
Herbs	<i>Cryptogramma acrostichoides</i> , <i>Penstemon menziesii davidsonii</i> , <i>Sedum oregonense</i> , <i>Juncus parryii</i>	<i>Sedum oregonense</i> , <i>Penstemon menziesii davidsonii</i> , <i>Chimaphila umbellata occidentalis</i>	<i>Chimaphila umbellata occidentalis</i> , <i>Linnaea borealis</i> , <i>Festuca occidentalis</i> , <i>Xerophyllum tenax</i> , <i>Penstemon cardwellii</i>
Mosses	<i>Rhacomitrium patens</i> , <i>R. lanuginosum</i> , <i>Dicranum scoparium</i> , <i>Hypnum fertile</i>	<i>Rhacomitrium patens</i> , <i>R. lanuginosum</i> , <i>Dicranum scoparium</i> , <i>Hypnum fertile</i>	<i>Rhacomitrium patens</i> , <i>R. lanuginosum</i> , <i>Dicranum scoparium</i> , <i>Hypnum fertile</i> , <i>Aulacomnium androgynum</i> , <i>Rhytidiadelphus triquetrus</i> , <i>Polytrichum juniperinum</i>

Source: Roach (1952).

Areas of Recent Vulcanism

The eruption and deposition of volcanic materials has been taking place in the Northwest up into recent times, particularly in the Cascade Range. Mount Lassen (in California) erupted early in this century and Mount St. Helens was last active about the middle of the 19th century. This activity has resulted in frequent occurrence of cinder cones, pumice and ash fields, lava flows, and laharic deposits³⁰ which support communities quite unlike those found on adjacent habitats. Some of these have been discussed in preceding sections, but at this time we would like to consider lava flow and mudflow communities in detail.

LAVA FLOWS AND LAVA-DAM LAKES

Pleistocene-Recent lava flows are conspicuous at many places in the Cascade Range; e.g., in central Oregon (Peterson and Groh 1966), the Santiam and McKenzie Pass areas (Taylor 1968) in the Oregon Cascade Range, and in the vicinity of Mount St. Helens and Mount Adams, Washington Cascade Range. These lava fields provide a rugged environment for pioneer plant communities, yet they are often surprisingly rich floristically, particularly in cryptogams.

The most extensive study of lava flow communities was conducted by Roach (1952) on the Nash Crater lava flows near Santiam Pass, Oregon. He recognized three associations which represented a series in development of substrate and community density and organization: the *Aceretum circinati lavosum*, *Pseudotsugeto-abietum lasiocarpae*, and *Pseudotsugetum-abietum grandis* associations. The major species found in these associations are listed in table 28. All of these associations are edaphic climaxes in which *Acer circinatum*, *Pseudotsuga menziesii* and *Abies lasiocarpa*, and *Pseudotsuga menziesii* are the respective dominants.

³⁰“The term, lahar, includes all of the broad textural range of debris flows and mudflows of volcanic origin . . . any unsorted or poorly sorted deposit of volcanic debris that moved and was deposited as a mass and owed its mobility to water.” (Mullineaux and Crandell 1962).

Some studies have also been made of the basaltic flows found in southern Washington (Franklin 1966; Franklin and Mitchell 1967). On one flow (near Wind River), a *Pseudotsuga menziesii*-*Abies lasiocarpa*-*Acer circinatum* community, very similar to the one described by Roach (1952), is present. The Wind River and Nash Crater flows lie almost entirely within the *Abies amabilis* Zone, however. Near Mount Adams is a large flow (Big Lava Beds) which extends from about 520 to 1,100 meters in elevation. Communities vary from *Pseudotsuga menziesii*-*Quercus garryana* at the lowest through *Pinus contorta*/*Arctostaphylos uva-ursi* to *Abies lasiocarpa*/*Xerophyllum tenax* (fig. 150) at the highest elevations (Franklin 1966). All of these communities are very rich in mosses and lichens and there are many vascular species present in niches and crevices, surprising in view of the xeric, sterile appearance of the substrate. Dis-

Figure 150. — An *Abies lasiocarpa*/*Xerophyllum tenax* community is found at about 1,200-meter elevation on the Big Lava Beds near Mount Adams (Gifford Pinchot National Forest, Washington).

Figure 151. — Lava flows have created lakes with widely fluctuating water levels by blocking stream drainages; Cottonwood, Sedge, and Fontinalis Zones were conspicuous around Goose Lake, an impoundment of this type (Gifford Pinchot National Forest, Washington).

cussion of *Pinus contorta* community will be deferred, since it is similar to many found on lahars and glacial outwash elsewhere.

Lava flows frequently blocked drainages of many small streams, and seasonal lakes or lakes with widely fluctuating water levels are not uncommon. Kienholz (1931) studied one of the latter type adjacent to Big Lava Beds (southern Washington). He recognized five zones around Goose Lake (fig. 151): Willow-Alder (*Salix sitchensis*-*Alnus rubra*); Sedge (*Carex* spp.); Fontinalis (*Fontinalis antipyretica gigantea*); Cottonwood (*Populus trichocarpa*); and Weed (*Artemisia tilesii*-*Stachys cooleyae*-*Scrophularia lanceolata*).

More frequently, lava-dammed lakes are filled during the winter months when underground drainage systems are inadequate and drain completely during the summer. Roach (1952) describes one of these which is covered primarily by a bog type vegetation dominated by *Carex sitchensis* and *Vaccinium occi-*

dentale. In nearby Fish Lake where the substrate is thin and rocky, a dense nearly pure community of *Carex aperta* and *C. rostrata* 1 meter or more in height develops during the short growing season.

MUDFLOWS

Lahars, including mud and debris flows as defined earlier, are common near the major volcanoes in the Cascade Range (Mullineaux and Crandell 1962; Tidball 1965; Crandell and Mullineaux 1967). Some of these are occupied by communities relatively normal in composition for the zone in which they occur (Franklin 1966). Others are sufficiently recent that they are obvious sites for studies of vegetation succession and soil development, such as some at Mount Rainier (Frehner 1957; Ballard 1963), Mount Lassen (Bailey 1963), and Mount Shasta (Dickson and Crocker 1953a, 1953b, 1954). Still others in the *Tsuga heterophylla* and *Abies amabilis*

Figure 152. — Mudflows are common features near the major volcanoes in the Cascade Range; the Kautz Creek mudflow occurred in 1947, burying and killing the original forest (photo courtesy Mount Rainier National Park).

Zones are occupied by climax stands of *Pinus contorta* (Franklin 1966). The status of the vegetation appears to be primarily a function of age and nature of the substrate.

Frehner's (1957) study of succession on the 1947 Kautz Creek mudflow (fig. 152) at Mount Rainier has shown that many conifers, typical of adjacent zonal forests, will invade recent mudflows. *Populus trichocarpa*, *Salix* spp., and *Alnus rubra* have been major pioneer species, however, and *Alnus rubra* had special importance as a consequence of its nitrogen-fixing abilities. Occurrence of standing snags appeared to be an important factor in the composition of the pioneering vegetation.

A *Pinus contorta*/*Arctostaphylos* community is found on some xeric laharic deposits (fig. 153), lava flows, and coarse glacial outwash in southwestern Washington and northwestern Oregon (Franklin 1966; Stephens 1966). This appears to be a stable climax type

on such habitats in many areas, although occasional specimens of more tolerant tree species such as *Pseudotsuga menziesii*, *Tsuga heterophylla*, or *Abies lasiocarpa* may be present; droughty years can eliminate many of these. In other cases, it is clearly successional to a *Pseudotsuga menziesii*, *P. menziesii*-*Pinus contorta*, or *Tsuga heterophylla* community. Although details of composition vary, the dominance of *Pinus contorta* and either *Arctostaphylos nevadensis* or *A. uva-ursi* in their respective layers (fig. 153) and a rich cryptogamic ground cover are distinguishing. Typical cryptogams are: *Rhacomitrium canescens* var. *ericoides*, *Cladonia grayii*, *Polytrichum juniperinum*, *Cladonia bellidiflora*, *C. ecmocyna* vars. *ecmocyna* and *intermedia*, *Stereocaulon paschale*, *Cladonia phyllophora*, *C. rangifera*, *Polytrichum piliferum*, *Cladonia coniocraea*, *Lecidea quadricolor*, *Cladonia macrophyllodes*, *Rhacomitrium heterostichum*, *R. sudeticum*, and *Aulacomnium androgynum*.

Figure 153. — *Pinus contorta*/*Arctostaphylos* communities are widespread on mudflows, glacial outwash, and lava flows in the Cascade Range of southern Washington and northern Oregon; this community is distinguished by a depauperate understory of *Arctostaphylos uva-ursi* or *A. nevadensis* and many species of lichens and mosses (Kalama River lahar, Gifford Pinchot National Forest, Washington).

Figure 154. — Vegetations on serpentine sites and adjacent nonserpentine soils often contrast sharply; in this Siskiyou Mountain area, open *Pinus jeffreyi* stands on serpentine (right) contrast with those of *Pseudotsuga menziesii*, *Pinus lambertiana*, and *Libocedrus decurrens* on nonserpentine soils (left).

Serpentine Areas

Serpentine areas are characterized by unusual plant communities and floras. Vegetation is invariably stunted on serpentine sites in comparison with that on adjacent nonserpentine soils. Sharp contrasts in physiognomy, composition, and productivity of communities are typical at margins of serpentine outcrops (fig. 154). The floras are unusual including endemics restricted to serpentine species not usually found in adjacent communities and "bodenvag" species which appear edaphically indifferent (Kruckeberg 1954, 1964, 1967; Whittaker 1954b, 1960; Waring 1969).

