

FOREST VEGETATION OF THE MONTANE AND SUBALPINE ZONES, OLYMPIC MOUNTAINS, WASHINGTON

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INTRODUCTION

One of the last frontiers for large scale ecological research in the United States has been the Pacific Northwest. Foresters have conducted silvicultural research in the area for many years, but until the late 1950's there had been few basic ecologic studies especially in the mountains near the coast. Daubenmire (1952, 1956) had done considerable work in the northern Rockies. Krajina and his students (Krajina 1965) began research during the late 1950's in the coastal and interior mountains in British Columbia, and Whittaker (1960) investigated the ecology of the Siskiyou Mountains in southern Oregon-northern California. Synecological studies in the Cascade Range began with the work of Franklin (1965, 1966).

Some pertinent points concerning the ecology of the Olympic Peninsula were first stated by Jones (1936), although the book was basically a flora. Sharpe (1956) studied the rain forests, which are narrowly confined to three broad river valleys open to the Pacific Ocean. The rain forest, dependent upon the ocean influence and typified by huge trees

and luxuriant vegetation, never extend to an elevation above 300 m. Sharpe's work was taxonomic in format, although a considerable portion was concerned with the phytosociology of carefully selected and narrowly defined plots.

This study is concerned with the forest vegetation of the montane and subalpine zones, part of a larger project to investigate the plant ecology of the Olympic Mountains massif. Dense coniferous forests cover the slopes of the Olympics from sea level to 1800 m, but this investigation is limited to those between 550 and 1800 m. Because so little was known about the ecology of these forests, several different kinds of data and observations were needed. Information was desired on the location, composition, and structure of the montane and subalpine forests; the relationships of the different community types to each other and how the pattern of species and communities is affected by temperature and precipitation. Additional information was sought on the role of fire in these forests; the effect of vegetation, environmental factors, and slope exposure on soil development; and the relationship of parent material and soil fertility levels to forest pattern. Finally, we wanted to know the position of the Olympic Mountain forests in the ecology and phytogeography of the Pacific Northwest mountain systems.

The nomenclature in this study follows the treatments of several authors, because of the lack of a comprehensive flora for the Pacific Northwest.

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Nomenclature is that of U.S. Forest Service (1965) for Gymnospermae, Hitchcock, *et al.* (1955, 1959, 1961, 1964) for Dicotyledonae, Hitchcock and Chase (1950) for grasses, and Peck (1961) for the lower vascular plants and Monocotyledonae. Exceptions are the treatments of *Blechnum spicant* and *Maianthemum dilatatum*, which follow Munz (1959).

Pseudotsuga menziesii var. *menziesii* is the only variety of Douglas fir found in the Olympics. Citation of the binomial elsewhere in this work indicates, therefore, only this variety. Voucher specimens are deposited in the Herbarium of the University of Illinois.

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STUDY AREA

LOCATION

The Olympic Peninsula, covering an area of *ca.* 10,400 km² in the northwest corner of Washington, is bounded on the west by the Pacific Ocean, on the north by the Strait of Juan de Fuca, and on the east by Hood Canal and Puget Sound. The Olympic Mountains constitute the center of the peninsula, and are one of the last true wilderness areas of the United States (Fig. 1). Figure 2 shows the major drainages in the Olympics, and some important landmarks.

Olympic National Park, officially established in 1938, occupies nearly 364,000 ha of the central mountains and a coastal strip. Olympic National Forest, *ca.* 252,000 ha adjoins the National Park boundary in many places. The National Forest and private land-owners carry on extensive logging operations, but the National Park boundaries were established before logging operations had penetrated the mountains very far, so that no forests within Olympic National Park have been cut. Most of the sampling for this study was conducted within the National Park boundaries, although some work was carried out in the National Forest on leave strips from clear-cutting operations.

GEOLOGY

Weaver (1937, 1945) and Danner (1955) have studied the geology of the Olympic Mountains, and their publications have served as the basis of the discussion below. Most of the rocks in the mountains originated in either of two geologic ages. The central and largest part of the Olympics consists of sedimentary rocks of the Soleduck Formation, deposited about 126 million years ago during the early Cretaceous period. Some volcanic rocks laid down during

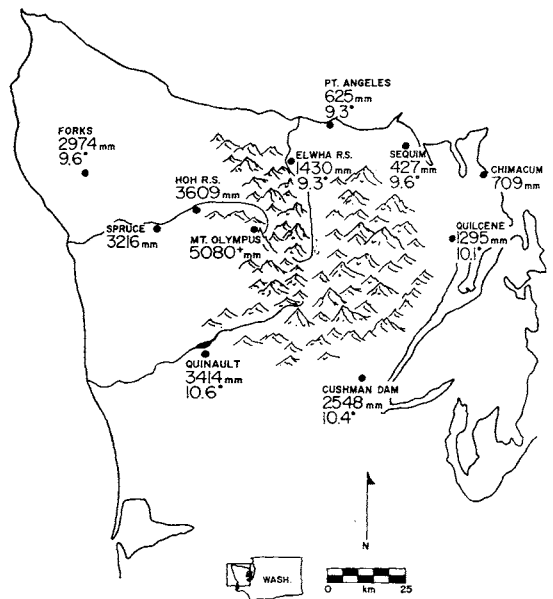


FIG. 1. Mean annual precipitation (mm) and temperature (°C) for selected stations on the Olympic Peninsula, Washington. Data are for observation periods of varying length.

this same period form a minor part of the geology. Metchosin Formation volcanics, formed during Eocene inundation, constitute the rim of the mountains on the north, east, and south. This formation covers considerably less area than the Soleduck Formation, and most of it lies in the National Forest. Along the east and south this formation is almost 19 km wide, but it is relatively narrow along the northern edge. Sediments deposited near the close of Eocene constitute the Crescent Formation, and are most obvious along this northern rim. Previously, rocks of this formation covered most of the Olympic Peninsula, but they have been subsequently eroded away.

The present topographic features of the Olympics were largely produced by two intervals of diastrophism, but were somewhat modified by glacial action and erosion during the Pleistocene. The mountains have a basic northwest-southeast course, over which has been imposed a north-south trend wrought by the Cascadian Revolution. The western mountains rise gently eastward from the ocean, with long ridges, 300 to 600 m high, stretching for 30 to 50 km before culminating in high peaks, such as Mt. Olympus and the Bailey Range. (Fig. 1). The central body of mountains from Mt. Olympus east for 40 km averages 1800 m in elevation. The northeast and southeast slopes are cut by deep valleys with steep sides and intervening sharp crests, so that the rugged eastern Olympics present a marked contrast to the western portion. As a result of the Puget Sound downwarping, the eastern Olympics plunge from 2100 m to sea level at Hood Canal in a distance of 13 km.

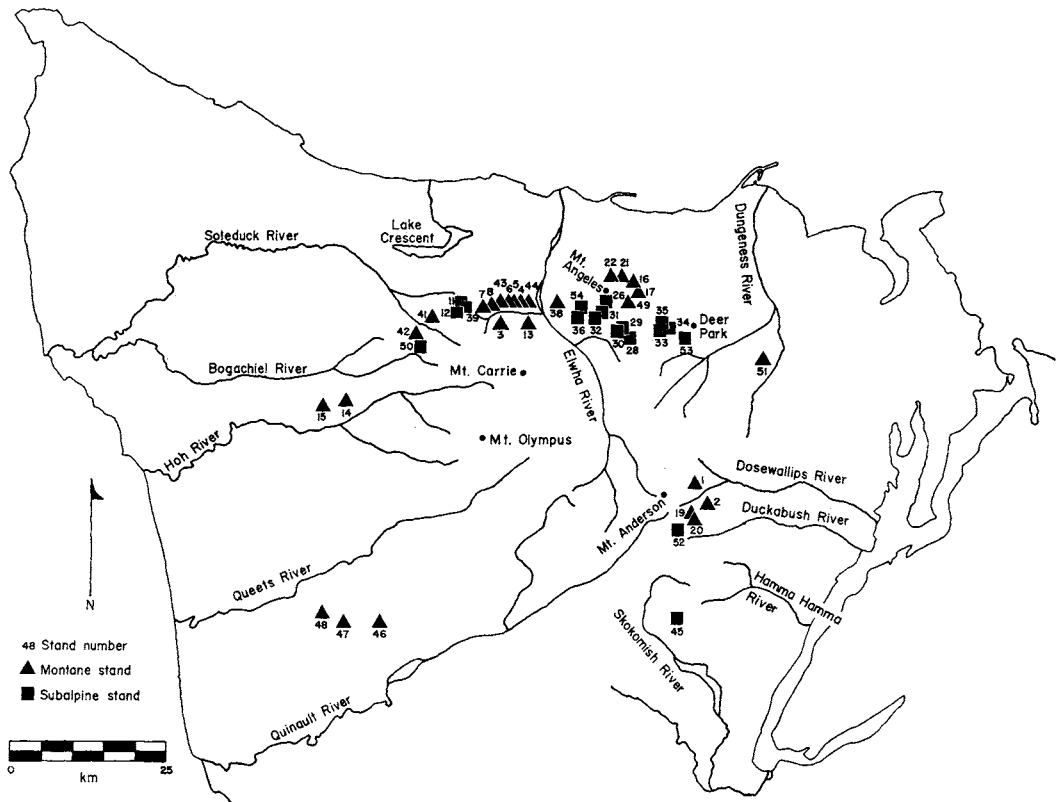


FIG. 2. Location of important geographic features and stands sampled in the Olympic Mountains.

Mountain glaciers have been the main sculpturing agents in the mountains. During maximum Pleistocene glaciation, many mountain glaciers pushed down their valleys, some probably reaching the ocean. Most of the major river valleys have a characteristic U-shape, evidence that valley glaciation was extensive. Continental glaciers from mainland British Columbia covered very little of the Olympic Peninsula. One lobe in Puget Sound reached only as high as 750 m on the eastern side of the peninsula. Another lobe in the Strait of Juan de Fuca pushed through Lake Crescent and the northern Soleduck Valley, but probably overrode very little of the mountainous portion of the peninsula.

CLIMATE

The climate of the Olympic Peninsula is distinctly maritime. The winters are mild and quite wet; the summers are cool and dry, although not nearly so dry as are the summers of more continental mountain systems. Owing to the orientation of the mountains, however, environmental regimes are highly varied. Within a distance of 65 km, one can go from the wettest location (500+ cm/yr) in the continental United States to the driest location (43 cm/yr) on the west coast outside of southern California. Table 1 gives mean monthly precipitation and mean monthly temperature for several stations on the peninsula.

The peninsula is about 120 km wide from the Pacific Ocean to Hood Canal; Mt. Olympus is only 51 km from the ocean. The ameliorating effect of the Pacific reaches far inland, keeping the general climate mild year-round. The diurnal and annual range in temperature at all stations is small, with those stations near water having a smaller range than those farther inland (Table 1). Mean annual temperatures are similar for all stations on the peninsula (Fig. 1; U.S. Weather Bureau 1965). Throughout the summer, temperatures on the coastal plain and lower elevations in the mountains usually range from 18° to 24° C during the day to 10° at night. In winter, maximum temperatures are around 4° to 8°, with minima about -1°. During very cold periods, minimum temperatures may fall to -9° to -12°, and maxima fail to reach 0° (Phillips 1963). Cold weather such as this rarely lasts more than a few days.

Topography is the most important control governing precipitation patterns on the Olympic Peninsula. The Olympic Mountains present an effective barrier to the moisture-laden westerly winds (Fig. 1). As the winds come off the ocean, they funnel up the broad valleys in the west, are forced to rise over the lower ridges, then over a mountain barrier dominated by Mt. Olympus and the peaks of the Bailey Range. This mountain barrier, which approximately bisects

TABLE 1. Mean monthly precipitation and temperature at selected U.S. Weather Bureau stations around the Olympic Peninsula. (Source: Phillips 1963; U.S. Weather Bureau 1965).

	Precipitation (mm)					Temperature (°C)				
	Quinsault R.S. 67 m	Cushman Dam 232 m	Elwha R.S. 105 m	Quilcene 38 m	Sequim 55 m	Quinsault R.S. 67 m	Cushman Dam 232 m	Elwha R.S. 105 m	Quilcene 38 m	Sequim 55 m
Jan.....	507	423	221	205	54	4.1	2.8	1.8	2.7	3.3
Feb.....	405	313	196	165	43	5.1	4.2	3.8	4.3	4.5
Mar.....	361	264	146	112	32	6.8	6.0	5.3	6.4	6.0
Apr.....	233	154	86	78	24	9.9	9.4	8.3	9.6	8.8
May.....	150	85	40	64	24	12.9	13.1	11.9	12.8	11.7
Jun.....	109	62	31	61	29	15.0	15.4	14.3	15.1	14.0
Jul.....	66	33	17	25	13	17.4	18.2	16.9	17.5	15.8
Aug.....	71	35	24	26	14	17.4	18.0	16.7	17.1	16.0
Sep.....	152	95	47	38	25	15.4	15.8	14.7	14.7	14.1
Oct.....	337	247	145	98	40	11.4	11.4	9.7	10.5	10.3
Nov.....	445	374	238	184	56	6.6	6.4	5.1	5.9	6.4
Dec.....	578	462	240	239	64	4.9	4.3	3.2	3.9	4.6
Tot.....	3414	2547	1431	1295	418	10.6	10.4	9.3	10.1	9.6

the peninsula, stretches for 30 km from north to south, and includes 12 major peaks. Mean annual precipitation west of the Bailey Range generally ranges from 2500 to 3200 mm along the coastal plain and valleys, and 3400 mm or more along some of the windward slopes (Fig. 1). LaChapelle (1960) estimates annual precipitation at Blue Glacier on Mt. Olympus at 3800 to 5000 mm. During the 1957/1958 IGY period, annual precipitation at Blue Glacier equaled 2580 mm.

East of this barrier, there is a rainshadow that is intensified by the jumble of tall peaks that constitute the eastern mountains (Fig. 1). Annual precipitation averages around 1400 mm immediately east of the Bailey Range, and drops to 1000 mm or less to the northeast. The Bailey Range thus separates the Olympics into an eastern and western section, and the dry eastern slopes contrast with the wet western slopes.

During winter, elevations below 600 m receive mostly rain; those between 600 and 1400 m, rain and snow; and those above 1400 m, mostly snow (Phillips 1963). Between 25 and 80 cm of snow usually falls in the lower valleys each year, whereas the higher mountains receive 760 to 1300 cm of snow (U.S. Weather Bureau 1965).

METHODS

VEGETATION

Following a general reconnaissance of the species distribution throughout the mountains, tentative community types (Langenheim 1962; Whittaker 1967) were recognized, based upon the various combinations of canopy trees and understory vegetation observed throughout the mountains. Rather than impose a random net of stands for sampling on the mountains, stands were selected based upon the recognition of relatively homogeneous populations of the tentative community types. Transition areas between the tentative community types were too narrow to include in the sampling. The only criterion for choosing a

stand for sampling were areas without large ravines, water seepageways, or rock outcrops. Figure 2 shows the location of the stands sampled in this study, and in addition, the important drainages in the mountains.

Quantitative data were gathered by measuring all trees 10.0 cm DBH or larger within the limits of either 0.04, 0.1, or 0.2 acre circular plots. Tree density and stand shape governed the size and number of plots used. The two *Abies amabilis-Tsuga heterophylla* stands were sampled with one line of 0.2 acre plots, about 65 m apart (seven plots). Because of the extent of the river terraces, these stands are usually about 100 m wide, and several compass lines were not possible. All other montane stands and three *Abies amabilis-Tsuga mertensiana* stands were sampled with fifteen 0.1 acre plots. These were taken at five points about 45 m apart along each of three compass lines. The *Abies lasiocarpa*, *Pinus contorta*, two *Abies amabilis-Tsuga mertensiana* and the two young *Pseudotsuga menziesii* stands were each sampled using ten 0.04 acre plots. These samples were on two compass lines of five plots each, about 30 m apart. Small plots were used because of the high tree density and irregularity of stand shape.

The understory was sampled at points 2 and 4 of each transect, except for 0.2 acre plots for which all seven points were sampled. Circular nested plots were used for the tree sapling-shrub layer (0.01 acre) and the herb layer (0.001 acre). Species in each layer were recorded and scored by cover class.

Data were compiled to give Importance Value Indices based on 300 (relative basal area, relative frequency, and relative density) for the tree species within each of the 45 stands (Brown and Curtis 1952). Cover classes were weighted for the sapling-shrub layer and herb layer to allow for the range difference in cover in the higher classes. Thus, cover class 1, which included cover from 0 to 1% was given a value of 1, whereas cover class 9, which included cover from 81 to 100%, was given a value of 90. Relative cover was determined using these

TABLE 2. Mean composition of the tree layers for the 7 major community types recognized in the montane and subalpine zones of the Olympic Mountains, Washington. Data are for Importance Value Indices (IVI) based on 100, constancy (C), mean density (T/ha), and mean basal area (m²/ha).

