

# VEGETATION OF THE SISKIYOU MOUNTAINS, OREGON AND CALIFORNIA<sup>1</sup>

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## I. INTRODUCTION

### NATURE OF THE STUDY

The Klamath Region, between the southern Cascade Range and the Pacific Ocean in southern Oregon and northern California, is an area of exceptional ecological interest. These old and geologically complex mountains support an exceedingly complex pattern of natural communities in relation to steep climatic gradients and diverse parent materials, and among these communities a prevailing climax, the Mixed Evergreen Forest, which has a central relation to other western forest vegetation. One area of the region, the Siskiyou Mountains along the California-Oregon border, was selected for vegetation study. Quantitative samples were taken over a wide range of topographic situations, climates, and parent materials for gradient analysis, seeking to relate distributions of plant populations and characteristics of communi-

ties to environmental gradients. Analysis and interpretation were based on the conception of the vegetation as a multi-dimensional pattern, and on study of the manner in which local patterns of vegetation in relation to topographic moisture gradients change along climatic gradients and from one parent material to another. The sections which follow include vegetation description, climax interpretation, community classification, floristic analysis, and consideration of species distributions for the pattern of Siskiyou forest vegetation in relation to four major environmental gradients—local topographic moisture, elevation, the diorite-gabbro-serpentine series of parent materials, and the east-west climatic gradient from the Pacific Coast inland.

### GEOLOGY

The dominating topographic features of the Pacific Coast states are the two chains of mountains which run parallel to the Coast from Canada to southern California, and the chain of valleys between them. The higher, inner mountain chain is formed by the Cascade Range and the Sierra Nevada; the lower, outer chain includes the "Coast Ranges" in a

<sup>1</sup> A contribution from the Department of Zoology, Washington State University, and the Department of Biology, Brooklyn College. This study was supported in part by the funds for biological and medical research of the State of Washington Initiative Measure No. 171. The author is indebted to M. Ownbey and A. Cronquist for determination of the plant collections, to D. I. Axelrod, R. W. Chaney, H. D. MacGinitie, and F. G. Wells for comments on the manuscript.

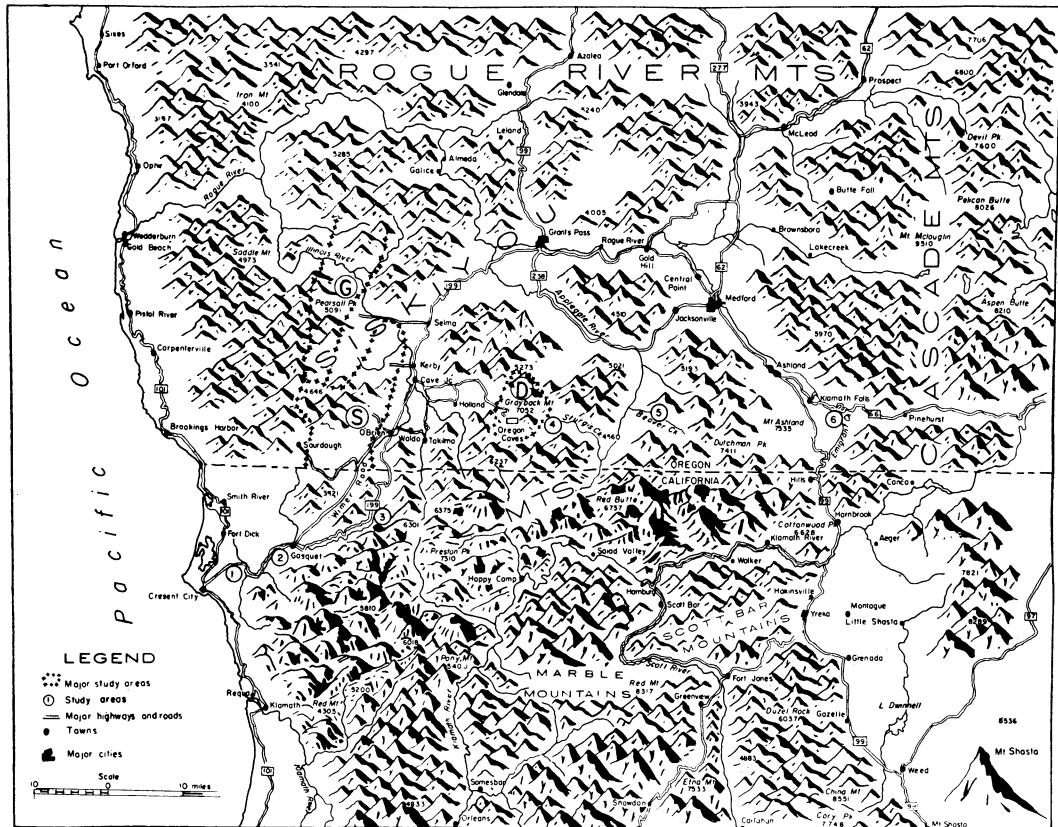


FIG. 1. Map of Siskiyou Mountains of California and Oregon in relation to other, adjacent ranges. Major study areas on three parent materials within the Mixed Evergreen Forest Region are outlined and marked with circled letters: (D) the diorite area, (S) the serpentinite area, (G) the area of gabbro and hornblende diorite. Study areas for the west-east climatic transect from the Coast inland are marked with circled numbers: (1) Mill Creek State Park (Sequoia forest), (2) South Fork, Smith River (coastal *Pseudotsuga* forest), (3) Siskiyou Fork, Smith River (mixed evergreen forest, more mesic phase), (4) Sturgis Creek (mixed evergreen forest), (5) Beaver Creek (mixed evergreen forest, more xeric phase), (6) Emigrant Creek (oak woodland, with *Pseudotsuga* forest in most mesic and valley grassland in most xeric sites).

broad sense. In northern California and southern Oregon a complex of mountains, the Klamath Ranges, extends from the Coast inland to the southern Cascade Mountains and interrupts the chain of valleys between the two mountain chains. Geographically the Klamath mountains are part of the coastal chain; but they differ from the Coast Ranges north and south of them in age and history, in geological character and complexity, in height and east-west extent. Their closest geological relations are not with the Coast Ranges, but with the Sierra Nevada and the older core of the Blue Mountain complex of Oregon (Fenneman 1931).

The Klamath Region, as it was outlined, described, and named by Diller (1894, 1902, 1903, 1906, 1914), extends north and south for about 390 km, and westward from the Cascade Mountains about 120 km, to reach the Pacific Coast between 41° and 43° north latitude, with a total area of about 34,000 km<sup>2</sup>. The Siskiyou Mountains are the northernmost of the

major mountain groups of the central Klamath Region; like other major ranges of the Region, they are a complex area of mountains rather than a well-defined ridge. The Siskiyou extend in an east-west direction along and on each side of the California-Oregon border, north of the Klamath River and south of the Rogue River. From the Pacific Coast they extend inland from low mountains, with elevations less than 1000 m near the coast, through the main area of mountains of intermediate elevations, including some peaks above 2135 m, to the low mountains which connect with the southern Cascade Range.

The older geological history of the Klamath Mountains is essentially the same as that of the Sierra Nevada (Diller 1894, 1903, 1906; Fenneman 1931). Extensive masses of sedimentary rocks were deposited in an inland sea in Devonian and Carboniferous time; and, at the close of the Paleozoic, these and other rocks were folded and raised into mountains. These mountains were worn down, and much of the area

submerged in Triassic and Jurassic time, while additional sediments and volcanic materials were deposited. At the close of the Jurassic, extensive deformation and intrusion occurred, accompanied by another uplift. A long cycle of erosion followed until, during the Cretaceous, the low mountains remaining subsided and were again largely submerged, with deposit of extensive sedimentary rocks.

At the close of the Cretaceous the Klamath Mountains were again uplifted; and they have existed, as at least low mountains, throughout the Cenozoic, with a complex history of uplift, subsidence, and erosion (Diller 1902). Results of this history are to be seen in wave-cut coastal terraces (Diller 1903, Fenneman 1931:463, Dicken 1952) and peneplain remnants (Diller 1902) in the Siskiyou Mountains. One of these, the Klamath peneplain, is of major significance in the study area. Erosion during the early Cenozoic reduced much of the region, by Miocene time, to a surface of low relief above which scattered mountain ranges rose. This peneplain was later subjected to repeated elevation and subsidence, and probably some tilting and deformation. The Klamath peneplain now appears as a dissected plateau, the surface of which in general rises from the Coast inland and from the north to the south. In the Siskiyou it is about 500 m near the coast, but rises to 1200 to 1350 m, 40 to 80 km inland; farther south in the Salmon and Yolla Bolly Mountains remnants appear at 1800 to 2200 m (Diller 1902, Fenneman 1931). In the central Siskiyou area, one may climb onto the peneplain by the Wimer Road and observe its surface in the serpentine and gabbro uplands west of the Illinois Valley. Sighting across the valley one may observe remnants of the surface in the lower, metavolcanic mountains, while the diorite monadnock of Grayback Mountain rises above it to 2148 m.

A great mass of ancient, closely folded and faulted rocks, generally metamorphosed, and intruded by igneous rocks, form the Klamath Mountains (Fenneman 1931). The consequence of their history of sedimentation, vulcanism, and igneous intrusion, uplifting, folding, faulting, and erosion is an extremely complex mosaic of rock types, a mélange of diverse parent materials. Peridotite and serpentine intrusions, characteristic of many mountains and island chains (Hess 1955), are especially extensive and conspicuous in vegetational effect. The deformation of these mountains was due to repeated compression from the east; and the folds thus formed are curved or crescent-like, striking southeast toward the Sierra Nevada in the southern part of the Klamath Region, northeast toward the Blue Mountains in the northern part (Diller 1914, Fenneman 1931). A trend toward the north-northeast is evident in the formations outcropping in the area of the Siskiyou studied (Wells *et al.* 1949, Wells & Walker 1953).

Geologic maps for Siskiyou quadrangles have been published by Diller (1903), Diller & Kay (1924), Maxson (1933), Wells (1939, 1940), Wells *et al.*

(1949), Wells & Walker (1953), and Cater *et al.* (1953). The Kerby and Grants Pass quadrangles (Wells *et al.* 1949, Wells 1940) include the main study areas in the central Siskiyou. In the Grants Pass quadrangle, the most extensive area is underlain by metavolcanic rocks of Paleozoic age; along with these occur a number of larger and smaller outcrops of diorite, thought to represent a single great batholith of Jurassic or Cretaceous age. Of these, the larger outcrop of quartz diorite (about 120 km<sup>2</sup>) which includes Grayback Mountain served as one study area. Other rocks on which vegetation could be observed in the area included various metasedimentary rocks—the marble in which the Oregon Caves occur, slate, argillite, and quartzite—and serpentine. In the Kerby quadrangle large areas of both serpentines and gabbros occur, together with various metavolcanic and metasedimentary rocks, granodiorite, hornblende diorite, dacite porphyry, and amphibole gneiss. The unmetamorphosed serpentines are predominantly saxonite, with small areas of dunite and pyroxenite. The fringes of the main peridotite mass and the smaller outcrops outlying from it are largely metamorphosed into serpentine rock in the narrower sense. The peridotite and serpentine together form a great sheet, thousands of meters, but probably not over 4500 m, in thickness intruded along planes of weakness into the other rocks of the area. The study of low-elevation serpentine vegetation was concentrated in the peridotite and serpentine area from Eight Dollar and Josephine Mountains west to Chetco Peak and south beyond Oregon Mountain into California. This, with a north-south extent of 90 km and an area exceeding 700 km<sup>2</sup>, is the largest body of ultramafic rock in the United States and perhaps in North America (Wells *et al.* 1946, Cater *et al.* 1953). The olivine gabbro study area, of about 36 km<sup>2</sup> including York Butte, is part of a larger belt of gabbro and hornblende diorite (over 260 km<sup>2</sup>), also intruded in Jurassic or Cretaceous time, lying north-west of but parallel to the serpentine area.

The complex rock pattern and history of the Klamath Mountains have produced no well-defined trend in stream drainage and ridge direction; the Siskiyou Mountains give the impression of “. . . a confusion of broken mountain ridges with steep and stony slopes . . .” (Peck 1941). The principal rivers of the Klamath Region cut transversely across it, running generally westward from the interior valleys, through deep canyons in the mountains themselves, to the ocean (Anderson 1902). Walls of these canyons are long, and often steep, inclines from the upland to the valley bottoms, interrupted in some cases by terraces remaining from past erosion cycles (Diller 1902, Fenneman 1931); valley bottoms are mostly narrow. Mountain slopes with an average grade of 30° or more through a range of 1000 m or more are common; over most of the region rugged mountain topography prevails. Although the Klamath peneplain is represented by rolling uplands in some areas

of the Siskiyou, the mountains of lower elevations are in general stream-eroded to topographic maturity.

Topography of higher elevations of the Klamath Mountains has been shaped by many local alpine glaciers; the description of glacial effects in the Trinity Alps by Hershey (1900) applies as well to the Siskiyou Mountains. Cirques, with steep rock walls with scanty vegetation and floors with tarns and mountain meadows, occur in the Grayback area and other higher mountains; but the fraction of the area showing glacial topography is small. The non-forest vegetation of the glacial topography is outside the concern of the present monograph.

#### THE CENTRAL RELATION OF THE KLAMATH FORESTS

To the ecologist familiar with both the Southern Appalachians and the Klamath Mountains, there are a number of striking parallels between these regions. Both are old mountains, with land surfaces which have been continuously occupied by vegetation throughout the Cenozoic, at least. Both persisted as monadnocks through major early Cenozoic cycles of erosion, culminating in the Schooley peneplain of the Southern Appalachians, the Klamath peneplain of this region. Both have been refuges for plant populations destroyed in other areas by glaciation, submergence of coastal plains, climatic desiccation, and, in the West, the great lava flows of the Interior. Both contain modern vegetation which is most nearly related to the widespread Arcto-Tertiary forests of the earlier Cenozoic. Both are areas of great vegetational diversity, and also areas of great floristic diversity and concentrations of narrowly endemic species. Both have "central" relations to the forest floras and vegetations of other, surrounding areas.

Figures are not available, but there is no doubt that the flora of the Klamath Region is extremely rich in numbers of species and numbers of narrow endemics for its latitude. Many genera show concentration of high proportions of their species, including endemics, in this area. Many of the endemics appear to be relicts of formerly wider distributions; in other cases species have probably spread from the Klamath Region to other areas of the West. Thus in the genus *Crepis*, a number of diploid species are now relict in the Klamath area, while genetic material from these has been used in apomictic polyploids which have spread over semi-arid environments of the Interior (Babcock & Stebbins 1938). The region possesses also a greater diversity of forest communities, in a more complex vegetation pattern, than any comparable area of the West. With the exception of more typical forms of the Pigmy Conifer Woodlands, all the plant formations dominated by trees of the western United States occur there, as they do in no other area.

Three interrelated reasons for this central relation may be given on the basis of the vegetational history of the West, the geological history and characteristics of the mountains, and their location. In

broadest statement, the history of western forests from Miocene time to the present has been one of progressive shrinkage toward the Coast and higher elevations, accompanied by progressive differentiation in the different areas of the West, while the diverse floristic elements of the Madro-Tertiary Geoflora were progressively expanding and differentiating in the Southwest and the drier lowlands of the Interior (Chaney 1947, 1948, Axelrod 1958, 1959). Forests most suggestive of the mixed forests of the Miocene are now restricted to the Southern Appalachians in the East, the Klamath Region and coastal California in the West. It is in these two areas that the combination of sufficiently favorable moisture conditions with sufficiently warm temperatures permit the existence today of remnants of the Arcto-Tertiary Geoflora. The significance of the Southern Appalachians in relation to the eastern forests has been extensively developed by Braun (1935, 1938, 1947, 1950).

A second basis of the central relation of the Klamath Region is in its climatic, topographic, and edaphic diversity, together with the age of the mountains. Climatic variation and topography permit a wide range of communities to exist in the region and in different situations in a given area. The different parent materials also have striking effects on floristic and vegetational diversity. Many of the narrowly endemic species in which the region is so rich occur on serpentine, gabbro, or other localized parent materials. Parent-material differences make possible also much of the distributional overlap in the region of species with diverse geographic relations. Thus, in the central Siskiyou, *Taxus brevifolia* in the southern part of its distribution occurs on diorite, *Pinus ponderosa* near the western limit of its distribution on gabbro, and *Pinus jeffreyi* near the northern limit of its distribution on serpentine; these three species appear in the same limited area, but not in the same stands.

The diversity of habitats has been characteristic of the area throughout its long history, although climatic gradients were probably less steep before middle Pliocene time. Even at the maximum development of the Klamath peneplain, mountains of diverse parent materials existed in the area. The region has at all times offered a complex mosaic of habitats, permitting species of diverse environmental requirements to persist in the area while changing climates eliminated some species elsewhere, and caused others to migrate north or south from the range, or to become largely restricted to the Interior east of the range, while leaving relict populations in the Klamath Region.

Finally, it may be observed that the location of the region makes it the meeting ground of floras of diverse climatic relations. In it the flora which may be broadly termed "Northwestern" meets part of the "Californian" flora, with representation also of the floras of the arid Interior and interior mountains. The Mixed Evergreen Forest climax itself is the

link between the coniferous Coast and Montane Forests on the one hand, and the broad-sclerophyll vegetation of California and Oregon on the other. More than any other area, the Klamath Region is central to the forest floras and forest vegetation of the West.

CLIMATE

The location and topography of the Klamath Region imply a wide range of climatic conditions, including steep climatic gradients from the Pacific Coast inland (Engelbrecht 1955). Coastal climates are strongly maritime, with high precipitations and humidities, abundant fog, limited ranges of temperatures, and low temperatures for their latitudes. The mountains paralleling the coast limit the extent of the maritime influences inland, and produce rapid climatic change toward drier, warmer, and more continental conditions in the interior valleys. Isoleths of January and July temperatures, annual range of temperature, annual precipitation, and relative humidity and evaporation, all tend to parallel the coast (Visser 1954). Kendrew (1937) observes of one aspect of these climatic gradients, that the contrast in temperature conditions between the coast at San Francisco and the Great Valley of California is as great as that between Scotland and North Africa, although the distance is only about 120 km.

Climatic data available for the Siskiyou Mountains themselves (Bowie 1934, Wells 1936, 1941, Sprague 1941) are summarized in Table 1. The stations are arranged in two sequences from the coast inland in California and in Oregon. Mean annual temperatures for low elevations in these mountains are rather consistently around 11.0-11.5°C. Average temperature conditions of valley stations are much the same throughout the area; but the inland stations are at higher elevations, and temperatures at comparable elevations are consequently warmer in the interior than on the coast. More marked contrasts appear in ranges of temperature. Mean monthly temperatures for January decrease from about 8.0° to 1.0-3.0°C, while those for July increase from about 15.0° to 21.0-23.0°C. The difference between these mean monthly temperatures, as an indication of the gradient from more equable maritime toward more variable continental climates, increases from about 7.0° on the coast to 19.0-21.5°C in the interior valleys. Similar trends may be observed in the extreme temperatures given in Table 1.

Mean annual precipitation decreases strongly from the coast inland, from values over 180 cm, through values of 80 to probably 150 cm in the central Siskiyou, to values below 50 cm in the interior valleys. The data for Waldo, in the Illinois Valley between the principal study areas, bear most directly on the work in the central Siskiyou. Siskiyou Summit is in the low mountains connecting the Siskiyou with the southern Cascade Range, and is thus not a part of the low-elevation sequence.

All the stations have maritime patterns of seasonal distribution of precipitation, with heaviest rainfall in

TABLE 1. Climatic data for stations at low elevations in the Siskiyou Mountains, from the Coast inland in California and Oregon.

	Distance from Coast, km	Elevation in m	Mean annual temperature, °C	Mean monthly temperatures, °C		Extreme temperatures, °C		Growing season in days	Annual precipitation, cm.	Per cent of precipitation in summer (4 mos. June-Sept.)	Annual snowfall, cm
				Jan.	July	Min.	Max.				
<b>California</b>											
Crescent City....	16	38	11.3	7.7	15.2	-7	39	230	193	6.5	
Happy Camp ..	64	700		3.2	22.1	-14	45	159	105	3.9	66
Scott Bar.....	92	549							63	6.0	
Yreka.....	122	801	10.8	1.0	22.0	-22	44	129	44	9.5	42
Montague.....	130	747	11.7	1.0	22.6	-26	43	141	31	14.9	24
<b>Oregon</b>											
Brookings.....	10	37	11.3	7.9	14.6	-8	38	269	187	8.9	3
Buekhorn Farm.	49	396	11.3	4.1	20.1	-14	42	150	180	3.9	65
Waldo.....	47	503	10.3	2.4	19.5	-17	43	155	126	5.8	84
Williams.....	80	457	11.1	3.7	19.4	-16	42	145	81	6.3	48
Grants Pass...	88	287	11.8	3.9	21.1	-18	45	132	74	6.5	22
Jacksonville...	106	500	11.4	2.6	21.6	-18	41	190	67	8.8	32
Talent.....	118	480	11.6	2.9	21.7	-17	42	170	42	13.6	21
Ashland.....	124	601	11.4	3.3	20.8	-17	41	182	50	12.8	45
Siskiyou Summit.	130	1363		0.6	18.3	-21	38		83	9.8	

winter, December and January, lightest in summer, July and August. The area is in the transition between the two Pacific Coast types of rainfall regime (Ward 1925, Kendrew 1937), the North Pacific with its limited summer rain and the California type with its practically rain-free summers. At Waldo the four months from November to February include 65% of the rainfall, the four months from June to September 6%. Maritime fogs, or low stratus, are a prominent feature of the coastal climate, where fog may be present 50% of the summer hours and where fog and fog-drip from trees contribute significantly to the humid conditions of the redwood belt (Cooper 1917, Byers 1953, Patton 1956, Oberlander 1956). Relative humidities may be assumed to decrease, and evaporation, hours of cloud-free sunlight, and diurnal temperature range to increase toward the interior; but data are not available.

In general character the climates of low elevations in the Siskiyou are warm-temperate, summer-dry, "Mediterranean" climates; corresponding to these climates, plant communities in which broad-leaved evergreen or sclerophyllous trees are prominent prevail over most of the range. The climates of these forests, and especially those of the redwood belt, are considerably more humid than those of Mediterranean Europe. Russell's (1926) application, with modifications, of the Köppen (1900, 1923) system recognized a mesothermal humid belt with equable temperatures near the coast (Csn), a belt of mesothermal humid, Mediterranean sclerophyll climates (Csb) inland from this, and warmer and drier woodland and steppe (Csa and Bsh) climates in the inner valleys, while microthermal climates occur at higher elevations. The Thornthwaite (1931, 1948) systems recognize a sequence from wet or perhumid conditions near the coast through humid in the main area of the range

to subhumid in the interior; low elevations of the area are microthermal by the criteria of the earlier system, cooler mesothermal by those of the later.

The work in the central Siskiyou had as one objective the comparison of vegetation patterns on three parent materials in the same climate. So steep are the climatic gradients across the Siskiyou that the three study areas on diorite, gabbro, and serpentine cannot have the "same" climate. They are all, however, in the same area of the central Siskiyou, represented approximately by the Waldo data. They are thought to be close enough to be reasonably comparable, and the consistency of the vegetational contrasts on these parent materials in different areas of the Siskiyou Mountains supports the conclusion that effects of parent materials far overshadow those of climate in the study areas.

#### CULTURE AND DISTURBANCE

The rugged topography and generally infertile soils of the Klamath Mountains have not offered resources which would draw a large population into the region. The largest city within the region is Medford, with a population somewhat over 19,000; most of the region is sparsely settled, and much of it is mountain wilderness. The greater part of the area is in National Forest land. The central and western Siskiyou of Oregon, in which most of the study was carried out, are within the Siskiyou National Forest, the eastern Oregon Siskiyou in the Rogue River National Forest. Extensive wilderness areas have been set aside in the Yolla Bolly, Salmon and Trinity Alps, and Marble Mountains; and small areas of the coastal redwood forests are protected as parks. In the Oregon Siskiyou the Oregon Caves National Monument includes typical mountain vegetation of the central Siskiyou, and an area of forests farther east is protected by the Mt. Ashland watershed. Two larger areas of the western Siskiyou are maintained by the Siskiyou National Forest as the Illinois Canyon and Kalmiopsis Limited Areas.

Only limited farming is carried on in the Klamath Region, although the upper Rogue River Valley is an important fruit-growing district. Parts of the Klamath Region are used as range land, although the forests of most of the region provide little food for stock. In the Siskiyou study areas, limited grazing in the forest lands of the serpentine areas seems not to have damaged their vegetation; limited grazing in the higher elevations of the diorite area has severely affected some of the drier mountain meadows. Gold was discovered in the Siskiyou in 1851 or 1852, and the local gold rush brought thousands of miners into the Galice-Kerby-Waldo area which includes the serpentine and gabbro mountains studied. Diller (1914, see also Diller & Kay 1909, Maxson 1933, Shenon 1933, Wells *et al.* 1940, 1949) mapped and described 52 placer mines and 67 lode mines and prospects in this area. Little more than marginal mining is carried on in the area now; and the mining settlements of Gold Rush times have shrunk to vil-

lages, or to fields with few vestiges of the old buildings.