Serpentine areas in this discussion refer to habitats with soils derived from ultramafic rocks either as peridotite and dunite (igneous forms) or as serpentinite (the metamorphic derivative) (Kruckeberg 1967). Such soils are typically low in total and adsorbed calcium and high in magnesium, chromium, and nickel (Walker 1954). Walker (1954) has analyzed the factors affecting plant growth on such sites and concluded the plants growing there must be tolerant of low calcium levels and one or more additional conditions; e.g., high nickel, chromium, or magnesium and physically unfavorable shallow soils.

There are three major serpentine areas in the Pacific Northwest (Whittaker 1954a; Kruckeberg 1964, 1967): (1) a large area in the Siskiyou Mountains of Oregon; (2) about 100 square miles in the Wenatchee Mountains, an eastern outlier of the Cascade Range; and (3) about 30 square miles in northwestern Washington near Mount Baker (Twin Sisters Mountain) and in parts of the San Juan Islands. Serpentine communities have been most thoroughly analyzed in the Siskiyou Mountains (Whittaker 1954b, 1960; Waring 1969) but Kruckeberg (1964, 1967) has provided general descriptions for the Washington serpentines.

SISKIYOU MOUNTAINS

Perhaps the outstanding feature of the Siskiyou serpentines is the *Pinus jeffreyi*/grass woodland which occupies the most xeric ser-

Figure 155. — Ultramafic rock outcrops in Washington typically consist of open woodlands and barren slopes; left, landscape mosaic on ultramafic slopes and, right, local outcrop of serpentine showing the extremely barren openings (Teaaway River drainage, Wenatchee National Forest; photos courtesy A. R. Kruckeberg).

pentine sites from 300- to 2,000-meter elevation (Whittaker 1960; Waring 1969). *Pinus jeffreyi* is typically the only tree species present in these open woodlands (fig. 154) along with a rather sparse growth of grasses (e.g., *Stipa lemmoni*, *Sitanion jubatum*, *Melica geyeri*, *Elymus glaucus*, and *Festuca ovina*) and occasional *Arctostaphylos viscida*. Forests, intermediate in elevation and moisture regime, are typified by a sparse and xerophytic appearance and dominated by a mixture of several conifers — *Pseudotsuga menziesii*, *Libocedrus decurrens*, *Pinus jeffreyi*, *P. monticola*, *P. lambertiana*, and *P. attenuata* (Whittaker 1960). Associated with them is a dense layer of sclerophyllous shrubs such as *Quercus vaccinifolia*, *Lithocarpus densiflora*, *Vaccinium parvifolium*, *Garrya buxifolia*, and *Umbellularia californica*. Herb coverage is generally low but rich in species. Whittaker (1954b, 1960) has commented at length on the “two-phase” or patchwise distribution of the shrub cover in these forests with essentially closed shrub patches alternating with herbaceous openings. On more mesic sites the shrubs form the matrix, but on more xeric sites the herbaceous openings are dominant.

Other community types described on Siskiyou serpentines include: *Chamaecyparis*

lawsoniana-*Pinus monticola*-*Pseudotsuga menziesii* stands, with a dense shrubby understory in ravines and draws, and higher elevation forests dominated by *Abies concolor* and *Pseudotsuga menziesii* and *Pinus monticola*, singly or collectively, over a *Xerophyllum tenax* and *Arctostaphylos nevadensis* understory.

Whittaker (1960) has provided a list of more useful serpentine indicator plants in the Siskiyou area. These include: (1) some dominants — *Pinus jeffreyi*, *P. monticola*, *P. attenuata*, *Quercus chrysolepis*, *Ceanothus cuneatus*, and *Arctostaphylos nevadensis*; and (2) species which are of more frequent occurrence on smaller serpentine areas — *Galium ambiguum*, *Pyrola dentata*, *Lomatium macrocarpum*, *Cheilanthes siliquosa*, *Rhododendron macrophyllum*, and *Darlingtonia californica*. *Xerophyllum tenax* is considered the most useful single indicator of small serpentine outcrops.

WASHINGTON SERPENTINES

Most ultramafic outcrops in Washington occur within forested zones, and communities consist of open woodland with barren slopes between the scattered stunted trees (fig. 155) (Kruckeberg 1964, 1967). In the Wenatchee

Figure 156. — The Columbia Gorge, the only nearly sea level break in the Cascade Range in Oregon and Washington and a major route for plant and animal migration between the western and eastern halves of these States; Beacon Rock, a large monolith, is visible (left center) in this east-facing view through the center of the Gorge.

Mountains, *Pseudotsuga menziesii*, *Pinus contorta*, and *Pinus monticola* are typical tree species at lower elevations and *Abies lasiocarpa* and *Pinus albicaulis* at higher elevations. *Juniperus communis* and *Arctostaphylos nevadensis* are typical shrubs. Herbs are found in serpentine openings, talus, etc., such as *Agropyron spicatum*, *Festuca viridula*, *Poa curtifolia*,* *Eriogonum pyrolaeifolium*,* *E. compositum*, *Silene parryi*, *Thlaspi alpestre*,* *Anemone drummondii*,* *Phlox diffusa*, *Arenaria obtusiloba*,* *Claytonia nivalis*,* *Lomatium cuspidatum*,* *Douglasia nivalis*,* *Achillea millefolium* var. *lanulosa*, *Senecio pauperculus*, *Cheilanthes siliquosa*,* and *Polystichum mohrioides* var. *lemmonii*.* Those species with asterisks (*) Kruckeberg³¹ considers serpentine indicator or character species.

³¹ Kruckeberg, Arthur R. 1964. Plant life on serpentines and other ultramafic rocks in northwestern North America. 13 pp., mimeo. (from talk given at X Int. Bot. Congr., Edinburgh, Scotland).

Serpentine areas in northwestern Washington have similarly sparse, open vegetation and an abundance of barren rock (Kruckeberg 1964, 1967). *Pinus contorta*, *Pseudotsuga menziesii*, *Rhacomitium canescens* var. *ericoides*, and *Cheilanthes siliquosa* seem to be characteristic on Twin Sisters Mountain. Stunted *Pseudotsuga menziesii*, *Pinus contorta*, *Juniperus scopulorum*, and *Arbutus menziesii*, along with dense herbaceous layers, are found on some of the San Juan serpentines.

The Columbia Gorge

The Columbia Gorge is an unusual physiographic feature which is of considerable importance to biologists (fig. 156). The Columbia River cut this nearly sea level route directly across the axis of the Cascade Range. As Detling (1966) pointed out, this is the only point between the Fraser River (in British Columbia) and Klamath River (in California) where a feature of this type is found. It has provided a major route for both plant and animal migration between the western and eastern halves of Washington and Oregon (Detling 1961, 1966, 1968). At the same time, it contains many species which are endemics or constitute relict populations.

The weather of the Columbia Gorge is as unique as its topography (Lynott 1966), since it provides a sea level transition from marine to continental climate in a region where they are otherwise separated by major mountain barriers. Strong winds are a dominant feature. During the winter, low-pressure systems move through the gorge on westerly winds, bringing heavy rains as a consequence of streamline convergence. Strong high-pressure systems east of the Cascade Range can bring gale-force easterly winds through the gorge, resulting in extremely hot dry weather during summer and fall and cold continental air during the winter. Marine low-pressure systems and this cold air may collide, particularly in the west end of the gorge, with blizzards, ice storms, and freezing rain the result.

These climatic features have profound effects upon the vegetation as Lawrence (1939) and Troll (1955) have pointed out. Tree crowns are markedly deformed or one-sided. In the east end of the gorge, they are flagged toward the east by the dominantly westerly winds. This is the result of wind training, not

breakage. At the west end of the gorge, trees typically lack branches on the easterly sides of the stem. This deformation is the result of branch breakage during the severe ice storms and destruction of buds and branches by dry east winds.

Another interesting ecological feature of the gorge is the opportunity it provides to

study the transition from xerophytic *Pinus ponderosa*-*Quercus garryana* forests on the east to the mesophytic *Pseudotsuga menziesii*-*Tsuga heterophylla* types on the west. Troll (1955) has provided an interesting vegetation profile (fig. 157) indicating the distribution and interdigitation of the various zones through this area.

Figure 157. — Vegetation profile through the Columbia Gorge and Cascade Range (from Troll 1955).

- Forests of *Pseudotsuga menziesii* with *Tsuga heterophylla* and *Thuja plicata*
- Forests of *Pinus ponderosa* and *Quercus garryana*
- Prairie (bunchgrass steppe of *Agropyron spicatum*)
- Forests of *Abies amabilis*, *A. procera*, *Pinus monticola*, *Tsuga heterophylla*, and *Chamaecyparis nootkatensis*
- Forests of *Pinus contorta*, *P. ponderosa*, *P. monticola*, *Larix occidentalis*, *Pseudotsuga menziesii*, and *Abies grandis*
- Subalpine forests of *Abies lasiocarpa*, *Tsuga mertensiana*, and *Pinus albicaulis*
- Alpine communities
- Snowfields and glaciers

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APPENDIX

BRIEF DESCRIPTION OF GREAT SOIL GROUPS

Descriptions follow those contained in "Soils of the Western United States" (Western Land Grant Universities et al. 1964). Soil horizon thickness classes are approximately: (1) very thin, less than 3 cm.; (2) thin, 3 to 10 cm.; (3) moderately thick, 10 to 20 cm.; (4) thick, 20 to 40 cm.; and (5) very thick, over 40 cm. All other classes and designations follow the "Soil Survey Manual" and supplement (U.S. Soil Conservation Service 1951, 1962).