COMMUNITY TYPE and species	IVI	C	T/ha	m ² /ha
ABIES AMABILIS-TSUGA HETEROPHYLLA/OXALIS (5 stands)				
<i>Abies amabilis</i>	53.1± 8.4	100	259	47.1
<i>Tsuga heterophylla</i>	45.2± 7.0	100	161	48.8
<i>Thuja plicata</i>	1.7± 2.9	40	2	1.8
ABIES AMABILIS-TSUGA HETEROPHYLLA (2 stands)				
<i>Abies amabilis</i>	59.3± 3.4	100	351	58.7
<i>Tsuga heterophylla</i>	34.4± 4.0	100	138	29.8
<i>Pseudotsuga menziesii</i>	4.1± 2.0	100	5	2.2
<i>Thuja plicata</i>	2.2± 1.5	100	2	0.1
TSUGA HETEROPHYLLA-PSEUDOTSUGA MENZIESII (8 stands)				
<i>Tsuga heterophylla</i>	45.5± 6.2	100	232	35.5
<i>Pseudotsuga menziesii</i>	39.1± 4.7	100	109	46.4
<i>Thuja plicata</i>	10.8± 10.0	75	49	3.9
<i>Abies amabilis</i>	3.6± 4.2	88	10	1.4
<i>Pinus monticola</i>	0.5± 0.7	38	1	0.3
<i>Picea sitchensis</i>	0.5± 1.4	13	1	0.2
PSEUDOTSUGA MENZIESII-TSUGA HETEROPHYLLA (7 stands)				
<i>Pseudotsuga menziesii</i>	56.5± 4.8	100	353	54.1
<i>Tsuga heterophylla</i>	30.0± 5.0	100	185	16.9
<i>Thuja plicata</i>	5.9± 4.6	86	22	1.6
<i>Taxus brevifolia</i>	4.5± 5.1	57	16	0.3
<i>Pinus monticola</i>	1.7± 2.0	71	2	0.4
<i>Abies amabilis</i>	1.4± 1.6	57	2	0.1
PSEUDOTSUGA MENZIESII (3 stands)				
<i>Pseudotsuga menziesii</i>	85.8± 8.5	100	554	93.4
<i>Tsuga heterophylla</i>	6.8± 5.5	67	20	0.9
<i>Pinus monticola</i>	4.1± 3.8	67	5	0.2
<i>Abies grandis</i>	3.3± 4.2	33	5	0.4
ABIES AMABILIS-TSUGA MERTENSIANA (5 stands)				
<i>Abies amabilis</i>	42.6± 9.8	100	346	47.3
<i>Tsuga mertensiana</i>	40.6± 6.2	100	306	47.6
<i>Chamaecyparis nootkatensis</i>	14.2± 10.2	60	91	12.0
<i>Pseudotsuga menziesii</i>	1.2± 2.0	20	1	1.9
<i>Abies lasiocarpa</i>	0.8± 1.2	40	2	0.1
<i>Pinus monticola</i>	0.8± 0.9	20	2	0.5
ABIES LASIOCARPA (9 stands)				
<i>Abies lasiocarpa</i>	67.7± 19.5	100	949	57.6
<i>Chamaecyparis nootkatensis</i>	9.2± 11.8	44	128	4.3
<i>Abies amabilis</i>	9.0± 11.6	78	72	4.5
<i>Tsuga mertensiana</i>	8.9± 11.2	56	94	5.4
<i>Pseudotsuga menziesii</i>	2.9± 4.8	33	12	2.4
<i>Pinus monticola</i>	2.3± 3.8	22	7	1.8

the individual stands, using these reduced Importance Values from all three vegetation layers in the formula

$$C = \frac{2w}{a + b} \times 100, \text{ where } C \text{ is the coefficient of similarity, } a \text{ and } b \text{ are the sums of Importance Values in stands A and B, and } w \text{ is the sum of the least common Importance Values of the two stands. Species were not adjusted in relation to their maximum values of frequency, density, and basal area or cover as in Bray and Curtis (1957). A two-dimensional ordination (Beals 1960) was then constructed from these similarity values to test the spatial patterning of sampled stands. The placement of stands along each axis utilized the Pythagorean theorem.}$$

Following the construction of the ordination, the stands were regrouped based upon the ordination, and the original tentative community types were modified to reflect the spatial pattern of the ordination. From this final grouping of stands, composite Importance Values were obtained to form the basis of Table 2, 3, and 4.

SOILS

Twenty-two soil pits were dug to determine the effect of vegetation on soil development and to see if soil fertility had an effect on the distribution of species and plant communities. Profiles were described following the USDA Soil Survey Manual (1951, 1962), and composite samples of each horizon were taken for later analyses. The soils were air-dried after collection. In the laboratory, the soil was passed through a 2 mm sieve, and analyses were carried out in duplicate on the 2 mm fraction. Soil moisture at 1/8 atmos. was obtained on a Pressure Plate Extractor; soil moisture at 15 atmos. on a 15-Bar Ceramic Plate Extractor (Soilmoisture Equipment Co., Cat. 60). Soil texture was determined by the hydrometer method (Bouyoucos 1951), except that the sand fraction was sieved out on a 0.053 mm sieve. Exchangeable bases and exchangeable hydrogens were obtained by the method of Brown (1943). The University of Wisconsin, Department of Soils, analyzed the soils for pH, organic matter, and available calcium, magnesium, phosphorus, and potassium. Soil pH was determined by the glass electrode method. Calcium and magnesium were extracted with N ammonium acetate and read with a Coleman Jr. Flame Photometer. Phosphorus was determined following the method of Laverty (1961). The remainder of the phosphorus extract was used for potassium determination on a Coleman Model 21 Flame Photometer. Organic matter percent was obtained by the Walkley-Black method (1934), modified for reading on a Coleman Model 8 Photo-Electric Calorimeter. This method is accurate for soils with less than 12.5% organic matter. Soils with more organic matter were ignited in a muffle furnace at 400° C for 8 hours, at Urbana. Total iron was obtained by atomic absorption at the Nu-Ag Soil Testing Laboratory, Rochelle, Illinois. Soil color was described

weighted values, then added to relative frequency to give an Importance Value Index based on 200 (Bazzaz 1968).

ORDINATION

Importance Value Indices for the tree, tree sapling-shrub, and herb strata were each reduced to 100. Coefficients of similarity were then calculated for

for moist soil using the Munsell Color Charts in natural light.

RESULTS

MONTANE FORESTS

Abies amabilis-Tsuga heterophylla/Oxalis Type

The most extensive forests in the Olympic Mountains comprise the *Abies amabilis-Tsuga heterophylla/Oxalis* community type. These forests occur from 550 to 1100 m on the western slopes of the main mountain barrier and on all the ridges stretching from there to near the ocean, but are absent east of the Bailey Range. Growing conditions in this area are favorable for excellent tree growth, because the forests are so close to the Pacific Ocean that the climate is mild year-round, precipitation is plentiful, and moisture stress is rare. These forests exhibit large, moderately spaced trees, a patchy tree sapling-shrub layer, and an extensive herb layer, testifying to the favorable climate. The community type has a mean of 422 trees/ha, mean basal area of 97.7 m²/ha, and mean DBH of 54 cm/tree. The *Abies amabilis-Tsuga heterophylla/Oxalis* forests occur on slopes of every aspect, for the macroclimate is so uniform that the effect of slope exposure is negli-

TABLE 3. Composition of the tree sapling-shrub layer and the herb layer for the 7 major community types recognized in the montane and subalpine zones of the Olympic Mountains, Washington. Data are for Importance Value Indices based on 100; + signifies species present, but IVI less than 3.0.

Species	<i>Abies amabilis-Tsuga heterophylla/Oxalis</i>	<i>Abies amabilis-Tsuga heterophylla</i>	<i>Tsuga heterophylla-Pseudotsuga menziesii</i>	<i>Pseudotsuga menziesii-Tsuga heterophylla</i>	<i>Pseudotsuga menziesii</i>	<i>Abies amabilis-Tsuga mertensiana</i>	<i>Abies lasiocarpa</i>
TREE SAPLINGS							
<i>Abies amabilis</i>	31.7	29.2	8.5	1.6	—	28.9	6.1
<i>Tsuga heterophylla</i>	27.7	14.0	28.5	14.1	4.1	—	—
<i>Thuja plicata</i>	—	16.8	3.2	0.4	—	—	—
<i>Pseudotsuga menziesii</i>	—	—	3.1	1.6	1.0	—	—
<i>Taxus brevifolia</i>	—	—	—	6.0	—	—	—
<i>Pinus monticola</i>	—	—	—	1.0	—	—	0.9
<i>Abies grandis</i>	—	—	—	—	3.8	—	—
<i>Tsuga mertensiana</i>	—	—	—	—	—	11.8	6.2
<i>Chamaecyparis nootkatensis</i>	—	—	—	—	—	2.7	5.6
<i>Abies lasiocarpa</i>	—	—	—	—	—	—	29.6
SHRUBS							
<i>Vaccinium ovalifolium</i>	24.7	17.8	9.3	5.1	—	—	—
<i>Vaccinium parvifolium</i>	9.3	8.9	14.5	6.0	—	+	+
<i>Menziesia ferruginea</i>	—	6.8	+	+	—	—	—
<i>Gaultheria shallon</i>	+	—	13.3	30.2	35.1	—	—
<i>Berberis nervosa</i>	+	—	4.7	12.0	16.2	—	—
<i>Acer circinatum</i>	—	—	3.1	4.6	—	—	—
<i>Linnæa borealis</i>	—	+	3.0	10.9	3.3	—	—
<i>Rosa gymnocarpa</i>	—	—	—	+	20.8	—	+
<i>Symphoricarpos albus</i>	—	—	—	—	6.3	—	—
<i>Vaccinium deliciosum</i>	—	—	—	—	—	34.2	4.4
<i>Rhododendron albiflorum</i>	—	—	—	—	—	12.6	9.1
<i>Pachistima myrsinites</i>	—	—	—	+	—	—	3.7
<i>Sorbus sitchensis</i>	—	+	—	—	—	—	3.3
<i>Vaccinium membranaceum</i>	+	+	+	+	—	+	26.0
Other species	2.8	3.0	3.7	3.1	9.4	5.2	3.9

Species	<i>Abies amabilis-Tsuga heterophylla/Oxalis</i>	<i>Abies amabilis-Tsuga heterophylla</i>	<i>Tsuga heterophylla-Pseudotsuga menziesii</i>	<i>Pseudotsuga menziesii-Tsuga heterophylla</i>	<i>Pseudotsuga menziesii</i>	<i>Abies amabilis-Tsuga mertensiana</i>	<i>Abies lasiocarpa</i>
HERBS							
Mosses	21.2	21.5	53.5	54.9	23.7	42.3	27.2
<i>Oxalis oregana</i>	26.7	—	—	—	—	—	—
<i>Blechnum spicant</i>	8.7	—	—	—	—	+	—
<i>Clintonia uniflora</i>	6.7	11.0	+	—	—	—	—
<i>Polystichum munitum</i>	5.1	+	6.2	+	+	—	—
<i>Lycopodium clavatum</i>	5.0	—	—	—	—	—	—
<i>Maianthemum dilatatum</i>	3.4	—	+	—	—	—	—
<i>Achlyis triphylla</i>	3.4	—	3.0	+	7.9	—	—
<i>Streptopus amplexifolius</i>	3.4	—	—	—	—	—	—
<i>Rubus pedatus</i>	+	22.6	+	—	—	6.6	3.4
<i>Streptopus curvipes</i>	+	8.1	+	—	—	—	—
<i>Listera caurina</i>	+	5.8	+	+	—	—	—
<i>Tiarella unifoliata</i>	—	8.9	3.2	—	—	+	—
<i>Pyrola secunda</i>	—	4.8	+	+	—	4.7	+
<i>Dryopteris dilatata</i>	—	4.2	3.4	—	—	—	—
<i>Trillium ovatum</i>	—	+	—	—	—	—	—
<i>Chimaphila menziesii</i>	—	—	7.8	7.8	+	—	—
<i>Chimaphila umbellata</i>	—	—	+	15.9	8.1	—	—
<i>Adenocaulon bicolor</i>	—	—	+	—	7.9	—	—
<i>Campanula scouleri</i>	+	—	—	+	7.3	—	+
<i>Vicia americana</i>	—	—	—	—	6.4	—	—
<i>Trisetum cernuum</i>	—	—	—	+	5.7	—	—
<i>Hieracium albiflorum</i>	—	—	—	+	5.3	—	+
<i>Bromus sp.</i>	—	—	—	+	4.9	—	—
<i>Madia madioides</i>	—	—	—	—	3.7	—	—
<i>Trientalis latifolia</i>	—	+	+	+	3.7	—	—
<i>Arenaria macrophylla</i>	—	—	—	—	3.6	—	—
<i>Rubus lasiococcus</i>	—	4.8	—	—	—	+	14.8
<i>Erythronium montanum</i>	—	—	—	—	—	29.2	13.4
<i>Xerophyllum tenax</i>	—	—	—	2.2	—	7.2	3.9
<i>Valeriana sitchensis</i>	—	+	—	—	—	+	6.9
<i>Polemonium pulcherrimum</i>	—	—	—	—	—	—	4.1
<i>Peucedanum racemosum</i>	—	—	—	—	—	—	+
<i>Lupinus latifolius</i> var. <i>subalpinus</i>	—	—	—	—	+	—	2.7
Other species	11.6	1.0	10.6	8.1	8.7	3.9	16.5

ble. Forests on north and south-facing slopes generally have the same structure and composition and any slight differences are not consistent throughout the zone.

Abies amabilis and *Tsuga heterophylla* dominate this community type (Table 2). Total basal area is similar for the two species (47.1 vs 48.8 m²/ha), but mean tree basal areas differ. *Tsuga heterophylla* averages 60 cm DBH, whereas *Abies amabilis* averages only 48 cm DBH. The larger trees are 350 to 400 years old.

Thuja plicata is a minor associate species in these forests, and occurs locally throughout the zone. This species grows where soil moisture is plentiful on sites such as creek banks and steep slopes with active seepageways. These areas are limited in extent, and thus are a minor physiographic feature.

Further evidence for composition of this community type and its extent throughout the western Olympics was obtained from sale and timber cruise records of the U.S. Forest Service in the Quinault and Soleduck Ranger Districts. Although these records deal only with tree species greater than 30 cm DBH, they are a good estimate of forest composition.

Sale records from the Quinault District show that both *Abies amabilis* and *Tsuga heterophylla* are the dominants of the forests, accounting for 70 to 99% of the sale volume. *Thuja plicata* was usually included in the sale records, but the volume was small. Invariably, when this species occurred in large amounts, the sale block was located along creeks or major drainage systems, or the block spanned both the montane and lowland zones. An insignificant amount of *Pseudotsuga menziesii* was sold from the montane zone in this district.

The ridges in the Soleduck District are generally low, and *Abies amabilis*-*Tsuga heterophylla* forest types are reported on only the higher ridges. *Pseudotsuga menziesii* was more commonly listed from cruises near the Soleduck River, which is near the eastern border of this western montane zone. Again, many of these cruises were at lower elevations, and along creeks. *Thuja plicata* was common along creeks. From these records, and from the quantitative data gathered in this study, there is little doubt that the *Abies amabilis*-*Tsuga heterophylla*/*Oxalis* community type is widespread and well-developed throughout the western Olympics.

The tree sapling-shrub layer is patchy in occurrence, and much of it is composed of tree reproduction of the two dominant canopy species. Mean cover values for reproduction are about the same for both species (*Abies amabilis* 17%; *Tsuga heterophylla* 15%). *Vaccinium ovalifolium* and *V. parvifolium* are the only important shrub species (Table 3). *Vaccinium ovalifolium* has a mean cover value of 10%; *V. parvifolium*, ca. 2%. Other shrub species have low constancies, being primarily local in occurrence. Mean cover for the total shrub constituent is 13%; for the layer, including tree reproduction, 45%.

The well-developed herb layer, of which *Oxalis oregana* is the dominant species, is the most noticeable aspect of the understory. Although mean cover value for the herb layer is 55%, some of the stands, and many other sites visited had herb layers with 90 to 100% coverage for large areas. Nineteen herbaceous species were sampled in the stands of this community type. *Oxalis oregana* has a high constancy throughout the zone, and is an indicator species. Other vascular species with high constancy are: *Blechnum spicant*, *Clintonia uniflora*, *Polystichum munitum*, and *Maianthemum dilatatum*. Other species in the herb layer are mostly local. Numerous species of moss are abundant throughout these forests.

Abies amabilis-*Tsuga heterophylla* Type

This community type is limited in extent in the Olympic Mountains, but provides a good comparison of similar forests in widely separated, but similar environments. These forests are confined to the alluvial flats and narrow valley slopes along rivers and creeks in the eastern montane zone. The environment along rivers and creeks is cool, owing to cold air drainage from the higher elevation. Soils are moist,

especially on the terraces. Rivers and creeks are fed by the tremendous snowmelt of higher elevations and flow throughout the summer. The soils are not as excessively drained as on the steep slopes to the west, and favorable soil moisture relations thereby compensate for the lower precipitation of the eastern location. These factors result in an environmental regime similar to that of the western montane zone, thus it is not surprising that a similar community develops. These forests are a little more densely stocked (496 trees/ha) than the western montane forests (422 trees/ha). Tree diameters are smaller, with 90.8 m²/ha and an average 48 cm DBH/tree. The centers of the largest trees are usually affected with heart rot, but estimated age for such trees is more than 300 years. Because these river terrace sites are localized, this forest type usually extends less than 100 m from the river edge. *Abies amabilis*-*Tsuga heterophylla* forests were observed in all the river valleys investigated in the eastern Olympics, and constitute an important part of the forest ecology.

Mean composition for the *A. amabilis*-*T. heterophylla* type is given in Tables 2 and 3. *Tsuga heterophylla* grows downstream to sea level in association with *T. plicata*. Apparently, the warmer temperatures on the lower slopes limit *A. amabilis* growth, and thus this community type occurs at higher elevations, generally between 760 and 1125 m. Temperature is more important than moisture in limiting *A. amabilis* distribution (U.S. Forest Service 1965). Moisture deficits appear not to be important here, since these are river terrace sites. Moreover, *T. plicata* always occurs on wetter sites than *A. amabilis* throughout the Olympics, and that species replaces *A. amabilis* in the river terrace forests below 760 m. Warmer temperature could produce a number of physiological effects, among them being higher evapotranspiration which *A. amabilis* may not be able to withstand. These forests are rather heavily dominated by *A. amabilis*, as the IVI of 59.3 would indicate. *Tsuga heterophylla* does well in these forests, but it is not as plentiful as downslope in the lowland forests.

The tree sapling-shrub layer is not well-developed in the *A. amabilis*-*T. heterophylla* forests, where mean cover is 35%. The two principal canopy trees are reproducing, although the value for *Abies* (13% cover) is more than twice as much as that for *Tsuga* (5% cover). This also reflects the size class distribution (see Table 9). There is good representation of *Thuja plicata* in the understory (11% cover).

Although the tree layer in this forest type is similar to the tree layer in the previous type, differences are apparent in the understory when comparing the two, both floristically and structurally. *Vaccinium ovalifolium* and *V. parvifolium*, the most important shrubs, occur in the same order as in the western montane zone, although *V. parvifolium* was present but not sampled in one of the stands. *Menziesia ferruginea* is also locally abundant. These three important shrubs have all been seen consistently in

other locations of the *A. amabilis*-*T. heterophylla* type in addition to the two stands sampled. Other shrub species are generally less common.