Lumber now forms the principal resource and industry of most of the Klamath Region. The coastal redwood belt contains immensely valuable timber lands; within the central Siskiyou Port Orford cedar (*Chamaecyparis lawsoniana*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), and to a lesser extent other species, form valuable timber stands. Lumbering practice at low elevations generally involves removal of the conifers of the mixed evergreen forests, leaving at least partial sclerophyll cover. With the relative depletion of more available timber farther north and consequent shift of lumbering activity toward the south, much of the forest area of the Siskiyou is being rapidly cut; and conservation and sustained-yield programs are little in evidence (Dickens 1952).

In the dry-summer climate of the Siskiyou, the forests are easily set afire; and fires of widely varying intensities have been frequent. The Klamath and other Indians are believed to have set fires in connection with hunting and warfare. In Gold Rush days and thereafter, fires were set prodigally, unintentionally from neglected camp-fires and intentionally to make travel easier, to clear the ground for prospecting, and for recreation. Miners are said to have set fires to enliven an evening's drinking with a mountain slope in flames. Fires were used to drive game, and there is a report of a successful hunt that bagged 18 elk through the destruction of 3 billion feet of timber (Forest Service 1940). Probably all lower-elevation mixed evergreen forests have been affected by less intense fires in the litter and undergrowth, at least; and most forests of higher elevations have been burned at some time (cf. Leiberg 1900).

#### LITERATURE

There are apparently no published studies of the vegetation of the Klamath Region, except the author's (Whittaker 1954b) earlier account of low-elevation diorite and serpentine vegetation in the Siskiyou Mountains. Brief descriptions of the Klamath Region are given by Harshberger (1911), Peck (1925, 1941), and Munger *et al.* (1926). Jepson (1923-5, 1935), Mason (1927), Peck (1941), and Detling (1948b) have commented on the concentration of narrowly endemic species in this region. Vegetation descriptions of other areas most pertinent to interpretation of the Siskiyou vegetation include Cooper (1922) on the broad-sclerophyll vegetation of California, Munz & Keck (1949, 1950, 1959), Jensen (1947), and Burcham (1957) on California vegetation types, Shreve (1927), Clark (1937), Bowerman (1944), and Sharsmith (1945) on the California Coast Ranges, Baker (1951), Merkle (1951), and Detling (1953, 1954) on the Oregon Coast Ranges, Grinnell & Storer (1924), Klyver (1931), and Oosting & Billings (1943) on the Sierra Nevada, Grinnell *et al.* (1930) on Mt. Lassen and Merriam (1899) and Cooke (1940, 1941,

1955) on Mt. Shasta, Becking (1956) on the Douglas-fir forests of the Northwest, and Hansen (1947) on northwestern vegetation and forest history.

The foreign studies most relevant to the present work are two studies dealing with vegetation of serpentine and normal soils and the mafic soils which are intermediate to them (Sočava 1927, Pichi-Sermolli 1948). General characteristics of serpentine vegetation as they appear in the Siskiyou and other parts of the world were reviewed by the author (Whittaker 1954a, 1954b); and this work includes (together with additional European papers cited by Novák 1923, Pichi-Sermolli 1948, and Rune 1953) a bibliography of world literature on serpentine vegetation. Citations which should be added to it are discussions of Balkan serpentine by Beck (1901) and Adamović (1909), an account of grass and herb communities on serpentine in an area of heath in Shetland (West 1912), descriptions of grassland and pine communities on serpentine in Hungary (Soó 1934, Zólyomi 1936), mention of the effect of gabbro in Greenland by Böcher (1933:13), and observations in Switzerland by Lüdi (1937) and in the California Coast Ranges by Sharsmith (1945). The extensive recent literature includes material on serpentine vegetation in Germany (Gauckler 1954) and Austria (Eggler 1954), Bosnia and Serbia (Ritter-Studnička 1953, 1956, Pavlović 1953, 1955, Krause & Ludwig 1956, 1957, Krause & Klement 1958), Scandinavia (Knaben 1952, Rune 1954b, 1954c, Kotilainen & Seivala 1954), Italy (Gismondi 1953), Cuba (Smith 1954), New Caledonia (Baumann-Bodenheim 1956), Japan (Yamanaka 1954, 1955, 1956, 1957, Hattori 1955, Taniguti 1958), Great Britain (Steele 1955, Coombe & Frost 1956a, 1956b, Spence 1957), Quebec, (Rune 1954a), and California (McMillan 1956). The basis of serpentine infertility has been discussed by Hunter & Vergnano (1952), Vergnano (1953a, 1953b), Minguzzi & Vergnano (1953), Martin *et al.* (1953), Walker (1954), Kruekeberg (1954), Walker *et al.* (1955), Croke (1956), Tadros (1957), and Krause (1958).

Taxonomic references used included Jepson (1923-5), Peck (1941), McMinn & Maino (1937), McMinn (1939), and Abrams (1940-51). Of these Peck (1941) applies most directly to the very localized flora of special parent materials in southwestern Oregon, where much of the study was carried out. Most plant names are in the form given in Peck's manual; names not included in it, or given here in a different form, are accompanied by authors' names where first mentioned. The more recent manual of Munz & Keck (1959) also includes most of the flora of the study areas.

## II. PROCEDURE

### STUDY AREAS

The quantitative part of this study deals with relations of plant populations, vegetation patterns, and floras to: (1) topographic moisture gradients from ravines to south-facing slopes, (2) elevation, on a

more typical soil parent-material in the central Siskiyou Mountains, (3) the parent-material series from diorite through gabbro to serpentine, in the central Siskiyou Mountains, and (4) the climatic gradient from humid-maritime to drier and more continental climates, from the Pacific Coast inland along the California-Oregon border. Within each elevation belt, parent material, and location along the maritime-continental gradient, samples were taken to represent the topographic moisture gradient. The study is based primarily on the comparison, not of individual communities or community-types, but of moisture-gradient patterns of vegetation as these change in relation to elevation, parent material, and the east-west climatic gradient.

The area of most intensive study was in the quartz diorite mountains lying behind Oregon Caves National Monument and including Grayback Mountain. This and the other study areas in the central Siskiyou may be reached by side roads leading from the series of villages (Kerby, Selma, Cave Junction, and O'Brien) along U. S. Highway 199 in the Illinois Valley in southernmost Oregon, back into the mountains east and west of the valley. The diorite area is best reached from the Oregon Caves, at the end of a road leading from Cave Junction, and a branch from this road up Grayback Creek. About 290 vegetation samples, from elevations between 550 and 2100 m, were taken from this area in the summer of 1949.

Study of effects of parent material was made possible by the existence, across the Illinois Valley, 27 km west and 52 km northwest from the diorite area, of extensive outcrops of serpentine and gabbro. These three rocks are part of a major gradient in characteristics of parent materials, represented by the sequence of intrusive, igneous rocks from acid or felsic granite, through intermediate diorite, to basic or mafic gabbro, and ultrabasic or ultramafic serpentine. No granite was available for study close to the other areas. The main area of serpentine studied is accessible on the historic and scenic Wimer Road leading southwest from O'Brien across Oregon Mountain, and other side roads leading in to Rough-and-Ready Creek, Tennessee Mountain, and Eight-Dollar Mountain. The gabbro area of York Butte is accessible by a trail to York and Panther Creeks from the end of a minor road leading west from Selma to Oak Flat. The serpentine sampling was carried out in the summers of 1949 and 1950, the gabbro sampling in the summers of 1950 and 1951. These serpentine and gabbro areas are low mountains, mostly not extending above the level of the Klamath peneplain (about 1200 m). The serpentine samples from this area were supplemented with samples from various other, smaller outcrops from all elevations in different parts of the Siskiyou Mountains.

For the study of vegetational gradation from the coast inland, more limited sample series were taken at low elevations on more typical parent-materials in six areas from coastal redwood forest inland to an in-

terior valley. Locations of these areas and their vegetation will be described in Part IV. Limited series of vegetation samples were taken also from a number of other parent materials, mainly metavolcanic rocks, marble, slate, argillite, and quartzite in the Oregon Caves area, from high-elevation forests in other areas of the Siskiyou, mainly near Ashland Peak and Preston Peak, and from successional communities. The study as a whole is based on 470 formal vegetation samples, of the type to be described, and supplementary field notes and plant collections.

#### VEGETATION SAMPLES AND SOIL DATA

As the basis of the gradient analysis 60 vegetation samples, representing the full range of moisture-gradient conditions within elevation belts of 1000 ft or 300 m, were sought from each of the three rock types at low elevations, and from all elevation belts on diorite. Within a given area of relatively undisturbed vegetation, the author and field assistant walked over the mountain surface without set plan, but usually either following a contour line or ascending a slope vertically. In the former case samples were taken from each new site or slope exposure which seemed favorable for sampling; in the latter case samples were taken at 200-ft (61 m) intervals of elevation. In either case actual location of samples was subjectively chosen—only stands were sampled which seemed of sufficient area and homogeneity and in reasonably undisturbed condition. After 40 of the 60 samples for an elevation belt were taken, the last 20 samples were, if necessary, selected to obtain a reasonably even representation of the different types of topographic sites.

Vegetation samples were based upon a 50-m steel tape, normally laid out perpendicular to the contour lines. All tree stems were recorded by diameters in a strip extending 10 m on each side of the tape. This tenth-hectare sample was supplemented by an additional tenth hectare between 10 and 20 m on each side of the tape, when stands were open or highly mixed, but sufficiently homogeneous to permit such expansion of the sample. Tree seedlings, shrubs, and herbs were counted in 25 one-meter-square quadrats; these quadrats were the alternate square meters along one side of the 50-m tape. To provide density as well as frequency information, an effort was made in all cases to count individual plants in the square meters, even though such counts have limited meaning for some plant species. When additional information on shrub or seedling populations was desired, a count of individual plants was made in a strip 5 m on each side of the tape. In stands with sparse herb growth the herb-layer samples were sometimes expanded to 50 sq m along the tape; and in all samples species observed outside the quadrats were recorded. Coverages were determined by recording the presence or absence of herb and shrub (and in more open stands, tree) cover at the 100 points which marked the corners of the 25 sq m undergrowth quadrats. Location and

environment, and evidence on fire-history were also recorded.

The most extensive work in gradient analysis in this country, apart from the author's, has been that of the Wisconsin group (Cottam & Curtis 1949, 1955, 1956, Curtis & McIntosh 1951, Brown & Curtis 1952, Hale 1955, Culbertson 1955, Curtis 1959), using forest samples based on random pairs of tree stems from relatively large areas of more level terrain. The type of sample developed by the author for the present study is adapted to mountain topography, where a sample concentrated within a more limited area is needed. For the present study the sample based on the 50-m steel tape was considered effective, reasonably rapid, and easily adapted to the variety of vegetation types studied.

An effort was made to collect herbarium specimens of all species dealt with in the study in sufficient numbers to represent different habitats in which the species occurred. The herbarium collection was determined, except for some groups sent to other specialists, by M. Ownbey and A. Cronquist; and the voucher specimens of mature plants were placed in the Herbarium of Washington State University.

Soil samples were collected from 15 stations, 5 from different topographic situations within each rock-type, to compare inorganic nutrient conditions in soils developed from the three parent materials. Analyses were carried out in the soils laboratory at Washington State University; a summary of the results is given in Table 2. The "xeromorphic" char-

TABLE 2. Soil analyses for three parent materials at low elevations in the central Siskiyou Mountains. Values are averages of 5 samples representing different topographic situations on each parent material.

	Quartz diorite	Olivine gabbro	Serpentine
Cation exchangeable capacity, m.e./100g. . . . .	21.7	31.8	21.2
Exchangeable cations, m.e./100g: Calcium. . . . .	9.8	7.9	3.3
Magnesium. . . . .	2.6	2.6	13.0
Potassium. . . . .	0.56	0.48	0.12
Sodium. . . . .	0.29	0.28	0.30
Hydrogen. . . . .	15.3	22.7	9.5
Soil Acidity (pH). . . . .	5.8	6.0	6.5

acter of serpentine vegetation (Whittaker 1954b) suggested to the author the desirability of comparing levels of available soil moisture in soils of the serpentine and diorite areas. On two occasions, in 1949 and 1951, series of soil samples were taken from different topographic sites in the two areas to determine moisture content by drying at 105°C. No significant differences between the two areas were established.

#### ARRANGEMENT OF SAMPLES IN TRANSECTS

The study of Siskiyou vegetation patterns is based on the premise that within each parent material, at



a given elevation in a limited area, one major environmental gradient is of such preponderant effect in determining differences of stable vegetation that other environmental differences may be treated as secondary to it. This gradient is the topographic "moisture gradient" leading from most mesic sites of ravines, through lower, or sheltered, mesic slopes, open north-facing and intermediate (east- and west-facing) slopes to open south- and southwest-facing xeric slopes. Along this gradient, the moisture conditions affecting plants undoubtedly change, but also physiognomy of the vegetation, and other factors of soil and climate, change. The "moisture gradient" is by no means simply a gradient of moisture, and it is not a factor gradient in the usual sense; it is a gradient of whole environmental complexes, a "complex-gradient" (Whittaker 1954e, 1956). It can never be assumed that moisture itself is the cause of an observed species distribution. The study is based, not upon any such assumption, but on accepting the complex-gradient as given, as a basis for ordering samples into transects and comparing vegetation patterns between different parent materials, elevations, and climates.

Since the moisture gradient is not subject to direct measurement in the conditions of this study, other means of arranging samples in sequence along the gradient must be sought. Techniques for ordering samples should, ideally, accomplish two things: (1) They should express, in an effective and sensitive manner, the relative positions of samples along the gradient in question. (2) They should indicate which samples are deviant, departing from the main body of samples along gradients of environment (or disturbance) other than that being studied, gradients which also may be subject to later study (cf. Bray & Curtis 1957). Formal statistical techniques may be adapted to ordering of samples and expression of their directions of interrelation (Goodall 1954a, Hughes & Lindley 1955). In the present study, however, the author has experimented with three less formal, quantitative but nonstatistical, approaches to sample arrangement or "ordination" (Goodall 1954b, *Ordnung* of Ramensky 1930).

The first technique was based directly on topographic relations of sites, and 10 types or groups of sites from most mesic to most xeric: (1) deeper ravines with flowing streams, (2) shallower or more open draws without streams, (3) lower, sheltered slopes, (4) open N-, NE-, and NNE-facing slopes, (5) open ENE and NNW slopes, (6) open E and NW slopes, (7) open ESE and WNW slopes, (8) open SE and W slopes, (9) open SSE and WSW slopes, and (10) open S, SW, and SSW slopes. Samples were grouped by these, into *composite topographic transects* for each elevation belt and parent material.

Topographic position alone is a relatively crude approach to moisture conditions of site. Over-all relations of most plant species to the moisture gradient

are effectively shown by the composite topographic transects, however; and the distributional relations thus indicated were the basis of the second ordination technique, the *composite weighted-average transects*. Species were grouped by the locations of their modes, or maximum population levels, along the gradient, as: (1) Mesic—centered in step 1 or 2, (2) Submesic—in steps 3 to 5, (3) Subxeric—in steps 6 to 8, and (4) Xeric—in steps 9 and 10 of the transect. Lists of species thus classified were prepared for each parent material and elevation belt and used as "ecological groups" (Ellenberg 1948, Whittaker 1954e, 1956) for the ordering of samples in that transect. Population measurements for species were multiplied by weights (the numbers of the ecological groups above); and the total of weighted values was divided by the unweighted total, in the weighted-average technique which was developed independently by Ellenberg (1948, 1950, 1952), Whittaker (1951, 1954e, 1956), Curtis & McIntosh (1951), and Rowe (1956). Bimodal species and those for which the composite topographic transect provided no significant indication of moisture-gradient relations were excluded from the computations.

Tree-stratum and undergrowth weighted averages were computed separately; the values used for the tree stratum were numbers of stems 1 cm dbh or over per 0.1 ha, for the undergrowth numbers of apparent

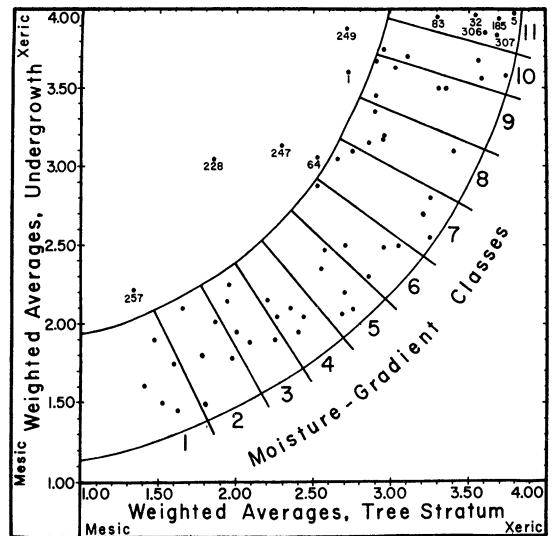


FIG. 2. Weighted-average technique for sample ordination along the moisture gradient. Low-elevation samples from quartz diorite are plotted by weighted averages for both undergrowth and tree stratum, and grouped in 10 classes, or gradient-steps, along the moisture gradient. In this and Fig. 3, numbered samples outside the 10 transect steps are "deviant" from the main body of samples for reasons of parent material, elevation, geographic location, or disturbance. Samples in transect step 11 are sclerophyll stands without *Pseudotsuga*, produced by fires on open south slopes, and more strongly xeric in composition than mature sclerophyll-*Pseudotsuga* stands of comparable sites.

plant individuals per 25 sq m. Fig. 2 illustrates the scatter-diagram which results when stands are plotted by weighted averages of the tree stratum on one axis, of the undergrowth on the other. The two values are necessarily correlated; a curvilinear relation such as illustrated results from the manner in which species are assigned to ecological groups. The oblique axis of the scatter-diagram was taken as the best indicator of relative position along the gradient; and in each case 10 segments of the scatter-figure containing 5-7 samples each were marked off, to provide the 10 steps of the transects. Sample deviance is sometimes expressed in wide departure from the axis of the scatter-figure, as indicated by the numbered samples and legend of Fig. 2.

With deviant samples eliminated by this means and judgment, the remaining 50 were grouped into 10 sets of 5 each. Within each set, tree and undergrowth populations were tabulated for areas of 0.5 hectare and 125 sq m, and coverages were averaged. Tree populations were also tabulated separately above and below arbitrary size limits set to distinguish canopy and smaller trees. Compiled tabulations for undergrowth included, for each species in each step of the transect, constancy, frequency, and density; from the data, presence, abundance, and an indication of contagion (Whitford 1949) could also be obtained.

The third series of transects, the *composite sample-comparison transects*, were based on measurement of percentage similarity of samples (see Part VI). If a stand at one extreme of the gradient is taken as a standard, then the degree to which other stands differ from it is in part an expression of their relative distances from it along the gradient. For a more sensitive expression of stand position, all samples of a transect were compared by undergrowth densities with three standards (each an average of 5 stands), (1) most mesic ravines, (2) intermediate, E-facing slopes, and (3) most xeric, S-, SW-, SSW-facing slopes. The resulting percentage similarities for a given stand were weighted from 1 to 3, and the weighted total divided by the unweighted total. The quotient, on the abscissa of Fig. 3, expresses the relation of the stand to the moisture gradient and is used to group the stands into transect steps. The unweighted total, on the ordinate, expresses the affinity of a sample to the main body of sample material as represented in the three comparison standards; low values provide an effective means of recognizing deviant samples.

#### EVALUATION OF TRANSECT TECHNIQUES

The three types of transects do not give equally satisfactory results, and none gave results as satisfactory as those of the weighted-average technique in the Great Smoky Mountains (Whittaker 1956). The lower sensitivity of weighted averages as moisture-gradient indicators in the Siskiyou is believed to result from the smaller extent of vegetational change along the moisture gradient (see Part VI) and

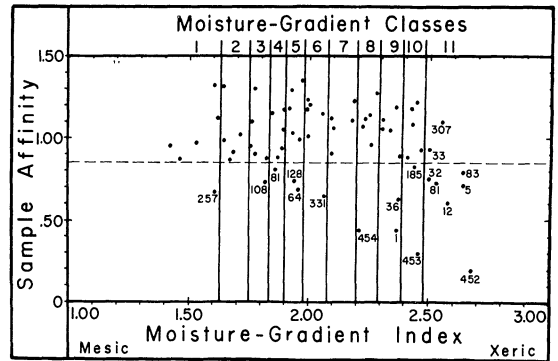


FIG. 3. Sample ordination by comparison with standards. Low-elevation vegetation samples from quartz diorite are plotted by moisture-gradient index (a weighted comparison with samples representing mesic ravines, intermediate open east slopes, and xeric south slopes) and by sample affinity (total of percentage similarities with these three comparison standards, as a measure of floristic consistency with the main body of transect samples from diorite). Samples are grouped into 10 classes, or transect steps, by position along the moisture-gradient index. Samples with affinities less than 0.85 are considered deviant from the main group of samples from low elevations on diorite.

the greater stand-to-stand irregularity resulting from fire. Quantitative indications of relative effectiveness of different techniques of stand ordination are possible, on the basis of certain assumptions about species distributions. It may be assumed, for example, that the more effective the sample ordination, the more each species distribution will be concentrated in part of the transect. Dispersions, or other indications of relative spread of species populations in the transects, may be used as an indication of effectiveness of the ordination technique. Or, it may be assumed that the more effectively is the natural distributional curve of the species represented in the transect, the less will be the irregular, up-and-down difference of population measurements for that species in successive steps of the transect.

In application to the Siskiyou material, lists of species were selected for diorite, gabbro, and serpentine, with the requirements that each species have relatively high population levels for significance of results, and have a distribution extending through several but not all 10 steps of the transects. The number of steps through which a species population extended was then taken as an indication of dispersion or spread; and these values were averaged for the species used to compare transects on a given soil. The sums of signless differences between successive density values in steps of transects for the same species, also averaged for these sets of species, provided an indication of relative smoothness *vs.* irregularity of the population curves in the transects. In each case, higher values indicate less effective sample ordination. The values obtained for relative spread

of species distributions in the topographic, weighted-average, and sample-comparison transects were: on diorite—8.1, 7.9, 8.2; on gabbro—8.3, 7.7, 8.0; on serpentine—8.7, 7.2, 7.6. Corresponding values for relative irregularities of species distributions in the transects were: on diorite—32.0, 20.7, 23.0; on gabbro—17.6, 15.0, 20.0; on serpentine—34.9, 32.2, 34.7.

TRANSECT TABLES

The main body of transect data for the central Siskiyou Mountains are presented in the following tables, considerably compressed for publication. Distributions of tree, shrub, and herb species in relation to the moisture gradient at low elevations on diorite, gabbro, and serpentine are given in Tables 3 to 11.

TABLE 3. Distributions of trees in a moisture-gradient transect for low elevations on quartz diorite in the central Siskiyou Mountains. Based on 50 stand samples of 0.1 or 0.2 hectares each from elevations between 2000 and 3000 ft (610-915 m) arranged in 10 transect steps of 5 samples each. All values in transect steps are numbers of stems over 1 cm dbh (i.e. from the 0.5-1.5 in class up) or, where indicated, 8 in (20 cm) or 15 in (37 cm) dbh or larger in 0.5 hectare. Transect constancy is the per cent of 50 samples, 0.1 hectare each, in the transect in which the species occurred as a tree over 1 cm dbh.