Azonal Soils

Alluvial

Alluvial soils are formed on recent alluvium and, therefore, exhibit very little profile development. A horizons are thin to moderately thick, light to dark in color, with low to moderate amounts of organic matter accumulation. B horizons are lacking, while the C is made up of stratified alluvium which is often stony or gravelly. Soil reaction ranges from moderately alkaline to medium acid.

Lithosols

Lithosols are well drained, shallow, generally stony soils over bedrock. A horizons are very thin to moderately thick, light to dark in color, with low to moderate amounts of incorporated organic matter. B horizons are lacking; a transitional AC horizon may be present. Soil reaction may vary from moderately alkaline to medium acid.

Regosols

Regosols are well to excessively drained, poorly developed soils formed in deep, unconsolidated materials. A horizons are very thin to moderately thick, light to dark colored, with low to moderate organic matter content.

B horizons are lacking, and the C is made up of uniform or stratified material. Reaction ranges from slightly acid to moderately alkaline. In dry areas, the soil may be calcareous.

Zonal Soils

Alpine Turf

Alpine Turf soils are formed under alpine grasses and herbs in high mountain areas having a cold, humid climate. These well to imperfectly drained soils have thin to thick black A horizons of moderate to high organic matter content. B horizons are lighter colored, generally stony, and may have noticeable increase in clay. The stony or gravelly C horizon may be layered by solifluction processes. Soil reaction is strongly acid in the surface and medium acid in the B.

Brown

Brown soils are formed under shrub-steppe in cool, semiarid climates. These well-drained soils have moderately thick, dark-brown A horizons of low organic matter content. B horizons typically have more clay and subangular blocky to prismatic structure. Soil reaction is slightly alkaline in the surface, and alkalinity increases with depth. A zone of calcium carbonate accumulation is generally present as a Bca or Cca horizon.

Brown Podzolic

Brown Podzolic soils are formed under forest in cool, humid climates. Soil drainage varies from well to imperfectly drained. O1 and O2 horizons are usually present. The A1 horizon is thin and dark grayish-brown in color. A very thin, intermittent A2 horizon may also be present. The brown-colored B horizon gives evidence of iron and humus accumulation but has no appreciable clay increase. Soil reaction is medium to strongly acid.

Chernozem

Chernozem soils are formed under steppe or shrub-steppe in cool, subhumid climates. These moderately well to well drained soils have moderately thick, very dark-brown to black A horizons of moderate organic matter content. B horizons usually contain more clay than the A, but may be distinguished solely on the basis of color and structural changes. Soil reaction becomes more alkaline with depth, and a zone of carbonate accumulation is generally present in the lower part of the B.

Chestnut

Chestnut soils are formed under steppe or shrub-steppe in cool, semiarid climates. These well-drained soils have dark-brown, moderately thick A horizons containing moderate amounts of organic matter. B horizons often contain more clay than the A but may be distinguished largely by color and structural changes. Structure in the B may be blocky, subangular blocky, or prismatic. Soil reaction becomes more alkaline with depth, and a zone of carbonate accumulation usually occurs in or below the B horizon.

Desert

Desert soils are formed under shrub-steppe in warm, arid climates. These well-drained soils have thin, light-colored A horizons of low organic matter content. Structure of the A is platy. B horizons typically show increased clay content and are as dark or darker colored than the A1. Reaction varies from neutral to strongly alkaline. Horizons of calcium enrichment, sometimes cemented with lime or silica, occur in or below the B horizon.

Gray-Brown Podzolic

Gray-Brown Podzolic soils are formed under forest in cool to cold, subhumid climates. They are well to imperfectly drained. A1 horizons are thin to moderately thick and very dark gray. A thin, light-colored A2 horizon occurs beneath the A1. B horizons contain

more clay than the A2 and have darker colors. Structure is blocky, subangular blocky, or prismatic. Reaction is medium acid in the surface and medium to slightly acid in the B horizon.

Gray Wooded

Gray Wooded soils are formed under forest in cold, subhumid climates. They are well to imperfectly drained. Thin to moderately thick O1 and O2 horizons are present at the soil surface. A thin A1 horizon is generally present. The A2 horizon is light colored, low in organic matter content, and has platy structure. The B horizon contains more clay than the A2 and has blocky or subangular blocky structure. Surface reaction is slight to medium acid and may approach neutrality with depth.

Noncalci Brown

Noncalci Brown soils are formed under shrub communities (e.g., chaparral) in warm, subhumid climates. These well to moderately well drained soils have moderately thick to very thick, brown or reddish-brown, massive A horizons of low organic matter content. B horizons contain more clay and are redder than the A. They may be massive or have blocky or prismatic structure. Hard layers caused by silica cementation commonly occur in the B. In addition, small amounts of carbonate may be present in the lower part of the B horizon.

Podzol

Podzol soils are formed under forest in cool to cold, subhumid climates. They are well to moderately well drained. Thin to thick (5 to 40 cm.) O1 horizons overlie thin to thick (5 to 25 cm.) O2 horizons. A2 (bleicherde) horizons are thin to thick, white to very pale brown, and very low in organic matter content. B horizons are much darker and contain accumulations of iron and humus. Structure ranges from very weak blocky to strong blocky or prismatic. Soil reaction is strongly to very strongly acid.

Prairie

Prairie soils are formed under grassland vegetation in cool, subhumid to humid climates. These well to imperfectly drained soils have thick, very dark A horizons generally containing large amounts of organic matter. B horizons typically have more clay but may be differentiated from the A largely by color and structural changes. Prairie soils exhibit decreasing acidity with depth, and accumulations of calcium carbonate may occur in the C horizon.

Reddish Brown Lateritic

Reddish Brown Lateritic soils are formed under forest in warm, humid climates. They are moderately well to well drained. A horizons are moderately thick, reddish brown, and of granular structure. Shotlike iron-magnesium concretions are commonly present. B horizons are red or reddish brown and have more clay than the A. Structure is typically moderate blocky or subangular blocky. Reaction varies from moderately to very strongly acid.

Sierozem

Sierozem soils are formed under shrub-steppe in cool, arid climates. These well-drained soils have thin, light-colored A horizons containing low amounts of organic matter. Soil structure is typically platy, especially in the upper portion. B horizons contain more clay and are often darker than the A. Calcium carbonate accumulations, often cemented, generally occur in the lower part of, or just below, the B horizon. Soil reaction ranges from mildly to strongly alkaline.

Sols Bruns Acides

Sols Bruns Acides soils are formed under coniferous forest vegetation in cool, humid climates. Soil drainage may vary from well to imperfectly drained. Thin O1 and O2 horizons are usually present at the soil surface. A horizons are thick, dark brown to dark reddish brown, and moderate to high in organic mat-

ter content. B horizons show no evidence of illuviated clay and are distinguished by color and structure (subangular blocky). Soil acidity generally increases with depth and ranges from medium to very strongly acid.

Western Brown Forest

Western Brown Forest soils are formed under forest in areas of forest-steppe transition and cool, semiarid to subhumid climates. These well or moderately well drained soils have moderately thick, dark-colored granular A horizons containing low to moderate amounts of organic matter. B horizons may show increased clay content but are usually distinguished by color and structural changes. Typical B horizon structure is subangular blocky. Reaction varies from slight to medium acid, and acidity commonly decreases with depth. A zone of calcium carbonate accumulation occurs in the lower B or upper C horizon.

Intrazonal Soils

Alpine Meadow

Alpine Meadow soils are formed under high-elevation meadows in cold to very cold and humid climates. These soils are imperfectly to poorly drained. The A1 horizon is thick, very dark brown to black, moderate to high in organic matter content, and frequently stony. B horizons are lacking. C horizons are stony, mottled, and gleyed. Soil reaction is strongly or very strongly acid.

Grumusols

Grumusols occur under grassland or grass-shrub vegetation in a variety of climatic zones. They are generally well drained except in depressional areas. A horizons are very thick, dark colored, and contain low to moderate amounts of organic matter. Montmorillonitic clay content is usually high. B horizons are lacking. C horizons have wide vertical cracks which typically extend up into the A

horizon. Carbonate accumulation may occur in the lower A or upper C horizon. Reaction varies from slightly acid to slightly alkaline.

Humic Gley

Humic Gley soils occur under meadows in virtually all climatic zones. They are poorly to very poorly drained. The A horizon is very dark colored and contains large amounts of organic matter. The B horizon is gleyed or mottled and is higher in clay content. Soluble salts may be present in weak to moderate concentrations. Soil reaction ranges from moderately alkaline to strongly acid.

Planosol

Planosols may occur under steppe, shrub-steppe, or forest and in a wide variety of climatic zones. They are imperfectly to poorly drained. A1 horizons are thick, dark colored, with moderate to high organic matter content. An A2 horizon of variable thickness underlies the A1; it is massive and mottled. B horizons contain appreciably more clay and have blocky or prismatic structure. A cemented layer may be present in the lower solum. Reaction varies from medium to mildly alkaline.

Solonchak

Solonchak soils occur under shrub-steppe in arid to semiarid areas. These poorly drained soils have thin, light-colored A horizons low in organic matter content. Salt crusts are commonly present on the surface. B horizons are lacking.

Solonetz

Solonetz soils occur under steppe or shrub-steppe in arid to semiarid areas. Soil drainage ranges from well to imperfectly drained. A horizons are thin, platy, light colored, and contain low amounts of organic matter. B horizons contain more clay and have blocky, prismatic, or columnar structure. Portions of the B horizon contain more than 15 percent of exchangeable sodium. A zone of carbonate enrichment, commonly cemented, occurs in the lower part of or below the B horizon. Soil reaction varies from neutral to very strongly alkaline.

Miscellaneous Land Type

Rockland

Rockland designates areas with only sparse vegetation, dominated by rock outcrops, rock rubble, boulders, or stones. Restricted areas of thin soils may be included, but in general, soil development is severely limited.