Rubus pedatus dominates the sparse herbaceous layer. This low growing herb may provide ground cover over large areas in this forest type. Mosses are also plentiful in this forest, and apparently the gravelly nature of the soil limits growth to those herbs which grow close to the surface and hold water around their aerial structures. Snow lies longer into the summer in the cooler river valleys than on the surrounding slopes, further limiting herbaceous growth to the lower-growing species. *Clintonia uniflora* seems to grow well in areas of late snowmelt, and is notably important in those areas of this forest type that have a late snowmelt. Other important herbaceous species in the *A. amabilis*-*T. heterophylla* community type are: *Tiarella unifoliata*, *Streptopus curvipes*, and *Listera caurina*. There is a significant lack of *Oxalis oregana* and *Blechnum spicant* in this forest type, indicating either a minor environmental difference, such as less fog, or merely a migrational barrier to these species.

Tsuga heterophylla-*Pseudotsuga menziesii* Type

The most majestic forests of the eastern montane zone are those of the *T. heterophylla*-*P. menziesii* type. These forests usually occur on north and east-facing slopes from 600 to 1100 m where conditions are cooler and moister than on south and west-facing slopes. In the Soleduck and Skokomish Valleys (Fig. 2), where precipitation is more plentiful, these forests occupy both north and south-facing slopes. Such sites have adequate moisture, and available sunlight is high because the eastern mountains have fewer cloudy days than the western mountains. These conditions account for the tremendous size some of the trees attain. The type has a mean basal area of 87.7 m²/ha, mean DBH of 53 cm/tree, and 400 trees/ha.

These forests are about 300 years old, so that *Pseudotsuga menziesii* is prominent. In these forests, *T. heterophylla* germinates under a *P. menziesii* canopy, but conditions are moist enough on these sites after disturbance that *T. heterophylla* can germinate and grow with *P. menziesii*. Consequently, the oldest *T. heterophylla* are approximately the same age as the *P. menziesii*. *Tsuga heterophylla* is a prolific seed producer, and seedlings germinate well in shade (U.S. Forest Service 1965). Third generation *Tsuga heterophylla* are now conspicuous in these stands.

Tsuga heterophylla and *P. menziesii* are the most important species in the tree layer (Table 2). Until recently, this type was probably dominated by *P. menziesii*, but the greater number of young *T. heterophylla* trees that attained 10 cm DBH only a short time ago (based upon increment borings), makes *T. heterophylla* the dominant species today. Successionally, this represents a major shift in dominants, from the principal seral species, *P. menziesii*, to a climax

species, *T. heterophylla*. *Pseudotsuga menziesii* will continue to decline in importance in the future.

Many small *Thuja plicata* trees occur in these forests. The small tree size is apparently a response to the drier environment and higher elevation of the montane zone. The species will continue to exist in the forest as a minor component.

Tsuga heterophylla saplings have a higher cover value than any other canopy species, showing that this species will continue to be dominant. Mean cover value for *T. heterophylla* reproduction is 17%. Because *P. menziesii* seedlings are shade intolerant (U.S. Forest Service 1965), the small saplings will die as light becomes limiting. The IVI values for *A. amabilis* saplings indicate the species can reproduce here, and may be better represented in the canopy layer in the future. Mean cover for *A. amabilis* saplings is 5%.

The important shrubs of this community type are: *Vaccinium parvifolium*, *Gaultheria shallon*, *Vaccinium ovalifolium*, *Berberis nervosa*, and *Linnaea borealis* (Table 3). The order of *Vaccinium* importance is reversed from the previous two forest types. *Gaultheria shallon* is found abundantly on the infrequent dry sites on these slopes, but has a low constancy throughout this community type. The remaining shrub species, with low constancies, occur mostly as single plants. Mean cover of the tree sapling-shrub layer is 50%.

The herb layer is poorly developed, although it has a mean cover value of 60%. Mosses account for more than half the importance value and 45% of the cover. The only important vascular species are *Chimaphila menziesii*, *Polystichum munitum*, *Tiarella unifoliata*, and *Listera caurina*. The remaining species of the herb list in Table 3 have low constancies in this forest type.

Pseudotsuga menziesii-*Tsuga heterophylla* Type

This community type occupies south and west-facing slopes in the eastern montane zone, between 550 and 1125 m. These slopes are warm, evapotranspiration is probably high, summer precipitation is low, and the soils are excessively drained. Consequently, there is little soil moisture during the growing season and trees are much smaller than those on sheltered slopes. Mean DBH is only 40 cm/tree, and basal area averages 73.4 m²/ha for the community type. The largest trees may reach 80 cm DBH, whereas those on the opposite slope grow as large as 115 cm DBH. Because the trees are smaller, the forests are more densely stocked than the previous types discussed, averaging 580 trees/ha. Above 900 m, where altitude results in a more moderate temperature, the forests are a little more open, and some trees exceed 100 cm DBH.

Pseudotsuga menziesii is the most important tree species in these 300 year old forests (Table 2). Following fire, the more moist conditions on north-facing slopes are favorable for *Tsuga heterophylla* germination, whereas the warm, dry, south-facing slopes are unfavorable. Thus, *T. heterophylla* is

absent from the latter until the densely stocked *P. menziesii* has thinned sufficiently, about 100 years after disturbance. The *P. menziesii* on north and south-facing slopes are about 250 to 300 years old. The oldest *T. heterophylla* are about 280 years old on north-facing slopes, but only about 180 years old on south-facing slopes, a reflection of the less favorable growing conditions on the latter sites. Some *P. menziesii* never get much larger than 30 cm because of competition, and increment borings showed that all *P. menziesii* regardless of size, are about the same age. Regression analysis showed that tree age had no significant effect (0.01 level) on tree size. Because of the drier conditions, succession to a *Tsuga heterophylla* forest takes longer on southern exposures, and *P. menziesii* will probably continue to dominate these forests for many years.

Thuja plicata is limited in this forest type, found only near ravines and drainage areas, and the trees are all quite small. Whenever *T. plicata* grows on moderately dry and warm sites, its growth is poor (U.S. Forest Service 1965). *Taxus brevifolia* may form a layer ca. 3 to 5 m tall, so thick that nothing grows beneath. Sometimes, these small trees are greater than 10 cm DBH, and must be counted in with the tree layer, but the best measure of *T. brevifolia* occurrence is obtained by an arbitrary lumping of these data with those from the tree sapling-shrub layer.

Tree reproduction in *P. menziesii*-*T. heterophylla* communities is almost exclusively *T. heterophylla* (Table 3). *Tsuga* saplings have a mean cover of 13%, whereas the total cover of all other canopy species is less than 1%. Of these, *P. menziesii* and *Pinus monticola* are limited by light, and will soon die. *Abies amabilis* and *Thuja plicata* reproduction was sampled, but the amounts were too small to permit speculation about compositional trends.

The extensive shrub layer is composed of taller plants than in the previous forest types (Table 3). *Gaultheria shallon*, the most important species, generally grows in tangles about 0.5 m high. In some places, it may reach more than 1 m, but these sites are at lower elevations in the montane zone, continuing downslope into the lowland forests. *Gaultheria shallon* is a dry site indicator in west coast mountains (Hansen 1947). In this and the *P. menziesii* type, it may often completely cover hundreds of square meters, to the virtual exclusion of every other species, even tree reproduction. *Berberis nervosa*, usually associated with *G. shallon*, is not as extensive. Most other shrub species have low IVI values, but those with higher constancies are: *Linnaea borealis*, *Vaccinium parvifolium*, *Taxus brevifolia* (mentioned above), *Vaccinium ovalifolium*, *Acer circinatum*, and *Rosa gymnocarpa*. These species number more than one-half those found in the shrub layer, and generally a majority of them can be found in any given stand. Other shrub species have low constancies, and low cover values. Mean cover for *G. shallon* is 37%, for *B. nervosa*, 7%, and for the tree sapling-shrub layer, 80%. This is one of

the most extensive shrub layers in any of the community types investigated (see Table 8).

The herb layer is poorly developed save for mosses, reflecting both the overall dry conditions and the extreme density of the shrub layer. Only three vascular species with high constancy are important: *Chimaphila umbellata*, *C. menziesii*, and *Xerophyllum tenax* (Table 3). Again, various species of moss constitute more than half the importance values, and have a mean cover of 47%. The herb layer as a whole has a mean cover of 55%. The remaining species are not consistently associated with this forest type.

Pseudotsuga menziesii Type

On exposed south or west-facing slopes in rain shadow areas, where more intense solar radiation and drying winds compound low precipitation, succession to a *Tsuga heterophylla* forest is long delayed. Even after 300 years, moisture relations do not favor *T. heterophylla* germination, so that in contrast to other eastern montane forests, communities on these sites are almost wholly composed of 270 to 300 year old *P. menziesii*. This community type may be found from sea level to 1400 m but most often at lower elevations in the montane zone (550 to 900 m). The *P. menziesii* type was observed in many river valleys in the Olympics, but was particularly common in the Elwha and Dungeness drainages (Fig. 2), and on the western slopes of Blue Mountain (Deer Park). Although there are no data, these areas probably receive the least precipitation. Moreover, the soils are excessively drained, and evapotranspiration is probably high, resulting in very dry sites.

Pseudotsuga menziesii trees dominate this forest type, with a mean IVI of 85.8 (Table 2). These seral communities are densely stocked with *P. menziesii*, but the canopy is somewhat open. The dry environment limits *T. heterophylla* reproduction, which requires a more shaded and moist environment. The forests average 584 trees/ha, with mean basal area of 94.9 m²/ha and mean diameter of 45 cm. *Pseudotsuga menziesii* averages 46 cm DBH with little deviation, whereas various tree sizes were encountered in other community types. This community type also occupies rocky slopes in the rain shadow area, but the *P. menziesii* are younger (180 to 230 years old), and the forests more open, indicating slower re-invasion after fire.

Although the remaining tree species are unimportant, because of the long life span of *P. menziesii* this community type represents an early stage of succession. Whenever *T. heterophylla* becomes established and grows to maturity, it serves as a nurse tree, enabling *Tsuga* seedlings to develop in its shade. *T. heterophylla* will thereby spread through these stands from small groves, replacing *P. menziesii* in the canopy but only after a lapse of several hundred years. *Abies grandis* is found in the montane zone in this forest type on the eastern side of the mountains, but is more commonly associated

with the lowland zone (Jones 1936). A few scattered *A. grandis* were found in this forest type on the western slope of Hurricane Ridge, and in the Dungeness Valley (Fig. 2).

There are two different phases of this forest type: 1) a shrub layer, and 2) an herb layer. Thus, although Table 3 shows combined values, both the shrub type and the herb type are common.

In stands with a well-developed shrub layer, cover averages 77% and of this total, *Gaultheria shallon* contributes 60%. Other important shrubs are: *Rosa gymnocarpa*, *Berberis nervosa*, and *Symphoricarpos albus*.

Another important shrub in this forest type, common on the western slopes of Blue Mountain is *Arctostaphylos uva-ursi*. This species has the same ecological position as *Gaultheria shallon*, which is absent from many of the Blue Mountain forests. These stands are limited in extent, and occur mainly on dry, rocky ridges.

Tree reproduction is sparse, except in the *T. heterophylla* groves. *Tsuga heterophylla*, the species most commonly found reproducing in this community type, has a mean cover value of ca. 1%. Within one of the groves, however, saplings provided 5 to 10% cover. This is not very high, but it is only within the last 20 to 30 years that *Tsuga* reproduction has started on these sites. Moreover, many of the young *Tsuga* in these groves quickly reach 10 cm DBH, so that they are counted in the tree layer.

Two *P. menziesii* stands that were sampled had well-developed herb layers, with a mean cover value of 60%. Mosses are the most important component (25%). Where a shrub layer is extensive, mean cover for the herb layer drops to 45%, with mosses accounting for 17%. Many vascular species in this community type are not found in moist areas. This is the only forest type in which grass species form a conspicuous part of the herb layer, with a mean total cover of 8%. The important vascular species in this layer are: *Chimaphila umbellata*, *Adenocaulon bicolor*, *Achlys triphulla*, *Campanula scouleri*, *Vicia americana*, *Trisetum cernuum*, *Hieracium albiflorum*, and a species of *Bromus*.

SUBALPINE FORESTS

Abies amabilis-Tsuga mertensiana Type

The forests of this community type occur from 1100 to 1650 m on slopes in the vicinity of the Bailey Range, where precipitation is high. Temperatures are lower, both from the altitude and from the oceanic influence. This type is also found from 1125 to 1400 m on cool, moist, north-facing slopes in the central part of the mountains, but is absent from the far eastern slopes, where the north-facing exposure apparently fails to compensate for the overall dry climate. Growing conditions are favorable, and with 109.4 m²/ha basal area, this is the only forest type studied with more than 100 m²/ha. These forests are dense (748 trees/ha) which is typi-

cal of the subalpine types. Although many trees grow larger than 120 cm DBH, mean DBH is only 43 cm. Near ridge crests in and around the Bailey Range, the steep topographic gradient limits tree size to about 30 cm DBH, and density increases sharply (over 1200 trees/ha).

Abies amabilis-Tsuga mertensiana forests are uncommon west of the slopes of Mt. Olympus, because the ridges are not high enough to support subalpine forest. The approximate western limit of this type is in the headwaters of the Bogachiel River (Fig. 2).

Abies amabilis and *Tsuga mertensiana* are the most important tree species in this community type accounting for over 80% of the canopy layer (Table 2). Forest pattern and ecology are about the same as between *A. amabilis* and *T. heterophylla* in the western montane zone. There are a few places with pure, dense stands of *Tsuga mertensiana*, mostly on exposed ridge crests.

Chamaecyparis nootkatensis, an ubiquitous species in the subalpine zone, is never a dominant species. Although this species is a minor component, it has a high constancy in this community type. *Pinus monticola*, *Pseudotsuga menziesii*, and *Abies lasiocarpa* are present as a result of canopy openings.

Abies amabilis is reproducing more abundantly than *Tsuga mertensiana*. *Abies amabilis* saplings have a cover value of 20%, as opposed to 3% for *T. mertensiana*, thus it is likely that *A. amabilis* will increase in importance in the future. *Chamaecyparis* reproduction is rare (1%).

The tree sapling-shrub layer is extensive in this community type. Including tree reproduction, there is an average cover value of 75%; for only shrubs, the value is 50%. *Vaccinium deliciosum* is the most important shrub species (Table 3), although it was sampled in only three of the five stands. This species is abundant around the Bailey Range, but absent from northern exposures in the eastern Olympics, where *Rhododendron albiflorum* assumes the dominant role. The other species have low constancies, and are important only locally.

This forest type has a poorly developed herb layer (mean cover 43%), probably in response to the heavy snow loads to which these forests are subjected each winter. Snow is deeper, and snowmelt is later in these forests than in nearby lush meadows because the canopy blocks solar radiation, thereby limiting both cover and floristic richness. Vascular species account for slightly less than half the herb cover in the *A. amabilis-T. mertensiana* forests, with *Erythronium montanum* the most important (Table 3). This species has a mean cover value of 15%, and is closely associated with sites that are released from winter snow late in summer, both in forests and subalpine meadows. Various species of moss again are the most important constituents of the herb layer, and have a mean cover value of 23%. *Xerophyllum tenax* and *Rubus pedatus* are notable, but other vascular species have low constancies and cover values.



FIG. 3. *Abies lasiocarpa* forests at 1550 m in the Hurricane Ridge area. This view, looking east, shows the sharp ridge crests typical of the eastern Olympics. Cox Valley, to the left, contains one of the rare stands of *Picea engelmannii* in the Olympics.

Abies lasiocarpa Type

The *Abies lasiocarpa* forests are extensive in the eastern Olympics, occurring from about 1300 to 1800 m on the higher exposed ridges. Downslopes, where the sites are more protected, particularly from the drying westerly winds, this forest type abruptly contacts *A. amabilis*-*T. mertensiana* forests or *P. menziesii*-*T. heterophylla* forests. In the west-central Olympics (Bailey Range), the *A. lasiocarpa* type is found high on the drier south-facing ridges. In the east-central section (Hurricane Ridge), the *A. lasiocarpa* forests occupy most aspects except north (Fig. 3), and have a greater altitudinal extent. In the far eastern section, these forests are also found on north-facing slopes, where the dry climate eliminates *A. amabilis*-*T. mertensiana* communities from the northern exposures. The *A. lasiocarpa* forests, in response to altitude and drier sites, are extremely dense with 1262 trees/ha. Moreover, the trees are small, with mean DBH only 28 cm/tree and mean basal area only 76.0 m²/ha.

Throughout the range of this type, *Abies lasiocarpa* is the dominant (Table 2). Depending upon local conditions, however, there may be any combination of minor components. Thus, in wetter areas, combinations of *A. amabilis* and *T. mertensiana* are found with *A. lasiocarpa*. At lower elevations in this zone, *A. lasiocarpa*-*A. amabilis* forests are encountered. On drier sites at lower elevations, quantities

of *C. nootkatensis* are mixed in with *A. lasiocarpa*. With the low temperatures of high elevations, there are pure stands of *A. lasiocarpa* (Fig. 6). Stand composition, especially with regard to the minor associates, may change from site to site, but the overall importance of *A. lasiocarpa* is always noticeable.

Chamaecyparis nootkatensis has a low constancy within this type, and is found where conditions are drier. The higher IVI is accounted for by its abundance in one of the stands sampled (#26 on Mt. Angeles; see Fig. 2). *Abies amabilis* and *Tsuga mertensiana* have higher constancies, *A. amabilis* being found in 78% of the stands. *Pseudotsuga menziesii* and *Pinus monticola* remain from earlier seral stages and are always minor constituents.

The tree sapling-shrub layer is not widespread in this forest type. The combination of high tree density, dry sites, and heavy winter snowfall limits the understory considerably. The greatest amount of tree reproduction is of *Abies lasiocarpa*, with a mean cover of 17%. The other three minor associates in the canopy layer each averages 3% sapling cover. Of the shrubs, *Vaccinium membranaceum* is the most important (average cover 14%), followed by *Rhododendron albiflorum* and *Vaccinium deliciosum* (Table 3). The remaining shrub species are all minor. Shrubs have a cover value of 20%; with tree reproduction included, the value is 43%.