Transect step	Sites										Transect Constancy	
	Mesic	1	2	3	4	5	6	7	8	9		Xeric
<b>Conifers</b>												
<i>Chamaecyparis lawsoniana</i> . . . . .	102	75		2								22
15 in (37cm) dbh/ and over	27	29										
<i>Pseudotsuga menziesii</i> . . . . .	128	96	153	107	79	78	63	50	86	44		98
15" and over . . . . .	41	46	50	59	48	54	50	31	42	18		
<i>Pinus lambertiana</i> . . . . .	1	1	1	5	2	5	6	3	8	6		44
15" and over . . . . .				1	2	1	6	2	5	1		
<i>Taxus brevifolia</i> . . . . .	63	53	26	4			1					24
<i>Abies concolor</i> . . . . .	1	1	2		2							12
<i>Libocedrus decurrens</i> . . . . .				1						12		4
<i>Pinus ponderosa</i> . . . . .											1	2
<b>Sclerophylls</b>												
<i>Lithocarpus densiflora</i> . . . . .	77	152	483	413	493	473	361	442	399	669		100
8 in (20cm) dbh/ and over . . . . .	11	6	9	3	6	13	18	14	14	34		
<i>Quercus chrysolepis</i> . . . . .	6	2	87	86	55	102	194	230	325	209		78
8" and over . . . . .			2	7	21	34	24	12	18			
<i>Arbutus menziesii</i> . . . . .	2	2	27	28	50	75	93	124	79	322		68
8" and over . . . . .	1	1	4	9	17	40	27	48	13	21		
<i>Castanopsis chrysophylla</i> . . . . .	23	34	89	79	44	52	11	20	43	162		74
8" and over . . . . .	1	2		1	3	2	1	3		1		
<b>Deciduous trees</b>												
<i>Alnus rubra</i> . . . . .	8	2										4
<i>Alnus rhombifolia</i> . . . . .	9	1										4
<i>Acer circinatum</i> . . . . .	110	53	185	9	12	2						26
<i>Acer macrophyllum</i> . . . . .	13	11	14	1	1	4	5					32
<i>Salix</i> sp. . . . .	3	1	6	1	5	1	1					18
<i>Cornus nuttallii</i> . . . . .	35	11	26	34	18	6	8	9	12	7		58
<i>Corylus rostrata</i> var. <i>californica</i> . . . . .	141	146	58	34	16		11	2	2	4		52
<i>Quercus kelloggii</i> . . . . .			3	1		1	1	7	7			18
<i>Amelanchier florida</i> . . . . .			6								3	4
<b>Arborescent shrubs</b>												
<i>Philadelphus lewisii</i> . . . . .	2		2									4
<i>Rhododendron californicum</i> . . . . .	15	4										4
<i>Holodiscus discolor</i> . . . . .	9	8	10	8	4	9	14					32
<i>Rhus diversiloba</i> . . . . .										2		2

These tables are intended to permit direct comparison of distributional relations of species, stand compositions, and vegetation patterns on the three parent materials as the basis of the discussions which follow. Only frequency values for undergrowth species can be given here from the density-frequency-constancy tabulations of the original transects; constancy and density values for the transects as wholes are summarized in the last columns. Distributional relations to elevation on diorite were approached through a series of transects for different elevation belts. In the condensed form given here in Tables 12 to 14 only average population values for whole transects are given for the various elevation belts—density and constancy values of trees and per mille frequencies of shrubs and herbs. Distributions of grasses, sedges, and rushes in relation to both parent materials and elevation are summarized in Table 15.

TABLE 4. Distributions of shrubs and seedlings in a moisture-gradient transect for low elevations on diorite in the central Siskiyou Mountains. Based on 50 undergrowth samples, each of 25, 1-m<sup>2</sup> quadrats, for elevations between 2000 and 3000 ft (610-915 m) arranged in 10 transect steps of 5 samples each. All values in transect steps are per cent frequencies in 100, 1-m<sup>2</sup> quadrats (based on 125, 1-m<sup>2</sup> quadrats per transect step). Transect constancy is the per cent of 50 samples, each of 25, 1-m<sup>2</sup> quadrats, in the transect in which the species occurred; total density is the number of apparent individuals in an area of 1000 sq m, based on density counts in 1250, 1-m<sup>2</sup> quadrats in the 10 steps of the transect. Observed presence in samples, outside the first 25, 1-m<sup>2</sup> quadrats, is indicated by 'x.'

Transect step	Sites										Transect Constancy	Total Density	
	Mesic	1	2	3	4	5	6	7	8	9			Xeric
<b>Conifer seedlings</b>													
<i>Chamaecyparis lawsoniana</i> . . . . .	2	2										6	5
<i>Taxus brevifolia</i> . . . . .	7	2	2	2								14	15
<i>Pseudotsuga menziesii</i> . . . . .		2	6					4	9	3	10	12	8
<i>Pinus lambertiana</i> . . . . .							2	2			1	1	1
<i>Libocedrus decurrens</i> . . . . .											8		2
<b>Broadleaf tree seedlings</b>													
<i>Acer circinatum</i> . . . . .	5	2	6	2									18
<i>Amelanchier florida</i> . . . . .	1	2	2										6
<i>Cornus nuttallii</i> . . . . .	1		1	1	1								8
<i>Corylus rostrata</i> var. <i>californica</i> . . . . .	1	9	7	5	3	1	3				1		32
<i>Castanopsis chrysophylla</i> . . . . .	2	2	6	8	4	1						2	6
<i>Lithocarpus densiflora</i> . . . . .	31	18	27	26	39	28	30	21	34	30	100	374	
<i>Quercus chrysolepis</i> . . . . .	3	8	6	13	5	20	21	14	14	14	64	148	
<i>Arbutus menziesii</i> . . . . .										1	1	4	2
<b>Shrubs</b>													
<i>Rhododendron californicum</i> . . . . .	2	1										6	4
<i>Vaccinium parvifolium</i> . . . . .	3	6		1	1							14	15
<i>Gaultheria shallon</i> . . . . .	31	32	19	25	19	10		8				32	537
<i>Rubus parviflorus</i> . . . . .	1	4		2	1				1	2		16	14
<i>Berberis nervosa</i> . . . . .	42	45	21	26	25	20	14	9	9			76	632
<i>Berberis pumila</i> . . . . .	2	1						10	13			2	16
<i>Rubus vitifolius</i> . . . . .	27	26	6	7	5	20	10	11	19	32	70	271	
<i>Rosa gymnocarpa</i> . . . . .	8	14	22	32	24	38	27	30	37	43	98	497	
<i>Rhus diversiloba</i> . . . . .		6	12	15	16	15	49	37	31	38	64	611	
<i>Holodiscus discolor</i> . . . . .			1		2			2				10	6
<i>Pachystima myrsinites</i> . . . . .				1						1		4	2
<i>Symphoricarpos hesperius</i> . . . . .			3	9			1	1	5			10	26
<i>Ceanothus integerrimus</i> . . . . .										x		0	0



TABLE 7. Distributions (frequencies) of shrubs and seedlings in a moisture-gradient transect for low elevations on olivine gabbro in the central Siskiyou Mountains. For basis of data see heading of Table 4.

Table 7: Distributions of shrubs and seedlings in a moisture-gradient transect. Columns include Sites, Mesic (1-10), Xeric, Transect Constancy, and Total Density.

TABLE 8. Distributions (frequencies) of herbs in a moisture-gradient transect for low elevations on olivine gabbro in the central Siskiyou Mountains. For basis of data see heading of Table 4.

Table 8: Distributions of herbs in a moisture-gradient transect. Columns include Sites, Mesic (1-10), Xeric, Transect Constancy, and Total Density.

(which could be excluded from the weighted averages) are thought to be the reason for its relative ineffectiveness in the Siskiyou transects.

III. VEGETATION DESCRIPTION

LOW ELEVATIONS ON DIORITE

In general character, the vegetation of low elevations on diorite is a forest of two tree strata—an upper stratum of evergreen needle-leaved trees and a lower one of sclerophyllous broad-leaved trees—forming together a closed canopy. In ravines, dominance of the upper tree stratum is shared by Pseudotsuga menziesii and Chamaecyparis lawsoniana. Three deciduous broadleaf trees—Acer macrophyllum, Alnus rubra Bong. (A. oregona Nutt), and A. rhombifolia—occur in small numbers among the larger stems. Among the smaller trees, two deciduous species, Cory-





TABLE 12. Distributions of trees in relation to elevation on quartz diorite in the central Siskiyou Mountains. Based on 6 moisture-gradient transects of different elevation belts; transects nos. 1 to 9 each included 50 stand samples of 0.1 or 0.2 hectare each in 10 transect steps, transect no. 11 included 16, 0.1 or 0.2 hectare samples in 8 transect steps. Density values are numbers of stems over 1 cm dbh (i.e. from the 0.5-1.5 in class up) or, where indicated, 8 in (20 cm) or 15 in (37 cm) or over in areas of 5.0 hectare per transect. Constancy values are per cents of the 50 (or 16) samples, 0.1 hectare each, of the transect in which the species occurred as a tree of the 1-in or larger diameter class.

Transect no. Elevations in feet Elevations in meters	1 1500-2500 460-670		3 2500-3500 670-1070		5 3500-4500 1070-1370		7 4500-5500 1370-1680		9 5500-6300 1680-1920		11 6300-7000 1920-2140	
	Dens.	Cons.	Dens.	Cons.	Dens.	Cons.	Dens.	Cons.	Dens.	Cons.	Dens.	Cons.
Conifers												
<i>Chamaecyparis lawsoniana</i> .....	93	13	499	46	439	54	370	32				
15'' and over.....	42		167		160		121					
<i>Taxus brevifolia</i> .....	215	16	185	26	10	12	54	12				
<i>Pinus ponderosa</i> .....	1	2					3	2				
<i>Pseudotsuga menziesii</i> .....	904	96	767	92	674	100	435	90	5	10		
15'' and over.....	378		506		604		330		4			
<i>Labocedrus decurrens</i> .....	1	2	15	6	8	6	72	24	11	12		
15'' and over.....			2		2		37		6			
<i>Abies concolor</i> .....	5	10	215	40	905	100	1602	100	1241	58		
15'' and over.....			11		143		477		404			
<i>Pinus lambertiana</i> .....	35	42	20	22	7	12	29	8	1	2		
15'' and over.....	14		13		7		9					
<i>Abies nobilis</i> .....					2	2	71	40	1260	92	2400	100
15'' and over.....					1		22		421		693	
<i>Tsuga mertensiana</i> .....							2	2	796	54	1338	75
15'' and over.....									205		368	
<i>Pinus monticola</i> .....									1	2	3	6
Sclerophylls												
<i>Lithocarpus densiflora</i> .....	4236	100	2007	76	54	6						
8'' and over.....	109		66		1							
<i>Quercus chrysolepis</i> .....	1422	90	463	48	59	8						
8'' and over.....	171		57									
<i>Arbutus menziesii</i> .....	856	82	341	56	72	16						
8'' and over.....	135		142		23							
<i>Castanopsis chrysophylla</i> .....	470	82	712	62	339	50	13	6				
8'' and over.....	18		103		24							
Deciduous trees												
<i>Fraxinus oregana</i> .....	4	2										
<i>Cornus nuttallii</i> .....	201	60	48	12								
<i>Quercus kelloggii</i> .....	22	18	11	8								
<i>Acer circinatum</i> .....	642	46	198	22	32	10						
<i>Acer macrophyllum</i> .....	61	24	32	24	17	4	15	8				
<i>Salix</i> sp.....	29	24	2	4	1	2	4	4				
<i>Alnus rubra</i> and <i>A. rhombifolia</i> .....	34	10	23	12	4	2	3	2				
<i>Amelanchier florida</i> .....	25	10	1	2	33	8	3	2				
<i>Corylus rostrata</i> var. <i>californica</i> .....	497	56	246	38	109	12	78	30	4	2		
<i>Acer glabrum</i> var. <i>douglasii</i> .....					14	6	190	24	23	10		
<i>Sorbus americana</i> .....							5	4				
Arborescent shrubs												
<i>Rhus diversiloba</i> .....	2	2										
<i>Philadelphus lewisii</i> .....	8	6										
<i>Rhododendron occidentale</i> .....	8	2										
<i>Ceanothus integerrimus</i> .....	4	4	15	10								
<i>Vaccinium parvifolium</i> .....	3	2	1	2	1	2						
<i>Holodiscus discolor</i> .....	171	38	33	20	55	18	53	18	5	2		
<i>Rhododendron californicum</i> .....			290	24	318	18	164	10				
<i>Quercus sadleriana</i> .....			1	2	24	6	17	2				
<i>Cornus stolonifera</i> .....					3	2	1	2				
<i>Lonicera conjugalis</i> .....							3	2	x	0		
<i>Ceanothus velutinus</i> .....							3	2				
<i>Prunus emarginata</i> .....									1	2		



TABLE 13. Distributions of shrubs and seedlings in relation to elevation on quartz diorite in the central Siskiyou Mountains. Based on 6 moisture-gradient transects for different elevation belts; transects nos. 1 to 9 each included 50 undergrowth samples of 25, 1-m<sup>2</sup> quadrats each in 10 transect steps, transect no. 11 included 16 samples of the same size in 8 transect steps. All values are per mille frequencies in transects (the number of 1-m<sup>2</sup> quadrats, among 1000 such quadrats, in which a species was observed, based on 1250, 1-m<sup>2</sup> quadrats in the ten steps of transects 1 to 9, 400, 1-m<sup>2</sup> quadrats in transect no. 11).<sup>1</sup> Observed presence in one or more samples of the transect, outside the 25 m<sup>2</sup> samples, is indicated by "x."

Transect no. Elevation in feet Elevation in meters	1 1500- 2500 460- 760	3 2500- 3500 760- 1070	5 3500- 4500 1070- 1370	7 4500- 5500 1370- 1680	9 5500- 6300 1680- 1920	11 6300- 7000 1920- 2140
<b>Conifer seedlings</b>						
<i>Chamaecyparis lassoniana</i> ...	2	13	7	9		
<i>Taxus brevifolia</i> .....	12	12	5	5		
<i>Pseudotsuga menziesii</i> .....	64	46	35	18		
<i>Pinus lambertiana</i> .....	7	4	2	1		
<i>Libocedrus decurrens</i> .....	2	11	1	4	2	
<i>Abies concolor</i> .....		7	90	68	28	2
<i>Abies nobilis</i> .....				8	64	100
<i>Tsuga mertensiana</i> .....					18	22
<b>Sclerophyll seedlings</b>						
<i>Lithocarpus densiflora</i> .....	291	174	4			
<i>Arbutus menziesii</i> .....	2		1			
<i>Castanopsis chrysophylla</i> .....	31	43	13	1		
<i>Quercus chrysolepis</i> .....	130	47	3	x	1	
<b>Deciduous tree seedlings</b>						
<i>Cornus nuttallii</i> .....	2	1				
<i>Acer macrophyllum</i> .....	2		9			
<i>Acer circinatum</i> .....	18	10	4	1		
<i>Corylus rostrata</i> var. <i>californica</i> .....	36	14	5	2		
<i>Amelanchier florida</i> .....	6	2	4	2	4	
<i>Acer glabrum</i> var. <i>douglasii</i> .....			1	2		
<b>Shrubs</b>						
<i>Rhododendron occidentale</i> .....	1					
<i>Symphoricarpos hesperius</i> .....	32	6	1			
<i>Berberis pumila</i> .....	17	15	2			
<i>Gaultheria shallon</i> .....	132	263	77			
<i>Berberis nervosa</i> .....	197	264	455	160		
<i>Pachystima myrsinites</i> .....	6	9	13	1		
<i>Rhus diversiloba</i> .....	226	85	1			
<i>Holodiscus discolor</i> .....	11	2	11	16		
<i>Symphoricarpos rivularis</i> .....	8	1	4	32	19	
<i>Vaccinium parvifolium</i> .....	14	48	22	1	1	
<i>Rubus vitifolius</i> .....	126	204	177	38	1	
<i>Rosa gymnocarpa</i> .....	273	199	102	126	24	
<i>Rubus parviflorus</i> .....	19	3	2	15	2	
<i>Ceanothus integerrimus</i> .....		x				
<i>Rhododendron californicum</i> .....		65	30	14		
<i>Rubus nivalis</i> .....		8	70	37		
<i>Quercus sadleriana</i> .....		21	22	8	18	
<i>Vaccinium membranaceum</i> .....		1	13	28	8	10
<i>Ribes lacustre</i> .....			2			
<i>Ribes marshallii</i> .....			1	58	211	157
<i>Ribes lobbii</i> .....			x	2		
<i>Cornus stolonifera</i> .....				x		
<i>Lonicera conjugalis</i> .....				x	6	x
<i>Ribes viscosissimum</i> .....				25	36	13
<i>Sambucus racemosa</i> var. <i>californica</i> (Greene) Jeps.....						2

TABLE 14. Distributions of herbs in relation to elevation on quartz diorite in the central Siskiyou Mountains. For basis of data see heading of Table 13.

Transect no. Elevation in feet Elevation in meters	1 1500- 2500 460- 760	3 2500- 3500 760- 1070	5 3500- 4500 1070- 1370	7 4500- 5500 1370- 1680	9 5500- 6300 1680- 1920	11 6300- 7000 1920- 2140
<i>Cynoglossum grande</i> .....	3					
<i>Claytonia perfoliata</i> .....	1					
<i>Epilobium minutum</i> .....	2					
<i>Satureja douglasii</i> .....	2					
<i>Lathyrus pauciflorus</i> .....	6	1				
<i>Cypripedium fasciculatum</i> .....	2	3				
<i>Boynkia elata</i> .....	2	12				
<i>Adiantum pedatum</i> var.						
<i>aleuticum</i> .....	4	3				
<i>Aralia californica</i> .....	4	1				
<i>Lonicera hispidula</i> .....	83	14				
<i>Tauschia kelloggii</i> .....	51	23				
<i>Campanula prenanthoides</i> .....	106	56	7			
<i>Madia nuttalliana</i> .....	22	7	3			
<i>Boschniakia hookeri</i> .....	2	2	2			
<i>Allotropa virgata</i> .....	1	2	1			
<i>Whipplea modesta</i> .....	140	35	212	21		
<i>Linnaea borealis</i> .....	179	128	96	30		
<i>Asarum caudatum</i> .....	1	1	8	17		
<i>Tolmiea menziesii</i> .....	x		5	2		
<i>Collomia heterophylla</i> .....	22	6	13	4		
<i>Psoralea physodes</i> .....	28	1	1	12		
<i>Cephalanthera austriana</i> .....	x	x	1	2		
<i>Listera caurina</i> .....	2	1	9	1		
<i>Anemone deltoidea</i> .....	23	24	126	163	62	
<i>Achlys triphylla</i> .....	193	307	805	542	128	
<i>Trientalis latifolia</i> .....	161	77	205	296	37	
<i>Pteridium aquilinum</i> var.						
<i>pubescens</i> .....	141	163	53	63	14	
<i>Viola sempervirens</i> .....	57	154	248	78	4	
<i>Apocynum pumilum</i> .....	102	66	58	68	45	
<i>Senecio bolanderi</i> .....	105	12	40	62	1	
<i>Tiarella unifoliata</i> .....	5	27	78	197	12	
<i>Galium triflorum</i> .....	34	45	165	190	64	
<i>Goodyearia decipiens</i> .....	38	40	91	49	1	
<i>Adenocaulon bicolor</i> .....	34	79	289	268	14	
<i>Vancouveria hezandra</i> .....	23	11	140	311	50	
<i>Disporum hookeri</i> .....	48	79	152	307	7	
<i>Iris chrysophylla</i> .....	10	14	8	20	11	
<i>Coptis laciniata</i> .....	5	32	6		11	
<i>Asarum hartwegii</i> .....	18	14	17	58	6	
<i>Clintonia uniflora</i> .....	5	21	81	172	15	
<i>Habenaria unalascensis</i> .....	1			x		
<i>Smilacina racemosa</i> .....	47	14	11	21	51	22
<i>Polystichum munitum</i> .....	88	53	42	17		2
<i>Trillium ovatum</i> .....	38	48	62	126	50	10
<i>Chimaphila menziesii</i> .....	7	42	46	56	66	38
<i>Chimaphila umbellata</i> var.						
<i>occidentalis</i> .....	96	160	258	92	12	2
<i>Pyrola picta</i> .....	5	4	8	16	55	47
<i>Hieracium albidiflorum</i> .....	93	58	160	172	202	197
<i>Phlox adurgens</i> .....	67	70	181	352	146	65
<i>Campanula scouleri</i> .....	10	29	171	328	204	35
<i>Arenaria macrophylla</i> .....	2		48	183	268	234
<i>Corallorhiza maculata</i> .....	x	9	5	13	5	7
<i>Fragaria vesca</i> var. <i>bracteata</i> .....	6	11	59	102	70	45
<i>Osmorhiza chilensis</i> .....	4	4	110	284	219	82
<i>Equisetum hyemale</i> var.						
<i>californicum</i> .....		2				
<i>Heuchera micrantha</i> .....	1					
<i>Galium bifolium</i> .....	1					
<i>Pleuricospora fimbriolata</i> .....	1					
<i>Cornus canadensis</i> .....	2					
<i>Mitella ovalis</i> .....	14	82				
<i>Listera cordata</i> .....	1	4				
<i>Pyrola uliginosa</i> .....	3	2				
<i>Gaultheria ovatifolia</i> .....	1	1				
<i>Corallorhiza striata</i> .....	x	2		x		
<i>Pyrola bracteata</i> .....	2	x		x		

diorite (see distributional groupings 5 & 6, part V). Important grasses include *Festuca occidentalis* and *F. ovina*, *Melica harfordii*, *Bromus suksdorfii*, and *Trisetum canescens*. The herb stratum on diorite includes a group of non-green vascular plants—*Cepha-*

Table 14 (Cont.)

Transect no.	1	3	5	7	9	11
Elevation in feet	1500-2500	2500-3500	3500-4500	4500-5500	5500-6300	6300-7000
Elevation in meters	460-760	760-1070	1070-1370	1370-1680	1680-1920	1920-2140
<i>Osmorhiza occidentalis</i> . . . . .		2	1		x	
<i>Vicia californica</i> . . . . .		1	32	121	30	
<i>Lathyrus polyphyllus</i> . . . . .		5	74	126	24	
<i>Pyrola secunda</i> . . . . .		1	25	63	122	112
<i>Claytonia spathulata</i> . . . . .		2	7	41	74	2
<i>Smilacina stellata</i> . . . . .		9	94	251	98	5
<i>Prunella vulgaris</i> . . . . .			1			
<i>Lilium columbianum</i> . . . . .			2			
<i>Sarcodes sanguinea</i> . . . . .			1			
<i>Trautvetteria carolinensis</i> (Walt.) Vaill. . . . .			8			
<i>Lotus oblongifolius</i> . . . . .			1			
<i>Mitella caulescens</i> . . . . .			14			
<i>Orobanche uniflora</i> . . . . .			3			
<i>Ranunculus uncinatus</i> var. <i>parviflorus</i> (Torr.) Benth. . . . .			1	1		
<i>Claytonia sibirica</i> L. . . . .			x	5		
<i>Habenaria sparsiflora</i> . . . . .			2	2		
<i>Streptopus amplexifolius</i> . . . . .			x	1		
<i>Circaea alpina</i> var. <i>pacifica</i> . . . . .			22	46		
<i>Athyrum felix-femina</i> . . . . .			12	9		
<i>Lewisia leana</i> . . . . .			2		x	
<i>Actaea spicata</i> . . . . .			2	135	58	
<i>Nemophila parviflora</i> . . . . .			16	37	15	
<i>Rubus lasiococcus</i> . . . . .			2	39	157	130
<i>Dicentra formosa</i> . . . . .			3	5	14	25
<i>Viola glabella</i> . . . . .			39	171	58	
<i>Claytonia parvifolia</i> . . . . .			2	1	12	22
<i>Veratrum insolitum</i> . . . . .			1	3	5	13
<i>Mitella diversifolia</i> . . . . .			1	22	18	5
<i>Corallorhiza mertensiana</i> . . . . .			x	1	6	2
<i>Bojkinia major</i> . . . . .				10		
<i>Heracleum lanatum</i> . . . . .				4		
<i>Listera convallarioides</i> . . . . .				1		
<i>Cardamine breweri</i> . . . . .				2		
<i>Pteropora andromedea</i> . . . . .				1		
<i>Pentstemon anguineus</i> . . . . .				x	4	
<i>Hackelia jessicae</i> . . . . .				5	20	
<i>Monardella odoratissima</i> . . . . .				2	14	
<i>Agastache urticaefolia</i> . . . . .				2	11	
<i>Aquilegia formosa</i> . . . . .				1	9	7
<i>Senecio triangularis</i> . . . . .				23	43	22
<i>Polygonum phytolaccaceaeifolium</i> . . . . .				4	2	5
<i>Viola sheltonii</i> . . . . .				2	20	13
<i>Arnica latifolia</i> . . . . .				79	365	253
<i>Phacelia magellanica</i> . . . . .				15	42	22
<i>Eriogonum aliciae</i> . . . . .				2	52	13
<i>Valeriana sitchensis</i> ssp. <i>sitchensis</i> . . . . .				42	265	308
<i>Angelica arguta</i> . . . . .				1	5	10
<i>Hydrophyllum occidentale</i> . . . . .				67	76	10
<i>Mertensia bella</i> . . . . .				2	26	7
<i>Erythronium oregonum</i> and <i>E.</i> <i>grandiflorum</i> . . . . .				1	3	7
<i>Mitella breweri</i> . . . . .				5	39	25
<i>Pentstemon nemorosus</i> . . . . .				2	128	254
<i>Pedicularis racemosa</i> . . . . .				9	90	200
<i>Artemisia douglasiana</i> . . . . .					3	
<i>Epilobium paniculatum</i> . . . . .					6	
<i>Pentstemon tolmiei</i> Hook. . . . .					11	
<i>Cryptogramma crispum</i> var. <i>acrostichoides</i> (R. Br.) C. B. Clarke . . . . .					1	
<i>Collinsia parviflora</i> . . . . .					2	
<i>Delphinium sonnei</i> . . . . .					7	2
<i>Saxifraga ferruginea</i> . . . . .					4	10
<i>Pentstemon newberryi</i> . . . . .					2	38
<i>Castilleja miniata</i> . . . . .					2	13
<i>Orogenia fusiformis</i> . . . . .					1	7
<i>Epilobium hornemannii</i> . . . . .					6	18
<i>Viola praemorsa</i> . . . . .					2	5

Table 14 (Cont.)