LIST OF PLANT SPECIES

The major sources for the scientific names of these species are Little (1953) for trees and a few shrubs, Hitchcock et al. (1955, 1959, 1961, 1964) for Dicotyledonae, and Peck (1961) for the remaining vascular plants. Mosses follow Lawton (1965) and lichens fol-

low Howard (1950) in most cases. Common names are according to Little (1953), Garrison, Skovlin, and Poulton (1967) and Peck (1961). Mosses, lichens, and liverworts are marked with an asterisk; no common names are given for these species.

Abies amabilis (Dougl.) Forbes
Abies concolor (Gord. & Glend.) Lindl.
Abies grandis (Dougl.) Lindl.
Abies lasiocarpa (Hook.) Nutt.

Pacific silver fir
White fir
Grand fir
Subalpine fir

Abies magnifica Murr. var. *shastensis* Lemm.
Abies procera Rehd.
Abronia latifolia Eschsch.
Acer circinatum Pursh
Acer glabrum Torr.
Acer glabrum var. *douglasii* (Hook.) Dipp.
Acer macrophyllum Pursh
Achillea millefolium L.
Achillea millefolium var. *lanulosa* Piper
Achlys triphylla (Smith) DC.
Actaea rubra (Ait.) Willd.
Adenocaulon bicolor Hook.
Agoseris heterophylla (Nutt.) Greene
Agoseris hirsuta (Hook.) Greene
Agropyron dasystachyum (Hook.) Scribn.
Agropyron spicatum (Pursh) Scribn. & Sm.
Agropyron subsecundum (Link) Hitchc.
Agropyron trachycaulum (Link) Malte.
Agrostis hallii Vasey
Agrostis rossae Vasey
Agrostis tenuis Sibth.
Aira caryophyllea L.
Aira praecox L.
Alnus rhombifolia Nutt.
Alnus rubra Bong.
Alnus sinuata (Reg.) Rydb.
Aloina rigida (Hedw.) Limpr.*
Amelanchier alnifolia Nutt.
Amelanchier pallida Greene
Ammophila arenaria (L.) Link
Anaphalis margaritacea (L.) B. & H.
Andraea nivalis Hook.*
Anemone deltoidea Hook.
Anemone drummondii Wats.
Anemone lyallii Britt.
Anemone occidentalis Wats.
Anemone oregana Gray
Anemone piperi Britt.
Angelica lucida L.
Antennaria alpina (L.) Gaertn.
Antennaria corymbosa E. Nels.
Antennaria dimorpha (Nutt.) T. & G.
Antennaria rosea Greene
Anthoxanthum odoratum L.
Apocynum androsaemifolium L.
Apocynum pumilum Greene
Arabis holboellii Hornem.
Arbutus menziesii Pursh
Arctostaphylos canescens Eastw.
Arctostaphylos columbiana Piper
Arctostaphylos hispidula How.

Shasta red fir
 Noble fir
 Yellow sandverbena
 Vine maple
 Rocky Mountain maple
 Rocky Mountain maple
 Bigleaf maple
 Western yarrow
 Western yarrow
 Deerfoot vanillaleaf
 Baneberry
 Trail plant
 Annual agoseris
 Woolly agoseris
 Thickspike wheatgrass
 Bluebunch wheatgrass
 Bearded wheatgrass
 Slender wheatgrass
 Halls bentgrass
 Ross bentgrass
 Colonial bentgrass
 Silver hairgrass
 Early hairgrass
 White alder
 Red alder
 Sitka alder

Saskatoon serviceberry
 Pale serviceberry
 European beachgrass
 Pearly everlasting

Threeleaf anemone
 Drummond anemone
 Lyall anemone
 Western pasqueflower
 Oregon anemone
 Piper anemone
 Sea-watch
 Alpine pussytoes
 Flattop pussytoes
 Low pussytoes
 Rose pussytoes
 Sweet vernal grass
 Spreading dogbane
 Low dogbane
 Holboell rockcress
 Pacific madrone
 Hoary manzanita
 Hairy manzanita
 Howell manzanita

Arctostaphylos nevadensis Gray
Arctostaphylos patula Greene
Arctostaphylos uva-ursi (L.) Spreng.
Arctostaphylos viscida Parry
Arenaria capillaris var. *americana* Davis
Arenaria formosa (Fisch.) Reg.
Arenaria macrophylla Hook.
Arenaria obtusiloba (Rydb.) Fern.
Arenaria pumicola Cov.
Aristida longiseta Steud.
Arnica cordifolia Hook.
Arnica latifolia Bong.
Arnica sororia Greene
Arrhenatherum elatius (L.) Mert.
Artemisia arbuscula Nutt.
Artemisia cana Pursh
Artemisia rigida (Nutt.) Gray
Artemisia spinescens Eat.
Artemisia suksdorfii Piper
Artemisia tilesii Ledeb.
Artemisia tridentata Nutt.
Artemisia tripartita Rydb.
Asarum caudatum Lindl.
Aster alpigenus (T. & G.) Gray
Aster canescens Pursh
Aster conspicuus Lindl.
Aster ledophyllus Gray
Aster occidentalis (Nutt.) T. & G.
Aster radulinus Gray
Aster scopulorum Gray
Aster subspicatus Nees
Astragalus arrectus Gray
Astragalus filipes Torr. ex Gray
Astragalus lentiginosus Dougl. ex Hook.
Astragalus miser Dougl. ex Hook.
Astragalus spaldingii Gray
Astragalus stemophyllus T. & G.
Atriplex confertifolia (Torr. & Frem.) Wats.
Atriplex nuttallii Wats.
Athyrium alpestre Butters
Athyrium filix-femina (L.) Roth
Aulacomnium androgynum (Hedw.) Schwaegr.*
Avena fatua L.
Balsamorhiza deltoidea Nutt.
Balsamorhiza hookeri Nutt.
Balsamorhiza sagittata (Pursh) Nutt.
Balsamorhiza serrata Nels. & Macbr.
Berberis aquifolium Pursh
Berberis nervosa Pursh
Berberis pumila Greene
Betula papyrifera Marsh.

Pine-mat manzanita
 Green manzanita
 Kinnikinnick
 White-leaved manzanita
 Fescue sandwort
 Slender mountain sandwort
 Bigleaf sandwort
 Blunt-leaved sandwort
 Crater Lake sandwort
 Red threeawn
 Heartleaf arnica
 Broadleaf arnica
 Sisters' arnica
 Tall oatgrass
 Low sagebrush
 Silver sagebrush
 Stiff sagebrush
 Bud sagebrush
 Suksdorf sagebrush
 Mountain wormwood
 Big sagebrush
 Threetip sagebrush
 Wild ginger
 Alpine aster
 Hoary aster
 Snowy aster
 Cascades aster
 Western aster
 Rough-leaf aster
 Crag aster
 Douglas aster
 Hangingpod milkvetch
 Threadstalk milkvetch
 Specklepod loco
 Starved milkvetch
 Spaldings milkvetch
 Hangingpod milkvetch
 Shadscale
 Nuttall's saltbush
 Alpine ladyfern
 Ladyfern

 Wild oat
 Puget balsamroot
 Hooker balsamroot
 Arrowleaf balsamroot
 Serrated balsamroot
 Tall Oregongrape
 Oregongrape
 Pygmy Oregongrape
 Northwestern paper birch

<i>Boschniakia strobilacea</i> Gray	Ground-cone
<i>Briza minor</i> L.	Little quaking grass
<i>Brodiaea coronaria</i> (Salisb.) Jeps.	Harvest brodiaea
<i>Brodiaea coronaria</i> var. <i>macropoda</i> Torr.	Harvest brodiaea
<i>Brodiaea multiflora</i> Benth.	Many-flowered brodiaea
<i>Bromus carinatus</i> H. & A.	California brome
<i>Bromus commutatus</i> Schrad.	Hairy brome
<i>Bromus laevipes</i> Shear	Chinook brome
<i>Bromus mollis</i> L.	Soft brome
<i>Bromus rigidus</i> Roth	Ripgut brome
<i>Bromus sitchensis</i> Trin.	Alaska brome
<i>Bromus tectorum</i> L.	Cheatgrass brome
<i>Bromus vulgaris</i> (Hook.) Shear	Columbia brome
<i>Calamagrostis nutkaensis</i> (Presl) Steud.	Pacific reedgrass
<i>Calamagrostis rubescens</i> Buckl.	Pinegrass
<i>Calochortus nitidus</i> Dougl.	Big-pod mariposa lily
<i>Caltha biflora</i> DC.	Twinflower marshmarigold
<i>Caltha leptosepala</i> DC.	Elkslip marshmarigold
<i>Campanula scouleri</i> Hook.	Scouler bellflower
<i>Cardamine bellidifolia</i> L.	Alpine bittercress
<i>Carex aperta</i> Boott	Columbia sedge
<i>Carex aquatilis</i> Wahl.	Water sedge
<i>Carex breweri</i> Boott	Brewer sedge
<i>Carex concinnoides</i> Mack.	Northwestern sedge
<i>Carex geyeri</i> Boott	Elk sedge
<i>Carex hoodii</i> Boott	Hood sedge
<i>Carex lyngbyei</i> Hornem.	Lyngbye's sedge
<i>Carex macrocephala</i> Willd.	Bighead sedge
<i>Carex nebraskensis</i> Dew.	Nebraska sedge
<i>Carex nigricans</i> C. A. Mey.	Black alpine sedge
<i>Carex obnupta</i> Bail.	Slough sedge
<i>Carex praegracilis</i> W. Boott	Clustered field sedge
<i>Carex rossii</i> Boott	Ross sedge
<i>Carex rostrata</i> Stokes	Beaked sedge
<i>Carex spectabilis</i> Dew.	Showy sedge
<i>Cassiope mertensiana</i> (Bong.) G. Don	Western cassiope
<i>Castanopsis chrysophylla</i> (Dougl.) A. DC.	Golden chinkapin
<i>Castanopsis chrysophylla</i> var. <i>minor</i> Benth	Small golden chinkapin
<i>Castilleja angustifolia</i> (Nutt.) G. Don	Northwestern paintbrush
<i>Castilleja arachnoidea</i> Greenm.	Cotton paintbrush
<i>Castilleja lutescens</i> (Greenm.) Rydb.	Yellow paintbrush
<i>Castilleja miniata</i> Dougl. ex Hook.	Scarlet paintbrush
<i>Castilleja parviflora</i> Bong.	Smallflower paintbrush
<i>Ceanothus cordulatus</i> Kell.	Mountain whitethorn ceanothus
<i>Ceanothus cuneatus</i> (Hook.) Nutt.	Narrow-leaved buckbrush
<i>Ceanothus integerrimus</i> H. & A.	Deerbrush
<i>Ceanothus prostratus</i> Benth.	Squawcarpet
<i>Ceanothus sanguineus</i> Pursh	Redstem ceanothus
<i>Ceanothus thyrsiflorus</i> Esch.	Blueblossom
<i>Ceanothus velutinus</i> Dougl. ex Hook.	Snowbrush ceanothus
<i>Ceanothus velutinus</i> var. <i>laevigatus</i> T. & G.	Varnishleaf ceanothus