The herb layer of the *A. lasiocarpa* forests is limited in extent, although floristically the richest of all forest types. Apparently, the same factors that limit the shrub layer in this forest type are even more effective in limiting herbs. Various species of moss are the most important component, sometimes being the only representative of this layer. Mean cover value for mosses is 14%. *Rubus lasiococcus* and *Erythronium montanum* are the most important vascular species (Table 3), again a response to the late-lying winter snow. These are followed by: *Valeriana sitchensis*, *Polemonium pulcherrimum*, *Xerophyllum tenax*, *Pedicularis racemosa*, and *Lupinus latifolius* var. *subalpinus*. All the herbaceous species in this forest type have low constancies, but high abundances in single stands makes each species important in the abstract community. The herb layer has a mean cover value of 45%.

Thirty-one herbaceous species were sampled in this community type. The floristic richness of this layer stems from the occasional small openings in the forests. These are floristically related to the lush subalpine meadows immediately upslope, into which the trees grade. When a sampling point fell in or near one of these openings, more species were encountered. Sampling points near forest openings were necessitated because small meadows are characteristic of the forest type.

COMMUNITIES ON RECENTLY DISTURBED SITES

The eastern Olympics have a long fire history. Many fire scars in the eastern section of the mountains date from within the last 100 years, indicative of the continuing importance of fire. Tree reinvasion

of these sites has been rapid in both montane and subalpine zones, and they are now populated by dense forests of small trees.

These young forests are dominated by the seral species *Pseudotsuga menziesii*, with some *Tsuga heterophylla*, *Thuja plicata*, and *Abies amabilis*. Stand 21 is a 65-year old *P. menziesii* community on a northeast-facing slope. Tree composition of this stand is given in Table 4. The forest is heavily dominated by *P. menziesii*, with small amounts of *T. heterophylla* and *T. plicata*. The stand is densely stocked with 1355 trees/ha. The trees are small, and self-pruning has removed many branches, creating poor conditions for understory development. *Tsuga heterophylla* reproduction is advanced, averaging 28% cover. Some *Thuja plicata* reproduction is present but accounts for only 7% cover.

Stand 22 is a 90-year old *P. menziesii* forest, on a north-facing slope, near stand 21 (Fig. 2). In this older stand on a cooler and moister site, *T. heterophylla* is more abundant, and even some *A. amabilis* is noted (Table 4). *Pseudotsuga menziesii* remains the most important species, however. This stand is more densely stocked than #21, with 1637 trees/ha, owing to the greater density of *T. heterophylla*. *Tsuga heterophylla* reproduction is most important, with a cover value of 37%, followed by *Thuja plicata* with 15%. From the values for both stands, these forests will rapidly become dominated by *T. heterophylla*, and there may be good representation of *T. plicata*. Most *P. menziesii* will succumb to competition, with an estimated 85 to 90% dying within 200 years.

On south-facing slopes, these forests are so densely stocked with *P. menziesii*, it is nearly impossible to walk through them. In this situation, *T. heterophylla* is absent, conditions being too dry yet to favor invasion by this species. There are well over 2000 stems/ha.

These stands, on north or south-facing slopes, generally have a poor ground cover, apparently in response to the extreme tree density. Before *P. menziesii* is well-established, however, shrub cover in particular may be high. A study of shrub and herb invasion of clear-cut, slash-burned *P. menziesii* forests in the montane zone of the Oregon Cascades was conducted by Yerkes (1960). This study showed that shrub species present in the forest before logging and burning dominated the extensive shrub vegetation that developed afterwards. Of the species listed by Yerkes (1960), *Linnaea borealis*, *Berberis nervosa*, *Vaccinium parvifolium*, and *Gaultheria shallon* are now present in the young *P. menziesii* stands in the Olympics. Although their cover value is not great, it appears that these species may be remnants of a previous, more extensive shrub vegetation. It appears that following wildfire in the Olympics, species that were previously present in the forest populate the site until crowded out by *P. menziesii*. They later increase in number as tree density decreases.

Tree species can reoccupy burned areas in the sub-

TABLE 4. Composition of the tree layer for communities on recently disturbed sites. Data are for Importance Value Indices (IVI), mean density (T/ha), and mean basal area (m²/ha).

Stand & species	IVI	T/ha	m ² /ha
Stand 21			
<i>Pseudotsuga menziesii</i>	79.4	1236	58.4
<i>Tsuga heterophylla</i>	12.1	82	2.5
<i>Thuja plicata</i>	8.5	37	1.0
Stand 22			
<i>Pseudotsuga menziesii</i>	4.89	778	46.0
<i>Tsuga heterophylla</i>	35.2	704	21.6
<i>Thuja plicata</i>	14.1	148	5.4
<i>Abies amabilis</i>	1.8	7	0.9
Stand 36			
<i>Abies lasiocarpa</i>	84.6	1384	57.9
<i>Pseudotsuga menziesii</i>	8.9	32	2.8
<i>Pinus monticola</i>	6.5	37	2.3
<i>Pinus contorta</i> composite (3 stands)			
<i>Pinus contorta</i>	73.6	1228	58.1
<i>Abies lasiocarpa</i>	25.6	259	15.8
<i>Abies amabilis</i>	0.8	5	0.2

alpine zone in either of two ways: 1) by directly seeding in and establishing a new forest, or 2) by invading fire-induced subalpine meadows. An example of the first process is stand 36 (Table 4). *Abies lasiocarpa* is the principal invader after fire in the subalpine zone, and is dominant in this 40-year old stand. The seral species *Pseudotsuga menziesii* and *Pinus monticola* are present in small amounts. This is at a low elevation in the subalpine zone (1460 m) where tree species apparently can successfully compete with meadow species on burned sites. As in the montane stands, this stand is densely stocked with 1453 trees/ha. There will be a reduction of ca. 30% in the number of *A. lasiocarpa* stems within 100 years, but because this species can reproduce in its own shade, this will remain an *A. lasiocarpa* community. *Abies lasiocarpa* reproduction has a cover value of 20%.

Pinus contorta forests represent another example of trees directly re-occupying burned sites. Three *P. contorta* stands were sampled, and a composite is given in Table 4. *Pinus contorta*, the dominant species, is strictly seral as there is no *Pinus* reproduction. The forests are dense, with 1492 trees/ha. One stand, 80 years old, averaged 2218 trees/ha. *Abies lasiocarpa* will eventually dominate these stands for it is increasing in importance, and has a high reproductive cover value of 22%. *Pinus contorta* forests are limited to the northeast mountains, in the vicinity of Deer Park (Fig. 2), where rainfall is low. These stands are found only on west and south-facing ridge tops from 1500 to 1800 m, wholly exposed to the drying winds. On other exposures at this same elevation, *A. lasiocarpa* is the dominant species. Moreover, many of these moister sites did not suffer in the same fire to which the *P. contorta* stands are responding. Maiden Ridge, west of Deer Park, has

a north-south orientation. A dense stand of 200-year old *P. contorta* was sampled on the west-facing slope, but at the same elevation on the east-facing slope, an *A. lasiocarpa* forest occurred. This same pattern is repeated on other ridges, where apparently the dry sites are limiting for *A. lasiocarpa* following fire.

An example of the second process of tree reoccupation of burned sites can be found in the area known as Waterhole Burn, a portion of the Hurricane Ridge complex. A wildfire apparently burned this area earlier than 1900, but meadow species, primarily *Festuca idahoensis*, *Lupinus latifolius* var. *subalpinus*, *Juncus* spp., *Vaccinium deliciosum*, and *Arenaria formosa* re-invaded the area. At the lower end of this burn (1550 m) there is a dense forest of 40-year old *A. lasiocarpa*. This forest is entirely different in appearance from the *A. lasiocarpa* stand discussed above. The former stand had almost no ground cover, whereas there are remnants of meadow species under the closed canopy of the 40-year old forest at Waterhole Burn. *Abies lasiocarpa* forest is slowly encroaching on the meadow through establishment of outlying trees which then permit seedling establishment under them. In this way, the canopy closes and eventually shades out the meadow species. The total distance from outlying 10-year old trees to dense 40-year old forest at Waterhole Burn is about 150 to 200 m. Further evidence that this is an adventive meadow resulting from a burn is found in the remains of trees destroyed in the fire, but not rotted (Fig. 4). These are abundant on the hillside, showing that a forest at one time reached the crest at nearly 1700 m. More conclusive proof that this is not beyond the range of *A. lasiocarpa* is found on an adjacent peak which apparently escaped burning and has an *A. lasiocarpa* forest to the top at 1700 m.

SOILS

MORPHOLOGY

The soils of the Olympic Mountains generally have weak development, as a result of several factors. The mountains are geologically young, and are still undergoing rapid erosion. A large percentage of the slopes were probably covered by alpine glaciers during Pleistocene, and scouring and plucking undoubtedly left a barren landscape for tree re-invasion. Thus, it is likely that there has been a short time period for soil development. Parent material is uniform throughout the extent of the mountains, where 80% of the substratum is sedimentary rock. Because the soils are largely derived from sandstone and other sedimentary material, they contain large quantities of rock, pebbles, and coarse sand. The soils are thus excessively drained, and water percolation as a soil forming factor has been negligible. Because the soils are snow covered from November through May, soil temperatures remain relatively uniform, so that freeze-thaw cycles with concurrent movement of particles at the freeze face are not prominent.

Fire has been an important factor in differential



Fig. 4. Waterhole Burn on Hurricane Ridge. The small trees are between 10 and 20 years old. They are invading a *Festuca-Lupinus* meadow which resulted from a burn more than 60 years ago. The numerous old logs in the photograph are evidence that forest previously extended to the crest at 1700 m.

soil development. Soils in the east have suffered repeatedly from forest-destroying wildfire, which destroys organic matter, accelerates leaching, and leads to physical changes in the upper solum (Ahlgren and Ahlgren 1960). Even slash-burning and groundfire have been shown to destroy much of the organic matter in the duff layer, and to reduce water holding capacity in western soils (Isaac and Hopkins 1937; Dyrness and Youngberg 1957). Another important effect is erosion. Following fire, rainfall removes quantities of surface soil from steep mountain slopes, and this may drastically alter the morphology (Retzger 1963).

Two Great Soil Groups are recognized in the Olympics: Brown Podzolics (Spodosols) and Lithosols (Entisols). Brown Podzolic soils generally develop under those community types which are relatively stable and where fire is rare. Lithosols are found where fire is frequent. Because Brown Podzolics represent a more advanced stage of soil development, they will be discussed first.

Brown Podzolics are most extensive and best developed in southern New England, although they have been reported from other areas, including northwestern Washington (Lyford 1946). The typical morphology of the Brown Podzolics was described by Lyford (1946) for the New England soils. The Olympic soils are more weakly developed than those in the East.

The *Abies amabilis-Tsuga heterophylla/Oxalis* forests occur on Brown Podzolics formed from Soleduck sediments, and show perhaps the best development of this group in the mountains.

Horizon	Description
O1	2 to 0 cm; thin layer of freshly fallen needles, twigs, and leaves; somewhat compacted from late lying snow.
A1	0 to 13 cm; very dark grayish brown (10 YR 3/2) friable silt loam; many roots,

decaying pieces of bark and other incorporated organic matter; 26% organic matter; extremely acid (pH 3.7); abrupt, wavy boundary.

- B 13 to 30 cm; dark yellowish brown (10 YR 4/4) friable sandy clay loam; 42% > 2 mm; weak subangular blocky; many roots; extremely acid (pH 4.1); gradual, wavy boundary.
- C 30 to 90+ cm; dark yellowish brown (10 YR 4/4) friable sandy clay loam; 39% > 2 mm; granular; few roots; extremely acid (pH 4.2).

Except for the weak subangular blocky structure, the B horizon was difficult to recognize in the field. Laboratory analyses for clay, iron, and organic matter indicate slightly better development in this horizon over the one below.

Lithosols are associated with areas that have had a high frequency of fire, and are necessarily found under communities with a large component of *P. menziesii* in the montane zone. Generally, the profile is similar from one stand to the next, even when parent material shifts from sedimentary to volcanic rock. The profile from a *Tsuga heterophylla*-*Pseudotsuga menziesii* stand is typical of sediments of the Soleduck Formation:

Horizon	Description
01	10 to 8 cm; very loose layer of freshly fallen needles, twigs, and leaves.
02	8 to 0 cm; very dark brown (10 YR 2/2) layer of decomposed organic matter, with some recognizable material; charcoal present; many large roots; very strongly acid (pH 4.8); abrupt, smooth boundary.
C1	0 to 28 cm; dark yellowish brown (10 YR 4/4) loose sandy loam; 67% > 2 mm; single grain; some large roots in upper part of horizon, but small roots throughout; charcoal present; very strongly acid (pH 4.7); diffuse, wavy boundary.
C2	28 to 65+ cm; dark yellowish brown (10 YR 4/4) loose sandy loam; 85% > 2 mm; single grain; small roots to bottom of pit; very strongly acid (pH 4.6); marked increased in rocks.

There are slight differences between the C1 and C2 horizons, the most noticeable of which is the definite increase in rocks. Charcoal as a result of fire is present in the upper part of all Lithosol profiles.

Somewhat better soil development than found in this study was reported for the broad terraces of the western river valleys at low elevations, where fire and steep topography are absent (Sharpe 1956). These soils were tentatively recognized as Gray-Brown Podzolics (Alfisols) and further investigation into these soils has not been undertaken.

TALBE 5. Soil moisture characteristics for soils in the Olympic Mountains, Washington.

Stand	Horizon	Moisture (%)		
		1/3 atmos.	15 atmos.	Available
14	A1	54.9	30.9	24.0
	B	38.6	19.8	18.8
	C	38.7	17.4	21.3
7	02	108.8	74.4	34.4
	B	21.5	9.2	12.3
	C	12.5	5.8	6.7
54	02	122.7	106.3	16.4
	A2	44.1	16.9	27.2
	B2	35.4	14.3	21.1
	B3	26.2	11.2	15.0
	C	16.7	6.9	9.8
26	02	119.9	62.6	57.3
	B21	30.0	15.9	14.1
	B22	26.7	14.9	11.8
	C	20.2	12.9	7.3
29	A1	52.9	26.5	26.4
	B	22.6	11.5	11.1
	C	20.4	9.4	11.0
3	02	120.8	78.2	42.6
	C1	34.9	13.1	21.8
	C2	28.6	12.4	16.2
16	02	110.2	77.5	32.7
	C1	17.1	8.1	9.0
	C2	16.4	7.8	8.6

Community types: (#14) *A. amabilis*-*T. heterophylla*/*Ozalis*; (#7) *A. amabilis*-*T. heterophylla*; (#54) *A. amabilis*-*T. mertensiana*; (#26) *A. lasiocarpa* with *C. nootkatensis* on volcanic soils; (#29) *A. lasiocarpa*; (#3) *T. heterophylla*-*P. menziesii*; (#16) *T. heterophylla*-*P. menziesii* on volcanic soil.

Franklin (1966) made an extensive survey of the soils of the western Cascades, perhaps the most complete description of mountain soils in western North America. He recognized seven Great Groups, ranging from Podzols and Brown Podzolics (Spodosols) to Alluvial soils (Entisols). Podzols and Brown Podzolics were the most frequently encountered Great Groups, with the other five relatively uncommon. Franklin, however, hesitated to show definite correlation between forest associations and soil groups.

Soil moisture values for different profiles are given in Table 5. As expected, lower horizons have lower available moisture. Where more clay is in the profile, slightly more moisture is available. Volcanic or stony soils appear to hold slightly less water at field capacity when compared to sedimentary soils. Considerably more moisture is held by the 02 than A1 horizons.

CHEMICAL PROPERTIES

There is great similarity among the various profiles examined, especially with regard to chemical properties, because they are derived largely from the same type of parent material. Dissimilarities are noted when comparing Brown Podzolic soils to Lithosols, but within either group only minor differences are found. Soil fertility does not seem an important

TABLE 6. Properties of selected soil profiles from the major community types in the Olympic Mountains, Washington.

Stand	Horizon	Classification	pH	CEC (me/100g)	Base Saturation %	Organic matter %	Clay %	Available ions			
								P (ppm)	K (me)	Ca (me)	Mg (me)
14.....	A1	BP	3.7	34.1	16.4	25.5	5.7	17	0.10	1.00	0.42
	B		4.1	20.4	25.4	4.5	26.1	2	0.10	0.50	0.21
	C		4.2	19.9	34.2	3.7	20.6	5	0.09	0.50	0.21
7.....	02	BP	3.8	71.6	15.4	86.2	—	54	0.67	3.25	0.83
	B		4.3	16.8	25.0	4.5	9.0	29	0.14	1.25	0.42
	C		4.6	11.6	31.9	3.5	8.4	32	0.14	2.50	0.83
54.....	02	BP	3.7	73.2	19.7	86.2	—	48	0.77	15.00	1.25
	A2		4.3	37.5	16.0	7.0	16.2	13	0.09	0.03	0.42
	B2		4.4	24.2	25.6	5.0	11.2	19	0.10	0.03	0.42
	B3		4.5	21.5	32.1	4.5	8.5	48	0.15	0.03	0.42
	C		4.8	15.3	40.5	2.7	7.1	53	0.14	0.03	0.42
29.....	A1	BP	3.6	35.6	13.2	8.0	8.3	50	0.23	1.00	0.21
	B		4.5	16.7	34.7	5.5	6.0	18	0.13	1.00	0.21
	C		4.9	12.1	45.5	4.2	7.5	30	0.10	0.63	0.21
26.....	02	BP	5.0	62.0	53.5	62.2	—	30	0.36	7.50	0.83
	B21		4.8	20.0	40.0	4.3	16.8	12	0.24	3.75	0.83
	B22		4.8	18.1	40.3	3.0	20.2	8	0.22	3.00	1.25
	C		4.6	14.7	40.8	1.6	21.2	4	0.25	8.63	2.92
3.....	02	L	4.8	61.9	49.4	78.3	—	29	0.39	5.25	0.83
	C1		4.7	16.6	31.3	3.3	17.9	34	0.13	1.50	0.42
	C2		4.6	13.4	42.5	2.3	14.6	35	0.08	0.38	0.42
5.....	02	L	4.7	68.1	51.7	80.2	—	35	0.53	7.50	1.25
	C1		4.6	14.4	25.0	3.8	19.3	34	0.22	2.25	0.42
	C2		4.6	15.7	27.4	4.3	16.3	110	0.22	1.00	0.42
16.....	02	L	4.1	63.2	34.2	76.0	—	32	0.49	4.50	0.42
	C1		5.0	10.6	57.5	2.3	11.3	34	0.23	2.00	0.42
	C2		5.3	8.7	64.4	1.8	8.8	33	0.22	3.75	0.83

Community types: (#14) *A. amabilis*-*T. heterophylla*/*Ozalis*; (#7) *A. amabilis*-*T. heterophylla*; (#54) *A. amabilis*-*T. mertensiana*; (#29) *A. lasiocarpa*; (#26) *A. lasiocarpa* with *C. nootkatensis* on volcanic soils; (#3) *T. heterophylla*-*P. menziesii*; (#5) *P. menziesii*-*T. heterophylla*; (#16) *T. heterophylla*-*P. menziesii* on volcanic soils. BP=Brown Podzolic; L=Lithosol. CEC=Cation Exchange Capacity.

factor in forest pattern in the Olympics. The soil nutrient status is largely the same from site to site, and nutrients are present in sufficient quantity that they are not limiting for a given tree species or community type. It may be that local nutrient status within a community type affects tree growth, but that aspect is not a part of this study. The general chemical properties of several profiles have been summarized in Table 6. The mineral horizons of the profiles should be emphasized in considering many of the trends in these soils.