Transect no.	1	3	5	7	9	11
Elevation in feet	1500-2500	2500-3500	3500-4500	4500-5500	5500-6300	6300-7000
Elevation in meters	460-760	760-1070	1070-1370	1370-1680	1680-1920	1920-2140
<i>Sanicula nevadensis</i> . . . . .					2	7
<i>Anemone quinquefolia</i> . . . . .					1	2
<i>Erysimum capitatum</i> . . . . .					1	7
<i>Sedum oregonense</i> . . . . .					23	10
<i>Aster siskiyouensis</i> . . . . .					85	242
<i>Ligusticum grayi</i> . . . . .					26	42
<i>Lupinus albeaculis</i> . . . . .					10	2
<i>Gayophytum nuttallii</i> . . . . .						2
<i>Castilleja pruinosa</i> . . . . .						2
<i>Eriophyllum lanatum</i> . . . . .						2
<i>Epilobium angustifolium</i> . . . . .						15
<i>Polygonum davisiae</i> . . . . .						25
<i>Calyptridium umbellatum</i> (Torr.) Greene . . . . .						5
<i>Phacelia procera</i> . . . . .						2

*lanthera austinae*, *Allotropia virgata*, *Corallorhiza maculata* and *C. striata*, *Pyrola picta* f. *aphylla* (Smith) Camp, *Pleuricospora fimbriolata*, and *Boschniakia hookeri*—which are rare or absent on the other soils.

In xeric stands (Fig. 4) the coverage of *Pseudotsuga* (and the smaller numbers of *Pinus lambertiana*) is relatively low, generally well below 50%. In most stands *Lithocarpus* is most numerous among smaller stems, but *Arbutus* and *Q. chrysolepis* share dominance with it. *Rosa gymnocarpa* and *Rhus diversiloba* are the principal shrub species, as in subxeric sites; these and the prostrate *Rubus vitifolius* are often the only shrub species present, apart from tree seedlings. Shrub coverage averages around 30%, but with tree seedlings making up most of this. Herb coverage is consistently low (1-7%), with *Pteridium aquilinum* var. *pubescens* the major species of the herb stratum (see Table 5, distributional groups 6 and 8).

Stands which are floristically similar to these, but without large trees of *Pseudotsuga* or *P. lambertiana*, occur on some slopes, especially south-facing ones. These stands are considered products of more severe fires, and fire-effects are reflected both in size-distributions of the sclerophyll canopy and in the fact that *Pseudotsuga* is present as seedlings, but absent as a tree.

Some trends along the moisture gradient in low-elevation diorite vegetation have been commented on (Whittaker 1953:49, 1954b). Among the trees, the deciduous broad-leaf growth-form predominates in numbers of stems of all sizes in mesic sites and declines to 1-2% of stems in xeric sites. Character of the canopy changes from evergreen needle-leaf dominance in mesic sites, with relatively small numbers of sclerophylls, to a two-level canopy of *Pseudotsuga* and the sclerophylls in submesic and subxeric sites, to a closed canopy of sclerophylls with an overgrowth of large *Pseudotsuga* in xeric sites. Shrub coverage

TABLE 15. Distributions of grasses and grass-like plants in relation to elevation on quartz diorite (transects 1-11), and in relation to parent-materials at low elevations (transects 1 and 3 on diorite, 18 on olivine gabbro, 15 on serpentine). Observed presence in the samples of a transect is indicated by "x." Per mille frequencies, and densities of apparent individuals, for 1000, 1-m<sup>2</sup> quadrats are given for all grass, sedge, and rush species together, based on 400, 1-m<sup>2</sup> quadrats in transect 11, 1250 quadrats in other transects.

Transect no.	1	3	5	7	9	11	18	15
Elevation in feet	1500-2500	2500-3500	3500-4500	4500-5500	5500-6300	6300-7000	1500-2500	2000-3000
Elevation in meters	460-760	760-1070	1070-1370	1370-1680	1680-1920	1920-2240	460-670	610-915
Parent material	diorite						gabbro serpentine	
<i>Festuca ovina</i> .....	x						x	x
<i>Festuca rubra</i> .....	x							
<i>Melica harfordii</i> .....	x	x					x	
<i>Luzula campestris</i> ....	x	x	x				x	x
<i>Trisetum canescens</i> ...	x	x	x	x			x	x
<i>Bromus suksdorfii</i> ....	x	x	x	x	x			
<i>Melica subulata</i> .....	x	x	x	x	x	x		
<i>Festuca occidentalis</i> ...	x	x	x	x	x	x	x	
<i>Festuca subulata</i> .....	x							
<i>Carex bolanderi</i> .....		x						
<i>Festuca subuliflora</i> ....		x	x	x				
<i>Bromus orcuttianus</i> ....			x					
<i>Carex laeviculmis</i> .....			x	x				
<i>Carex mertensii</i> .....			x	x				
<i>Luzula parviflora</i> ....			x	x				
<i>Pleuropogon refractus</i> ..			x	x				
<i>Glyceria striata</i> .....				x				
<i>Luzula spicata</i> .....				x		x		
<i>Carex tracyi</i> .....					x	x		
<i>Carex rossii</i> .....					x	x		
<i>Trisetum spicatum</i> ....					x	x		
<i>Poa bolanderi</i> .....					x	x		
<i>Juncus parryi</i> .....						x		
<i>Poa nervosa</i> .....						x		
<i>Elymus glaucus</i> .....					x	x		x
<i>Bromus carinatus</i> .....						x		
<i>Juncus ensifolius</i> .....							x	
<i>Festuca californica</i> ....							x	
<i>Carex multicaulis</i> .....							x	
<i>Eriophorum crinigerum</i> ..							x	x
<i>Carex debilisformis</i> ....							x	x
<i>Agrostis hallii</i> .....							x	x
<i>Stipa lemmonii</i> .....							x	
<i>Carex angustior</i> .....								x
<i>Calamagrostis</i>								
<i>koeleroides</i> .....								x
<i>Poa rhizomata</i> .....								x
<i>Melica geyeri</i> .....								x
<i>Bromus breviaristatus</i> ..								x
<i>Danthonia californica</i> ..								x
<i>Koeleria cristata</i> .....								x
<i>Sitanion jubatum</i> .....								x
All graminoid species								
Frequency/1000 m <sup>2</sup> ...	110	96	269	307	304	227	182	728
Density/1000 m <sup>2</sup> ....	269	211	731	789	845	490	451	6066

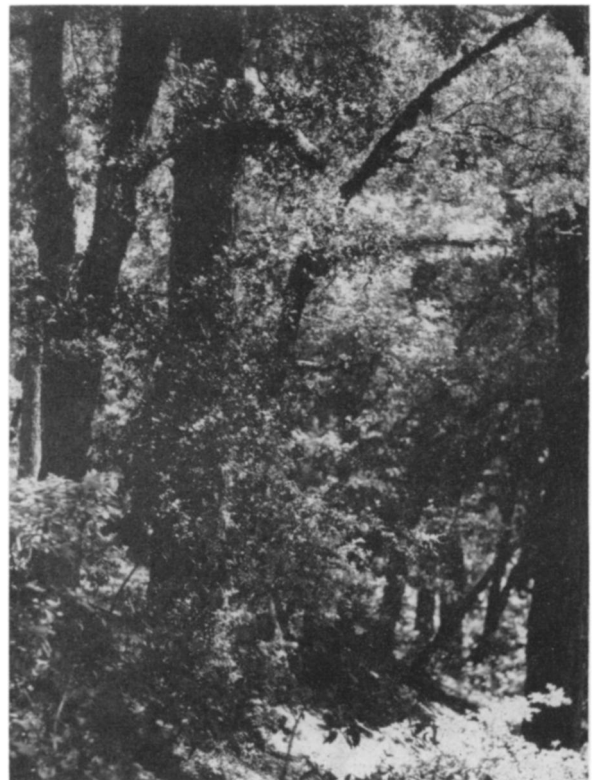


FIG. 4. View within a sclerophyll-Pseudotsuga forest on diorite on an open SE slope, inclination 30°, at 670 m, Oregon Caves area, Siskiyou Mts., Ore. *Pseudotsuga menziesii*, *Quercus chrysolepis*, and few *Lithocarpus densiflora*; *Rhus diversiloba*, *Rosa gymnocarpa*, *Lonicera hispidula*, *Polystichum munitum*, *Hieracium albiflorum*, *Whipplea modesta*. July 19, 1950.

continuum, three community-types are distinguished—Chamaecyparis-Pseudotsuga forest with few sclerophylls and many deciduous stems in mesic sites, Pseudotsuga-sclerophyll stands with two-level canopies in intermediate sites, and sclerophyll-Pseudotsuga stands with quite open growth of conifers in xeric sites.

LOW ELEVATIONS ON GABBRO

The general description of the diorite vegetation as "mixed evergreen forest" can apply also to the gabbro vegetation pattern at low elevations. Apart from over-all physiognomic similarity and the sharing of some species, however, the two vegetation patterns are quite different. The gabbro vegetation is much more open than that on diorite (cf. Figs. 4 and 5). Average densities of large stems of conifers (37 cm dbh and over) were less than half as great on gabbro (8.4 stems/ha vs. 20.5 on diorite); and density of larger sclerophyll stems is much lower on gabbro in more xeric sites. It is consequently possible to stand on one hillside in the gabbro area and look through the canopy to the soil on another, nearby hillside (Fig. 6); in the diorite area one cannot similarly look through the dense evergreen canopies. The undergrowth strata on gabbro are in general of lower cover-

is moderate, averaging 20-35% throughout the transect; herb coverage is low, declining from an average of 12% in mesic to 6% in xeric sites. The whole vegetation pattern, dominated as it is by larger evergreen needle-leaved and smaller evergreen sclerophyll trees, may be described as Mixed Evergreen Forest (Munz & Keck 1949); but the gradual changes along the moisture gradient make mesic and xeric stands very unlike one another. Within this vegetational



FIG. 5. View within a more open *Pinus-Pseudotsuga-sclerophyll* forest on gabbro, on an open east slope, inclination  $35^\circ$ , at 370 m near Panther Creek, Siskiyou Mts., Ore. *Pinus lambertiana*, *Arbutus menziesii*, *Quercus chrysolepis*, *Rhus diversiloba*, *Polygala californica*, *Whipplea modesta*, *Chimaphila umbellata* var. *occidentalis*. July 15, 1951.

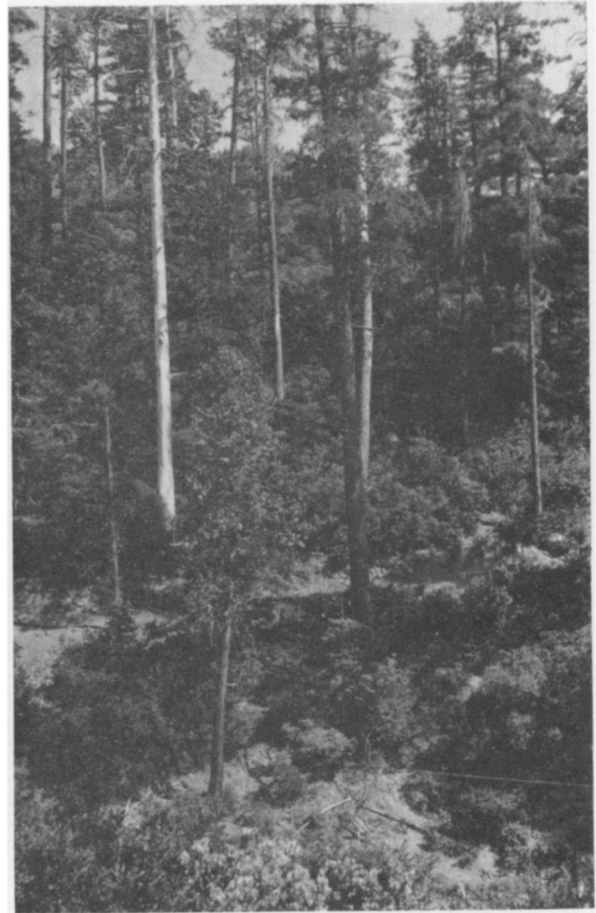


FIG. 6. View into a *Pinus-Pseudotsuga-Quercus* stand on gabbro from across a ravine; the stand photographed is on a NW slope,  $32^\circ$  inclination, 400 m, York Creek, Siskiyou Mts., Ore. *Pinus lambertiana*, *Pseudotsuga menziesii*, *Quercus chrysolepis*, *Lithocarpus densiflora*, *Umbellularia californica*. *Kalmiopsis leachiana* occurs in this stand and on ridge above. July 8, 1950.

age than on diorite, and of quite different floristic composition.

Stands of ravines in the gabbro area are dominated by *Pseudotsuga menziesii* and *Chamaecyparis lawsoniana*; but significant numbers of *Pinus lambertiana*, *P. ponderosa*, and *Libocedrus decurrens* also occur. Below the quite open canopy is an open stratum of sclerophylls; deciduous tree species are much less numerous on gabbro than on diorite (Table 6). Shrub coverage in ravines is patch-like and variable, but generally low; *Rhododendron occidentale* is the principal species. The stream-side herb flora is much richer in species than on diorite (Table 8). Like the rest of the gabbro flora, it includes some species which are shared with the diorite flora, some shared with the serpentine flora (see distributional group 1, Part V), and some (*Luina hypoleuca*, *Peltiphyllum peltatum*, *Epipactis gigantea*, *Erigeron cervinus*) encountered only in the gabbro transect. A number of sedges and rushes are conspicuous in the herb stratum of ravines on gabbro and serpentine (see distributional group 1).

On mesic and submesic slopes, the stands are dominated by *Pseudotsuga* and *P. lambertiana*, in a quite open tree stratum, together with a denser, but not closed, lower stratum of sclerophylls. Estimated coverages for the two strata averaged 40% for the

conifers, 80% for the sclerophylls. The relative importance of *P. lambertiana* is much greater than on diorite; the ratio of larger stems of *P. lambertiana* to *Pseudotsuga* was about 2:3 on the average on gabbro and only 1:20 on diorite. Three of the major sclerophylls—*Lithocarpus densiflora*, *Quercus chrysolepis*, and *Arbutus menziesii*—are shared with the diorite vegetation; but the sclerophyll stratum on gabbro includes two major species, *Umbellularia californica* and *Arctostaphylos cinerea* Howell, which are essentially absent from the diorite vegetation.

The principal shrub species on gabbro are *Rhus diversiloba*—the usual shrub dominant—, and *Rhamnus californica* var. *occidentalis* and *Vaccinium ovatum*, both of which are rare or absent on diorite. Shrub coverage increased from averages of 10-12% in submesic sites to 20-32% in xeric ones; herb coverage was low, averaging between 2% and 7% throughout the transect. The rare endemic shrub *Kalmiopsis leachiana* occurs in some, more xeric stands. Grasses

of broad distribution in the gabbro transect include *Melica harfordii*, *Festuca occidentalis*, *F. californica*, and *Trisetum canescens*, together with the rush *Luzula campestris*.

In most xeric stands on gabbro (transect steps 7-10) *Pseudotsuga* is strongly outnumbered by pines (*P. lambertiana* and *P. ponderosa*). These stands are unlike the *Pseudotsuga*-dominated forests on diorite, and like the serpentine vegetation, in the mixture of pines with *Pseudotsuga* and *Libocedrus* in the upper tree stratum and in the low coverage of this stratum (below 50% and in some stands below 20%). The xeric stands on gabbro differ also from those on diorite in the occurrence of *Arctostaphylos cinerea* as the most numerous small tree and in the low coverage of the sclerophyll stratum (10 to 40%).

The gabbro vegetation is thus in general more open, less strongly dominated by *Pseudotsuga*, with greater importance of pines and smaller of deciduous trees, than that on diorite. *Libocedrus* and *P. ponderosa* are absent from low-elevation diorite in this area, except as rare large individuals presumably surviving from past disturbance. On gabbro they are present along most of the moisture gradient, with all size classes including current reproduction represented; presumably the more open structure of gabbro vegetation makes possible their reproduction there. Physiognomic trends along the moisture gradient are less striking on gabbro than on diorite. Coverage of conifers declines somewhat, and proportion of pines among them increases, along the gradient from mesic to xeric. Sclerophyll coverage declines along the gradient from submesic to xeric; but sclerophyll stem numbers increase toward more xeric sites because of the larger numbers of small stems of *Arctostaphylos*.

#### LOW-ELEVATIONS ON SERPENTINE AND THE TWO-PHASE EFFECT

The vegetation of serpentine is still more open than that of gabbro (Fig. 7); even in mesic sites the



FIG. 7. A serpentine landscape at low elevations in the Siskiyou Mts., Ore.; view of Eight-Dollar Mountain, west-facing slopes, from Oak Flat Road, July 9, 1950. Open *Pinus jeffreyi* woodlands occur on the most open W- and SW-facing slopes, mixed conifers with patchy or 2-phase shrub undergrowth in somewhat less xeric situations, and denser (but still rather open) stands of *Chamaecyparis lawsoniana*, *Pinus monticola*, and *Pseudotsuga menziesii* on most mesic slopes and in ravines.

low-elevation serpentine stands have a characteristic sparse and xerophytic appearance. In the tree stratum, pines are more numerous than *Pseudotsuga* and other conifers, and deciduous broad-leaved trees are absent. The sclerophyllous trees are also virtually absent, as trees, from serpentine. Some of these sclerophylls are very much in evidence on serpentine, however, as shrubs. *Quercus chrysolepis* is represented on serpentine by var. *vaccinifolia* (Kell.) Engelm., the most abundant single shrub species there; *Lithocarpus densiflora* is represented by var. *echinoides*, *Umbellularia californica* by an unnamed shrubby variant, and *Castanopsis chrysophylla* by var. *minor* (uncommon in the study area). *Quercus garryana* occurs on serpentine as the shrubby var. *breweri* (Engelm.) Jeps. Among other trees and shrubs a series of congeneric pairs appear in non-serpentine and serpentine floras, with the serpentine species in each case of smaller stature: *Amelanchier florida* and *A. gracilis* Heller, *Garrya fremontii* and *G. buxifolia*, *Rhamnus purshiana* and *R. californica* var. *occidentalis*, *Holodiscus discolor* and *H. dumosus* (Nutt.) Heller, *Ceanothus integerrimus* and *C. pumilus*, *Berberis nervosa* and *B. pumila*. The impression given by the serpentine vegetation is that, as the physiognomic changes evident from diorite to gabbro vegetation are carried a step further onto serpentine, the coniferous tree stratum is reduced to an open stand mostly of smaller pines, the sclerophyllous tree stratum shrunken to a shrub layer, and the other broad-leaved trees and shrubs replaced by smaller shrubs and dwarf shrubs.

Stands of ravines on serpentine (Whittaker 1954b: Fig. 2) are still more open than those on gabbro, with *Chamaecyparis lawsoniana* and *Pinus monticola* each contributing about 3% of the coniferous stems (Table 8). *P. monticola*, however, is a small tree on serpentine, and among larger stems *Chamaecyparis* is strongly dominant. As on gabbro, there are numerous small stems of *Rhododendron occidentale* along the streams; and most other shrubs of the serpentine flora may occur in ravines at low coverages. In the herb stratum the distinctive character of the serpentine flora is apparent; rare and narrowly endemic species (*Cypripedium californicum*, *Rudbeckia californica*, *Darlingtonia californica*, *Trillium rivale*, *Lilium howellii* and *L. occidentale*) are mixed with more widespread species of bogs and other moist situations (see Table 11, distributional groups 1 and 4).

Tree strata on submesic and subxeric sites are typically mixtures of several conifers—*Libocedrus*, *Pseudotsuga*, *Pinus jeffreyi*, *P. monticola*, *P. lambertiana*, and in some stands *P. attenuata*. Tree coverage of these stands is low, generally below 50%, but shrub coverage is high, often over 80% in submesic stands, giving these a most distinctive physiognomy of small conifers in open growth above a dense, low sclerophyllous shrub stratum (Fig. 8). Shrub coverages increase along the moisture gradient from 20-50% in ravines to 50-90% in submesic stands,



FIG. 8. A stand of a mesic slope on serpentine at low elevations; SE-facing slope above Cedar Creek, near the Wimer Road, at 650 m, Siskiyou Mts., Ore. An open stand of *Chamaecyparis lawsoniana*, *Pinus monticola* and *Pseudotsuga menziesii* above a dense evergreen shrub layer, 90% coverage, dominated by *Lithocarpus densiflora* var. *echinoides* and *Quercus chrysolepis* var. *vacciniifolia*. October 10, 1951.

and then decrease to 20-50% in subxeric and 0-20% in xeric stands. *Quercus chrysolepis* var. *vacciniifolia*, *Lithocarpus densiflora* var. *echinoides*, *Vaccinium parvifolium*, *Garrya buxifolia*, and *Umbellularia californica* are the principal species and form the canopy of shrubs of middle height—generally below, but approaching 1 m, with *Umbellularia* extending somewhat higher.

Herb coverages in submesic sites on serpentine were relatively low, ranging from 1 to 20% and averaging 11%, but increased along the moisture gradient to 10-40%, averaging 30%, in subxeric sites. Composition of the floristically rich herb stratum may be judged from Table 11. Grasses and grass-like plants included *Poa rhizomata*, *Trisetum canescens*, *Melica geyeri*, *Luzula campestris*, *Calamagrostis koe-*

*leroides*, and an abundant but undetermined small *Carex* sp.

In most stands of intermediate sites on serpentine, the shrubs show a patch-wise distribution, giving undergrowth of these stands a two-phase character of essentially closed shrub cover alternating with shrub-less openings with grasses and other herbs (Whittaker 1954b). Since shrub cover is high in submesic sites but declines toward more xeric ones, there is a reversal of phase along the moisture gradient. In submesic stands the shrubs form the continuous phase with discontinuous openings (Whittaker 1954b: Fig. 3); but as shrub cover falls below 50% in subxeric sites, the grassy openings form the continuous phase with discontinuous shrub patches (Fig. 9). Diameters of patches of the discontinuous phase in the samples were mostly 2-5 m, with occasional larger or smaller ones.

In such two-phase vegetation the distributions of shrub populations are necessarily non-random; but the tendency toward correlation with one of the phases applies to populations other than those of the dominant shrubs. Ten samples from vegetation of two-

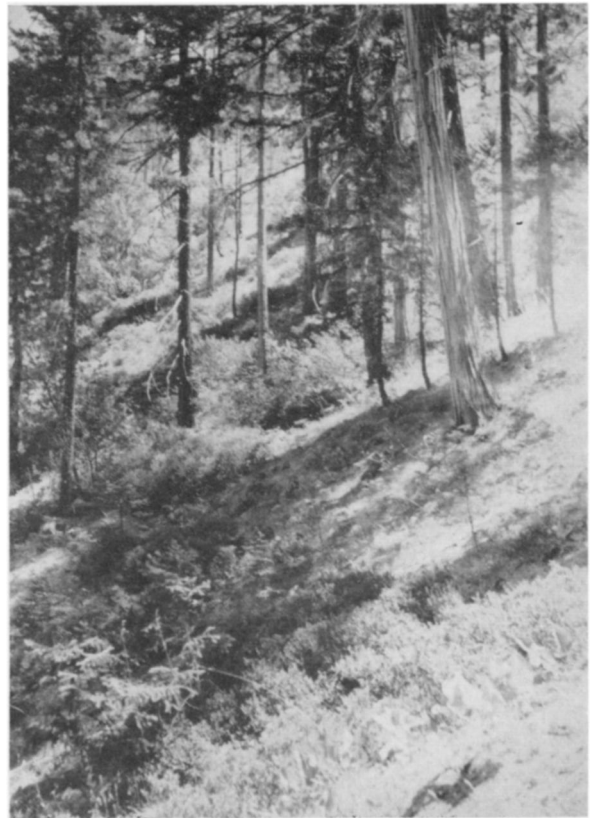


FIG. 9. A mixed-conifer stand with 2-phase undergrowth on serpentine, open ENE slope, 25° inclination, 740 m, on Tennessee Mtn. in the Siskiyou Mts., Ore. *Pinus jeffreyi*, *P. monticola*, *P. lambertiana*, *Libocedrus decurrens*, *Pseudotsuga menziesii*, in open stand (about 40% coverage), scattered shrub patches (24% coverage) dominated by *Quercus chrysolepis* var. *vacciniifolia*, and sparse grass (29% coverage). July 18, 1950.

phase character were selected, evenly divided between submesic and subxeric stands and numbers of herb and shrub quadrats; and plant populations were tabulated by their occurrence in quadrats assigned, by their predominant character, to either the shrub or herb phase. Table 16 summarizes results for species

TABLE 16. Two-phase relations of species populations in serpentine vegetation of the central Siskiyou Mountains.