Ceanothus velutinus var. *velutinus*

Dougl. ex Hook.

Celtis douglasii Planch.

Cercocarpus betuloides Nutt. in T. & G.

Cercocarpus ledifolius Nutt. in T. & G.

Chaenactis douglasii (Hook.) H. & A.

Chamaecyparis lawsoniana (A. Murr.) Parl.

Chamaecyparis nootkatensis (D. Don) Spach

Cheilanthes gracillima D. C. Eaton

Cheilanthes siliquosa Maxon

Chimaphila menziesii (R. Br.) Spreng.

Chimaphila umbellata (L.) Bart.

Chimaphila umbellata var. *occidentalis* Blake

Chrysothamnus nauseosus (Pall.) Brit.

Chrysothamnus nauseosus var. *albicaulis*

Hall. & Clem.

Chrysothamnus viscidiflorus (Hook.) Nutt.

Cicuta douglasii (DC.) Coult. & Rose

Circaea alpina L.

Cirsium vulgare (Savi) Airy-Shaw

Cladonia bellidiflora (Ach.) Schaer.*

Cladonia coniocraea (Flk.) Spreng.*

Cladonia grayii Merr.*

Cladonia ecmocyna (Ach.) Nyl.*

Cladonia ecmocyna var. *intermedia* (Robb.) Thoms.*

Cladonia macrophyllodes Nyl.*

Cladonia phyllophora Hoffm.*

Cladonia rangiferina (L.) Wigg.*

Claytonia megarhiza (Gray) Parry ex Wats.

Claytonia megarhiza var. *nivalis* (English)

C. L. Hitchc.

Clintonia uniflora (Schult.) Kunth

Collinsia parviflora Lindl.

Convolvulus soldanella L.

Coptis laciniata Gray

Coptis occidentalis (Nutt.) T. & G.

Corallorhiza maculata Raf.

Cornus canadensis L.

Cornus glabrata Benth.

Cornus nuttallii Aud. ex T. & G.

Corylus cornuta Marsh. var. *californica* (DC.) Sharp

Cotula coronopifolia L.

Crataegus columbiana Howell

Crataegus douglasii Lindl.

Cryptantha affinis (Gray) Greene

Cryptogramma acrostichoides R. Br.

Cuscuta salina Engelm.

Cynosurus echinatus L.

Dactylis glomerata L.

Danthonia californica Boland.

Danthonia intermedia Vasey

Snowbrush ceanothus

Hackberry

Birchleaf mountainmahogany

Curlleaf mountainmahogany

Falseyarrow

Port-Orford-cedar

Alaska-cedar

Lace-fern

Podfern

Little prince's pine

Western prince's pine

Western prince's pine

Tall gray rabbitbrush

Whitestem gray rabbitbrush

Tall green rabbitbrush

Western waterhemlock

Alpine circaea

Common thistle

Alpine springbeauty

Alpine springbeauty

Queencup beadlelily

Littleflower collinsia

Coast morningglory

Cutleaf goldthread

Western goldthread

Spotted coralroot

Bunchberry dogwood

Brown dogwood

Pacific dogwood

California hazel

Bird brassbuttons

Columbia hawthorn

Black hawthorn

Slender cryptantha

Parsley-fern

Salt-marsh dodder

Hedgehog dogtail

Orchardgrass

California danthonia

Timber danthonia

<i>Darlingtonia californica</i> Torr.	California pitcher-plant
<i>Daucus carota</i> L.	Wild carrot
<i>Deschampsia atropurpurea</i> (Wahl.) Scheele	Mountain hairgrass
<i>Deschampsia caespitosa</i> (L.) Beauv.	Tufted hairgrass
<i>Descurainia pinnata</i> (Walt.) Britt.	Pinnate tansymustard
<i>Dicranum fuscescens</i> Turn.*	
<i>Dicranum scoparium</i> Hedw.*	
<i>Dipsacus sylvestris</i> Huds.	Common teasel
<i>Disporum hookeri</i> (Torr.) Britt.	Hooker's fairybells
<i>Disporum smithii</i> (Hook.) Piper	Smith's fairybells
<i>Distichlis spicata</i> (L.) Greene	Seashore saltgrass
<i>Distichlis stricta</i> (Torr.) Rydb.	Alkali saltgrass
<i>Douglasia nivalis</i> Lindl.	Snow douglasia
<i>Draba aureola</i> Wats.	Great alpine whitlow-grass
<i>Drepanocladus aduncus</i> (Hedw.) Warnst.*	
<i>Dryas octopetala</i> L.	White mountain avens
<i>Dryopteris linnaeana</i> C. Chr.	Oak fern
<i>Dryopteris dilatata</i> (Hoffm.) A. Gray	Mountain woodfern
<i>Elymus caput-medusae</i> L.	Medusahead wildrye
<i>Elymus cinereus</i> Scrib. & Mer.	Giant wildrye
<i>Elymus flavescens</i> Scribn. & Sm.	Yellow rye-grass
<i>Elymus glaucus</i> Buckl.	Blue wildrye
<i>Elymus mollis</i> Trin.	Dune wildrye
<i>Elymus triticoides</i> Buckl.	Creeping wildrye
<i>Epilobium alpinum</i> L. var. <i>clavatum</i> (Trel.) C. L. Hitchc.	Alpine willowweed
<i>Epilobium angustifolium</i> L.	Fireweed
<i>Epilobium latifolium</i> L.	Red willowweed
<i>Epilobium paniculatum</i> Nutt.	Autumn willowweed
<i>Equisetum maximum</i> Lam.	Giant horsetail
<i>Erigeron aureus</i> Greene	Golden fleabane
<i>Erigeron filifolius</i> Nutt.	Threadleaf fleabane
<i>Erigeron linearis</i> (Hook.) Piper	Lineleaf fleabane
<i>Erigeron peregrinus</i> (Pursh) Greene	Peregrine fleabane
<i>Eriodictyon californicum</i> (H. & A.) Greene	Yerba santa
<i>Eriogonum compositum</i> Dougl. ex Benth.	Northern buckwheat
<i>Eriogonum douglasii</i> Benth. in DC.	Douglas buckwheat
<i>Eriogonum heracleoides</i> Nutt.	Wyeth buckwheat
<i>Eriogonum latifolium</i> Smith	Broad-leaved eriogonum
<i>Eriogonum marifolium</i> T. & G.	Mountain buckwheat
<i>Eriogonum microthecum</i> Nutt.	Slenderbush buckwheat
<i>Eriogonum niveum</i> Dougl. ex Benth.	Snow eriogonum
<i>Eriogonum piperi</i> Greene	Piper buckwheat
<i>Eriogonum pyrolaefolium</i> Hook. ex A. Murr.	Oarleaf buckwheat
<i>Eriogonum sphaerocephalum</i> Dougl. ex Benth.	Rock buckwheat
<i>Eriogonum thymoides</i> Benth. in DC.	Thyme buckwheat
<i>Eriogonum umbellatum</i> Torr.	Sulfur buckwheat
<i>Eriophorum angustifolium</i> Roth.	Tall cottongrass
<i>Eriophyllum lanatum</i> (Pursh) Forbes	Common woolly sunflower
<i>Erodium cicutarium</i> (L.) L'Her.	Filaree
<i>Erythronium montanum</i> Wats.	Avalanche fawnlily