The soils under seral forests (Lithosols) are very strongly acid (pH 4.6 to 5.0), whereas those under stable vegetation (Brown Podzolics) generally have extremely acid conditions (pH 4.1 to 4.5). One important exception to this latter range is found in stand 26, which has a large quantity of *Chamaecyparis nootkatensis* (Table 6). This species, as other members of the Cupressaceae, stores calcium (J. Franklin—personal communication). When the foliage is incorporated into the litter and solum, the pH is higher because of the larger amounts of calcium. The mineral horizons of this profile have larger amounts of calcium than any of the other

profiles considered in Table 6. This calcium relationship becomes more apparent in considering the pH change with depth under this stand (#26). From a high of 5.0 in the 02 horizon, pH drops continually to a low of 4.6 in the C.

The higher pH in Lithosols apparently results from fire which produces ash and releases calcium. Isaac and Hopkins (1937) showed that clear-cut and slash-burned areas changed from original very strongly acid conditions (pH 5.0) to alkaline conditions (pH 7.6) in the duff layer after burning. Austin and Baisinger (1955) found that slash-burning changed pH values from 4.5 to 7.6 on sites in western Oregon and Washington. Ahlgren and Ahlgren (1960) list 20 papers that showed that fire causes a decrease in acidity. It is likely that portions of the surface zone would be similarly affected. Higher pH values persist until salts have been leached from the profile. This can vary from one month to 10 years, depending on a combination of factors (Ahlgren and Ahlgren 1960).

Cation exchange capacity (CEC) for Lithosols varies from 8.7 to 16.6 me, whereas the range for Brown Podzolics is from 11.6 to 24.2 me (Table 6).

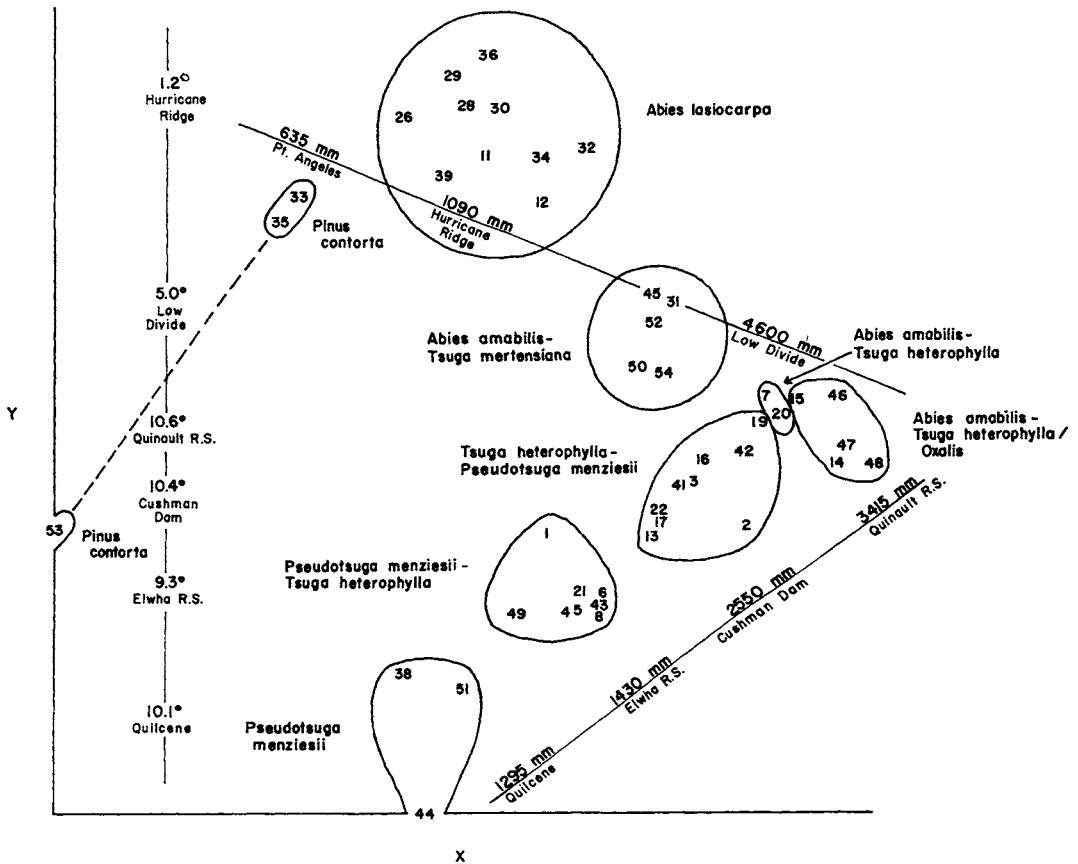


FIG. 5. Stand position on a two-dimensional ordination for 45 stands sampled in the montane and subalpine zones. Lines delimit community types, which are named for the dominant species. Environmental data are for precipitation and temperature; see text for explanation.

The C horizons have the low CEC values. Base saturation for either soil group varies from about 25 to 40% in the upper horizons and increases with depth. Cation exchange capacity results from a number of factors, the most important of which are percent organic matter and percent clay. Organic matter varies from 1.8 to 4.3% in Lithosols, and from 1.6 to 5.5% in Brown Podzolics; again the lowest values are in the C horizon. Clay percentages are not very different from Lithosols to Brown Podzolics, but the low CEC values are found with low clay percentages, unless high organic matter compensates.

Lithosols have higher phosphorus values in the upper horizons than Brown Podzolics, although phosphorus amounts show unusual trends in the C horizons. Fire is an important agent for releasing nutrients, and thus larger amounts of phosphorus are found under seral forests (Ahlgren and Ahlgren 1960). The relatively high phosphorus value for stand 7 (Table 6) probably did not result directly from burning. This *Abies amabilis-Tsuga heterophylla* forest is surrounded by forest that burned about 300 years ago. It is likely that large quanti-

ties of ash blew in and washed downslope through erosion after fire, thereby accumulating under these forests on the relatively flat river bottoms.

There are few differences in the other three available nutrients shown in Table 6. Generally, as the result of fire and the release of nutrients, there are higher levels of potassium and calcium in the Lithosols, although calcium levels are erratic. Only stand 3 has a potassium level approximately the same as in the Brown Podzolics. The higher calcium in stand 26, where *Chamaecyparis* is abundant, has already been mentioned. Magnesium is about the same for each group. The occurrence of stand 26 on volcanic soils, although it is a Brown Podzolic, may have some connection with higher levels of available K, Mg, and Ca as compared to the other stands.

DISCUSSION

FOREST PATTERN

A two-dimensional ordination was constructed to graphically illustrate the interrelationships of individual stands and groups of stands. See Methods section for details on constructing the ordination. Stand

clusters which are segregated on the graph are considered distinct community types, and have been named after the important species (Fig. 5). Although the stand numbers go to 54, the ordination comprises only 45 stands. Numbers were allocated for sampling vegetation other than forests, and have not been included in the ordination. Two major groupings are present in the ordination, the lower one representing the montane zone and the upper one the subalpine zone (Fig. 5).

The ordination graphically shows the relationship of forest pattern to mean annual temperature and precipitation from Weather Bureau stations data. Because of the extent of the Olympics, with great distances separating the community types, it was not feasible to obtain data on temperature, precipitation, or soil moisture during this study. Thus, Weather Bureau stations within or characteristic of a given community type as indicated by isothermal and isohyetal analysis (Soil Conservation Service and U.S. Weather Bureau 1965; U.S. Weather Bureau 1965), have been used for the environmental data. The exceptions to this are the temperature values for Low Divide and Hurricane Ridge, which are calculated using lapse rates of 5.6° per 1000 m. The temperatures for Low Divide and Hurricane Ridge were calculated based on mean annual temperatures at Lake Quinault Ranger Station and Elwha Ranger Station, respectively. Larsen (1930) showed that forest zonation in the Rocky Mountains of Idaho and Montana was determined chiefly by air temperature and precipitation. It has been further shown that different levels of summer drought control distribution of plant associations in the northern Rockies (McMinn 1952). These same two elements were used to show the distributional relationships of plant associations in the Mt. Rainier Province of the Cascade Mountains, Washington (Franklin 1966). In this latter case, only qualitative estimates were available.

Stands are arranged on the Y axis on the basis of temperature regime, with high temperature at the bottom and low at the top. The temperature regime in the subalpine zone is lower than that for the montane zone, showing the effect of altitude on zonation. The effect of ocean proximity on air temperature becomes important at the community level. Generally, those community types farthest away from the ocean influence (top and bottom of Y axis) have greater temperature extremes, whereas moderate temperatures prevail in those nearest the ocean influence (middle of Y axis). See also Table 1 for data on temperature extremes over the peninsula.

The X axis locates stands in relation to a moisture gradient, with drier conditions to the left and wetter conditions to the right. Those community types near the right side of the ordination generally receive more summer rain and have better soil moisture relations, than those near the left, which are influenced by the rainshadow (see Table 1). An exception to this is the *A. amabilis*-*T. heterophylla* type, which lies in the eastern mountains and generally does not receive as much summer rain as other community

types on the wetter side of the ordination. Here, the moister conditions associated with the river terraces compensate for the lower precipitation of the eastern location, producing an environment similar to that of the western montane zone.

Ordination analysis not only provides a graphical illustration of vegetational interrelations of the community types and the relation of community types to environmental complexes, but it also allows consideration of a given factor. In the Olympic forest ordination, temperature, primarily controlled by altitude, broadly separates the different forest zones. Within each zone, moisture relations segregate out community types, but it is the temperature-moisture regime complex that finally positions a community type on the graph and shows its relation to all other community types in these mountains.

The general environmental characteristics of each community type were given under results. Further characteristics of the environmental regimes of each can be interpreted from the ordination. Communities at the right center of the ordination, with fewer environmental extremes, exhibit the most favorable growing conditions. This is shown by data for the three *Abies amabilis* forest types, which have greater basal areas (90.8 to 109.4 m²/ha) than the other forest types (58.1 to 94.9 m²/ha). Community types at the left side occur on drier sites and generally consist of denser stands of smaller trees. The combination of low temperature and dry climate results in the smallest trees high in the subalpine zone (1262 trees/ha and 76.0 m²/ha in the *Abies lasiocarpa* type, and 1228 trees/ha and 58.1 m²/ha in the *Pinus contorta* type).

COMMUNITY TYPE DIVERSITY

Although the community types tend to occupy particular environmental regimes on the ordination, there may be noticeable variation within a given forest type. This is a normal situation in forest associations, in which variation may range from open stands in which the ground cover is mainly heliophytic herbs or shrubs to dense stands, with such heavy shade that only sciophytic species are present (Daubenmire 1952). Daubenmire (1952) further pointed out that there are two sources of variation in vegetation. One is directly proportional to the floristic richness of a community. Here, chance dissemination and survival produces unpredictable variation within a community even when the environment is uniform. Habitat type differences constitute the second source of variation, but in this instance, when any aspect of the vegetational pattern is known, the remainder is predictable.

Site differences are the predominant source of variation in the Olympic ordination. The ordination is based upon phytosociological data (Importance Values) of the species present, including floristic richness. The patterning of stands on the ordination results from a quantitative measure of floristic variability as regulated by site differences and not by floristic richness alone. The various combinations of

a small number of species differentiate the community types (Tables 2 and 3), and these combinations are related to site variability. Thus, the greater the site variation (environmental gradient) within the community type, the greater will be the variation among the stands that community type comprises.

The mean X and Y co-ordinates of each community type were determined by averaging the X and Y co-ordinates of all stands within the given community type. Thus, it was possible to plot a mean location for each community type, and to measure in ordination units the deviation of each stand of the type from the mean location. Mean stand distance and standard deviation from the mean distance were calculated for each community type (Table 7). This results in a measure of the environmental gradient

TABLE 7. Within community type variability on the two dimensional ordination. Data are for mean stand distance from the mean co-ordinates of the given community type, and for standard deviation from the mean distance (S), and are equal to units of the ordination scale.

Community Type	# Stands	Mean Distance	S
<i>Pinus contorta</i>	3	31.1	9.9
<i>Pseudotsuga menziesii</i>	3	8.2	3.3
<i>Abies lasiocarpa</i>	10	7.5	3.2
<i>Tsuga heterophylla</i> - <i>Pseudotsuga menziesii</i>	9	5.6	3.0
<i>Abies amabilis</i> - <i>Tsuga heterophylla</i> / <i>Oxalis</i>	5	4.4	1.9
<i>Pseudotsuga menziesii</i> - <i>Tsuga heterophylla</i>	8	4.0	2.7
<i>Abies amabilis</i> - <i>Tsuga mertensiana</i>	5	4.0	1.8
<i>Abies amabilis</i> - <i>Tsuga heterophylla</i>	2	1.4	0.0

present, based upon quantitative floristic diversity, in the different types. The variations present in the Olympic forests will now be considered by community type, in decreasing order of variation.

The *Pinus contorta* type occupies a very broad temperature range. Two stands (33 and 35) are close together, and 53 is far away on the ordination (Fig. 5), resulting in a large mean distance (Table 7). Besides being younger by 120 years, stand 53 occupies a very dry, south-facing slope, where evapotranspiration apparently makes conditions so dry that not even moss is present. There is, therefore, a large floristic difference in the understory among these stands. *Pinus contorta* is not uncommon on the Olympic Peninsula. Jones (1936) reports this species in many dry habitats in the lowland zone (prairies, dry gravelly soil) and in the coastal forests, but not from the subalpine zone. Krummholz *P. contorta* have been reported from high elevations on the lee side of Gray Wolf Ridge, but this species does not occur there in forest structure (Arno 1967). It is likely that forests of *P. contorta* in the subalpine zone are limited to the very dry northeastern section of the mountains, where the lowest precipitation that will support a forest is received.

The *Pseudotsuga menziesii* type varies with respect to understory development. Mean distance is 8.2

(Table 7). Stand 44 has a well-developed shrub layer, whereas stands 38 and 51 contain more herbs (Fig. 5). Stands with extensive shrub layers tend to occupy warmer sites, where *Gaultheria shallon* or *Arctostaphylos uva-ursi* do well. Stands with an herb phase seem to occur where frequent fog lowers the temperature. Thus, stand 38 is on the west-facing slope of Hurricane Ridge where orographic clouds pile up, and stand 51 is in the Dungeness Valley where fog comes inland from the Strait of Juan de Fuca (Fig. 2). Neither site receives much rain, but sites with fog have an understory that favors herbaceous growth.

The *Abies lasiocarpa* type occupies a broad environmental range. Overall conditions are cold, but summer moisture varies from moist to approaching very dry. Variations in these forests (mean distance 7.5) results from IVI differences of minor canopy associates, which are better indicators of moisture differences than *A. lasiocarpa*. *Abies lasiocarpa* seems to tolerate greater extremes of moisture than *A. amabilis*, *T. mertensiana*, or *C. nootkatensis*. Stands 11, 12, 32, 34, and 39, located on sites with better moisture relations (Fig. 5), have good representation of *Abies amabilis* and *Tsuga mertensiana*. The remaining stands are almost wholly composed of *Abies lasiocarpa* and are found on dry sites at much higher elevations. Pure *A. lasiocarpa* stands range from 1450 to 1800 m, whereas other species are mixed in from 1280 to 1450 m.

Variation in the *Tsuga heterophylla*-*Pseudotsuga menziesii* community type ranges from stand 13, which occupies a relatively dry site near the mouth of the Boulder Creek Valley, to stand 19, near the bottomland of the Dosewallips River (Fig. 2) where cold air drainage results in a cool, moist environment (Fig. 5). Stand 13 is densely stocked with smaller trees (586 trees/ha and 35 cm DBH/tree), and *Gaultheria shallon* is abundant in the shrub layer. Stand 19, however, is more open, with larger trees (232 trees/ha and 68 cm DBH/tree) and mesophytic shrubs such as *Oplopanax horridum*. Another comparison can be made between stands 41 and 42 (Fig. 5). These are in the Soleduck Valley, with stand 41 on a south-facing slope and stand 42 on a north-facing slope (Fig. 2). Ordinarily, southern exposures in the eastern montane zone support *P. menziesii*-*T. heterophylla* forests. The Soleduck Valley, however, is generally open to the northwest (Fig. 2), and thus precipitation is high enough that south-facing slopes support *T. heterophylla*-*P. menziesii* communities. Similar environmental relations were found in the Skokomish Valley (Fig. 2), where *T. heterophylla*-*P. menziesii* forests occupy both exposures. Stand 22, a 90-year old *P. menziesii* forest on a northern exposure, contains large amounts of *T. heterophylla*, so that it is positioned in the *T. heterophylla*-*P. menziesii* type (Fig. 5).

The *Abies amabilis*-*Tsuga heterophylla*/*Oxalis* type covers the largest area and occupies slopes of every aspect, yet has little variability because of the moderating effect of the ocean. Mean distance is 4.4

(Table 7). Structure and composition of these forests may vary slightly with slope exposure, but not consistently throughout the western montane zone. For example, stand 15 is dominated by *A. amabilis* and lacks a well-developed herb layer. In stand 46 there is a better developed herb layer, and *T. heterophylla* is barely more important than *A. amabilis*, yet both of these stands are on west-facing slopes.