	CONSTANCY	DENSITY		FREQUENCY		FREQUENCY RATIO
		No. of individuals in 125 m <sup>2</sup>		No. out of 125 1-m <sup>2</sup> quadrats in which observed		
	(10 samples)	open	shrub	open	shrub	open/shrub
<b>Shrubs</b>						
<i>Quercus chrysolepis</i> var. <i>vacciniifolia</i> . . . . .	10	20	186	16	85	0.19
<i>Umbellularia californica</i> . . . . .	5	4	8	2	8	0.25
<i>Garrya buxifolia</i> . . . . .	6	9	34	7	22	0.32
<i>Amelanchier gracilis</i> . . . . .	5	5	12	4	10	0.40
<i>Lithocarpus densiflora</i> var. <i>echinoides</i> . . . . .	4	12	31	9	17	0.53
<i>Vaccinium parvifolium</i> . . . . .	3	27	47	7	12	0.58
<i>Arctostaphylos viscida</i> . . . . .	5	12	13	10	11	0.9
<i>Rhamnus californica</i> var. <i>occidentalis</i> . . . . .	5	14	13	12	11	1.1
<i>Rosa gymnocarpa</i> . . . . .	5	16	8	10	7	1.4
<i>Berberis pumila</i> . . . . .	6	39	27	17	12	1.4
<i>Arctostaphylos nevadensis</i> . . . . .	3	25	11	10	5	2.0
<i>Convolvulus polymorphus</i> . . . . .	6	19	4	14	4	3.5
<b>Herbs</b>						
<i>Whipplea modesta</i> . . . . .	8	48	131	15	34	0.44
<i>Trientalis latifolia</i> . . . . .	8	67	98	13	24	0.54
<i>Xerophyllum tenax</i> . . . . .	6	53	36	18	22	0.82
<i>Phlox speciosa</i> . . . . .	7	22	34	14	12	1.2
<i>Iris bracteata</i> . . . . .	10	159	157	48	47	1.0
<i>Viola lobata</i> . . . . .	5	73	45	17	17	1.0
<i>Aster brickelliioides</i> . . . . .	4	22	14	8	7	1.1
<i>Lomatium howellii</i> . . . . .	4	10	8	7	6	1.2
<i>Balsamorhiza deltoidea</i> . . . . .	6	46	32	24	19	1.3
<i>Galium ambiguum</i> . . . . .	10	122	62	29	18	1.6
<i>Ceanothus pumilus</i> . . . . .	6	110	33	27	13	2.1
<i>Lomatium triternatum</i> . . . . .	6	39	11	15	6	2.5
<i>Hieracium cynoglossoides</i> var. <i>nudicaule</i> . . . . .	6	22	8	12	4	3.0
<i>Eriogon foliosus</i> var. <i>confinis</i> . . . . .	4	34	9	6	2	3.0
<i>Carex</i> sp. . . . .	4	117	28	19	6	3.2
<i>Horkelia sericata</i> . . . . .	2	72	9	12	3	4.0
<i>Eriophyllum lanatum</i> var. <i>achillaeoides</i> . . . . .	2	8	1	4	1	4.0
<i>Polygala californica</i> . . . . .	4	8	1	6	1	6.0
<i>Senecio fastigiatus</i> . . . . .	2	16	1	7	1	7.0
<i>Cheilanthes siligiosa</i> . . . . .	5	10	1	9	1	9.0
<i>Cordylanthus viscidus</i> . . . . .	4	20	0	9	0	
<i>Zygadenus micranthus</i> . . . . .	4	12	0	7	0	
<i>Perideridia oregana</i> . . . . .	2	4	0	3	0	

represented by significant numbers in 125 quadrats of each phase. Of the shrub species, the first six are necessarily concentrated in the shrub phase, for they form the shrub canopy of this phase. Of the other species one (*Rosa gymnocarpa*) is often part of the shrub canopy but occurs also in the openings;

*Arctostaphylos viscida* is taller, and *Berberis pumila*, *Arctostaphylos nevadensis*, and *Convolvulus polymorphus* are lower than the shrub canopy, and occur independently of it.

Relations of herb species to the phases are significantly correlated with their moisture-gradient relations. *Whipplea* and *Trientalis*, the only species concentrated in the shrub phase, are the only species whose distributional centers are in mesic or mesic-submesic sites; and they are also the only herb species listed which occur in the well-shaded herb stratum on diorite. The next 8 species listed, *Xerophyllum* to *Galium ambiguum* are centered in submesic, or submesic and subxeric, sites; the last 13 species are centered in subxeric or xeric sites. In general, the more a species population is concentrated toward the mesic end of the gradient, the more it is concentrated also in the shrub phase; the more a species is concentrated toward more xeric sites, the more it is concentrated in the open phase. Grasses in general show marked concentration in the open phase, but significant data are not available for individual species. Such data suggest different responses of species populations to the somewhat different microclimatic and soil conditions underneath the shrubs and in the grassy openings. It appears that these micro-environments may also influence tree distributions through effects on seedlings. *Pseudotsuga*, *P. monticola*, and *P. attenuata* tended to be concentrated in the shrubs; *Libocedrus* to be indifferent or less strongly concentrated in the shrubs; *P. jeffreyi* to be concentrated in the open.

The two-phase character is developed in quite different degrees in different stands. The condition is most easily recognized in those stands in which the proportions of shrub cover and opening are relatively even. Comparison of samples with regard to disturbance and succession suggests that the two-phase effect is characteristic of climax, rather than successional, stands. The two-phase effect seems best developed in some stands with well-developed soil, but poorly developed in stands with more rocky, clearly immature soils. It seems best developed also in those stands least disturbed by fire, but poorly developed in stands with more severe fire effects.

Two-phase vegetation, with reversal of phase along an environmental gradient, is known for other circumstances—as the break-up of taiga and krummholz into tundra in the far North (Rousseau 1952), the transition of deciduous chaparral into semi-desert in the Wasatch Mountains (Hayward 1948), and the aspen groveland (Coupland & Brayshaw 1953, Lynch 1955). In these circumstances the two-phase character seems transitional, an "ecotone" of the "mosiac-insular" type considered by Nytzenko (1948) the most common kind of ecotone. In a broad sense, the two-phase vegetation of the Siskiyou serpentine is a transition between closed forests of high elevations and the open pine steppes of low elevations and most xeric sites (Fig. 12). The two-phase vegetation is an extensive community-type, diverse within

itself, however, with a distinctive physiognomy, and many character-species which are centered within it rather than in forest or pine steppe. Species populations show all degrees of correlation with one or another of the phases; the phases are by no means distinct and relatively immiscible communities in mosaic arrangement.

Too facile a description of this vegetation as "an ecotone between two communities" may do more to obscure than clarify its significance, for the meanings of "ecotone" and "community" in this description are scarcely understood by ecologists. The author would prefer a different descriptive interpretation. The open tree stratum on serpentine makes possible well-developed undergrowth communities of high coverage. Along the whole of the moisture gradient the undergrowth is of mixed shrubs, and grasses and other herbs; but the shrub populations are concentrated in submesic sites, the grasses in more xeric ones. Along the moisture gradient from submesic to xeric sites, there is gradual shift of balance between these two major components of the undergrowth, as the extent of the woody strata which the sites can support declines. Since there is also a tendency for the shrubs to grow in closed patches, the vegetation assumes a two-phase character with the relative importance of the phases shifting continuously along the moisture gradient.

In stands of xeric sites shrub coverage ranges downward to zero. Undergrowth of these stands is predominantly of grasses, in rather sparse growth; grass-like plants include *Stipa lemmoni*, *Sitanion jubatum*, *Melica geyeri*, *Elymus glaucus*, *Festuca ovina*, *Bromus breviaristatus*, *Danthonia californica*, *Agrostis hallii*, *Koeleria cristata*, *Carex* sp., and *Luzula campestris*. With these occur many broad-leaved herb species (Table 11, distributional groupings 7 and 9). In some xeric stands *P. jeffreyi* is the only tree species present, in very open stand (Fig. 10). *Libocedrus* occurs in smaller numbers in



FIG. 10. Jeffrey pine woodlands with widely scattered *Arctostaphylos viscida* and grassy floor, on dry flats and lower slopes on serpentine. Oak Flat Road, about 400 m, Siskiyou Mts., Ore., October 9, 1951.

most, and *Pseudotsuga* in some stands. *Arctostaphylos viscida* forms a very open high-shrub stratum in some stands. Physiognomically these stands, with their pines in scattered growth above a

grassy floor, are unlike anything yet described; they are of the widespread physiognomic type which may be termed pine steppe or pine woodland.

Although pine woodlands are of very wide occurrence, the two-phase stands of intermediate sites on Siskiyou serpentine are most distinctive. Their physiognomy—mixed conifers in open growth above a dense scrub-oak stratum with grassy openings—is scarcely duplicated elsewhere to the author's knowledge, although pine heath and mixed conifers with heath or chaparral are reported from serpentine in other areas (Ritter-Sudnička 1953, Yamanaka 1954, 1956, 1957, McMillan 1956). Neither physiognomic type occurs on diorite or gabbro in the study area. Comparing the three vegetation patterns described here, there is progressive reduction of tree-stratum coverage and biomass from diorite through gabbro to serpentine; while undergrowth strata are better developed on serpentine. Compared with the other vegetations, the serpentine vegetation suggests a shift of the concentration of plant life from the tree stratum downward toward the shrub and herb strata (Whittaker 1954b). Viewing serpentine vegetation as a whole, a comparable shift of vegetational biomass toward the lower strata along the moisture gradient is suggested—from the trees in most mesic sites to a highly developed shrub stratum in intermediate and herb stratum in xeric sites. Within the serpentine vegetation the herb and shrub strata show a distinct inverse correlation, such as is encountered in some vegetation conditions (Whittaker 1956) but not in others, and not on the other soils in the Siskiyou.

Within the Siskiyou Mountains at low elevations, serpentine vegetation shows a general consistency with what has been described; but climatic variation, the extreme localization of some of the species, and probable variation in chemistry of serpentine rocks imply differences in floras from one outcrop to another. Smaller outcrops of serpentine, such as may be observed west and northwest from the diorite study area, often support vegetation and floras which are intermediate to those of serpentine and more typical soils. Extent of development of the serpentine flora on one of these outcrops seems in general to be directly proportional to its size and inversely proportional to its distance from one of the larger serpentine areas. Departing also from what has been described are the dense stands of young stems of *Pinus attenuata* encountered in many areas, and the Jeffrey pine woodlands on private land near the valleys, with shrub strata dominated by *Ceanothus cuneatus*. These conditions are thought to be products of disturbance, the former by fire and the latter by grazing.

#### FOREST VEGETATION OF HIGHER ELEVATIONS ON DIORITE

Although intensive study was concentrated in a single area, serpentine vegetation was observed at all elevations in other areas of the Siskiyou Mountains.



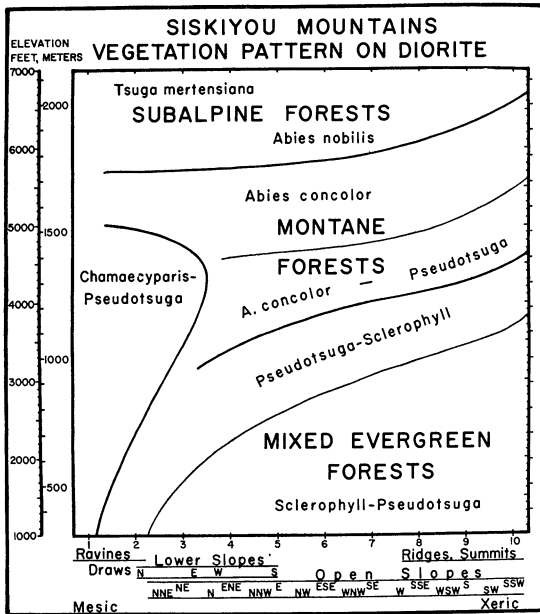


FIG. 11. Mosaic chart of vegetation on quartz diorite, central Siskiyou Mountains, Oregon.

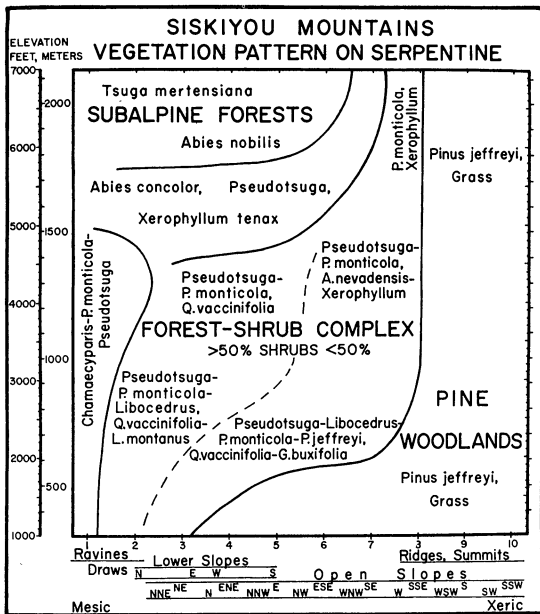


FIG. 12. Mosaic chart of vegetation on peridotite and serpentine, central Siskiyou Mountains, Oregon (*L. montanus* = *Lithocarpus densiflora* var. *echinoides*).

The diorite vegetation was intensively sampled at all elevations in the principal study area. Figs. 11 and 12 present "mosaic charts" (Whittaker 1956) for the two patterns in the central Siskiyou, based on 270 vegetation samples on diorite, 70 vegetation samples and 90 other field records of serpentine stands.

In the diorite pattern the sclerophylls are concentrated in the low-elevation, xeric sites, the lower right corner of Fig. 11. With increasing departure from these sites, toward either more mesic situations or higher elevations, the proportion of sclerophylls in the stands decreases. This distributional relation, and the complex relations of moisture conditions to both topography and elevation, imply an oblique boundary for the sclerophyll-Pseudotsuga type. Beyond this boundary the Pseudotsuga stands form a transition, to Chamaecyparis-Pseudotsuga stands at lower and *Pseudotsuga-Abies concolor* stands at higher elevations.

The Chamaecyparis-Pseudotsuga forests, which are rather narrowly restricted to ravines and most mesic slopes at lower elevations, expand toward higher elevations onto many sheltered slopes and some open northerly ones. The character of these forests changes gradually as they are followed from the low elevations already described to elevations above 1200 m. Representation of the sclerophylls and all other broad-leaved trees decreases toward higher elevations, while *Abies concolor* becomes increasingly important. Shrub coverage is low; the low-elevation species *Rosa gymnocarpa*, *Berberis nervosa*, and *Rubus vitifolius* are joined by other species largely restricted to forests of higher elevations—*Quercus sadleriana*, *Ribes marshallii*, *Vaccinium membranaceum*. The change in the herb stratum toward higher elevations is more conspicuous; for herb coverage increases to 20-60%, with many mesophytic species including most of these of low-elevation mesic stands and montane forests (distributional groups 3, 6, 10, and 11).

At elevations between 1200 and 1850 m (4000-6000 ft) "Montane Forests" occur, dominated by Pseudotsuga and *Abies concolor* at lower, by *A. concolor* at higher, elevations. Chamaecyparis is present in some stands of more mesic situations, *Libocedrus decurrens* in some stands of more xeric situations. The only broad-leaved trees of significance are *Acer glabrum* var. *douglasii* and *Corylus rostrata* var. *californica*; sclerophylls are wholly absent above lower elevations of the montane forests. Shrub coverage is low, generally 0-10%, with *Rosa gymnocarpa*, *Berberis nervosa*, *Rubus vitifolius*, and *Holodiscus discolor* the principal species. The herb stratum is floristically rich and of high, though variable coverage—30-80% in most stands, but as high as 90% and below 10% in some stands. These forests show, in less marked degree, the gradation from rich to poor herb strata to be described for the subalpine forests. Herb species include *Achlys triphylla*, the species of greatest density and coverage, and many others of distributional groupings 6, 10, and 11, together with some species of groupings 3 in more mesic sites and 12 toward higher elevations. Average composition of these forests is indicated by data for the 1370-1680 m elevation belt in Tables 12-15.

At elevations approaching 1850 m the *A. concolor* forests are usually mixed with *Abies nobilis* Lindl. (*A. procera* Rehd.), sometimes with *Tsuga mertensiana*.

At elevations above 1850 m, subject to differences in exposure and topographic situation, the latter species become the dominants of subalpine forests. At still higher elevations, above about 1920 m, *T. mertensiana*



FIG. 13. *Abies nobilis* forest of high elevations in the Siskiyou Mts., Ore. A NE-facing slope on Dutchman Peak, 1920 m, July 14, 1950.

and *A. nobilis* are the only tree species represented in the stands; these are subalpine forests without birches or any other broadleaf associates. Most stands contain both dominants. Proportions of the two are not strongly correlated with elevation or site, suggesting that stand composition is to some extent determined by chance in the newer stands which have developed following fires, or in the primary successions on glacial topography. Within the subalpine forest pattern, however, there is some tendency for *A. nobilis* to predominate toward lower elevations and more xeric sites, *T. mertensiana* toward higher elevations and more mesic sites. Canopy coverages average somewhat less than in the montane forests, and in some stands are below 50%.

Average composition of the subalpine forests is indicated by data for the 1920-2140 and 1680-1920 m elevation belts in Tables 12-15. These forests show a very wide range of herb-stratum coverages—from less than 1% to more than 90%—and great variation in appearance from relatively open stands with lush and floristically rich herb strata to denser stands with almost bare floors of needles and twigs. The former are characterized by a group of herbs—*Arnica latifolia*, the species of highest density and

coverage, *Achlys triphylla*, *Campanula scouleri*, *Arenaria macrophylla*, *Anemone deltoidea*, *Valeriana sitchensis* ssp. *sitchensis*, *Phlox adsurgens*, *Osmorhiza chilensis*, *Hieracium albiflorum*, *Claytonia spathulata*, *Viola glabella*, *Actaea spicata*, *Galium triflorum*, *Trillium ovatum*—with high densities and with constancies of 80-100% in such stands. In stands of low herb coverage some of these, especially *Arnica latifolia*, *Campanula scouleri*, *Hieracium albiflorum*, and *Arenaria macrophylla*, are still present, but represented by few individuals. Along with these, the herb strata include *Chimaphila menziesii*, *Pyrola secunda*, *Pyrola picta*, *Corallorhiza maculata*, and toward lower elevations, *Chimaphila umbellata* var. *occidentalis*; the evergreen ground heaths are a conspicuous part of the sparse herb strata in such stands but are of low constancy in stands with well-developed herb strata. One may recognize at least three distributional groupings or unions among undergrowth species of these forests (cf. Oosting & Billings 1943), although these groupings intergrade: (1) Species with maximum population levels in stands with rich herb strata, and limited occurrence in stands with poor herb strata and in meadows or other open communities, (2) Species of extensive occurrence in meadows and other open communities, which also occur in stands with rich herb strata (see distributional groupings 11 and 12), and (3) Species which are of greatest importance in stands with poor herb strata. The low coverages of the shrub stratum, in which *Ribes marshallii* is the only important species, are correlated with the herb coverages; in stands with herb coverages over 70%, shrub coverages averaged 5%, in those with herb coverages of 2% or less, 0%. Average undergrowth coverages decrease along the moisture gradient from N- to S-facing slopes and from the 1370-1680 to the 1920-2140 m elevation belt; and at any elevation and exposure are inversely correlated with tree-stratum density.

The general character of the diorite vegetation shown by the mosaic chart is a pattern of mixed evergreen forests at low elevations which is gradually transformed toward higher elevations into montane and subalpine coniferous forest. Apart from the *Chamaecyparis-Pseudotsuga* stands, the vegetation types form a series of belts or zones toward higher elevations; in life-zone terminology (Hall & Grinnell 1919, Jepson 1923-5, Grinnell 1935, Cooke 1941) the Mixed Evergreen Forest is presumably to be identified with the Upper Austral, the forests of *Pseudotsuga* and *Abies concolor* with the Transition and those of *A. nobilis* and *T. mertensiana* with the Canadian and Hudsonian zones.

A kind of relative discontinuity, defined by growth-forms and not species distributions, between subalpine forests and those of lower elevations was described by the author for the Great Smoky Mountains (Whittaker 1956). No such relative discontinuity could be detected in the Siskiyou pattern; the Subalpine and Montane Forests are continuous with

one another, and the latter with the Mixed Evergreen Forests. Abrupt forest-edges occur between high-elevation forests and meadows; but within the forests themselves the vegetation on diorite is a single, continuously intergrading pattern from most mesic sites to most xeric, and from lowest elevations to highest. Low-elevation vegetation patterns on serpentine and gabbro are correspondingly continuous; and the more limited samples from higher elevations on serpentine indicate, though they are insufficient to demonstrate, the full continuity of the serpentine pattern.

#### VEGETATION OF HIGHER ELEVATIONS ON SERPENTINE

The serpentine vegetation, described for elevations of 610-920 m, has much the same character up to elevations of 1100 and 1200 m, and down to elevations of 300 m and less. Toward lowest elevations, however, there is striking expansion of the Jeffrey pine woodlands so that these, rather than the two-phase stands, become the prevailing vegetation type on serpentine slopes of low elevations (Figs. 10, 12).

The *Chamaecyparis-P. monticola* stands are more narrowly restricted to ravines than the comparable *Chamaecyparis-Pseudotsuga* stands on diorite. Some expansion toward higher elevations occurs, and stands dominated by *Chamaecyparis* with *P. monticola* and *Pseudotsuga* were encountered on slopes and flats up to 1400 m. Such stands had high shrub coverages, 65 and 83% in two samples, with *Quercus chrysolepis* var. *vaccinifolia*, *Lithocarpus densiflora* var. *echinoides*, and *Vaccinium parvifolium* the dominant shrubs, and low herb coverages (1-2%), with various of the species of mesic and submesic stands at lower elevations.

The vegetation types which prevail on intermediate sites and intermediate elevations, and thus have a central position in the Siskiyou serpentine pattern, have been grouped together as the "forest-shrub complex." The diverse stands of this grouping are in general characterized by open canopies of mixed conifers, and well-developed undergrowths in which dominance is shared in varying proportions between evergreen shrubs and grasses or grass-like plants. In stands of higher elevations, 1100-1400 m, *Pseudotsuga* and *P. monticola* are the dominant trees, with *Chamaecyparis* toward more mesic and *P. jeffreyi* toward more xeric sites, *Libocedrus* toward lower and *Abies concolor* toward higher elevations. Undergrowths are of the same general character and composition described for lower elevations, with *Quercus chrysolepis* var. *vaccinifolia* the principal shrub and *Xerophyllum tenax* most conspicuous in the herb stratum. Toward still higher elevations, above about 1400 m, stands of the complex extend upward in subxeric sites between the *A. concolor* forests and pine woodlands. In these stands *Pseudotsuga* and *P. monticola* are dominant, and the two-phase undergrowth is replaced by lower strata of quite different appearance and composition, with *Arctostaphylos*

*nevadensis* the principal shrub and *Xerophyllum tenax* the principal herb.

At highest elevations, *Pinus monticola* occurs in very open stand above an undergrowth strongly dominated by *Xerophyllum tenax*. Physiognomically such *Xerophyllum*-rich stands have the appearance of pine "steppes." Floristically they are much like the high-elevation Jeffrey pine woodlands to be described, but contain also some species of the *A. concolor* forests. In a stand of the type which was studied, at 2040 m on a west-facing slope of Big Red Mountain, the coverage of *P. monticola* was below 30%, with few stems of *A. concolor* and *P. jeffreyi*. Shrub coverage was 24%, predominantly *Arctostaphylos nevadensis*, but with *Amelanchier gracilis* present; *Xerophyllum* predominated in a floristically rich herb stratum of 57% coverage.

At elevations mostly between 1370 and 1770 m, montane forest stands dominated by *A. concolor* and *Pseudotsuga* with *P. monticola*, *P. jeffreyi*, and *Libocedrus* often present, occur. These are more open stands than the montane forests on diorite, with coverages generally between 40% and 70%. Shrub coverages were rather low and herb coverages high, 13 and 48% in a representative sample, with *Arctostaphylos nevadensis* and *Xerophyllum tenax* the stratal dominants. The latter forms, in many of these stands, an apparently "grassy" undergrowth. Flora of the undergrowth includes both some species characteristic of serpentine and some of those of high-elevation diorite vegetation. At higher elevations closed stands of *Abies nobilis* were encountered in the Observation Peak and Big Red Mountain serpentine areas near Ashland Peak. Physiognomically they differed little from comparable stands on diorite, but many herb species characteristic of high-elevation forests on diorite were not recorded in the stands observed.