<i>Eurhynchium oreganum</i> (Sull.) J. & S.*	Winterfat
<i>Eurotia lanata</i> (Pursh) Moq.	California fescue
<i>Festuca californica</i> Vasey	Brome fescue
<i>Festuca dertonensis</i> (All.) Asch. & Graeb.	
<i>Festuca elatior</i> L. var. <i>arundinacea</i>	
(Schräd.) Weinm.	Alta fescue
<i>Festuca idahoensis</i> Elm.	Idaho fescue
<i>Festuca myuros</i> L.	Rattail fescue
<i>Festuca occidentalis</i> Hook.	Western fescue
<i>Festuca octoflora</i> Walt.	Sixweeks fescue
<i>Festuca ovina</i> L.	Sheep fescue
<i>Festuca rubra</i> L.	Red fescue
<i>Festuca scabrella</i> Torr.	Rough fescue
<i>Festuca subulata</i> Trin.	Bearded fescue
<i>Festuca viridula</i> Vasey	Green fescue
<i>Fontinalis antipyretica</i> Hedw. var.	
<i>gigantea</i> (Sull.) Sull.*	
<i>Fragaria chiloensis</i> (L.) Duchesne	Coast strawberry
<i>Fragaria vesca</i> L. var. <i>bracteata</i> (Heller) Davis	Western wood strawberry
<i>Fragaria virginiana</i> Duchesne var. <i>platypetala</i>	
(Rydb.) Hall	Broad-petaled strawberry
<i>Franseria chamissonis</i> Less.	Silver beach-weed
<i>Fraxinus latifolia</i> Benth.	Oregon ash
<i>Galium aparine</i> L.	Cleavers bedstraw
<i>Galium boreale</i> L.	Northern bedstraw
<i>Galium divaricatum</i> Lam.	Spreading bedstraw
<i>Galium triflorum</i> Michx.	Sweetscented bedstraw
<i>Garrya buxifolia</i> Gray	Box-leaved garrya
<i>Garrya elliptica</i> Dougl.	Silk tassel bush
<i>Garrya fremontii</i> Torr.	Bear bush
<i>Gastridium ventricosum</i> (Gouan) Schinz. & Thell.	Nit grass
<i>Gaultheria shallon</i> Pursh	Salal
<i>Gayophytum diffusum</i> T. & G.	Spreading gayophytum
<i>Gayophytum ramosissimum</i> Nutt. ex T. & G.	Hairstem groundsmoke
<i>Geranium viscosissimum</i> F. & M.	Sticky geranium
<i>Geum macrophyllum</i> Willd.	Largeleaf avens
<i>Gilia capitata</i> Sims	Globe gilia
<i>Gilia nuttallii</i> Gray	Nuttall gilia
<i>Glaux maritima</i> L.	Sea milkwort
<i>Glehnia leiocarpa</i> Mathias	Beach silver-top
<i>Goodyera oblongifolia</i> Raf.	Rattlesnake plantain
<i>Grayia spinosa</i> (Hook.) Moq.	Spiny hopsage
<i>Grindelia stricta</i> DC.	Oregon gum-plant
<i>Gymnomitrium varians</i> (Lindb.) Schiffn.*	
<i>Haplopappus liatrifolius</i> (Greene) St. John	Palouse haplopappus
<i>Haplopappus stenophyllus</i> Gray in Torr.	Narrow-leaved haplopappus
<i>Helianthella uniflora</i> (Nutt.) T. & G.	False sunflower
<i>Heracleum lanatum</i> Michx.	Common cowparsnip
<i>Hieracium albertinum</i> Farr	Western hawkweed
<i>Hieracium albiflorum</i> Hook.	White hawkweed
<i>Hieracium cynoglossoides</i> Arv.-Touv.	Houndstongue hawkweed

<i>Hieracium gracile</i> Hook.	Slender hawkweed
<i>Holcus lanatus</i> L.	Common velvetgrass
<i>Holodiscus discolor</i> (Pursh) Maxim.	Creambush oceanspray
<i>Holodiscus glabrescens</i> Heller	Gland oceanspray
<i>Holosteum umbellatum</i> L.	Jagged chickweed
<i>Homalothecium megaptilum</i> (Sull.) Robins.*	
<i>Hulsea nana</i> Gray in Torr.	Dwarf hulsea
<i>Hydrophyllum fendleri</i> (Gray) Heller var. <i>albifrons</i> (Heller) Macbr.	Fendler waterleaf
<i>Hylocomium splendens</i> (Hedw.) Bry. Eur.*	
<i>Hypericum anagalloides</i> C. & S.	Bog St. Johnswort
<i>Hypericum perforatum</i> L.	Common St. Johnswort
<i>Hypnum circinale</i> Hook.*	
<i>Hypnum fertile</i> Sendt.*	
<i>Hypochaeris radicata</i> L.	Spotted catsear
<i>Iris chrysophylla</i> How.	Slender-tubed iris
<i>Iris douglasiana</i> Herb. var. <i>oregonensis</i> Fost.	Douglas iris
<i>Iris missouriensis</i> Nutt.	Western iris
<i>Iris tenax</i> Dougl.	Oregon iris
<i>Isothecium spiculiferum</i> (Mitt.) Ren. & Card.*	
<i>Jaumea carnosa</i> (Less.) Gray	Jaumea
<i>Juncus balticus</i> Willd.	Baltic rush
<i>Juncus drummondii</i> E. Mey.	Drummond rush
<i>Juncus effusus</i> L.	Common rush
<i>Juncus falcatus</i> E. Mey.	Sickle-leaved rush
<i>Juncus lesueurii</i> Boland.	Salt rush
<i>Juncus parryi</i> Engelm.	Parry's rush
<i>Juncus phaeocephalus</i> Engelm.	Brown-headed rush
<i>Juniperus communis</i> L.	Common juniper
<i>Juniperus occidentalis</i> Hook.	Western juniper
<i>Juniperus scopulorum</i> Sarg.	Rocky Mountain juniper
<i>Koeleria cristata</i> (L.) Pers.	Prairie junegrass
<i>Lactuca serriola</i> L.	Prickly lettuce
<i>Lagophylla ramosissima</i> Nutt.	Slender rabbitleaf
<i>Lappula redowskii</i> (Hornem.) Greene	Western stickseed
<i>Larix lyallii</i> Parl.	Subalpine larch
<i>Larix occidentalis</i> Nutt.	Western larch
<i>Lathyrus bijugatus</i> White	Pinewoods peavine
<i>Lathyrus littoralis</i> (Nutt.) Endl.	Beach peavine
<i>Lathyrus polyphyllus</i> Nutt. ex T. & G.	Pacific peavine
<i>Lathyrus sphaericus</i> Retz.	Grass pea
<i>Lecidea quadricolor</i> (Dicks.) Borr. ex Hook.*	
<i>Ledum glandulosum</i> Nutt.	Mountain labradortea
<i>Ledum glandulosum</i> var. <i>columbianum</i> (Piper) C. L. Hitchc.	Mountain labradortea
<i>Ledum groenlandicum</i> Hulten	Bog labradortea
<i>Leptarrhena pyrolifolia</i> (D. Don) R. Br.	False saxifrage
<i>Leptodactylon pungens</i> (Torr.) Nutt.	Granite gilia
<i>Libocedrus decurrens</i> Torr.	Incense-cedar
<i>Ligusticum apiifolium</i> (Nutt.) Gray	Parsleyleaf licoriceroot
<i>Ligusticum grayi</i> Coult. & Rose	Gray's lovage

<i>Lilaeopsis occidentalis</i> Coult. & Rose	Western lilaeopsis
<i>Linaria dalmatica</i> (L.) Mill.	Dalmatian toadflax
<i>Linnaea borealis</i> L.	Twinflower
<i>Listera caurina</i> Piper	Western twayblade
<i>Listera convallarioides</i> (Sw.) Nutt.	Broad-lipped twayblade
<i>Lithocarpus densiflorus</i> (Hook. & Arn.) Rehd.	Tanoak
<i>Lolium perenne</i> L.	Perennial ryegrass
<i>Lomatium angustatum</i> St. John	Few-fruited lomatium
<i>Lomatium cuspidatum</i> Math. & Const.	Pointed-leaved lomatium
<i>Lomatium dissectum</i> (Nutt.) Math. & Const.	Lace-leaved leptotaenia
<i>Lomatium macrocarpum</i> (Nutt.) Coult. & Rose	Bigseed lomatium
<i>Lomatium triternatum</i> (Pursh) C. & T.	Nineleaf lomatium
<i>Lonicera conjugialis</i> Kell.	Purpleflower honeysuckle
<i>Lonicera hispidula</i> (Lindl.) Dougl. ex T. & G.	
var. <i>vacillans</i> (Benth.) Gray	California honeysuckle
<i>Lonicera involucrata</i> (Rich.) Banks	Bearberry honeysuckle
<i>Luetkea pectinata</i> (Pursh) Kuntze	Luetkea
<i>Lupinus albifrons</i> Benth.	White-leaved lupine
<i>Lupinus caudatus</i> Kell.	Tailcup lupine
<i>Lupinus latifolius</i> Agardh	Broadleaf lupine
<i>Lupinus leucophyllus</i> Dougl. ex Lindl.	Velvet lupine
<i>Lupinus lepidus</i> Dougl. ex Lindl.	Prairie lupine
<i>Lupinus littoralis</i> Dougl. ex Lindl.	Shore lupine
<i>Lupinus saxosus</i> Howell	Rock lupine
<i>Lupinus sericeus</i> Pursh	Silky lupine
<i>Lysichitum americanum</i> Hult. & St. John	Skunkcabbage
<i>Madia madioides</i> (Nutt.) Greene	Woodland tarweed
<i>Maianthemum bifolium</i> DC. var. <i>kamschaticum</i> (Gmel.) Jeps.	
<i>Marah oreganus</i> (T. & G.) Howell	False lily-of-the-valley
<i>Melica bulbosa</i> Geyer	Oregon wild cucumber
<i>Melica geyeri</i> Munro	Oniongrass
<i>Melica harfordii</i> Boland.	Geyer oniongrass
<i>Menziesia ferruginea</i> Smith	Harford melic
<i>Mesembryanthemum chilense</i> Molina	Rustyleaf
<i>Microseris troximoides</i> Gray	Sea fig
<i>Mimulus lewisii</i> Pursh	False agoseris
<i>Mimulus nanus</i> H. & A.	Lewis monkeyflower
<i>Mimulus tilingii</i> Reg.	Dwarf monkeyflower
<i>Mitella stauropetala</i> Piper	Clustered monkeyflower
<i>Mnium insigne</i> Mitt.*	Sideflower miterwort
<i>Mnium menziesii</i> (Hook.) C. Müll.*	
<i>Monotropa hypopitys</i> L.	
<i>Montia sibirica</i> (L.) Howell	Pinesap
<i>Muhlenbergia filiformis</i> (Thurb.) Rydb.	Western springbeauty
<i>Myosotis micrantha</i> Pall. ex Lehm.	Pullup muhly
<i>Myrica californica</i> Cham.	Smallflower forgetmenot
<i>Oenanthe sarmentosa</i> Presl ex DC.	Waxmyrtle
<i>Oplopanax horridum</i> (J. E. Smith) Miq.	Water parsley
<i>Opuntia polyacantha</i> Haw.	Devilsclub
<i>Oryzopsis hymenoides</i> (R. & S.) Ricker	Plains pricklypear
	Indian ricegrass