Variation on a smaller order is noted within the *Pseudotsuga menziesii*-*Tsuga heterophylla* community type (Table 7 and Fig. 5). Stand 49 is located on a drier site in the eastern section, where rainfall is lower than for the other stands. Stand 1 is located low in the Dosewallips Valley where cold air drainage produces a cooler environment. The effect of increasing moisture on *T. heterophylla* importance is illustrated by stands in two community types. Stands 44, 4, 5, and 6 (Fig. 5) are all located on a south-facing slope in the Boulder Creek Valley, progressing from east to west with relative moisture increasing in the same direction (Fig. 2). *Tsuga heterophylla* IVI progressively changes with the increase in moisture from stand 44 (IVI 7.8) to stand 6 (IVI 34.1). Stand 21 is a 60-year old *P. menziesii* forest and is positioned in this community type because of the abundance of that species.

The *Abies amabilis*-*Tsuga mertensiana* forests occupy a narrow environmental range (mean distance 4.0). They are closely associated with ocean influence in the vicinity of the Bailey Range, and are on northern exposures to the east where the aspect approximates sites farther west. The forests are similar floristically, the criterion by which stands are positioned on the graph (Fig. 5), though structurally they may differ. Moderate slopes support stands of large trees, but on steep ridge crest, tree size is markedly decreased, and density increases to well over 1200 stem/ha. The Hoh River-Soleduck River divide and the Soleduck River-Boulder Creek divide support good examples of these dense forests.

The *Abies amabilis*-*Tsuga heterophylla* type has the smallest environmental range, because it is found on specialized sites, closely associated with the cool, moist environment of rivers and creeks in the eastern montane zone (Fig. 5). There is little variation between the two stands sampled (Table 7), except that stand 20, at a lower elevation than stand 7, has a better developed shrub layer. This variation, apparently the result of later snowmelt at higher elevations, was noted in other river valleys throughout the eastern Olympics.

Considering the closeness of stands 7, 15, 19, 20, 46, and others in that area of the ordination, one might question the separation of stands into different community types (Fig. 5). This criticism would be based solely upon floristics and ordination analysis, whereas this study has considered community dynamics. These stands are very near one another on the graph, primarily because they occupy similar environmental regimes. They are floristically similar but vegetationally distinct.

Stand 19 is a *Tsuga heterophylla*-*Pseudotsuga*

menziesii stand on a slope above stand 20, an *Abies amabilis*-*Tsuga heterophylla* stand on a river terrace. Many differences can be listed for these two stands, including past history, stand dominants, tree size and spacing, and relative development of shrub and herb layers. When these aspects of community dynamics are compared, there is little doubt that these represent different communities.

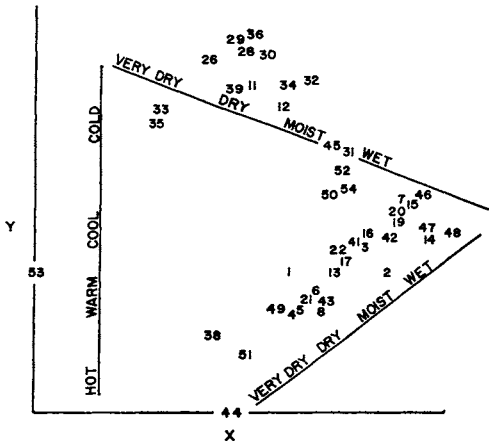
The separation of stands 7 and 20 from stands 14, 15, 46, 47, and 48 focuses on an important comparison between the two *A. amabilis*-*T. heterophylla* forest types. Although floristically similar, with the same tree dominants, shrub, and herb flora, the structural differences in the understory, plus the lack of *Oxalis oregana* and *Blechnum spicant* in the eastern forest, justifies the separation into two distinct community types (Fig. 5). The forests of the western mountains, with deeper soils and abundant precipitation, have a well-developed herb layer (total cover 55%) while the shrub layer is correspondingly reduced. The forests of the eastern mountains occupy gravelly river flats, where the understory is sparse. The shrub layer is about equal in cover to the western montane forests, but the herb layer is much reduced. Moreover, the dominant herb in the eastern forests is *Rubus pedatus*, an uncommon species in the western forests.

Comparisons of similarity values for these seven stands reveal that stands 7 and 20 are more similar to each other (62.5) than they are to any of the other five stands. The most similar stand to either stand 7 or 20 is stand 47, which has a similarity value with stand 7 of 61.0. Stand 15 is the nearest stand of the western montane zone to stands 7 and 20 on the ordination, and has similarity values of 52.3 and 59.1 respectively. Similarity values for the five stands in the *A. amabilis*-*T. heterophylla*/*Oxalis* type range from 50.6 (stands 14 and 15) to 80.9 (stands 46 and 47), with a mean value of 68.4 ± 7.7 .

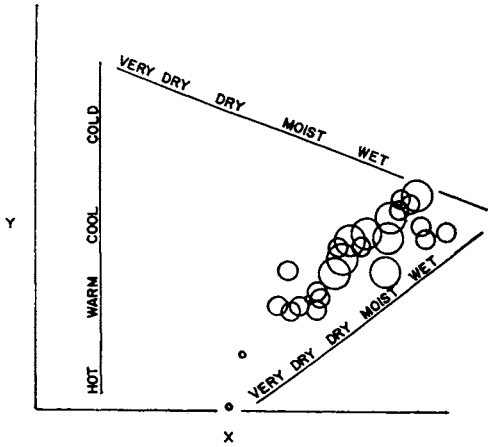
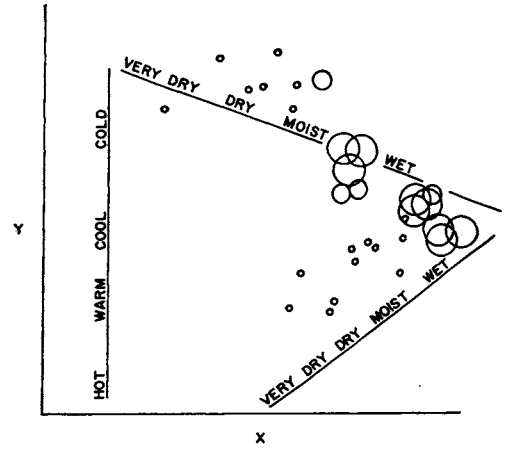
DISTRIBUTION OF IMPORTANT TREE SPECIES

Plant communities are composed of species, so that the ultimate distribution of a given community type must necessarily be governed by the tolerances of the species to the different environmental complexes within the mountains. The distribution by importance of the five major tree species in the Olympics was plotted over the ordination analysis (Fig. 6). In any stand, only one species dominates; there may or may not be a subdominant species, but if present, there is not more than one; there may be several minor associates.

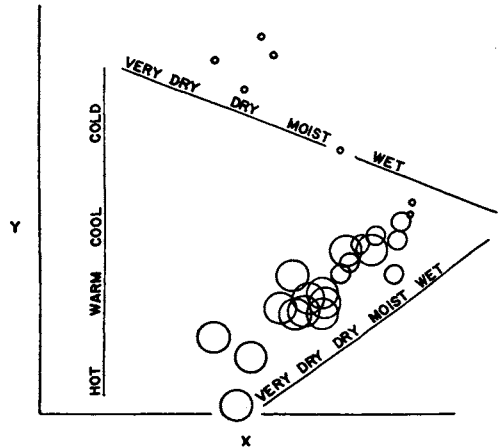
Abies amabilis, the most important and widespread species in the montane and subalpine forests of the Olympics, characteristically grows in a cool, wet climate (Fig. 6). This climax species reaches its best development in the Olympics from 450 to 1400 m on the western slopes, where ocean proximity produces a moderate climate. It apparently is excluded from the stands at either altitudinal extreme by temperature rather than moisture regime (U.S. Forest Service 1965). *Abies amabilis* was present in 31 of



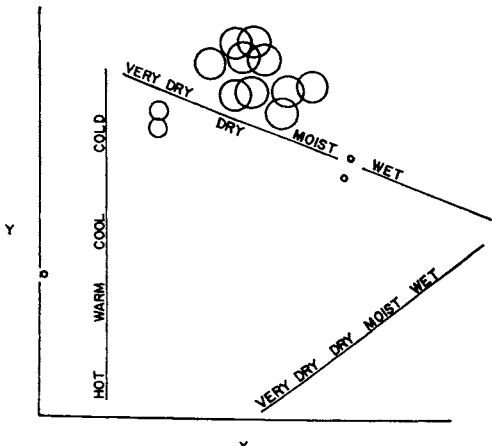
ABIES AMABILIS



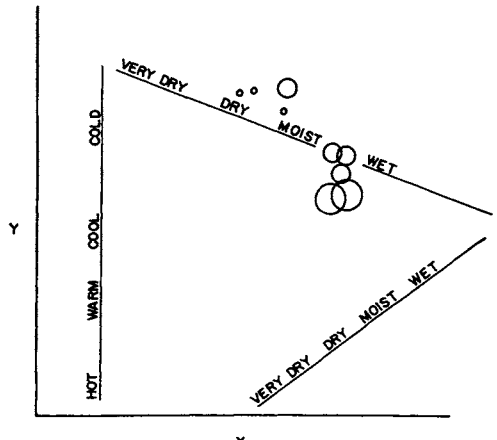
TSUGA HETEROPHYLLA



PSEUDOTSUGA MENZIESII



ABIES LASIOCARPA



TSUGA MERTENSIANA

the 45 stands used in the ordination, and dominates three community types. This is a very tolerant species (Baker 1949; U.S. Forest Service 1965; Krajina 1965). The term "tolerance" has long carried the implication of the ability of a species to withstand certain levels of shade. Although the word is necessarily vague and cannot have scientific limits placed upon it, Baker (1949) recognized that more than shade was involved. He used several features of a tree species, including reproduction, crown density, clear length, leaf characters, and changes with age in compiling new tolerance tables. *Abies amabilis* may not fully occupy its tolerance range because of poor migratory capacities (Schmidt 1957). The seeds are wind disseminated, but are too large to be carried far from the mother trees. Mammals and birds are insignificant in seed distribution (U.S. Forest Service 1965). There is an indication from Fig. 6, and from data presented in the results, that *A. amabilis* may some day become more important in other forest types in the Olympics.

Tsuga heterophylla is found from the dry to wet sites in the montane zone, but is most important on moist sites. *Tsuga heterophylla* is a very tolerant species. It is less tolerant than *Abies amabilis*, about the same as *Thuja plicata*, but more tolerant than *Pseudotsuga menziesii* (Baker 1949; U.S. Forest Service 1965). The principal factor limiting *T. heterophylla* distribution is moisture; if enough moisture is available, it will successfully compete with other species (U.S. Forest Service 1965). This species produces the greatest amount of seed of any tree species in the Olympics, even in dense stands (U.S. Forest Service 1965). *Tsuga heterophylla* requires better soil than *P. menziesii*, but will germinate and survive on a wide variety of seedbeds, even sterile soil if enough moisture is present (Hansen 1947). This explains why in the eastern montane zone which burned about 300 years ago, *T. heterophylla* can be 280 to 300 years old on moist, north-facing slopes, yet only about 180 years on dry, south-facing slopes. In the western mountains, where the forest floor is deeply covered with herbs, ferns, and shrubs, the small seeds of *T. heterophylla* germinate only on stumps and fallen trees. Some seedlings survive and eventually grow to maturity (U.S. Forest Service 1965).

Pseudotsuga menziesii, the only important seral species in the montane zone, is most abundant on dry and very dry sites (Fig. 7). When compared with its associate species in the Olympics, *P. menziesii* is shade intolerant (Baker 1949; U.S. Forest Service 1965). Apparently shade intolerance of seedlings is the limiting factor for *P. menziesii* (Hansen 1947). Plant cover heavier than 25% may be progressively harmful to seedling development. *Pseu-*

dotsuga menziesii seedlings are found in the Olympic forests, but they rarely survive to sapling stage in the forests. Because *P. menziesii* is a seral species, its importance in these forests will decline in the future, barring major wildfire. Several authors have commented that this species would have vanished from the Olympic forests long ago were it not for repeated fire (Judd 1915; Hanzlik 1932; Munger 1940).

Tsuga mertensiana is found prominently in the mesic environments of the subalpine zone (Fig. 6). Long, cold winters, short growing seasons, with much of the abundant precipitation falling as snow characterize the climate of the *Tsuga mertensiana* zone. Soil moisture is the most important soil characteristic in relation to *T. mertensiana* development (U.S. Forest Service 1965), and the species has its greatest importance on the wet end of the scale. This is the most restricted of the major tree species in the Olympics. *Tsuga mertensiana* is a tolerant species, and is considered a climax species of forests in which it is a major component (U.S. Forest Service 1965). In the *A. amabilis*-*T. mertensiana* forests, such as those forests in the Olympics, however, it may not continue to dominate because reproduction is not nearly so vigorous as that of *A. amabilis* (U.S. Forest Service 1965).

Abies lasiocarpa is most important on cold, dry sites throughout the high eastern mountains (Fig. 6). This is a tolerant tree species throughout its life span, more tolerant than any of its associates (Baker 1949; U.S. Forest Service 1965). Because it can reproduce in its own shade, *A. lasiocarpa* is a climax species in the high forest zone of the Olympics. This species grows in a cold climate, and will tolerate very poor soil moisture conditions (U.S. Forest Service 1965). Daubenmire (1965) found temperature to be more important than moisture in *A. lasiocarpa* distribution.

UNDERSTORY PATTERN

Although the feature that links stands of any one community type together is tree layer composition, this study is of plant communities, not merely tree layers, so that understory variation strengthens community type distinction. Floristic and structural shifts in the understory are important factors in differentiating community types, and also serve to relate various stands to a given type (Daubenmire 1952; Whittaker 1960; Whittaker and Niering 1965; Krajina 1965; Franklin 1966; Dyrness and Youngberg 1966).

A variety of Ericaceous species are the most important shrubs, with species of *Vaccinium* especially prominent in most community types (Table 3). *Rhododendron albiflorum* is abundant in the eastern sub-

Fig. 6. Importance of the five major tree species plotted over stand position on the two-dimensional ordination. No symbol is placed over a stand from which a species is absent. Circle size indicates species importance in a stand as follows: largest circle—dominant species, IVI greater than 45; middle circle—sub-dominant species, IVI between 20 and 45; smallest circle—minor associate, IVI less than 20. See Fig. 5 for actual data on precipitation and temperature.

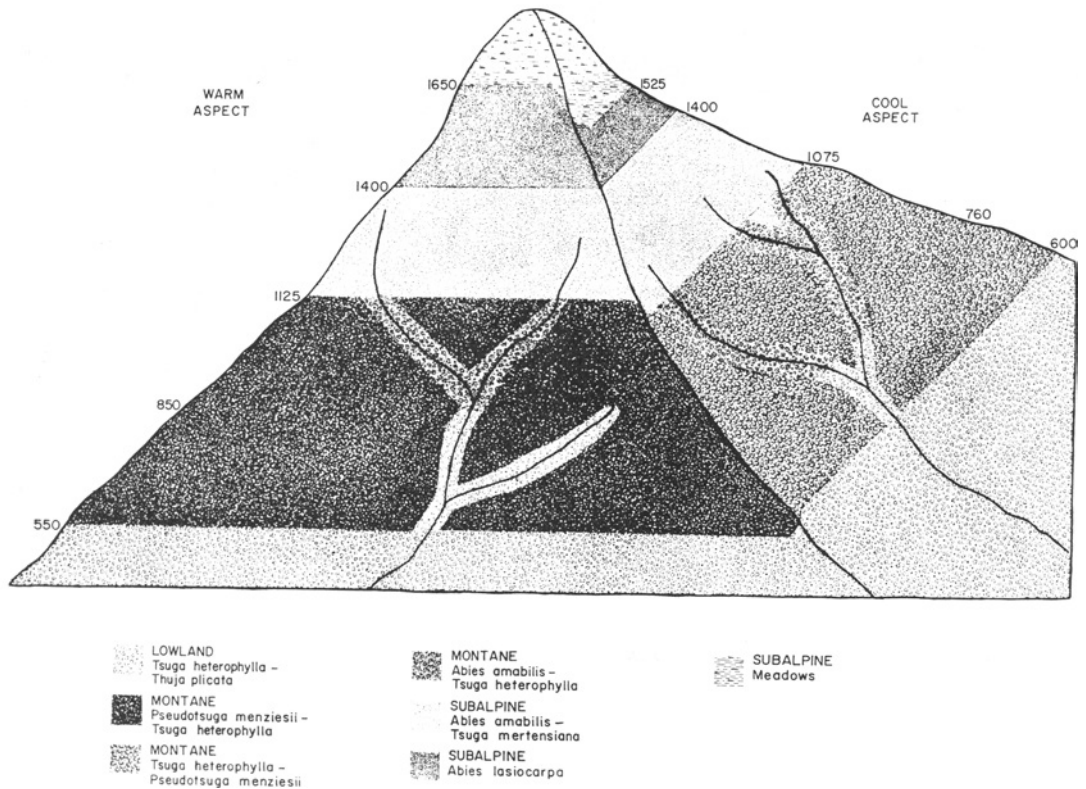


FIG. 7. Slope aspect modification of altitudinal zonation and forest pattern in the Olympic Mountains.

alpine zone. *Gaultheria shallon* is a dry site indicator in the Coast Ranges (Hansen 1947). Large expanses of *G. shallon* are common under seral forests on exposed sites. *Menziesia ferruginea* is an excellent indicator of the *A. amabilis*-*T. heterophylla* forest. Although not a dominant species in the shrub layer, *M. ferruginea* reaches its greatest abundance in these forests in the Olympics.

The herbaceous layer is usually rich and varied. Mosses are prominent in most community types, as are ferns. Individual species, such as *Oxalis oregana*, *Chimaphilla umbellata*, *Rubus pedatus*, and *Erythronium montanum* stand out in particular forest types.

Table 8 is a comparison of structural development of the understory for the major community types in the Olympics. Many times floristic composition can be linked to structural development to further indicate similarities and differences.

FOREST ZONATION

In order to understand the ecology of these forest it is necessary to consider the altitudinal zonation found in the Olympic Mountains, the causes of this sequence and at what altitudes a shift in forest type takes place. Slope aspect must be taken into account, however, for it can modify the zonal pattern by acting upon temperature, moisture, insolation, and wind.