Most xeric sites on serpentine are occupied by pine steppes or woodlands at all elevations. Floristic composition of these gradually changes upward from that already described at low elevations to the quite different flora of high-elevation stands. *P. monticola* and *A. concolor* occur in some of the high-elevation Jeffrey pine steppes, and *Libocedrus* is often absent. Shrubs included *Chrysothamnus nauseosus* var. *occidentalis*, *Amelanchier gracilis*, *Ceanothus cuneatus*, *Holodiscus dumosus*, and *Quercus chrysolepis* var. *vaccinifolia*, with coverage below 10%. Grasses were *Melica subulata*, *Sitanion hystrix*, *Festuca ovina*, *Bromus breviaristatus* and *B. carinatus*, and *Trisetum canescens*. *Xerophyllum tenax* was the principal herb species; other herbs shared with the low-elevation serpentine flora included *Cheilanthes siliquosa*, *Monardella odoratissima* var. *glauca*, *Eriophyllum lanatum* var. *lanceolatum*, *Eriogonum nudum*, *Castilleja miniata*, *Phlox diffusa*, *Achillea lanulosa*, *Phacelia dasyphylla* var. *ophitidis*, and *Silene campanulata* var. *orbiculata* Rob. Other species of the high-elevation pine steppes were *Iris chrysophylla*, *Vicia californica*, *Arenaria macrophylla*, *Aster siskiyouensis*,

*Pedicularis racemosa*, *Anemone quinquefolia*, *Eriogonum aliciae*, *Astragalus whitneyi* Gray, *Orthocarpus copelandii*, *Anemone drummondii*, *Sedum obtusatum* ssp. *boreale* Clausen, *Linum lewisii*, *Pentstemon azureus* ssp. *parvulus* (Gray) Keck, *Eriogonum umbellatum*, *Calochortus elegans* var. *nanus* Wood., *Senecio integerrimus* var. *exaltatus* (Nutt.) Cronq., *Erysimum capitatum*, *Polystichum scopulinum* (Eaton) Maxon, *Aster shastensis* var. *eradiata*, and *Leucopinus leucophyllus*.

Sample coverage is inadequate to prepare a mosaic chart for gabbro vegetation. In the low elevations studied, the *Chamaecyparis-Pseudotsuga* type is more narrowly restricted to ravines than on diorite. Because of the greater openness of the gabbro stands, the sclerophyll-*Pseudotsuga* is in immediate contact with *Chamaecyparis-Pseudotsuga*, without an intervening *Pseudotsuga-sclerophyll* type. The more xeric stands on gabbro, with pines predominant and a quite open sclerophyll stratum, represent a third physiognomic type within the Mixed Evergreen Forests (see Part V).

South of the main study area, in the area of Youngs Peak, Sanger Lake, and Preston Peak, a distinctive high-elevation forest pattern occurs, with varied mixtures of *Picea breweriana*, *Abies concolor* and *A. nobilis*, *P. monticola*, *Pseudotsuga*, and *Libocedrus* in rather open stands. In more mesic sites near 1500 m stands of *Chamaecyparis* with *P. breweriana* and *P. monticola* occur; and in more xeric ones stands of *A. concolor* with *Pseudotsuga* and *Libocedrus*. Toward higher elevations true spruce-fir stands occur, dominated by *P. breweriana* and *A. nobilis*, with *P. monticola* also present. Shrub and herb coverages were generally low, with *Vaccinium membranaceum* and *Quercus sadleriana* the principal shrubs, *Achlys triphylla* and *Chimphilla umbellata* var. *occidentalis* the principal herbs. This high-elevation pattern is in some respects intermediate to those of diorite and serpentine. Since observations for middle elevations are lacking, its continuity with the low-elevation pattern described for gabbro cannot be established.

#### IV. CLIMAX INTERPRETATION

The complex vegetation of the Siskiyou raises several problems of climax interpretation. Those to be discussed are: (1) The role of fire, (2) The question of edaphic climaxes, (3) The basis of comparing climax vegetation for different parent-materials and climates, (4) Gradation of climax vegetation along climatic gradients, and (5) Prevailing or "climatic" climax types for this area.

##### FIRE EFFECTS AND EDAPHIC CLIMAXES

The forests of the Siskiyou exist in a summer-dry, "Mediterranean" climate. During the dry season the forests are inflammable, and the means of igniting them have not been lacking. Essentially all the low-elevation vegetation described has been burned recently enough for fire-signs to be detected in the form

of charcoal in the soil, bark-burns or burned stumps, or in stand composition; it is believed that no low-elevation stand unaffected by fire was observed. All this vegetation is consequently "disturbed" in this sense; but it does not follow from this that the vegetation is to be interpreted as simply secondary.

Self-maintaining, all-age forest stands show a characteristic J-curve for the relation of numbers of tree stems to diameters of stems. Plotted with numbers of stems on a logarithmic scale, these curves become somewhat convex upward (Whittaker 1956) in the form illustrated in Fig. 14 by no. 8, *Pinus jeffreyi*

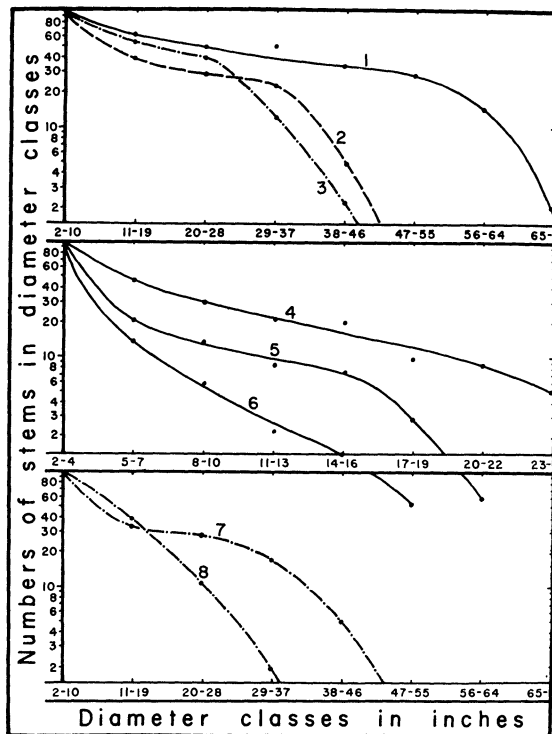


FIG. 14. Stand curves of stem numbers vs. diameters for principal trees at low elevations in the central Siskiyou Mountains, with numbers of stems on a logarithmic scale. Top—*Pseudotsuga menziesii* on quartz diorite (1), olivine gabbro (2), and serpentine (3). Middle—three sclerophylls on diorite, *Arbutus menziesii* (4), *Quercus chrysolepis* (5), and *Lithocarpus densiflora* (6). Bottom—two pines on serpentine, *Pinus lambertiana* (7), and *P. jeffreyi* (8).

on serpentine soils. A wide variety of all-age and presumably climax stands have been found to have curves of this form, though it is by no means the only possible one for climax forests. When stand curves for different species on different soils in the low-elevation Siskiyou are plotted, these curves (with the exception of *P. jeffreyi*) show an interesting and consistent departure from this singly-convex form, as illustrated in Fig. 14.

Increment borings permit some interpretation in relation to tree ages and history of the area. Three

phases of the curves may be recognized in relation to three historic periods: (1) A pre-white period, extending back from somewhat more than a century to several centuries ago, which is reflected in an essentially normal, convex curvature for the largest size-classes in the curves. (2) The historic period of a century or somewhat more, during which the forests were more frequently burned. The resulting reduced reproduction, or heavier mortality among younger trees, is reflected in the flattened intermediate sections of the curves. (3) A more recent period of protection from fire, during which the frequency of fires has been less, and the rate of tree reproduction and survival of younger trees greater, as indicated in the concave, uppermost sections of the curves.

In relation to fire-disturbance and the climax state of these forests, the curves suggest: (1) The older trees are several centuries old; they have survived the more intensive burning by white man and still dominate the upper levels of the tree strata and characterize the vegetation. (2) The general similarity of the curves implies that the different species have been affected in similar ways by increase and decrease of fire frequency. (3) The mixed conifer-sclerophyll dominance of these stands is not a product of more recent, more severe burning; the balance between the two groups in community dominance has been similar, though not necessarily identical, throughout the history represented. (4) The principal effect of less severe fires in this vegetation seems to be not in radical change in community composition, but in reducing the seedling survival, and hence eventually reducing stand density, for both conifers and sclerophylls.

If this vegetation is obviously not, on the one hand, climax vegetation unaffected by fire, neither, on the other hand, is it a vegetation of fire-successions. It may be regarded, rather, as a fire-adapted vegetation of a summer-dry climate, in which fires of varying frequencies and intensities and varying sources—white man, Amerind, and lightning—have for a very long time been part of its environment. If the term "climax" is to be applied in such circumstances, it seems supposititious to apply it to the non-existent vegetation which might develop after centuries of complete fire protection. The climax may better be regarded as that reasonably stable and self-maintaining vegetation which exists in this area, in adaptation to fires and other factors of environment. It may be understood in this case that the climax, or fire-climax, condition embodies a degree of population instability and irregularity resulting from fires affecting different areas in a patch-wise fashion at irregular intervals.

It further appears that vegetation patterns of different parent materials have been similarly affected by fire; no one of them is fire-successional to another. It seems inconceivable that the three vegetation patterns of diorite, gabbro, and serpentine, with their different physiognomies and floras in relation to different nutrient economies, should ever converge

to the same climax even in the absence of fire (Whittaker 1954b). The problem of edaphic climaxes, however, goes beyond the fact that there are three different climax patterns in the same climate. If so marked a difference of climax occurs on these three, and gabbro is intermediate to the other two, it is reasonable to suppose that rocks intermediate to the diorite and gabbro, or gabbro and serpentine observed, would support still different, intermediate vegetation. Granite, the fourth member of the series, is known to support vegetation different from diorite in some areas (Williams 1933). Moreover, the geological diversity of the Siskiyou involves many rock types other than the granite-serpentine series. Close by the diorite area one may observe vegetations of marble, quartzite, slate, and argillite, which differ from the vegetation of diorite and gabbro, especially in more xeric sites. There may be, within the same climate, many climax vegetation patterns differing in different ways and different degrees in response to different parent materials. If one sets aside the vegetation of serpentine as highly anomalous, there still remain the climax patterns, differing in many details, of these other rocks. If one regards these climaxes as part of "the same" climax formation, Mixed Evergreen Forest, one must recognize that they are "the same" in membership in a man-made class of forest communities, but not vegetationally "the same" in plant populations or details of physiognomy. Any statement that one of these vegetations represents the true, climatic climax surely represents an arbitrary choice of what is to be thought a "normal" or "typical" parent material and vegetation pattern.

It was one of the assumptions of the monoclimate theory that the climax, given time for development of a mature soil, should be independent of soil parent material. The diversity of climaxes in the Siskiyou seems to contradict this assumption. The extent to which differences of parent material are reflected in differences of vegetation must be influenced by various factors other than properties of the rocks themselves—climate, physiography, and fire, the general character of the vegetation and soils, floristics and the kinds of plants available to form and dominate communities. Two parent materials may well support different climax vegetations in one set of circumstances, but in another support vegetation which seems not significantly different. But it is suggested that the statement that climax is independent of soil parent material may be replaced by understanding that a significant difference in parent material may usually imply some degree of difference in climax vegetation.

#### THE COENOCLINE AND CLIMAX COMPARISON

Within each parent material and elevation belt there is conspicuous vegetational gradation from ravines to southwest slopes; the vegetation forms a continuous pattern, or vegetational spectrum, in relation to the topographic moisture gradient. So far as can be determined, in stands not recently and

severely disturbed, vegetation and soil are in the climax condition along the whole of the moisture gradient, at least in the sense that they are in steady-state in relation to the mountain-slope environments in which they exist. "The climax" on a given parent material is consequently not a particular kind of stand, but the whole climax pattern in relation to the moisture gradient (cf. Whittaker 1951, 1956). Considering also elevation and the three soils, climax vegetation in the central Siskiyou may be conceived as a highly diversified, generally continuous, multi-dimensional pattern comprising all the stabilized vegetation described in relation to the moisture, elevation, and diorite-to-serpentine gradients, and other vegetation undescribed.

A principal concern of the present work is with comparison of vegetation patterns of different climates and parent materials. Comparison for different climates, at least, can be based on "climatic climax"; but there are limitations to the effectiveness of such comparison, for the community-types to be designated "climatic climax" must be chosen from the vegetational gradient by an ecologist. Much that is significant about vegetational expression of climate may be lost sight of if a single climatic climax type is selected, to the neglect of the rest of the vegetation pattern. Comparison of vegetation from one area to another may be most effective if based, so far as possible, on the whole moisture-gradient patterns for each area.

The expressions community gradient, or pattern, or spectrum, or ecological series have been used in the preceding sections of this work, but a shorter term may be desirable. The term *ecocline* was suggested by Clements (1936), apparently for sequences of climax communities along environmental gradients, but has been little used. The term may be a useful one; and an *ecocline* may be conceived as a gradation in characteristics of ecosystems along an environmental gradient, a gradation which may be underlain or caused by a particular environmental gradient, but is usually expressed in complexly interrelated changes in all aspects of ecosystems. *Ecocline* has been applied also (Huxley 1943) to the genetic gradients or clines within species populations along ecosystemic gradients. For the environmental aspect of the ecosystemic gradient the term *complex-gradient* has been suggested (Whittaker 1954c, 1956), and the term *catena* is in use for the more strictly edaphic aspect (see also terms suggested by Major 1951). For the gradient of natural communities in an ecocline, the term *coenocline* is here proposed; the coenocline and complex-gradient together constitute the ecosystemic gradient or total ecocline.

If the climax on mature, stream-eroded topography is conceived as a "coenocline," then comparison of climaxes for different climates and parent materials may be facilitated by means of further abstraction, to express average or general character of coenoclines. Three approaches to such abstraction

have been suggested by the author (Whittaker 1956). *Average climax composition* is the average composition of climax stands in a given area, or within a given coenocline. *Intermediate climax stands* are intermediate, or median, to the extremes of a coenocline, as determined by the midpoint of a transect, by percentage similarity or coefficient of community comparison with the extremes, or other means. In some cases, as in the kind of topography dealt with here, open east-facing slopes are approximately intermediate to the extremes of the moisture gradient. The *prevailing climax type* is the community-type, whatever the criteria chosen to define it as a type, which comprises the majority of the climax stands in a given area or a given coenocline.

These concepts underly the present work in various ways. Vegetation has been sampled, the samples arranged in composite transects, the transects interpreted, and the vegetation itself described, in terms of moisture-gradient coenoclines. Tables 3-11 summarize community composition and the distributions of plant populations in coenoclines in such a way that these may be directly compared from one parent material to another. Tables 12-14 summarize relations of diorite vegetation to elevation in terms of average climax composition, and Tables 3-11 permit a similar summary in relation to the three parent materials at low elevations. The floristic analysis of Part VI is based primarily on species lists for coenoclines, and the comparison of these in terms of life-forms and growth-forms, species-diversities, and areal types. The problem of prevailing climax types for the Siskiyou will be considered in the section which follows.

#### EAST-WEST GRADATION AND THE PREVAILING CLIMAX TYPE

In order to supplement the work in the central Siskiyou with information on low-elevation climaxes, at least, for other areas of the range, a series of small-scale studies were made from the Coastal Sequoia forests at the western end, to the vegetation of the interior at the eastern end of the Siskiyou Mountains. At each study area six vegetation samples were taken at low elevations, in different topographic positions representing the moisture gradient—ravines, mesic lower slopes, and open NE, E, SE, and S or SSW slopes—along with other notes on the character of moisture-gradient coenoclines. Since each study was a limited transect, this phase of the work was designed as a transect of transects, representing change in low-elevation vegetation patterns along the climatic gradient from the more humid and maritime to the drier and more continental extremities of the Siskiyou Mountains. Some features of the climatic changes along this gradient are indicated in Table 1. The study areas (see Fig. 1), and vegetation patterns, were as follows:

1. Mill Creek State Park, Del Norte County, Calif., in hills or low mountains, about 8 km from the coast,

at elevations of 120-180 m, in coastal Sequoia forest. Stands were strongly dominated by *Sequoia sempervirens* in the upper tree stratum and *Tsuga heterophylla* in the middle tree stratum in all topographic situations. Smaller numbers of *Pseudotsuga menziesii*, *Abies grandis*, and *Chamaecyparis lawsoniana* also occurred, and, in more mesic sites, *Thuja plicata* and *Picea sitchensis*. The lower tree stratum of broad-leaved species included *Lithocarpus densiflora*, *Corylus rostrata* var. *californica*, *Acer circinatum*, and *Umbellularia californica*, but was of very low coverage and density in all sites (averaging only 80 stems/ha). The high shrub stratum, dominated by the arborescent coastal ecotypes of *Vaccinium ovatum* and *V. parvifolium* was, in contrast, highly developed; and in the S-facing stands this stratum formed a dense underbrush, with 3000 and 300 stems/ha respectively for the two species. More important undergrowth plants, besides these, included *Gaultheria shallon*, *Rhododendron californicum*, *Oxalis oregana*, *Polystichum munitum*, *Blechnum spicant* (L.) J. E. Smith, *Viola sempervirens*, *Galium triflorum*, *Trillium ovatum*, *Disporum smithii*, *Whipplea modesta* and, in ravines *Rubus spectabilis*, *Rhododendron occidentale*, and *Adiantum pedatum* var. *aleuticum*. Herb coverage (20-85%) was much higher than in the main Siskiyou study area, shrub coverage was variable from 1-10% in mesic to 70-95% in xeric sites. In stands of mesic flats the shrub cover approached zero and the herb coverage 90% or more, dominated by *Polystichum munitum* and *Oxalis oregana*.

2. In the hills above the Smith River near its junction with the South Fork, at elevations of 180-210 m, about 14 km from the nearest point on the coast, at the inland edge of the Sequoia range, Del Norte County, Calif. Few, widely scattered, large Sequoia occurred in stands strongly dominated in the upper tree stratum by *Pseudotsuga*. The lower tree stratum was dominated by *Lithocarpus* and (in less xeric stands) *Corylus*, averaging around 400 stems/ha each. *Arbutus menziesii*, *Quercus chrysolepis*, and *Cornus nuttallii* also occurred, predominantly in more xeric sites. As in the coast forest, *Vaccinium ovatum* dominated the high shrub stratum, reaching 2500-4000 small stems/ha; *Vaccinium parvifolium* and *Rhamnus purshiana* also occurred, along with numerous stems of *Rhododendron californicum*. Shrub coverages increased from 15-25% to 70-95%, herb coverages decreased from 60-70% to 0-10% along the moisture gradient. In general character this coenocline is one of *Pseudotsuga* forests with limited sclerophyll and heavy evergreen shrub undergrowth, physiognomically very similar to the Sequoia forests of slopes, but with a somewhat greater range of physiognomic and floristic variation along the moisture gradient.

3. Along the Smith River at its junction with the Siskiyou Fork, about 34 km from the coast, Del Norte County, Calif., on lower slopes with elevations between 350 and 450 m on slate soils. Forest stands were dominated by *Pseudotsuga* and, in mesic sites,

*Chamaecyparis*; of the four coastal conifers only *Tsuga heterophylla* occurred, in small numbers in mesic sites. *Lithocarpus* was the principal small tree, averaging 600 stems/ha; and the other principal small trees of the mixed evergreen forests were present. *Vaccinium ovatum*, *V. parvifolium*, *Rhododendron californicum*, and *Gaultheria shallon* were major shrubs; but the number of *Vaccinium* stems was much lower than in the preceding transects, reaching 250-750 small stems/ha in drier sites. Shrub coverage increased from 25-30% to 50-75%, herb coverage decreased from 30-40% to 0-5% along the moisture gradient. In general character this coenocline is one of mixed evergreen forests, gradating from *Chamaecyparis-Pseudotsuga* stands in ravines to sclerophyll-*Pseudotsuga* stands on xeric slopes, as in the diorite vegetation of the main study area.

4. Low-elevation vegetation already described—that of diorite (and metavolcanic rocks) in the Oregon Caves area, Josephine County, Ore., at 460-760 m, about 75 km from the coast—may serve as the fourth transect of the series. Sclerophyll density was still higher than in the Siskiyou Fork transect—averaging 800 stems/ha for *Lithocarpus* and 600 stems/ha for other species. Deciduous small trees averaged about as dense (250 stems/ha) as at Siskiyou Fork. *Vaccinium ovatum*, *V. parvifolium*, and *Rhododendron californicum*, on the other hand, were infrequent. Herb coverage decreased from 8-20% to 0-8% along the moisture gradient, and shrub coverage was between 10 and 40% in most stands.

5. Above Sturgis Creek, near Steve Peak, Josephine County, Ore., 15 km east from the Oregon Caves area, on metavolcanic rocks at elevations of 850-980 m. The vegetation was also mixed evergreen forest in predominant character, but showed effects of somewhat drier and more continental climate in a number of features. Three dominant species of the preceding vegetation patterns—*Chamaecyparis lawsoniana*, *Lithocarpus densiflora*, and *Gaultheria shallon*—were absent. Sclerophyll density, which had risen in the preceding series of transects, fell to an average of 500 stems/ha (from about 700 at comparable elevations in the Oregon Caves area), predominantly *Quercus chrysolepis* with smaller numbers of *Arbutus menziesii* and *Castanopsis chrysolepis*. Numbers of deciduous tree stems were higher—250 stems/ha in contrast to about 120 at comparable elevations in the Oregon Caves area—and included more numerous stems of *Quercus kelloggii* Newb. in more xeric stands. Important shrubs included *Berberis nervosa*, *Rhus diversiloba*, *Rubus vitifolius*, and *Rosa gymnocarpa*; they included also species rare in or absent from the Oregon Caves diorite transect—*Rubus leucodermis* and *R. parviflorus*, *Rosa spaldingii*, *Berberis piperiana*, and in xeric sites *Ceanothus integerrimus* and *Arctostaphylos viscosissimum* Peck. The herb stratum included most of the species familiar in the Oregon Caves area and some additional ones. Herb coverages decreased from 7-18% in more mesic to 0-5% in more xeric sites; shrub coverage was gen-

erally between 10 and 40%. Difference from the Oregon Caves diorite vegetation was most conspicuous in the south-facing slopes, where *Pseudotsuga* shared dominance with *Pinus ponderosa* and *P. lambertiana* in open stands with well-developed shrub strata. Pine dominance appeared to be at least partly a consequence of fire; but such stands are not encountered even as a consequence of burning in the Oregon Caves area on metavolcanic rock or diorite.

6. Near Beaver Creek, 105 km from the coast, on granite at elevations between 640 and 850 m, Jackson County, Oregon. More mesic stands were dominated by *Pseudotsuga* with a poorly developed sclerophyll layer; the (fire-affected) stands of south-facing slopes were dominated by *Pinus ponderosa* and *Pseudotsuga* in open growth. Representation of sclerophyll species (*Q. chrysolepis* and *Arbutus*) was still lower—200 stems/ha; representation of deciduous trees other than oaks only 170 stems/ha. *Quercus kelloggii* and *Q. garryana*, however, were in this area major small-tree species, contributing about 220 stems/ha on the average, with populations of 270 and 550, 150 and 390 stems/ha in the south-slope samples. Important shrubs included *Berberis nervosa* and *B. piperiana*, *Rubus vitifolius* and *R. leucodermis*, *Rhus diversiloba*, *Rosa gymnocarpa* and, in xeric sites, *Ceanothus integririmus*, *Arctostaphylos viscosissimum* and *A. viscida*. Herb stratum coverages decreased from 12-25% to 5-12%, shrub coverages increased from 7-25% to 20-50% along the moisture gradient. In general character the coenocline is one of *Pseudotsuga* forests with sclerophylls gradating into *Pinus-Pseudotsuga*-deciduous oak forests in xeric sites. The transition from mixed evergreen forest to oak woodland is represented in approximate equality of sclerophylls and deciduous oaks in the pattern as a whole, and pre-dominance of the oaks over sclerophylls in more xeric sites.

7. The final transect of the series was near Emigrant Creek, near Steinman in Jackson County, Oregon, at elevations between 820 and 1070 m, on andesite, 140 km from the Pacific Coast. Stands of ravines and mesic lower slopes were dominated by *Pseudotsuga* with *P. ponderosa* and *Libocedrus* present. Deciduous species in these coniferous forests included *Acer macrophyllum*, *Alnus rhombifolia*, and *Fraxinus oregana*. On the open NE slope *Pseudotsuga* shared dominance with *P. ponderosa* and *Libocedrus* in open stand, with a well-developed lower tree stratum (50% coverage) dominated by *Quercus garryana*. The conifers were absent from less mesic stands (open E and SE slopes), except for scattered *P. ponderosa*; these stands were oak woodlands of *Q. garryana* and *Q. kelloggii* with moderate tree (65 and 45%) and grass (20 and 60%) coverage. Sclerophylls were unimportant in either coniferous forest or oak woodland; only a few stems of *Arbutus* were recorded in the former. *Ceanothus integririmus*, *Arctostaphylos viscida*, and *Cercocarpus betuloides* were important high shrubs. Oak coverage decreased while grass coverage increased toward most xeric sites,

and open S and SW slopes supported grassland without or with widely scattered oaks. The grassland, severely disturbed, was dominated by *Elymus caput-medusae* where analyzed. This final vegetation pattern represents shrinkage of conifer forest into most mesic sites, reduction of the sclerophyll element to insignificance, and appearance of the oak woodland and valley grassland communities of the Interior as part of the coenocline, at the eastern end of the Siskiyou. The transitions from the Siskiyou vegetation to that of the Cascades and Interior are more complex than this single transect indicates; but the pattern described is that characteristic of low elevations in the interior valleys of the Rogue and Umpqua Rivers (Peck 1941).