<i>Osmaronia cerasiformis</i> (T. & G.) Greene	Indian plum
<i>Osmorhiza chilensis</i> H. & A.	Mountain sweetroot
<i>Oxalis oregana</i> Nutt. ex T. & G.	Oregon oxalis
<i>Oxyria digyna</i> (L.) Hill	Alpine mountainsorrel
<i>Pachistima myrsinites</i> (Pursh) Raf.	Oregon boxwood
<i>Parnassia fimbriata</i> Konig	Rockymountain parnassia
<i>Peltigera aphthosa</i> (L.) Willd.*	
<i>Penstemon aridus</i> Rydb.	Stiffleaf penstemon
<i>Penstemon cardwellii</i> Howell	Cardwell's penstemon
<i>Penstemon cusickii</i> Gray	Cusick penstemon
<i>Penstemon davidsonii</i> Greene	Davidson penstemon
<i>Penstemon procerus</i> Dougl.	Tinybloom penstemon
<i>Penstemon rydbergii</i> A. Nels.	Rydberg penstemon
<i>Penstemon speciosus</i> Dougl. ex Lindl.	Royal penstemon
<i>Petasites frigidus</i> (L.) Fries var.	
<i>nivalis</i> (Greene) Cronq.	Alpine coltsfoot
<i>Phacelia hastata</i> Dougl. ex Lehm.	Whiteleaf phacelia
<i>Phacelia heterophylla</i> Pursh	Varileaf phacelia
<i>Philadelphus lewisii</i> Pursh	Mockorange
<i>Philonotis fontana</i> (Hedw.) Brid.*	
<i>Phleum alpinum</i> L.	Alpine timothy
<i>Phlox diffusa</i> Benth.	Spreading phlox
<i>Phlox douglasii</i> Hook.	Tufted phlox
<i>Phlox gracilis</i> (Hook.) Greene	Pink annual phlox
<i>Phlox hoodii</i> Rich.	Hoods phlox
<i>Phlox longifolia</i> Nutt.	Longleaf phlox
<i>Phyllodoce empetrifolia</i> (S.W.) D. Don	Red mountainheath
<i>Physocarpus malvaceus</i> (Greene) Kuntze	Mallow ninebark
<i>Picea engelmannii</i> (Parry) Engelm.	Engelmann spruce
<i>Picea sitchensis</i> (Bong.) Carr.	Sitka spruce
<i>Pinus albicaulis</i> Engelm.	Whitebark pine
<i>Pinus attenuata</i> Lemm.	Knobcone pine
<i>Pinus cembra</i> L.	Swiss stone pine
<i>Pinus contorta</i> Dougl.	Lodgepole pine
<i>Pinus jeffreyi</i> Grev. & Balf.	Jeffrey pine
<i>Pinus lambertiana</i> Dougl.	Sugar pine
<i>Pinus monticola</i> Dougl.	Western white pine
<i>Pinus ponderosa</i> Laws.	Ponderosa pine
<i>Pinus pumila</i> Regel	Japanese stone pine
<i>Plantago lanceolata</i> L.	English plantain
<i>Plantago maritima</i> L.	Seaside plantain
<i>Plantago patagonica</i> Jacq.	Indianwheat
<i>Plantago subnuda</i> Pilgr.	Tall coast plantain
<i>Plectritis macrocera</i> T. & G.	Longhorn plectritis
<i>Poa ampla</i> Merr.	Alpine bluegrass
<i>Poa compressa</i> L.	Canada bluegrass
<i>Poa curtifolia</i> Scribn.	Mt. Stuart bluegrass
<i>Poa cusickii</i> Vasey	Cusick bluegrass
<i>Poa macrantha</i> Vasey	Seashore bluegrass
<i>Poa nervosa</i> (Hook.) Vasey	Wheeler bluegrass
<i>Poa pratensis</i> L.	Kentucky bluegrass
<i>Poa pringlei</i> Scribn.	Pringle bluegrass

<i>Poa scabrella</i> Torr.	Pine bluegrass
<i>Poa secunda</i> Presl	Sandberg bluegrass
<i>Pogonatum alpinum</i> (Hedw.) Roehl*	
<i>Pohlia nutans</i> (Hedw.) Lindb.*	
<i>Polemonium californicum</i> Eastw.	California polemonium
<i>Polemonium elegans</i> Greene	Slender polemonium
<i>Polemonium pulcherrimum</i> Hook.	Skunkleaf polemonium
<i>Polygonum bistortoides</i> Pursh	American bistort
<i>Polygonum newberryi</i> Small	Newberry fleecflower
<i>Polygonum paronychia</i> Cham. & Schlect.	Nailwort knotweed
<i>Polygonum phytolaccaefolium</i> Meisn. ex Small	Pokeweed fleecflower
<i>Polystichum munitum</i> (Kaulf.) Presl	Swordfern
<i>Polytrichadelphus lyallii</i> Mitt.*	
<i>Polytrichum juniperinum</i> Hedw.*	
<i>Polytrichum norvegicum</i> Hedw.*	
<i>Polytrichum piliferum</i> Hedw.*	
<i>Populus tremuloides</i> Michx.	Quaking aspen
<i>Populus trichocarpa</i> Torr. & Gray	Black cottonwood
<i>Porella navicularis</i> (L. & L.) Lindb.*	
<i>Potentilla anserina</i> L.	Silver weed
<i>Potentilla flabellifolia</i> Hook. ex T. & G.	Fanleaf cinquefoil
<i>Potentilla fruticosa</i> L.	Shrubby cinquefoil
<i>Potentilla glandulosa</i> Lindl.	Gland cinquefoil
<i>Potentilla gracilis</i> Dougl. ex Hook.	Beauty cinquefoil
<i>Prunella vulgaris</i> L. var. <i>lanceolata</i> (Bart.) Fern.	Heal-all
<i>Prunus avium</i> L.	Mazzard cherry
<i>Prunus emarginata</i> Dougl.	Bitter cherry
<i>Prunus virginiana</i> L.	Common chokecherry
<i>Prunus virginiana</i> var. <i>melanocarpa</i> (A. Nels.) Sarg.	Chokecherry
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	Douglas-fir
<i>Psoralea lanceolata</i> Pursh	Lanceleaf scurfpea
<i>Pteridium aquilinum</i> (L.) Kuhn. var. <i>pubescens</i> Underw.	Bracken fern
<i>Pterospora andromedea</i> Nutt.	Pine drops
<i>Ptilidium californicum</i> (Aust.) U. & C.*	
<i>Puccinellia pumila</i> (Vas.) Hitchc.	Alaska alkali grass
<i>Purshia tridentata</i> (Pursh) DC.	Bitterbrush
<i>Pyrola asarifolia</i> Michx.	Large pyrola
<i>Pyrola picta</i> Smith in Rees	Whitevein pyrola
<i>Pyrola secunda</i> L.	One-sided wintergreen
<i>Quercus chrysolepis</i> Liebm.	Canyon live oak
<i>Quercus garryana</i> Dougl.	Oregon white oak
<i>Quercus kelloggii</i> Newb.	California black oak
<i>Quercus sadleriana</i> R. Br.	Sadler oak
<i>Quercus vaccinifolia</i> Kellogg	Huckleberry oak
<i>Raillardella argentea</i> Gray	Raillardella
<i>Ranunculus flammula</i> L.	Smaller creeping buttercup
<i>Ranunculus occidentalis</i> Nutt.	Western buttercup
<i>Rhacomitrium canescens</i> (Hedw.) Brid. var. <i>ericoides</i> (Brid.) B.S.G.*	