TABLE 8. Comparison of the various strata in the major community types in the Olympic Mountains.

Community Type	Mean Cover (%)			
	Tree Saplings	Shrubs	Vascular Herbs	Mosses
<i>Abies amabilis</i> - <i>Tsuga heterophylla</i> / <i>Oxalis</i>	31	14	45	10
<i>Abies amabilis</i> - <i>Tsuga heterophylla</i>	20	15	22	15
<i>Tsuga heterophylla</i> - <i>Pseudotsuga menziesii</i>	25	25	29	31
<i>Pseudotsuga menziesii</i> - <i>Tsuga heterophylla</i>	13	67	10	48
<i>Pseudotsuga menziesii</i>	2*	75*	25**	35**
<i>Abies amabilis</i> - <i>Tsuga mertensiana</i>	25	50	23	20
<i>Abies lasiocarpa</i>	23	20	24	21

*shrub phase only; **herb phase only

Figure 7 shows the general forest zonation in the central mountains, and further compares the altitudinal sequence on a warm aspect (generally south-facing) with a cool aspect (generally north-facing). Usually, stands on a warmer, drier aspect are denser and have smaller trees than stands at a corresponding altitude on a cooler, moister aspect.

Thuja plicata, one of the dominant species of the lowland zone, is closely associated with a favorable soil moisture balance. Low soil moisture was shown to impair *T. plicata* growth on Vancouver Island (McMinn 1960), and a study in the Rocky Mountains found this species limited to sites with at least

12% soil moisture in August (Larsen 1940). *Thuja plicata* has requirements similar to *Tsuga heterophylla*, but apparently requires moister soil and more humus for seed germination (Hansen 1947). Throughout its range, *T. plicata* is found on stream bottoms, moist flats, terraces, gentle lower slopes, and in moist gulches and ravines (U.S. Forest Service 1965). This precisely describes the site locations for *Thuja plicata* in the Olympic Mountains, and strongly infers that soil moisture conditions of the steeper mountain slopes above 550 to 600 m are unfavorable for *T. plicata* abundance. Therefore, the species is a minor associate in the montane zone.

By using *T. plicata* importance as a measure of the extent of the lowland forest, the lowland zone contacts the montane zone at about 550 m on warm aspects and at 600 m on cool aspects. The steeper slopes, coupled with the excessively drained soils, limit *T. plicata* abundance, causing an abrupt shift to montane forest. The altitudinal range of *T. plicata*, however, increases along rivers, moist ravines, and seepage ways in the Olympics. For example, in a moist ravine in the Dosewallips Valley, *Thuja plicata* was the dominant species in the ravine (IVI 47.2), with *Tsuga heterophylla* and *Pseudotsuga menziesii* well represented. A *P. menziesii*-*T. heterophylla* forest occupied the adjacent slope, with *T. plicata* minor (IVI 3.2). Similar instances were recorded many times throughout the eastern montane zone.

The contact of the montane and subalpine zone is about 1100 to 1200 m throughout most of the mountain system, increasing to about 1450 m on the far eastern side of the mountains. Generally, the change from montane to subalpine forest is abrupt along these altitudinal limits, with distinct changes in the tree layer and the understory.

The factor most closely associated with zonal change in mountain systems is the shift to lower temperatures with increasing altitude. One factor in the Olympics that integrates temperature with kind and amount of precipitation, cold air drainage, exposure to solar radiation, and canopy density is early season snowline. Snow generally melts from the montane zone during early spring, and by June snowline is at ca. 1100 m, the lower limit of subalpine forests. Snowmelt takes longer in the subalpine zone, since temperatures are lower and snow is deeper. Orloei (1965) felt that the division between the wet subzone of the coastal *Tsuga heterophylla* zone and the *Tsuga mertensiana* zone in British Columbia was directly influenced by snow accumulation. Snow accumulation is considerable in the *T. mertensiana* zone during the winter months, but in the lower zone snow duration becomes insignificant in the British Columbia forests. Values for British Columbia showed that snow depth varied from 4 to 250 cm in the montane zone, but from 90 to 680 cm in the subalpine zone (Krajina 1965). The importance of snow impact on the subalpine forests in British Columbia is further emphasized by the extensive discussion of snow depths in relation to various plant associations of the *T. mertensiana* zone by

Brooke (1965), whereas Orloei (1965) discounts this environmental factor in describing the *T. heterophylla* zone. Higinbotham and Higinbotham (1954), studying moss communities on Mt. Rainier, found extensive evidence of snow pack in the subalpine forest, but did not mention this fact from the montane zone. This supports the use of early season snowline as an indicator of the causes in the differentiation of the two upper forest zones in the Olympics. The montane forests on warm slopes extend to about 1125 m, whereas those on cool slopes reach to 1075 m (Fig. 7). The reason is that winter snows are likely to be heavier, and snowmelt delayed, at a lower elevation on cool exposures, so that the change in temperature governing the break from montane forest becomes critical at a lower elevation on cooler exposures.

There are two types of contact between the montane and the subalpine zone: contact in the river valleys, and contact on the slopes. Considering the former, zonal interdigitation in the river valleys is common. Cold air drainage down the valley allows subalpine tree species to grow as small trees down-slope into the montane zone. Moreover, with the exchange of air up and down the valley the environment does not change rapidly with elevation. Avalanche tracks usually end in the valley bottom, and many times subalpine trees are seen growing at the bottom of avalanches. Often this is well into the montane zone, where the seeds had been carried by the snow. The most important consideration in valley zonation is that *A. amabilis*-*T. heterophylla* communities contact *A. amabilis*-*T. mertensiana* communities (Fig. 7). *Abies amabilis* is the dominant species in both forests, and both have similar physiognomy, which precludes determination by forest appearance. For these reasons, it is difficult to put a precise altitudinal limit on either forest zone in the valleys; a gradual transition is most frequently encountered.

Ocean proximity maintains a moderate climate on the western mountain slopes where two *A. amabilis* dominated communities are in contact, with similar physiognomy. Again, a gradual transition is encountered.

The contact between montane and subalpine forests on eastern slopes is distinct, because there is little interdigitation and the communities are floristically different. Environmental shifts are more abrupt on slopes, where steeper topography results in more rapid temperature changes, as evidenced by distinct early season snowline near the contact of the two zones. In the eastern Olympics, therefore, there is usually a marked contact of the forests containing *P. menziesii* with the subalpine forest.

The *A. amabilis*-*T. mertensiana* forests are generally found in the lower subalpine zone, where the slopes are wet. These forests abruptly contact the *Abies lasiocarpa* forests above, at about 1400 m on either slope. The reasons for this are complex, and not altogether clear, but it seems to result from an interaction of temperature and soil moisture. Tem-

perature is the most important factor governing the distribution of *Abies amabilis* (U.S. Forest Service 1965). Temperatures are lower upslope, but if temperature alone were the cause, it is likely that upper elevations would be floristically different on the opposing aspects. There is, however, an important change in soil moisture characteristics. At about this altitude in the Olympics, the slopes steepen appreciably, so that excessive drainage is common, and the soil mantle is thin, with many rock outcrops. Thus, soil moisture conditions probably deteriorate to a point that, compounded by the unfavorable temperature and exposure to prevailing winds, *A. amabilis* can no longer successfully compete as a dominant tree species. Figure 6 indicates that the range of *A. amabilis* may extend farther into the subalpine zone, notably stand 34, but these sites are in the cool, moist portion of the zone.

Abies lasiocarpa can successfully compete with other tree species in the rigorous climate of the high eastern subalpine zone, and this species dominates the highest forested zone in the Olympics. This forest type extends to 1650 m on south-facing slopes, but to only 1525 m on north-facing slopes (Fig. 7). Again, the predominant limiting factor is snowmelt. North-facing slopes are released much later than south-facing slopes from winter snow, with the result that dense forests cannot develop at higher elevations on the cool exposures.

The Hoh River-Soleduck River divide (Fig. 2) provides an excellent example of differential snowmelt. Snow melts early on the south-facing ridge of this divide (Hoh drainage), and thus a dense forest of *Tsuga mertensiana* is found to the ridge crest at 1500 m. Snowmelt is delayed on the north-facing ridge (Soleduck drainage), however, with the result that forest is excluded and wet subalpine meadows develop. This north-facing meadow is the Seven Lakes Basin area, and is an outstanding example of lowered forest line because of late snowmelt. Ordinarily Seven Lakes Basin is snow-free only during August and September, and in some cases snow lies there year-round. It is not difficult to see why forests are excluded from these situations. On south-facing slopes, snow pack eventually becomes limiting to forest development above 1650 m, where forests grade into subalpine meadows.

Abies lasiocarpa forests contact subalpine meadows at their upper limit, although scattered trees and krummholz clumps of *A. lasiocarpa* and less often *T. mertensiana* and *C. nootkatensis* continue upslope for some distance. These meadows may be dominated by various heath species (*Phyllodoce empetriformis*, *Cassiope mertensiana*, *Vaccinium deliciosum*) in the vicinity of the Bailey Range, by *Carex albionigra* and *Polygonum bistortoides* in wet areas, or by *Festuca idahoensis*, *Phlox diffusa*, *Arenaria capillaris*, and *Lupinus latifolius* var. *subalpinus* in drier areas (Kuramoto 1968).

FIRE

Fire is an exceedingly important environmental factor in the Olympics. It is evident from the results and composition of each community type that the effects of fire have been superimposed on climatically and topographically controlled forest patterns in these mountains. Fire has been most frequent in the dry sector of the Olympics (east of the Bailey Range). Wet conditions do not favor thunderhead formation over the windward slopes, so that lightning, the principal cause of natural fires, is rare. The general forest pattern in these mountains thus shows predominantly seral forests in the east and predominantly stable forests in the west.

The principal seral species in the lowland and montane zones is *Pseudotsuga menziesii*. The seral eastern montane forests show old, single generation *P. menziesii* slowly being replaced by *T. heterophylla*. On typical sites throughout the eastern montane zone, *P. menziesii* are from 270 to 300 years old, based on increment borings. This indicates that a series of major fires destroyed the montane and lowland vegetation about 300 years ago. The repeated occurrence of Lithosols throughout the eastern montane zone, coupled with charcoal through the soil profile, supports this conclusion. Through the normal course of succession, *P. menziesii* seeded-in and is now being replaced by other species. On extremely rocky slopes or atypical areas, *P. menziesii* is between 180 and 230 years old, implying a slower rate of invasion after fire, or that subsequent fires occurred.

On the basis of present forest composition and reproduction, most of the eastern montane forests will be ultimately dominated by *T. heterophylla*. *Abies amabilis* is present in many of the eastern forests, yet the small amount of reproduction indicates the species will remain minor. Slope aspect currently plays an important role in the distinction of the three community types (*T. heterophylla*-*P. menziesii*; *P. menziesii*-*T. heterophylla*; and *P. menziesii*). With time, however, it is possible that at least the first two types will become *T. heterophylla* forests. At present there is little indication that *P. menziesii* will be replaced on some of the dry spur ridges and slopes.

Recent years have seen a decline in another seral species after fire in the Olympics, *Pinus monticola*. It was earlier written that the climax forest in the montane zone ". . . is essentially a hemlock-fir complex with a sprinkling of western white pine, and should be designated the *Tsuga heterophylla*-*Abies amabilis*-*Pinus monticola* climax forest" (Jones 1936). The role of *P. monticola* was misinterpreted, for the species is found sporadically in seral forests of *P. menziesii* in the montane zone. It occasionally grows in the subalpine forests, and is exceedingly rare in those forests dominated by *A. amabilis*.

Many of the *P. monticola* present in the forests 30 years ago are dead or dying today, primarily from white pine blister rust. A second reason for the disappearance of this seral species is that many in-

dividuals are approximately 300 years old. The usual life span is 300 to 400 years, and the species does not reproduce well in shade (U.S. Forest Service 1965). Thus, natural old age replacement and white pine blister rust will result shortly in *Pinus monticola* becoming a rare species in the Olympic forests.

The forests dominated by *A. amabilis* are relatively stable forests. *Pseudotsuga menziesii* lives for more than 500 years, and *A. amabilis*, *T. heterophylla*, and *T. mertensiana*, which replace *P. menziesii*, may exceed 400 years of age (U.S. Forest Service 1965). Because there is little *P. menziesii* in these forests, and *Abies amabilis* and *Tsuga spp.* are over 300 years old, it is doubtful that these forests have been burned within at least the last 600 to 800 years.

Franklin (1966) plotted number of trees against size class to determine the successional direction of a forest association. This method is most useful in estimating minor directional changes in mature forests. It applies poorly to the early seral stages of the montane forests and to the *Abies lasiocarpa* forests in the Olympics, principally because there is not enough diversity in tree size. In size class distribution tables, seral species are either absent from, or have fewer trees in, a smaller size class than a larger one (Franklin 1966). Table 9 gives the size class distribution for mean number of trees/ha for the three community types dominated by *A. amabilis*. For these forest types, both *Abies* and *Tsuga* have representatives in all four size classes. Because there are more *A. amabilis* in the smaller and younger size classes in each community type, it is postulated that *A. amabilis* will become the major climax species in each type. This concurs with the pattern in the Cascades, in which *T. heterophylla* or *T. mertensiana* is giving way to *A. amabilis* (Franklin 1966). *Tsuga* can only germinate on fallen logs and stumps, not on the thick forest floor (U.S. Forest Service 1965), and such sites are precarious at best. Thus, the survival rate for *Tsuga* will be less than for *Abies*, which can germinate on many seedbeds. From the data we have in hand it is likely that *Tsuga spp.* will continue to grow in these forests, but not as abundantly as *A. amabilis* (Table 9).

Most of the *Abies lasiocarpa* forests originated after the same fire that burned the montane forests 300 years ago. These appear to be climax forests, however, exhibiting several generations of the dominant canopy species. *Abies lasiocarpa* is the first species to re-invade burned areas in the subalpine zone. Being more tolerant than any of its associates, it is also the climax species. *Abies lasiocarpa* is a short-lived tree, because the species easily succumbs to heart rot (U.S. Forest Service 1965). Individuals older than 250 years may be found, but many trees die at an early age. There is a rapid turnover in *A. lasiocarpa*, and thus several generations may be observed in these forests.

TREE INVASION INTO LATE-MELTING SNOW BASINS

Abies lasiocarpa and *Tsuga mertensiana* are invading some snow basins in the Olympics. Such sites

TABLE 9. Size class distribution for mean number of trees/ha for the three community types dominated by *Abies amabilis*.

Community Type and species	Size Class (cm)			
	I 10-30	II 30-75	III 75-120	IV over 120
ABIES AMABILIS-TSUGA HETEROPHYLLA/ OXALIS				
<i>Abies amabilis</i>	157	68	27	7
<i>Tsuga heterophylla</i>	79	45	27	12
<i>Thuja plicata</i>	+	+	+	+
ABIES AMABILIS-TSUGA HETEROPHYLLA				
<i>Abies amabilis</i>	126	183	22	+
<i>Tsuga heterophylla</i>	52	55	17	3
<i>Pseudotsuga menziesii</i>	+	+	2	—
<i>Thuja plicata</i>	2	—	—	—
ABIES AMABILIS-TSUGA MERTENSIANA				
<i>Abies amabilis</i>	143	167	15	—
<i>Tsuga mertensiana</i>	94	192	14	+
<i>Chamaecyparis nootkatensis</i>	21	54	1	—
<i>Abies lasiocarpa</i>	1	+	—	—
<i>Pseudotsuga menziesii</i>	—	—	—	1
<i>Pinus monticola</i>	—	1	—	—

+species present, but less than 1/ha

occur along east and north-facing exposures the length of Hurricane Ridge, from Hurricane Hill to Obstruction Point, where *A. lasiocarpa* is the most common invading species. Farther west, *T. mertensiana* is invading ecologically similar sites in Seven Lakes Basin and in the Bailey Range.

Quantitative data on tree invasion were gathered in two snow basins near Hurricane Ridge. A transect was established in each basin, running from the center to the outer edge. Perpendicular lines were established, along alternate sides of each transect, at 3 m intervals. Three circular plots were sampled on each line, 3 m² plots for saplings less than 1.5 m in height and 12.5 m² for plots with taller saplings. The number of individuals in each of the five height classes were recorded per plot. The data are presented on the basis of 10 m² for plots. An average of five (range: two to nine) individuals per height class were aged on each transect.

With increasing distance from the latest melting snow, there is an increase in height class of the saplings (Table 10). This suggests past years or groups of years when snow melted earlier enough to permit the establishment of seedlings. In years showing a decrease in snow load, snow melts out of these basins earlier than in years with heavier snow loads, and thus the habitat becomes suitable for tree growth. *Abies lasiocarpa* and *Tsuga mertensiana* have apparently taken advantage of this and seeded out into the meadows (Fig. 8). The mean age of the various height groups shows there were only certain groups of years when seedlings became established. The similarity in age of seedlings 0.5 to 3.0 m tall in transect 1, however, shows a better correlation of sapling height with length of the snow-free season than a height-age correlation. The number of seed-

TABLE 10. Density and age of *Abies lasiocarpa* seedlings and saplings invading snowbank sites near Hurricane Ridge. The data are expressed on the basis of 10 m² plots.

Distance (m) outward from treeless area	Height Class (m)				
	0.1	0.1-0.5	0.5-1.5	1.5-3.0	3.0
	Transect #1				
2.....	48.9	53.4	—	—	—
5.....	72.6	74.6	—	—	—
8.....	98.2	47.0	—	—	—
11.....	68.1	53.4	—	—	—
14.....	44.8	67.2	—	—	—
19.....	3.8	9.0	4.2	5.4	—
24.....	7.8	23.2	6.6	10.4	—
29.....	4.6	4.2(0.6*)	2.2(0.2*)	7.0(0.2*)	3.4
34.....	4.6	13.0	6.6	6.4(0.2*)	0.6(0.6*)
Mean age.....	11±5	24±2	42±4	43±5	40±7
	Transect #2				
2.....	2.2(1.0+)	2.2	1.0	—	—
5.....	10.6	18.2	2.2	—	—
8.....	23.4(1.0+)	48.0	7.4	—	—
11.....	19.2	29.8	16.0	—	—
14.....	4.8	21.0	27.8	5.8	—
19.....	5.0	24.0	4.6	3.2	—
24.....	3.2	13.6	23.2	4.2	—
Mean age.....	10±1	15±4	16±6	—	—

**Tsuga mertensiana*; +*Chamaecyparis nootkatensis*FIG. 8. *Abies lasiocarpa* invading meadow areas on Hurricane Ridge as a result of a previous period of early snowmelt.

lings less than 10 cm tall decreases rapidly where saplings greater than 0.5 m occur (Table 10). This is probably a response to reduced light levels with sapling growth.