Of the conclusions from this climatic transect, a series of trends may first be observed:

a) Stature and coverage of the coniferous high-tree stratum decreases progressively from the great Sequoia forests eastward. In inverse relation to this, the density of deciduous broadleaf trees increases toward the east. Maximum densities of sclerophylls (and of all broadleaf trees taken together) were in the Oregon Caves area near the middle of the transect, and the sclerophylls decrease toward both ends of the transect.

b) Both shrub and herb coverages decrease from the Sequoia forests to the middle of the transect, then increase again to the eastern end of the transect (though these trends are complicated by variations with site in a given area). Undergrowth coverages thus show some inverse correlation with development of the sclerophyll stratum.

c) Floristic trends in representation of life-forms, growth-forms, and areal types will be discussed in Part VI.

d) Distributions of species change in relation to the topographic gradient. (1) There is a general narrowing of species amplitudes toward the east. Many species occupy the whole of the topographic moisture gradient at Mill Creek, apparently none more than part of the gradient at Emigrant Creek. (2) Distributions of species (and community-types) shift along the moisture gradient in such a manner as to compensate for more or less humid climates. Species of wide amplitudes near the coast are increasingly restricted to the mesic end of the gradient toward the interior; species occurring in the interior transects are increasingly displaced toward the xeric end of transects nearer the coast. (3) Ecotypic populations show complex relations to parent materials and the climatic gradient. Many species largely restricted to "special" parent materials (serpentine, gabbro, quartzite, slate, argillite, marble), generally with more open or xeromorphic vegetation in one area, occur in the vegetation of "normal" parent materials (granite, diorite, andesite, metavolcanic rocks) in a drier and more continental climate toward the east. In contrast to this, several species (*Vaccinium parvifolium*, *V. ovatum*, *Vancouveria chry-*



*santha*, *Galium ambiguum*, *Polygala californica*) had ecotypic populations widely distributed in the humid coastal forests, and other populations largely restricted to serpentine and gabbro in the drier climate of the main study area.

Second, the results indicate that the prevailing climaxes of the Siskiyou at low elevations are: (1) Sequoia forest near the Coast, (2) a belt of coastal Pseudotsuga forest within this, (3) Mixed Evergreen Forests over the greatest part of the range between these coastal Forests and the interior valleys, (4) Oak Woodlands in these valleys at the eastern end of the range. The Oregon Caves study area on diorite, within the area of maximum development of the sclerophylls, is thought as "representative" of the mixed evergreen forests at their best development in the Siskiyou as any area known to the author. In relation to the Mixed Evergreen Forest region as a whole, however, it represents not average or median conditions, but those of maximum stand density toward the northern and mesophytic limits of these forests.

A final result of significance is the continuity of vegetational change along the climatic gradient studied (cf. Whittaker 1956). This continuity can scarcely be perfect, considering the irregular topography and effects of parent materials. But with allowance for these, the climatic gradient was expressed in gradual transformation of communities in both physiognomy and floristic composition, in shifts of position along the moisture gradient for both species populations and community-types, and not in abrupt transition. This continuity is the more impressive in that four formations—the Coast Forest, Mixed Evergreen Forest, Oak Woodland, and Valley Grassland—are involved. One can divide the continuity by prevailing climaxes and major community-types, but these approaches do not clarify the underlying quantitative relations. The approach through comparison of moisture-gradient patterns makes possible some quantitative analysis of the gradual transformation of community-types and vegetation patterns along a climatic gradient.

## V. PROBLEMS OF CLASSIFICATION

There are many ways of classifying vegetation; and most studies are influenced not merely in form of presentation, but in the way vegetation is observed and sampled, by the author's particular approach to classification. One object of the present study was to take samples which could be used to compare different approaches to classification. The preceding description embodies the author's own approach through physiognomy and dominance. The same material may be considered, however, in relation to several major vegetation units—the formation, dominance-type, sociation, association, and union.

### FORMATIONS

A formation is a grouping of communities which are similar in physiognomy and in broader environmental relations (cf. Beadle & Costin 1952, Whittaker

1957). Four formations—Coast Forest, Mixed Evergreen Forest, Oak Woodland, and Valley Grassland—appear in the climatic transect; three other forest formations—Montane Forest, Subalpine Forest, and Pine Woodland—occur in other environments. The Montane Forests and Subalpine Forests are in these mountains physiognomically continuous with one another. If they are to be separated as formations, as is customary, it must be on the basis of environmental relations, primarily elevation, and broad floristic and geographic relations, to the western Montane Forests and circumboreal taiga, not physiognomy. The yellow pine woodlands or pine steppes of the western states are often treated as part of the Montane Forest Formation. Their physiognomy is fundamentally different, however; and they may well, even though they intergrade with the closed Montane Forests, be regarded as a separate formation. Pine woodlands appear both on serpentine in the central Siskiyou (dominated by *P. jeffreyi*) and in drier situations of middle and higher elevations in the eastern part of the range (dominated by *P. ponderosa*).

The Mixed Evergreen Forests have affinities with the sclerophyll vegetation complex of California. Two major community-types have been recognized in this complex—the chaparral of shrubs and the broad sclerophyll forest dominated by trees (Cooper 1922, Oosting 1956). Among the associations of the broad-sclerophyll forest formation Cooper (1922) recognized one, the *Lithocarpus densiflora-Quercus chrysolepis-Arbutus menziesii* association, as characteristic of lower altitudes of the north Coast Ranges of California. He further observed that this association is itself somewhat a transition between broad-sclerophyll and coniferous types; for it rarely occurs without a sprinkling of conifers, especially Pseudotsuga, and its principal species occur commonly as an understory in the Pseudotsuga and Sequoia forests. Cooper's Lithocarpus-Quercus-Arbutus association is part of the Mixed Evergreen Forest, as designated by Munz & Keck (1949, 1950, 1959) and understood in this paper. The sharing of dominance between evergreen needle-leaved and sclerophyllous trees, and the transitional relation to the sclerophyll vegetation on the one hand, the Coastal and Montane Forests on the other, are essential features of this community-type.

The Mixed Evergreen Forest is unrecognized as a major community-type in its own right in many accounts (Weaver & Clements 1938, Oosting 1956). It is evidently transitional between sclerophyll and conifer forests, but only in the sense that many major community-types are transitional between other community-types. More critical than its transitional relation in evaluating the Mixed Evergreen Forest are the facts that: (1) It is itself a grouping of a number of dominance-types or associations. (2) It is the regional climax of an extensive area of the Klamath Region and north California Coast Ranges. (3) It possesses, especially on some parent materials,

a wealth of character-species largely or wholly restricted to it. The author advocates recognition of the Mixed Evergreen Forest as one of the major community-types of western North America and, because its definition is physiognomic, prefers to regard it as a formation. The characterization suggested for it is: mixed forest with an upper tree stratum of needle-leaved evergreen or coniferous and a lower tree stratum of broad-leaved evergreen or sclerophyllous species, but with these varying widely in coverage and density in different stands. Either one or both of these strata may be either relatively dense or quite open, but as both become open the formation gradates into pine-oak woodland.

A much more complex pattern of physiognomic types of vegetation exists in the western states than in the eastern, and in many cases the formations seem to intergrade as parts of longer physiognomic continua. These circumstances suggest that the approach developed by Beard (1944, 1955) in the tropics may be appropriate to western vegetation. The approach permits the conception of physiognomic relations of vegetation through larger numbers of more narrowly defined formations, arranged in formation-series complexly intersecting one another in relation to major gradients of environment. The author is not prepared to erect a system of formations and formation-series for the whole of the Klamath Region. The material discussed suggests, however, these major relations on more typical soils: (1) At low elevations, from the Coast inland, with decreasing precipitation and increasing continentality—Coast Forest, Mixed Evergreen Forest, Oak Woodland, and Valley Grassland. (2) At low elevations, in maritime environments near the Coast, with increasingly humid climates—Chaparral, Broad-Sclerophyll Forest, Mixed Evergreen Forest, and Coast Forest. (3) In the central Siskiyou Mountains, from low elevations to high—Mixed Evergreen Forest, Montane Forest (and ponderosa pine woodland in some drier sites), Subalpine Forest.

#### DOMINANCE-TYPES AND SOCIATIONS

Within the formations accepted by the author for the Siskiyou Mountains, various *dominance-types* defined by species dominance may be recognized. Within the Subalpine Forests *Abies nobilis* and *Tsuga mertensiana* dominance-types, within the Montane Forests *Abies concolor* and *Pseudotsuga menziesii*, dominance-types, within the Coast Forests *Sequoia sempervirens* and *Pseudotsuga menziesii* dominance-types may be distinguished. Such types defined by a single dominant species are "consociations" in Clementsian terminology (Clements 1928, 1936, Weaver & Clements 1938).

The author attempted to classify samples from mixed evergreen forests by combinations of dominant species, to see whether the stands would fall naturally into groups representing well-defined dominance-types. They did not, and a large number of types intergrading with one another resulted. These may

be grouped into three more broadly defined dominance-types: Chamaecyparis-Pseudotsuga forests of mesic sites, with deciduous and sclerophyll lower-tree strata, forming closed stands on diorite and more open ones with Libocedrus and *P. lambertiana* on gabbro. (2) Pseudotsuga-Lithocarpus-Arbutus forests, with other sclerophylls present and in some circumstances dominant and with wide variation in coverage of the tree strata, occurring along most of the moisture gradient on diorite and in less xeric sites on gabbro. Pseudotsuga-sclerophyll and sclerophyll-Pseudotsuga physiognomic subtypes are distinguished within this dominance-type (Part III). (3) Open Pinus-Pseudotsuga-*Q. chrysolepis*-Arctostaphylos forests of more xeric sites on gabbro and eastward from the main study areas.

Vegetation types defined by dominant species of the various strata, or by combinations of stratal unions, are properly termed *sociations* (Du Rietz 1930, 1936, Nordhagen 1937, 1943, Braun-Blanquet 1951, Hanson 1953, Böcher 1954); such units permit a finer division of the vegetation into more numerous types than dominance-types based on the uppermost stratum alone. An effort was also made to classify the Siskiyou samples by stratal dominants, with results similar to those on dominance-types: a very large number of sociations, intergrading with one another through various combinations of dominance in the different strata, differing widely in extensiveness or importance, many of them of no observable significance in relation to environmental difference, resulted. Much of the Siskiyou vegetation is relatively rich in species and shows no well-defined dominance in the lower strata. Certain community-types with well-marked stratal dominance (e.g. *Abies concolor*-*Arctostaphylos nevadensis*-*Xerophyllum tenax* forest and *Pinus jeffreyi*-*Arctostaphylos viscida*-*Stipa lemmoni* woodland on serpentine, *Sequoia sempervirens*-*Tsuga heterophylla*-*Vaccinium ovatum*-*Polystichum munitum* Coast Forest) are conveniently defined in the manner of sociations. But the experiments with classification of Siskiyou vegetation support the European experience, that the sociation is a unit best suited to communities with marked stratal dominance such as occur, for the most part, in floristically poor vegetation.

#### ASSOCIATIONS

The principal vegetation unit of phytosociology is the *association*, defined primarily by character-species—species of narrower ecological amplitudes which are largely or wholly restricted to or, at least, centered in, stands of a given community-type (Braun-Blanquet 1932, 1951). The samples taken from the Siskiyou vegetation were intended to be relatively complete floristically and suitable for classification into associations, although they include no data on bryophytes and lichens. The transects provide an effective picture of the distributional relations which underlie problems of floristic classification.

The transects show that population centers or distributional modes, and also the limits of distributions, are scattered along the various gradients studied. Species populations do not form well-defined groups of character-species with similar or congruent distributions. Character-species groupings must be created by the phytosociologist, and there are a number of ways in which the species of a given vegetation pattern may be grouped without violating their distributional relations (cf. Whittaker 1956). It is consequently often possible to choose character-species groupings which fit into community-types recognized initially by physiognomy, dominance, and environmental relations. It cannot be assumed that these units, secondarily defined by floristic composition, will be the same as the units which would be recognized by a phytosociologist who sought to base his work primarily on floristic composition. It is at least possible, however, to bring these two major approaches to vegetation classification into some accommodation to each other. Full discussion of the floristic approach to classification of this vegetation is outside the scope of the present monograph; but

character-species groupings by which the author's community-types may be defined as associations (or, more probably, higher units of this system) are indicated in the following section on distributional groupings.

QUANTITATIVE APPROACHES TO CONTINUITY AND SPECIES GROUPING

The work on classification included also experiments on quantitative methods by which relative discontinuities and natural clusters of species might be objectively revealed from the transect tables. The first of these methods is designed as an aid to the recognition of different rates of change between community-types. Percentage similarities (see Part VI) were computed between successive steps of the transect tables, for each of the three strata on each of the three parent materials. The resulting values are plotted in line graphs (upper halves of Figs. 15-17). Most of the graphs are of the form to be expected in continuously gradating vegetation—points generally at the same level, but with some zig-zag up and down due to chance variations in stand composition. Low points appear between the first and second steps on gabbro and serpentine. The change indicated is that from riparian communities of wet

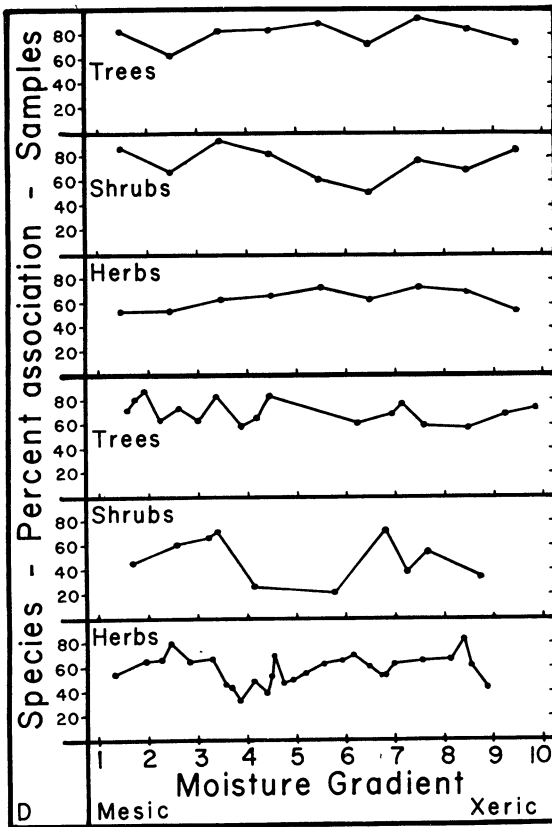


FIG. 15. Sample and species associations in a transect of the moisture gradient at low elevations on diorite. Above—percentage similarities of successive steps of the transect, for the tree, shrub, and herb strata. Below—percentage similarities of distributions of pairs of species, for the three strata.

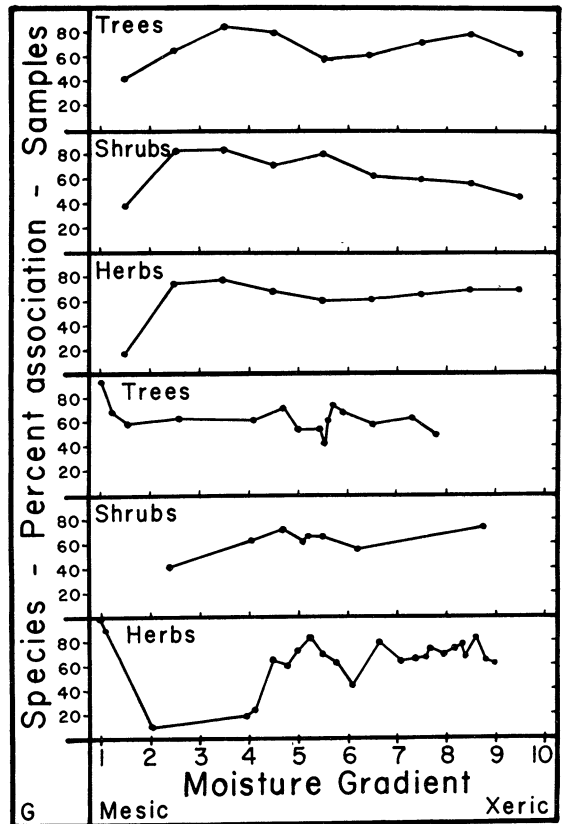


FIG. 16. Sample and species associations in a transect of the moisture gradient at low elevations on gabbro.

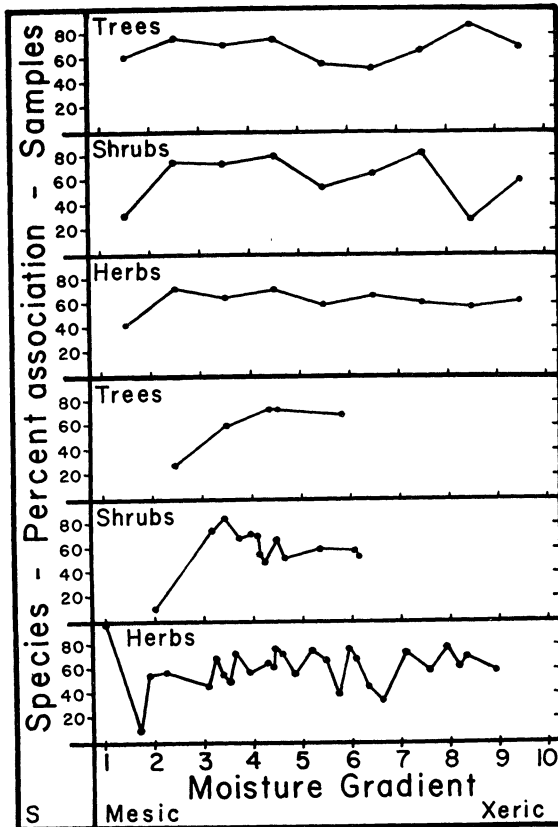


FIG. 17. Sample and species associations in a transect of the moisture gradient at low elevations on serpentine.

soils along stream-sides to the communities of mesic slopes above the ravines. It may be interpreted as a steeper gradient of community composition in response to a steeper environmental gradient, rather than as a vegetational discontinuity occurring along a uniform gradient. Two other low points—in the shrub strata between steps 8 and 9 of the serpentine transect, 6 and 7 of the diorite transect—appear to result from sample irregularity without vegetational discontinuity, and suggest caution in the interpretation of such data.

The other technique is designed to reveal natural clusters of species populations in the transects. For each species represented by significant numbers of individuals, two values were computed: (1) The mean position of the population in relation to the transect gradient, computed from  $\frac{\sum nx}{\sum x}$ , in which  $x$  is the num-

ber of individuals of the species in a given step of the transect,  $n$  the number of the step in the transect. These values may bear little relation to population centers or modes, but provide an indication of relative positions along the gradient. (2) The percentage similarity of species distributions for all pairs

of species, by the formula  $PS_d = \sum \min(a, b)$ , in which  $a$  is the per cent of the total population of species A in the transect table which occurs in a given step of the table, and  $b$  the same for species B (Whittaker & Fairbanks 1958). Percentage similarities of distribution were computed for all possible pairs of species in a given stratum for a given transect table, and the resulting values were arranged in matrices or Kulezyński triangles. Species were then arranged in sequence on the basis of their "mean positions"; and for each pair of species contiguous in the sequence, a point was entered in the species-association diagrams indicating the distributional association value from the matrix on the ordinate, the mid-point between the mean positions of the two species on the abscissa.

Natural clusters of species should appear as clusters of points in the diagram which are both of high values for distributional similarity, and close together in mean position along the abscissa. Individualistic scattering of species distributions should be reflected in points which are neither very high nor very low but moderate and variable, forming an irregular, zig-zag line. It is the latter pattern which appears in the results, in the lower halves of Figs. 15-17. The species of the most distinctive union of the vegetation described, the shrubs of the two-phase serpentine vegetation, do not show very strong distributional association with one another, or generally higher association with one another than with other shrubs with distributions overlapping theirs. The graphs do indicate distinct clusters of undergrowth species in ravines (points 1 on the transects); these clusters again represent the distinctive stream-side communities. The species which these clusters comprise are easily shown to be individualistic in their distributional relations to elevation, the three soil parent materials, and geography; they are clustered in relation to the range of environments represented by a given transect, but not in their over-all distributions. Results thus support conclusions suggested in a previous study (Whittaker 1956:22). Natural clusters are weakly developed in, or absent from, most of the vegetation studied, but may be present in some circumstances. Where they occur, as in the stream-side communities, they are not exceptions to the principle of species individuality; and their recognition is dependent on the range of conditions over which distributional relations of species are observed. What is a natural cluster in relation to one transect or one local vegetation pattern may not be a natural cluster in a broader range of vegetational observation.

#### DISTRIBUTIONAL GROUPINGS

Species occurring in significant numbers in the principal study area, at low elevations on serpentine or gabbro or at any elevation in forests on diorite, have been classified into distributional groupings. Despite the arbitrariness of such groupings, they may have real usefulness; they are used here to summarize

distributional relations of the Siskiyou species dealt with, to avoid repetitious listing of species in the vegetation descriptions, and to provide some definition of major community-types by character-species groupings. A distributional grouping, within a given stratum or life-form, is regarded as a *union* (Lippmaa 1935, 1939, Du Rietz 1936, Oosting & Billings 1943, Billings 1945, Braun-Blanquet 1951:47-49, Daubenmire 1952, Whittaker 1956). The groupings given here are based on broad relations to topographic moisture gradients, elevation, and parent material as represented in the transects; they are not intended to reflect any distributional relation outside the range of environments covered by these transects. Most species can be found outside the indicated distribution patterns, which are intended to represent more frequent occurrence in communities, and to exclude very scattered occurrence at transect constancies of less than 6 or 8%. Certain species with complex distributional relations, or morphologically distinct populations in different habitats, are listed more than once.

1. Riparian species, occurring predominantly on or near stream-banks in ravines at lower (and middle) elevations, in forests in which *Chamaecyparis lawsoniana* occurs as a dominant.

On diorite (character-species of *Chamaecyparis-Pseudotsuga* forests) at lower, or at middle (\*) elevations: Herbs—*Aralia californica*, *Athyrium filix-femina*\*, *Carex laeviculmis*\*, *C. mertensii*\*, *Claytonia spathulata*, *Listera cordata*, *Luzula parviflora*\*, *Pleuropogon refractus*\*, *Satureja douglasii*, *Tolmiea menziesii*\*.

On diorite and gabbro (character-species of *Chamaecyparis-Pseudotsuga* forests): Trees—*Alnus rhombifolia*, *A. rubra*. Herbs—*Boykinia elata*, *B. major*.

On gabbro (character-species of *Chamaecyparis-Pseudotsuga* forests): Herbs—*Epipactis gigantea*, *Erigeron cervinus*, *Juncus ensifolius*, *Peltiphyllum peltatum*, *Woodwardia fimbriata*.

On gabbro and serpentine (occurring in *Chamaecyparis-Pseudotsuga* and *Chamaecyparis-P. monticola-Pseudotsuga* ravine forests of these two parent materials): Shrub—*Rhododendron occidentale*. Herbs—*Carex debiliformis*, *Cypripedium californicum*, *Darlingtonia californica*, *Eriophorum crinigerum* (Gray) Beetle, *Habenaria sparsiflora*, *Rudbeckia californica*, *Tofieldia glutinosa ssp. occidentalis* (Wats.) C. L. Hitchc.

On serpentine (character-species of *Chamaecyparis-P. monticola-Pseudotsuga* forests): Shrubs—*Physocarpus capitatus*, *Rosa californica*. Herbs—*Carex angustior*, *Castilleja miniata*, *Galium multiflorum*, *Helenium bigelovii*, *Lilium occidentale*, *Trillium rivale*.

2. Lower-elevation mesic species of diorite, or diorite and gabbro (\*), centered in *Chamaecyparis-Pseudotsuga* forests but occurring also in more mesic *Pseudotsuga-sclerophyll* forests: Trees—*Acer circinatum*, *Amelanchier florida*\*, *Salix* sp., *Taxus brevifolia*.

Shrubs—*Gaultheria shallon*\*, *Philadelphus lewisii*, *Vaccinium parvifolium*. Herb—*Polystichum munitum*.

3. Mesic forest species of lower and middle elevations on diorite, or diorite and gabbro (\*), centered in and character-species for *Chamaecyparis-Pseudotsuga* forests, but occurring also in more mesic *Pseudotsuga-sclerophyll* forests at lower, and montane forests at middle, elevations, and in many cases in lower subalpine forests: Trees—*Acer macrophyllum*\*, *Corylus rostrata* var. *californica*. Shrubs—*Holodiscus discolor*\*, *Pachystima myrsinites*, *Rhododendron californicum*. Herbs—*Cephalanthera austinae*, *Coptis laciniata*, *Heuchera micrantha*, *Linnaea borealis*, *Listera caurina*, *Mitella ovalis*, *Pyrola bracteata*, *Senecio bolanderi*, *Viola sempervirens*.