<i>Rhacomitrium heterostichum</i> (Hedw.) Brid.*	
<i>Rhacomitrium lanuginosum</i> (Hedw.) Brid.*	
<i>Rhacomitrium patens</i> (Hedw.) Hueb.*	
<i>Rhacomitrium sudeticum</i> (Funck) B.S.G.*	
<i>Rhamnus californica</i> Esch. var.	California coffee berry
<i>occidentalis</i> (How.) Jeps.	Cascara
<i>Rhamnus purshiana</i> DC.	Cascades azalea
<i>Rhododendron albiflorum</i> Hook.	Pacific rhododendron
<i>Rhododendron macrophyllum</i> G. Don	Western azalea
<i>Rhododendron occidentale</i> (T. & G.) Gray	Pacific poison oak
<i>Rhus diversiloba</i> T. & G.	Smooth sumac
<i>Rhus glabra</i> L.	Skunkbrush sumac
<i>Rhus trilobata</i> Nutt. in T. & G.	
<i>Rhytidiadelphus loreus</i> (Hedw.) Warnst.*	
<i>Rhytidiadelphus triquetrus</i> (Hedw.) Warnst.*	
<i>Rhytidiopsis robusta</i> (Hook.) Broth.*	
<i>Ribes cereum</i> Dougl.	Wax currant
<i>Ribes lacustre</i> (Pers.) Poir.	Prickly currant
<i>Ribes marshalli</i> Greene	Hupa gooseberry
<i>Ribes menziesii</i> Pursh	Menzies gooseberry
<i>Ribes velutinum</i> Greene	Desert gooseberry
<i>Ribes viscosissimum</i> Pursh	Sticky currant
<i>Rosa eglanteria</i> L.	Sweetbriar rose
<i>Rosa gymnocarpa</i> Nutt.	Baldhip rose
<i>Rosa nutkana</i> Presl	Nootka rose
<i>Rosa woodsii</i> Lindl.	Woods rose
<i>Rubus lasiococcus</i> Gray	Dwarf blackberry
<i>Rubus nivalis</i> Dougl. ex Hook.	Snow dewberry
<i>Rubus parviflorus</i> Nutt.	Thimbleberry
<i>Rubus pedatus</i> J. E. Smith	Strawberry-leaf blackberry
<i>Rubus spectabilis</i> Pursh	Salmonberry
<i>Rubus ursinus</i> Cham. & Schlecht.	Trailing blackberry
<i>Rumex acetosella</i> L.	Sheep sorrel
<i>Rumex venosus</i> Pursh	Veiny dock
<i>Salicornia ambigua</i> Michx.	Woody glasswort
<i>Salix hookeriana</i> Barr.	Coast willow
<i>Salix nivalis</i> Hook.	Snow willow
<i>Salix scouleriana</i> Barr.	Scouler's willow
<i>Salix sitchensis</i> Sanson in Bong.	Sitka willow
<i>Salsola kali</i> L.	Russian thistle
<i>Sambucus cerulea</i> Raf.	Blue elderberry
<i>Sambucus racemosa</i> L. var. <i>melanocarpa</i>	
(Gray) McMinn	Black elderberry
<i>Sanicula bipinnatifida</i> Dougl. ex Hook.	Purple sanicle
<i>Sanicula crassicaulis</i> Poepp.	Western snake-root
<i>Sarcobatus vermiculatus</i> (Hook.) Torr.	Black greasewood
<i>Sarcodes sanguinea</i> Torr.	Snow plant
<i>Satureja douglasii</i> (Benth.) Briq.	Yerba buena
<i>Saussurea americana</i> Eat.	Saussurea
<i>Saxifraga tolmiei</i> T. & G.	Tolmie saxifrage
<i>Scapania bolanderi</i> Aust.*	
<i>Scirpus americanus</i> Pers.	Three-square

Scirpus pacificus Britt.
Scirpus setaceus L.
Scirpus validus Vahl
Scrophularia lanceolata Pursh
Sedum oregonense (Wats.) Peck
Selaginella wallacei Hieron.
Senecio fremontii T. & G.
Senecio integerrimus Nutt.
Senecio pauperculus Michx.
Senecio sylvaticus L.
Sequoia sempervirens (D. Don) Endl.
Sherardia arvensis L.
Sidalcea malvaeflora (DC.) Gray
Sidalcea oregana (Nutt.) Gray
Silene acaulis L.
Silene parryi (Wats.) Hitchc. & Maguire
Sisymbrium altissimum L.
Sisyrinchium californicum (Ker) Dryand.
Sitanion hystrix J. G. Sm.
Sitanion jubatum J. G. Sm.
Smelowskia calycina (Steph.) C. A. Mey.
Smelowskia ovalis M. E. Jones
Smilacina sessilifolia (J. G. Bak.) Nutt.
Smilacina stellata (L.) Desf.
Solidago canadensis L.
Solidago missouriensis Nutt.
Spiraea betulifolia Pall. var. *lucida*
(Dougl.) C. L. Hitchc.
Spiraea douglasii Hook.
Spiraea douglasii var. *menziesii*
(Hook.) Presl
Sporobolus cryptandrus (Torr.) Gray
Spraguea umbellata Torr. in Smith
Stachys cooleyae Heller
Stachys mexicana Benth.
Stellaria crispa Cham. & Schlecht.
Stereocaulon paschale (L.) Hoffm.*
Stipa californica Merr. & Davy
Stipa columbiana Macoun
Stipa comata Trin. & Rupr.
Stipa lemmonii (Vas.) Scribn.
Stipa lettermanii Vasey
Stipa occidentalis Thurb.
Stipa thurberiana Piper
Streptopus curvipes Vaill.
Struthiopteris spicant (L.) Weis.
Symphoricarpos albus (L.) Blake
Symphoricarpos mollis Nutt. var. *hesperius*
(G. N. Jones) Cronq.
Symphoricarpos rotundifolius Gray
Synthyris reniformis (Dougl.) Benth.
Taraxacum officinale Weber

Pacific coast bulrush
Bristle-leaved sedge
American great bulrush
Lanceleaf figwort
Creamy stonecrop
Wallace's selaginella
Low mountain senecio
Western groundsel
Balsam groundsel
Woodland groundsel
Coast redwood
Bluefield madder
Mallow sidalcea
Oregon checkermallow
Moss silene
Parrys silene
Tumbleweed
Golden blue-eyed grass
Bottlebrush squirreltail
Big squirreltail
Alpine smelowskia
Short-fruit smelowskia
Slim solomonplume
Starry solomonplume
Canada goldenrod
Missouri goldenrod

Shinyleaf spirea
Douglas spirea

Menzies spirea
Sand dropseed
Pussypaws
Cooleys hedge nettle
Great hedge nettle
Crisped starwort

California needlegrass
Columbia needlegrass
Needle and thread
Lemmon needlegrass
Letterman needlegrass
Western needlegrass
Thurber needlegrass
Purple twistedstalk
Deerfern
Common snowberry

Creeping snowberry
Round-leaved snowberry
Snowqueen
Common dandelion

<i>Taxus brevifolia</i> Nutt.	Western yew
<i>Tellima grandiflora</i> (Pursh) Dougl.	Alaska fringe cup
<i>Tetradymia canescens</i> DC.	Gray horsebush
<i>Thalictrum occidentale</i> Gray	Western meadow-rue
<i>Thlaspi alpestre</i> L.	Blue pennycress
<i>Thlaspi arvense</i> L.	Penny-cress
<i>Thuja plicata</i> Donn	Western redcedar
<i>Tiarella trifoliata</i> L.	Three-leaved coolwort
<i>Tiarella unifoliata</i> Hook.	Western coolwort
<i>Tolmiea menziesii</i> (Pursh) T. & G.	Youth-on-age
<i>Torilis arvensis</i> (Huds.) Link	Field hedge-parsley
<i>Torilis nodosa</i> (L.) Gaertn.	Knotted hedge-parsley
<i>Tortula brevipes</i> (Lesq.) Broth.*	
<i>Tortula ruralis</i> (Hedw.) Gaertn., Meyer & Schreb.*	
<i>Tortula princeps</i> De Not.*	
<i>Trautvetteria caroliniensis</i> (Walt.) Vail	False bugbane
<i>Trientalis latifolia</i> Hook.	Starflower
<i>Trifolium gymnocarpon</i> Nutt.	Tufted clover
<i>Trifolium longipes</i> Nutt.	Long-stalked clover
<i>Trifolium macrocephalum</i> (Pursh) Poir.	Big-headed clover
<i>Trifolium willdenovii</i> Lehm.	Spring-bank clover
<i>Triglochin maritima</i> L.	Seaside arrow-grass
<i>Trillium ovatum</i> Pursh	White trillium
<i>Trisetum canescens</i> Buckl.	Tall trisetum
<i>Trisetum cernuum</i> Trin.	Nodding trisetum
<i>Tsuga heterophylla</i> (Raf.) Sarg.	Western hemlock
<i>Tsuga mertensiana</i> (Bong.) Carr.	Mountain hemlock
<i>Ulex europaeus</i> L.	Common gorse
<i>Umbellularia californica</i> (Hook. & Arn.) Nutt.	California laurel
<i>Urtica dioica</i> L.	Bigsting nettle
<i>Vaccinium alaskaense</i> Howell	Alaska huckleberry
<i>Vaccinium caespitosum</i> Michx.	Dwarf huckleberry
<i>Vaccinium deliciosum</i> Piper	Blueleaf huckleberry
<i>Vaccinium membranaceum</i> Dougl. ex Hook.	Big huckleberry
<i>Vaccinium occidentale</i> Gray	Western bog huckleberry
<i>Vaccinium ovalifolium</i> Smith	Ovalleaf huckleberry
<i>Vaccinium ovatum</i> Pursh	Evergreen huckleberry
<i>Vaccinium parvifolium</i> Smith	Red huckleberry
<i>Vaccinium scoparium</i> Leiberger	Grouse huckleberry
<i>Valeriana sitchensis</i> Bong.	Sitka valerian
<i>Vancouveria hexandra</i> (Hook.) Morr. & Dec.	White inside-out-flower
<i>Veratrum viride</i> Ait.	American false hellebore
<i>Veronica peregrina</i> L.	Purslane speedwell
<i>Vicia americana</i> Muhl. ex Willd.	American vetch
<i>Vicia americana</i> var. <i>truncata</i> Brew.	American vetch
<i>Vicia tetrasperma</i> (L.) Moench	Slender vetch
<i>Viola glabella</i> Nutt.	Wood violet
<i>Viola sempervirens</i> Greene	Evergreen violet
<i>Whipplea modesta</i> Torr.	Whipple vine
<i>Xerophyllum tenax</i> (Pursh) Nutt.	Common beargrass
<i>Zigadenus fremontii</i> Torr.	Fremont deathcamas
<i>Zigadenus paniculatus</i> (Nutt.) Wats.	Foothill deathcamas

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