Similar patterns of tree invasion into subalpine meadows have been reported for the British Columbia Coast Range (Brink 1959), and for Mt. Rainier National Park (Franklin, *et al.* 1966). In the former area, most trees were 20 to 40 years old, while in the latter location trees 20 to 45 years old predominated. Our data show age groupings of 8 to 15, 20 to 25, and 35 to 45 years with several one and two year old seedlings also present. The data from these three mountain systems on seedling establishment and from melt rate of glaciers (Meier 1965) point to previous

periods of warmer and drier climate which has permitted tree invasion into areas from which these species were previously excluded.

AVALANCHE EFFECTS

The higher elevations in the Olympic Mountains receive from 6 to 12 m of snow each year (U.S. Weather Bureau 1965), and the steep, rugged topography produces numerous snow avalanches. When an avalanche descends through the forests, it rips and tears most of the trees in its path. Because avalanches seem to follow the same tracks year after year, a different vegetation develops in response to continued avalanche activity. *Alnus sinuata* and *Chamaecyparis nootkatensis* have springy, resilient branches and leaders, and are best able to withstand the repeated onslaughts (U.S. Forest Service 1965). *Alnus sinuata* most frequently grows in these tracks, which may have more than 1200 m of vertical relief. Generally, this species is low growing, not taller than 5 m, and very dense. In many places, the small stems are so thick it is impossible to walk through the thickets. Often, *C. nootkatensis* will occupy these sites at higher elevations, sometimes coming farther downslope in response to cold air drainage.

COMPARISON OF THE OLYMPIC FORESTS WITH FORESTS OF OTHER MOUNTAIN SYSTEMS IN THE NORTHWEST

Care must be taken when comparing the Olympic forest patterns with forests in similar environmental regimes in other mountain systems. The Olympics present a rugged, convoluted system of high, sharp ridges and deep, narrow valleys rather than the roll-

ing topography frequently encountered in other mountain systems. In mountain ranges with less complex topography, there is an obvious crest or divide, with the forest and zonation sequences on the east side much different from that on the west. In the northern Rockies, for example, one needs only to compare forests of the eastern slope with the western to realize this important fact. The Bailey Range-Mt. Olympus complex, however, which constitutes the crest of the Olympics, is not obvious because of the complex topography of the mountains. The effectiveness of this barrier to moisture and moderating temperatures, and the resultant patterning in the eastern and western Olympics must be taken into account, just as is environment and patterning on eastern and western slopes in other mountain systems.

The flora of the Olympic Peninsula has previously been compared with the Mt. Baker area and the Mt. Rainier area (Jones 1936). Jones found that of the total flora of Mt. Baker, only 40 species and varieties of vascular plants were absent from the Olympic Peninsula, whereas 107 species and varieties of the total flora of Mt. Rainier National Park were lacking from the Olympics. This is an indication that the strongest affinities of the Olympics are to the north, and is an important consideration to bear in mind when comparing the Olympic forests to forests of other areas.

An extensive survey of the forests of the western slope of the Cascades in southern Washington and northern Oregon was conducted by Franklin (1966), who earlier classified the Cascade and Coast Ranges into several ecological provinces for silvicultural purposes (Franklin 1965). The number of references in this study to Franklin's work attest to the great similarity of Olympic and Cascade forests. The senior author conducted an extensive reconnaissance of the Washington Cascades in the summer of 1967 for the Inter-Campus Educational and Scientific Preserves Committee (Washington Universities). His experiences on that reconnaissance form the basis for much of the discussion to follow.

Except for the lack of *Picea stichensis* and the lush rain forest development of the western Olympic valleys, the forest types in the western Cascades are similar to those of the western Olympics. Beginning with the lowland *Tsuga heterophylla*-*Thuja plicata* zone, the vegetation passes through montane *Abies amabilis*-*Tsuga heterophylla* and subalpine *A. amabilis*-*T. mertensiana* forests to open subalpine meadows. This is the same sequence reported for the Olympics. The constant association of *Abies amabilis* with *Tsuga heterophylla* or *Tsuga mertensiana* in the Cascades and Olympics laces together the phyto-geography of the Pacific Northwest. The duplication of many associates in these forests underscores their affinities.

The *A. amabilis*/*Oxalis oregana* association of the Mt. Rainier Province is found chiefly on well-watered lower slopes and benches. Although rare in that area, it was felt that this type would be more com-

mon in coastal areas of *A. amabilis* (Franklin 1966). This is the case, for the extensive *A. amabilis*-*T. heterophylla*/*Oxalis* community type in the Olympics apparently owes its existence to the wet conditions of the coastal location. Many species important in the *A. amabilis*/*Oxalis oregana* association of the Cascades are likewise important in the corresponding forests of the Olympics. The *A. amabilis* forests in the Olympics are fairly uniform, whereas Franklin (1966) recognized 12 different associations in the Cascade. The difference centers around the greater compositional diversity of the understory in the Mt. Rainier area when compared to Mt. Baker or the Olympics. Franklin (1965) attributed this compositional diversity to a lack of sufficient, continuous elevation for extensive forest development in the Mt. Rainier area. The south Washington Cascades are low, gently rolling mountains as compared to the complex steep topography of the North Cascades and Olympics. To this must be added the absence of moderating ocean proximity and greater compositional diversity related to more frequent fires followed by successional stages.

In subalpine forests, of both mountain systems, *Abies amabilis* and *Tsuga mertensiana* are dominant species, although many of the understory components are not the same in both ranges. Nevertheless, the extent of this forest type in the subalpine zone of both mountain systems again shows their similarities.

The greatest similarity of the Olympic forests apparently lies with those in the Mt. Baker region. Their forest composition (Franklin 1965) and structure have been shown to be very similar to those in the Olympics. The major forests in the Mt. Baker area are *Tsuga heterophylla*-*Thuja plicata*-*Pseudotsuga menziesii* in the lowland zone, *Abies amabilis*-*Tsuga heterophylla* (with *Streptopus curvipes* and *Oxalis oregana* important in the herb layer) in the montane zone, and *A. amabilis*-*T. mertensiana* in the subalpine zone, merging to parkland and subalpine meadows. The forests of the Mt. Baker region, as those in the Mt. Rainier province, show more variation in stability and age than do the forests of the western Olympics. Some forests show excellent stability and old age, with almost pure *A. amabilis* in places, whereas other forests show evidence of burning within the past 400 years. *Pseudotsuga menziesii* is a common component of many of the *A. amabilis*-*T. heterophylla* forests of the Mt. Baker area, in contrast to the absence of this species from comparable forests in the Olympics.

The forest composition of the eastern Olympic Mountains is unique when compared with other Pacific Northwest east-slope forests. The lowland zone of the Olympics is composed of *Tsuga heterophylla*-*Thuja plicata*-*Pseudotsuga menziesii* and a small amount of *Abies grandis* is present. The lowest forested zone in the eastern Cascades is dominated by *Pinus ponderosa*, with mixtures of *P. contorta* in the north (Okanogans), entirely different from the lowest zone in the eastern Olympics. *Tsuga*

heterophylla-Thuja plicata forests are common along the rivers and creeks of the eastern Cascades.

The montane zones provide the most striking comparisons. Both presently are responding to major fires about 300 years ago, and as such are heavily dominated by *P. menziesii*. Whereas the Olympic eastern montane forests will eventually be dominated by *Tsuga heterophylla*, only a very narrow band of the eastern Cascade *P. menziesii* forests will ever be dominated by *T. heterophylla*. This band lies approximately within six km immediately east of the Cascade crest. Farther east, over the greatest area of the eastern Cascade montane zone, *Abies grandis* will be the climax species, principally because conditions are unfavorable for *T. heterophylla*. Where the two species overlap in the Cascades, *A. grandis* is seral to *T. heterophylla* (U.S. Forest Service 1965).

In the subalpine zone, *Abies lasiocarpa* dominates most of the eastern Olympic forests. *Abies amabilis* and *Tsuga mertensiana* are important on cool, moist slopes in the east-central mountains, but give way to *A. lasiocarpa* farther to the east. East of the Cascade crest, forests of *Pinus contorta*, *Picea engelmannii*, and *Abies lasiocarpa* clothe the high ridges, with *P. engelmannii* likely to be the major climax species (Franklin and Mitchell 1967). *Abies amabilis* and *Tsuga mertensiana* may be found on many different sites in the subalpine zone of the eastern Cascades, but they drop out farther east. *Picea engelmannii* is not reported to occur farther west than the Cascade crest through Washington and Oregon to Mt. Shasta (U.S. Forest Service 1965). Park Service personnel have recently found *Picea engelmannii* growing in small isolated stands in the eastern Olympics. The authors have not seen the populations of *P. engelmannii*, but correspondence with Mr. Robert Kaune and Mr. Eric Burr of Olympic National Park, yielded the following information. Three stands have been located to date, in Cameron Creek, Cox Valley, and Pat's Prairie. The latter stand is a bog site in Olympic National Forest, and clear-cut logging has already removed $\frac{1}{3}$ of the stand. *Picea engelmannii* is growing there in association with *Chamaecyparis nootkatensis*, *Abies lasiocarpa*, *A. amabilis*, *Pinus monticola*, and *Pseudotsuga menziesii*. The largest of these stands is in the Cameron Creek drainage occupying about 16.2 ha of valley bottom at the foot of an avalanche slope. *Picea engelmannii* there is in association with *A. lasiocarpa*, *A. amabilis*, *T. mertensiana*, and *Juniperus communis*. *Picea engelmannii* averages ca. 60 cm DBH, with the largest being 213 cm DBH and 54.6 m tall.

Picea engelmannii, however, is not an important tree species in the Olympics. This notable lack of *P. engelmannii* in the forests there and the greater occurrence of *A. amabilis-T. mertensiana* forests in the eastern Cascades set the two zones apart.

Franklin and Trappe (1963) mention extensive avalanche scars in the Northern Cascades. There, the deeply dissected and rugged topography is similar to the Olympics, but different from the Mt. Rainier area. Avalanche tracks in the Mt. Baker area are

dominated by species of *Alnus*, *Acer*, or herbaceous species. *Chamaecyparis nootkatensis* and less often *Abies lasiocarpa* were components of the Mt. Baker avalanche scars. This is similar to the avalanche scars in the Olympics. Most often these latter sites are covered with dense stands of *Alnus sinuata*, but *Chamaecyparis nootkatensis* is frequently observed at upper elevations of the avalanche track.

Krajina and his students (Krajina 1965) have done considerable work in the coastal and interior mountains of British Columbia. Much of their work has dealt with lowland forests, but the *Abies amabilis-Tsuga heterophylla* wetter subzone of the coastal *T. heterophylla* zone is equivalent to *A. amabilis-T. heterophylla/Oxalis* forests in the Olympics. *Tsuga heterophylla* apparently is the major climax species in British Columbia (Orloci 1965). There are many similarities between the subalpine *Tsuga mertensiana* zone (Brooke 1965; Peterson 1965) and the *A. amabilis-T. mertensiana* forests of the Olympics. Many of the character understory species for the zone in British Columbia are the same for the zone in the Olympics.

Farther east, in the Rockies of eastern Washington and northern Idaho, there is a strong coastal element in the forests (Daubenmire 1952). Zonation in the Olympic Mountains is quite different from that in the northern Rockies. The lowest zones in the Rockies are composed of *Pinus ponderosa* and *Pseudotsuga menziesii*. These forests grade into forests of *Thuja plicata* and *Tsuga heterophylla*, approximately equivalent to the lowland zone of the Olympics. Upslope from this zone, the forest becomes dominated by *Abies lasiocarpa* and *Picea engelmannii*. This is a different sequence from that in the western Olympics, where *Abies amabilis* forests separate the lowland and subalpine zones. Daubenmire (1968) has recently pointed out that *A. lasiocarpa* in the northern Rockies occupies the coldest and wettest sites. This is slightly different from the Olympics, where *A. lasiocarpa* grows in the highest forested zone, on the coldest sites, but not the wettest sites in the mountains.

The affinity of the Olympic forests with those to the south is not strong. There is similarity in forest composition and structure through the northern Oregon Cascades, but a major change in the composition of the forests takes place in the vicinity of Crater Lake (Franklin 1965). *Tsuga heterophylla* and *Abies amabilis* are relatively inconspicuous and limited in distribution. Climax forests in this province are dominated by *Abies magnifica* var. *shastensis* and *Tsuga mertensiana* at high elevations. *Pinus monticola* and *Pinus contorta* are also common.

The major shift in forest composition carries over into the Siskiyou Mountains. The Olympic forests have very little in common with those of the Siskiyou. Species more typical of areas south into California, including several broadleaf trees, are prominent in these mountains. *Abies amabilis-Tsuga heterophylla* forests are local (Franklin 1965). *Abies concolor*, *Chamaecyparis lawsoniana*, *Abies nobilis*,

Pinus jeffreyi, *Libocedrus decurrens*, and several species of *Quercus* are all prominent in the Siskiyou Mountains and constitute the largest part of the vegetation. These species and forest types are better related to the Sierra Nevada.

The *Abies amabilis* zone has only recently come under intensive investigation by ecologists who now recognize the ecological importance of these forests. This investigation of the Olympic Mountain forests largely completes the phytogeography of an important forest type in the Pacific Northwest. Those forests dominated by *Abies amabilis* in association with *Tsuga heterophylla* or *Tsuga mertensiana* have been shown to be closely allied with the same forest types in the Cascades of Washington, northern Oregon, and the coastal and interior ranges of British Columbia. In each of these places, a cool maritime climate favors these lush forests of large trees. The unique character of the eastern Olympic forests in the Pacific Northwest has also been shown.

SUMMARY

This study concerned the ecology of montane and subalpine forests of the Olympic Mountains, Washington. These mountains are primarily derived from Cretaceous sediments with some Eocene volcanics. The climate ranges from a mild, wet maritime on the windward slopes to a mild, rain-shadow on the lee slopes to the east and north.

Data were gathered on forest composition, tree age, and soils to relate the mosaic of forest communities to the environmental regimes of the mountains. With the aid of a two-dimensional ordination the forest stands were grouped into the following major community types:

A. Montane Zone

1. *Abies amabilis*-*Tsuga heterophylla*/*Oxalis* in the Western Olympics from 550 to 1100 m under a maritime climate; an extensive herb layer but patchy shrub layer is characteristic.
2. *Abies amabilis*-*Tsuga heterophylla* on river terraces from 760 to 1125 m in the eastern Olympics; well developed shrub but depauperate herb layers.
3. *Tsuga heterophylla*-*Pseudotsuga menziesii* from 600 to 1100 m on northern and eastern exposures in the eastern Olympics; poorly developed understory.
4. *Pseudotsuga menziesii*-*Tsuga heterophylla* on southern and most western exposures from 550 to 1125 m in the eastern and drier mountains; an extensive shrub but poorly developed herb layer.
5. *Pseudotsuga menziesii* forests on dry, exposed sites from 550 to 900 m in the eastern Olympics and in recent fire areas; a shrub layer predominates in the driest forests, with an herbaceous layer characteristic of stands with more frequent fog.

B. Subalpine Zone

1. *Abies amabilis*-*Tsuga mertensiana* on all ex-

posures west of the main mountain crest and on northern exposures to the east, from 1100 to 1650 m; an extensive shrub but depauperate herb layer is characteristic.

2. *Abies lasiocarpa* in the eastern Olympics from 1300 to 1800 m; the understory is poorly developed due to the dense forest canopy.

Community types on recently disturbed sites, mainly from fire, include widespread *Pseudotsuga menziesii* forests at lower elevations, *Pinus contorta* forests at higher elevation on southern exposures in the northeast sector, and *Abies lasiocarpa* elsewhere in the drier subalpine forests.

The understory shrub and herb layers were important aids in determining forest types. Ericaceous species, especially those of *Vaccinium*, were important.

Community type diversity was related to the diversity of environments within each forest type. The forest types were ranked in order of decreasing stand diversity ranging from *Pinus contorta* stands which occupy a wide environmental gradient to the *Abies amabilis*-*Tsuga heterophylla* type that is confined to specialized sites on river terraces.

The ordination of the five major tree species showed that the location and environmental regime of each forest type is largely governed by the tolerance ranges of the dominant species. These patterns for species follow closely those patterns of the forest types.

The break from lowland to montane forest seems to be controlled by soil moisture with the indicator species *Thuja plicata* extending upslope along rivers and moist ravines. The change from montane to subalpine seems controlled by the spring melt of snow (by early June) from the montane forests. With cooler temperatures and deeper snow, melt is delayed until late June and July in the subalpine forests. Where snow remains until August, herbaceous or dwarf shrub subalpine meadows occur.

The drier eastern slope forests were extensively burned about 300 years ago. This has resulted in an abundance of *Pseudotsuga menziesii* in these forests. Although burned in the past, the *Abies lasiocarpa* forests appear stable. Fire has been rare in the wetter western slope forests. Here, *Abies amabilis*, *Tsuga heterophylla*, and *Tsuga mertensiana* are prominent.

Soil morphology has been greatly influenced by fire. Brown Podzolics (Spodosols) develop under relatively stable forests where fire is rare. Lithosols (Entisols) are found under seral forests where much of the solum has been destroyed by reoccurring fires and subsequent erosion. Profiles in both groups are poorly developed.

Soil fertility levels apparently have no effect on community type distribution. Brown Podzolics had more favorable cation exchange capacities than Lithosols, but fertility levels did not appear limiting for tree growth. Parent material differences had no effect on forest pattern.

The Olympic Mountain forests have strong affinities with the northern Cascade Range and coastal and interior ranges in British Columbia. The basic plant ecology, zonation, and dominant canopy species are similar in all three mountain systems. The affinities of these forests with the southern Oregon Cascades and the Siskiyou Mountains are not as strong as with the northern ranges. The affinities with the western slope forests in the Rocky Mountains of Idaho and Montana and also less pronounced.

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