4. Mesic species of low elevations on serpentine (character-species of the forest-shrub complex) or on serpentine and gabbro (\*): Tree—*Pinus monticola*. Shrubs—*Amelanchier gracilis*\*, *Berberis pumila*, *Garrya buxifolia*, *Juniperus sibirica*, *Lithocarpus densiflora* var. *echinoides*, *Quercus chrysolepis* var. *vaccinifolia*, *Rosa gymnocarpa*, *Umbellularia californica* (shrubby population), *Vaccinium parvifolium*. Herbs—*Angelica arguta*, *Antennaria suffruticosa*, *Arnica spathulata* var. *eastwoodiae*\* (Rydb.) Mag., *A. parviflora* ssp. *parviflora*\*, *Aster brickelliioides* Greene, *Epilobium rigidum*, *Haplopappus racemosus* ssp. *congestus* (Greene) Hall, *Ligusticum apifolium*, *Lilium howellii*, *Lomatium howellii*\*, *Lotus oblongifolius*\*, *Lupinus latifolius* var. *columbianus*, *Sancicula peckiana*, *Tauschia glauca*, *Vancouveria chrysantha*.

5. Species with broad moisture-gradient distributions at lower elevations on diorite, or diorite and gabbro (\*), character-species of Mixed Evergreen Forests in a broad sense, occurring also in *Chamaecyparis-Pseudotsuga* forests: Trees—*Arbutus menziesii*\*, *Castanopsis chrysophylla*, *Cornus nuttallii*\*, *Lithocarpus densiflora*\*, *Quercus chrysolepis*\*. Shrubs—*Berberis pumila*, *Rhus diversiloba*\*, *Symphoricarpos hesperius* G. N. Jones, Herbs—*Allotropia virgata*\*, *Lathyrus pauciflorus*, *Lonicera hispidula*\*.

6. Species with broad moisture-gradient distributions at lower and middle elevations on diorite, or on diorite and gabbro (\*), occurring in mixed evergreen and *Chamaecyparis-Pseudotsuga* forests of lower elevations and montane forests of middle elevations, and in many cases extending into lower subalpine forests: Shrubs—*Berberis nervosa*, *Rosa gymnocarpa*, *Rubus parviflorus*\*, *R. vitifolius*. Herbs—*Achlys triphylla*, *Adenocaulon bicolor*, *Apocynum pumilum*, *Bromus suksdorfii*, *Galium triflorum*, *Festuca occidentalis*\*, *Goodyera decipiens*, *Iris chrysothylla*\*, *Melica harfordii*.

7. Species with broad moisture-gradient distributions at low elevations on gabbro and serpentine:

On gabbro: Trees—*Pinus ponderosa*, *Umbellularia californica*. Shrubs—*Garrya fremontii*, *Vaccinium ovatum*. Herbs—*Carex multicaulis*, *Festuca californica*, *Galium bolanderi*.

On gabbro and serpentine: Tree—*Libocedrus decurrens*. Shrubs—*Convolvulus polymorphus*, *Holodiscus dumosus*, *Rhamnus californica* var. *occidentalis*. Herbs—*Galium ambiguum*, *Polygala californica*, *Polystickum munitum* var. *imbricans*, *Pyrola dentata*, *Schoenolirion album*, *Viola lobata*, *Xerophyllum tenax*.

On serpentine: Tree—*Pinus attenuata*. Shrub—*Arctostaphylos nevadensis*. Herbs—*Balsamorhiza deltoidea*, *B. platylepis*, *Calamagrostis koeleroides*, *Cordylanthus viscidus*, *Hieracium cynoglossoides* var. *nudicaule* Gray, *Iris bracteata*, *Lotus crassifolius*, *Phlox speciosa*, *Sedum laxum*.

8. Species of lower elevations in more xeric sites on diorite and gabbro, character-species of sclerophyll-Pseudotsuga forests (including Pinus-Pseudotsuga-Quercus-Arctostaphylos forests on gabbro):

On diorite: Herbs—*Collomia heterophylla*, *Cypripedium fasciculatum*, *Festuca rubra*, *Madia madioides*, *Psoralea physodes*, *Tauschia kelloggii*.

On diorite and gabbro: Tree—*Quercus kelloggii*. Herbs—*Boschniakia hookeri*, *Campanula prenanthoides*, *Pteridium aquilinum* var. *pubescens*.

On gabbro: Tree—*Arctostaphylos cinerea*. Shrub—*Ceanothus integerrimus*. Herb—*Hieracium bolanderi*.

9. Species of more xeric sites at lower elevations on serpentine, or on serpentine and gabbro (\*). The former are character-species for the *Pinus jeffreyi* woodlands on serpentine; the latter occur also in Pinus-Pseudotsuga-Quercus-Arctostaphylos forests on gabbro: Tree—*Pinus jeffreyi*. Shrubs—*Arctostaphylos viscida*, *Quercus garryana* var. *breweri*. Herbs—*Achillea lanulosa*, *Agrostis hallii*\*, *Bromus brevibracteatus*, *Calochortus howellii*, *C. tolmiei*, *Ceanothus pumilus*\*, *Cheilanthes siliquosa*, *Danthonia californica*, *Elymus glaucus*, *Epilobium paniculatum* var. *hammondi*, *Erigeron foliosus* var. *confinus*\*, *Eriogonum nudum*\*, *E. ternatum* Howell, *Eriophyllum lanatum* var. *achillaeoides*\*, *Horkelia sericata*, *Koeleria cristata*, *Lomatium macrocarpum*, *L. triternatum*, *Melica geyeri*, *Monardella odoratissima* var. *glaucula*\*, *M. villosa* var. *subserrata*\*, *Pentstemon laetus* ssp. *roezlii* (Regel) Keck, *Perideridia oregana*, *Phacelia dasphylla* var. *ophitidis*, *Senecio fastigiatus*\*, *Sidalcea malvaeflora* ssp. *elegans*\* (Greene) C. L. Hitch., *Sitanion jubatum*, *Stipa lemmoni*\*, *Zygadenus micranthus*.

10. Species occurring at or centered in middle elevations, 1200-1800 m, on diorite, character-species for the montane forests dominated by *Pseudotsuga menziesii* and *Abies concolor*. Many of these species extend into low elevations in *Chamaecyparis-Pseudotsuga* forests, and some (\*) were recorded frequently from open situations as well as forests: Trees—*Abies concolor*, *Acer glabrum* var. *douglasii*. Shrub—*Rubus nivalis*. Herbs—*Actaea spicata* L., *Anemone deltoidea*, *Asarum caudatum*, *A. hartwegi*, *Circaea alpina* var. *pacifica* (Aesch. & Mag.) M. E. Jones, *Clintonia uniflora*, *Corallorhiza striata*, *Festuca sub-*

*liflora*, *Habenaria sparsiflora*, *Hackelia jessicae*\*, *Lathyrus polyphyllus*, *Nemophila parviflora*, *Osmorhiza occidentalis*\*, *Tiarella unifoliata*, *Vancouveria hexandra*, *Viola glabella*\*, *Vicia californica*.

11. Species of middle- and higher-elevation forests, occurring in both montane and subalpine forests, or both these forests and more open situations (\*): Shrubs—*Quercus sadleriana*, *Ribes marshallii*, *R. viscosissimum*, *Symphoricarpos rivularis*, *Vaccinium membranaceum*. Herbs—*Agastache urticifolia*\*, *Arenaria macrophylla*, *Arnica latifolia*, *Artemisia douglasiana*\*, *Campanula scouleri*, *Claytonia spathulata* Dougl., *Corallorhiza maculata*, *Dicentra formosa*, *Fragaria vesca* var. *bracteata*, *Hydrophyllum occidentale*\*, *Luzula spicata*, *Mitella diversifolia*, *Monardella odoratissima*\*, *Osmorhiza chilensis*, *Phacelia magellanica*\* Coville, *Polygonum phytolaccaefolium*\*, *Pyrola secunda*, *Rubus lasiococcus*, *Senecio triangularis*\*, *Smilacina stellata* (L.) Desf.

12. Species of forests of high elevations, centered above 1800 m, character-species of subalpine forests dominated by *Tsuga mertensiana* and *Abies nobilis*, and species of both these forests and more open situations (\*): Trees—*Abies nobilis*, *Tsuga mertensiana*. Shrub—*Lonicera conjugalis*\*. Herbs—*Anemone quinquefolia*, *Angelica arguta*, *Aquilegia formosa*\*, *Aster siskiyouensis*, *Bromus carinatus*\*, *Carex rossii*, *C. tracyi*\*, *Castilleja miniata*\*, *Claytonia parvifolia* Moc., *Corallorhiza mertensiana*, *Delphinium sonnei* Greene, *Elymus glaucus*\*, *Epilobium hornemanni*, *Erigeron aliciae*\*, *Erysimum capitatum*\* (Dougl.) Greene, *Ligusticum grayi*\*, *Lupinus albicaulis*\*, *Mertensia bella*, *Mitella breweri*, *Orogenia fusiformis*, *Pedicularis racemosa*, *Penstemon anguineus*, *P. nemorosus*, *P. newberryi* Gray, *Poa bolanderi*\*, *Polygonum davisiae*\*, *Sanicula nevadensis*\*, *Saxifraga ferruginea*, *Smilacina racemosa* var. *glabra*, *Trisetum spicatum*, *Valeriana sitchensis* ssp. *sitchensis*, *Veratrum insolitum*\*, *Viola praemorsa*, *V. sheltonii*.

13. Parent-material ubiquitousists, occurring at low elevations on diorite, gabbro, and serpentine: Trees—*Chamaecyparis lawsoniana*, *Pinus lambertiana*, *Pseudotsuga menziesii*. Herbs—*Adiantum pedatum* var. *aleuticum*, *Chimaphila umbellata* var. *occidentalis*, *Disporum hookeri*, *Festuca ovina*, *Luzula campestris*, *Smilacina racemosa*, *Trientalis latifolia*, *Trisetum canescens*, *Whipplea modesta*.

14. Elevation ubiquitousists, occurring in forests of all elevations on diorite: Herbs—*Campanula scouleri*, *Chimaphila menziesii*, *Chimaphila umbellata* var. *occidentalis*, *Festuca occidentalis*, *Hieracium albiflorum*, *Melica subulata*, *Phlox adsurgens*, *Pyrola picta*, *Smilacina racemosa*, *Trillium ovatum*.

## VI. FLORISTIC COMPARISONS

Floristic comparisons for different vegetation patterns and communities in the Siskiyou Mountains are summarized in three tables (17, 18, 20). These tables are intended to show the manner in which life-form composition, growth-form composition and species-diversities, and geographic relations of floras

change in relation to four major environmental gradients—the diorite-gabbro-serpentine series of parent materials, local topographic moisture gradients on each of these, elevation on diorite, and the east-west climatic gradient. The basic unit of comparison is the transect flora—the list of species (with presence values of 4% or more) in a given transect of 50 samples. One list (1920-2140 m on diorite) included all species in a 16-sample transect; and the lists for the east-west climatic gradient are based on all species of 6-sample transects. The comparisons for different moisture-gradient conditions and community-types in the central Siskiyou are based on lists of species occurring more than once in the mesic, intermediate, and xeric ranges of the transects (steps 1-2, 3-7, 8-10). The lists for mesic, intermediate, and xeric sites correspond to community-types: on diorite—Chamaecyparis-Pseudotsuga, Pseudotsuga-sclerophyll, and sclerophyll-Pseudotsuga forests; on gabbro—Chamaecyparis-Pseudotsuga, sclerophyll-Pseudotsuga, and Pinus-Pseudotsuga-Quercus-Arcostaphylos forests; on serpentine—Chamaecyparis-*P. monticola*-Pseudotsuga forest, mixed conifer stands with two-phase undergrowth (forest-shrub complex), Jeffrey pine woodland.

LIFE-FORMS AND GROWTH-FORMS

In the life-form spectra for lower elevations in the central Siskiyou (Table 17), floristic dominance is shared equally by phanerophytes and hemicyptophytes, with smaller, but substantial, numbers of chamaephytes and geophytes and few therophytes. These spectra represent the mixed evergreen forests and express the temperate, moderately humid forest climate of the region. Very similar spectra have been obtained for eastern deciduous forests, as represented in the spectra for Appalachian cove forest (mixed mesophytic) and Long Island oak-chestnut forest in Table 17. The spectra give no indication of the wide differences in climate and physiognomy of these forests on opposite sides of the continent; life-form spectra are relatively insensitive to some differences of environment and community character, highly sensitive to others. The "normal spectrum" for the flora of the world computed by Raunkiaer (1918, 1934) is often used as a standard of comparison. For detailed comparisons among temperate-zone forests a different kind of standard may be appropriate—one representing mesophytic, floristically rich forests of unglaciated areas, midway between the phanerophyte dominance of the tropics and warm-temperate forests and the hemicyptophyte dominance of cooler-temperate forests. The very similar spectra for Arcto-Tertiary remnants on opposite sides of North America suggest such a spectrum. Averaging two spectra for the Mixed Mesophytic Forest of the East (Withrow 1932, Cain 1945) and two for the Mixed Evergreen Forest in the West (South Fork and Beaver Creek, for the transition to redwood forest and a more continental phase) gives the gen-

TABLE 17. Relations of life-forms to environments in the Siskiyou Mountains, per cents of species in floras of transects and site groupings.

	Phanerophytes	Chamaephytes	Hemicyptophytes	Geophytes	Therophytes	No. of species
<b>A. Central Siskiyou Mtns., by parent materials, 610-915m</b>						
Quartz diorite.....	32	12	30	24	2	84
Olivine gabbro.....	32	14	32	19	2	101
Serpentine.....	20	19	44	15	3	116
<b>B. Central Siskiyou Mtns., by sites, 610-915m</b>						
On diorite—Mesic.....						
Intermediate.....	35	14	28	21	2	72
Xeric.....	33	10	33	22	2	79
Xeric.....	31	8	42	13	0	47
On gabbro—Mesic.....						
Intermediate.....	34	11	33	21	1	73
Intermediate.....	30	22	35	12	1	72
Xeric.....	29	23	38	8	2	66
On serpentine—Mesic.....						
Intermediate.....	27	19	35	18	1	88
Intermediate.....	25	24	39	12	1	102
Xeric.....	15	17	43	14	11	76
<b>C. Central Siskiyou Mtns., by elevation belts on diorite</b>						
460-760 m.....	35	10	32	19	3	86
760-1070 m.....	33	12	33	20	3	92
1070-1370 m.....	30	9	37	20	4	99
1370-1680 m.....	25	10	40	21	4	106
1680-1920 m.....	18	14	44	18	6	98
1920-2140 m.....	10	17	54	12	7	72
<b>D. West-East climatic gradient across Siskiyou, low elevations</b>						
Mill Creek.....	48	5	34	13	0	41
South Fork.....	38	10	29	23	0	58
Siskiyou Fork.....	40	9	31	20	0	56
Sturgis Creek.....	33	12	37	16	2	93
Beaver Creek.....	30	14	37	15	4	102
Emigrant Creek.....	27	5	35	10	23	81
<b>E. Comparable spectra from other areas</b>						
Cove forest, Great Smoky Mts., Tenn. (Cain 1945).....						
	36	4	30	26	3	113
Mixed mesophytic forest, Cincinnati, Ohio (Withrow 1932).....						
	34	4	34	23	4	127
Chestnut Oak forest, Long Island, N.Y. (Cain 1936).....						
	35	11	33	21	1	92
Oak-hickory climax, Piedmont, N. Car. (Oosting 1942).....						
	60	0	36	4	0	89
Mediterranean live-oak forest, 0-500 m elev. (Braun-Blanquet 1936).....						
	54	9	24	9	4	
Beech forest, Cevenne Mts., 1000-1500 m elev. (Braun-Blanquet 1936).....						
	2	4	52	40	2	
Subalpine forests, Great Smoky Mts. (Cain 1945).....						
	21	2	57	17	3	301
Subalpine forests, Olympic Mts., Wash. (Jones 1936).....						
	12	7	49	31	1	
Subalpine forests, Mt. Rainier, Wash. (Jones 1938).....						
	11	8	47	31	3	
Serpentine and gabbro in Tuscan (Pichi-Sermolli 1948).....						
	11	9	40	15	26	405
"Normal spectrum" (Raunkiaer 1918, 1934).....						
	46	9	26	6	13	
Mid-temperate mesophytic forests.....						
	34	8	33	23	2	

eralized "mid-temperate mesophytic forest" spectrum entered in Table 17.

Effects of parent material within a given climate are indicated by the first three spectra of this table.

All three spectra have the general pattern of the mixed evergreen forests; but from diorite through gabbro to serpentine the phanerophytes and geophytes decrease, while chamaephytes and hemicyptophytes increase. The effect of the topographic moisture gradient at low elevations on diorite, as represented in the second series of spectra, appears in reduction of chamaephytes, increase in hemicyptophytes and therophytes toward drier sites. Somewhat comparable results appear in the contrast of north and south-facing slopes within the same climate in the eastern forests by Oosting (1942), Cantlon (1953), and Miller & Buell (1956). Generally similar trends in relation to site moisture appear also in the low-elevation gabbro and serpentine floras. The xeric serpentine spectrum, representing Jeffrey pine woodland, is the lowest in phanerophytes of the low-elevation Siskiyou forests, and is similar in character to the spectrum for ophiolitic soils (serpentine and gabbros) in a drier Mediterranean climate as given by Pichi-Sermolli (1948, see Table 17). Changes in life-form representation with elevation in mountains, such as have been shown in other areas by Guyot (1920), Hansen (1930), Raunkiaer (1934), Gelting (1934), Braun-Blanquet (1936, see Table 17), Jones (1936, 1938), Allan (1937), Davidsson (1946), Cain (1950), Dansereau (1957), and Costin (1959), are indicated in the third series of spectra. The decline of the phanerophytes and increase of the chamaephytes and hemicyptophytes toward higher elevations are consistent with observations in other areas; the slight increase in therophytes is in contrast to results in most other areas. The spectra for subalpine forests in the Siskiyou (1670-1920 and 1920-2140 m) resemble those of other subalpine or Canadian zone forests (Table 17) in proportions of phanerophytes and hemicyptophytes, but differ in other respects. As suggested by the larger per cent of therophytes, subalpine climates in the Siskiyou are probably drier than in the other ranges.

The fourth series of spectra, finally, represent the change in climates from the coastal redwood forests at Mill Creek to the interior valley at Emigrant Creek; the central Siskiyou (Oregon Caves area) diorite sample fits into this series between Siskiyou Fork and Sturgis Creek. Since life-form spectra give little expression of the difference between maritime and continental climates, the gradient in question is primarily one of decreasing climatic humidity. The four gradients studied parallel one another to some extent in the kind of departure from the spectra of the mixed evergreen forests, or the generalized mid-temperate mesophytic forest, they produce. In this area an approach toward a more "extreme" environment, whether of parent material, elevation, or topographic or climatic dryness in almost all cases implies a decrease of phanerophytes and geophytes and an increase of therophytes.

Table 18 summarizes the distribution of growth-forms over some of the same range of environments. A number of trends in the representation of growth-

TABLE 18. Relations of growth-forms and species-diversities to environments in the Siskiyou Mountains.

	Numbers of species in floras of transects and site groupings					Average number of species in vegetation samples					
	Trees	Shrubs	Forbs	Grammoid	Total	Trees	Shrubs	Forbs	Grammoid	Total	
<b>A. Central Siskiyou Mtns., by parent materials, 610-915 m</b>											
Quartz diorite.....	17	13	46	8	84	43	7.9	4.0	10.7	0.9	23.5
Olivine gabbro.....	16	19	54	12	101	45	7.0	3.4	11.0	1.4	22.8
Serpentine.....	9	18	73	16	116	59	4.5	6.2	16.5	2.9	30.1
<b>B. Central Siskiyou Mtns., by sites, 610-915 m</b>											
On diorite—Mesic.....	15	11	42	4	72	42	9.7	4.5	11.7	0.7	26.6
Intermediate.....	15	11	48	5	79	50	7.6	3.9	11.0	1.2	23.7
Xeric.....	9	6	27	5	47	53	6.5	3.7	9.3	0.7	20.2
On gabbro—Mesic.....	16	10	40	7	73	41	7.0	4.0	10.3	0.8	22.1
Intermediate.....	10	13	44	5	72	52	7.0	2.8	9.9	1.5	21.2
Xeric.....	10	11	40	5	66	48	7.0	3.5	13.3	2.0	25.8
On serpentine—Mesic.....	9	18	56	5	88	59	5.3	8.3	18.4	2.2	34.2
Intermediate.....	9	19	68	6	102	72	5.2	6.6	16.8	2.5	31.1
Xeric.....	6	7	49	14	76	72	2.7	2.6	14.0	4.0	23.3
<b>C. Central Siskiyou Mtns., by elevation belts on diorite</b>											
460-760 m.....	18	13	47	8	86	42	7.8	3.8	11.3	1.1	24.0
760-1070 m.....	19	15	50	8	92	44	6.1	4.2	11.9	0.6	22.8
1070-1370 m.....	15	12	62	10	99	55	3.8	4.4	20.2	1.0	29.4
1370-1680 m.....	13	13	70	10	106	39	3.5	3.4	24.5	1.4	32.8
1680-1920 m.....	6	8	76	8	98	36	2.5	1.7	18.4	1.7	24.3
1920-2140 m.....	3	3	58	8	72	50	1.8	0.7	14.0	1.5	18.0
<b>D. West-East climatic gradient across Siskiyou, low elevations</b>											
Mill Creek.....	11	8	17	5	41	74	5.0	3.7	6.5	0.2	15.4
South Fork.....	11	11	33	3	58	46	5.2	5.0	8.6	0.7	19.5
Siskiyou Fork.....	13	10	30	3	56	57	7.3	5.0	9.4	0.3	22.0
Sturgis Creek.....	17	16	48	12	93	42	7.8	6.7	17.5	1.7	33.7
Beaver Creek.....	13	17	57	15	102	37	7.2	7.2	15.0	2.6	31.9
Emigrant Creek.....	10	12	44	15	81	33	4.2	3.8	12.0	3.7	23.7

forms in these floras are evident. Numbers of tree species may be observed to decrease (1) from diorite through gabbro to serpentine, (2) from low elevations toward higher ones, (3) from the central Siskiyou (Oregon Caves and Sturgis Creek) toward the Pacific Coast, (4) from the central Siskiyou toward the drier interior, and (5) from mesic sites toward xeric within the central Siskiyou. Numbers of shrub species (1) increase somewhat from diorite to gabbro and serpentine, (2) decrease toward higher elevations, (3) increase from the Coast to the eastern Siskiyou (Beaver and Sturgis Creeks), and (4) decrease from mesic sites toward xeric ones within the central Siskiyou. The decline in shrub species toward higher elevations parallels that for trees and is part of the very general decrease in floristic diversity of woody strata toward the north and toward higher elevations (cf. Whittaker 1956:11).

The increase in numbers of shrub species from the the Coast toward the Interior is paralleled among the herbs. The data for Emigrant Creek suggest that these trends do not extend beyond the floristically rich communities of the eastern Siskiyou into those



of the continental Interior. Because of the disturbance at Emigrant Creek, however, the numbers of shrub and herb species there cannot be relied upon as comparable with those of the other transects. The increase in numbers of graminoid species along this same gradient into the drier and more open vegetation of the Interior is marked.

Within each of these growth-forms, trends in the representation of evergreen *vs.* deciduous forms appear, notably along the climatic gradient from the Coast inland. Evergreen forms are strongly dominant in all strata in the redwood forests at Mill Creek, they are predominant in the woody strata, at least, of the mixed evergreen forests of the central Siskiyou, but in the oak woodlands at Emigrant Creek deciduous forms are strongly dominant in all strata. The most striking expression of continentality in these floras is not in life-form spectra, but in the representation of evergreen forms both in numbers of species in floras and in community and stratal dominance.

#### SPECIES-DIVERSITIES

The data in Table 18 bear on another problem of community relations to environment—that of species-diversities, or the relative richness of communities in numbers of species. Studies of species-diversity (Fisher *et al.* 1943, Williams 1945, 1947, 1951, 1953, 1954, Preston 1948, Simpson 1949, Whittaker 1952, MacArthur 1957, Hairston 1959) have dealt mostly with animal populations, in which measurements can be based on numbers of species *vs.* numbers of individuals. Although measurements of this type can be applied to plants (Williams 1950, Margalef 1949, 1951, 1958, Black *et al.* 1950, Patrick *et al.* 1954, Hopkins 1955, Whittaker 1956, Dahl 1957, Curtis 1959) the author has preferred, because of the problem of what constitutes an individual among many plants, to deal with numbers of species in fixed sampling areas—whether the individual community-samples or the combined areas of the samples for a moisture-gradient transect.

There may be a general tendency for species-diversity, community productivity and biomass, development of the woody strata, and differentiation of the community into strata, to decrease from environments which are “favorable” in the sense of being warm, moist, and equable, toward environments which are “unfavorable” or “extreme” in their low temperatures, or aridity, or instability, or low nutrient levels, or high salinities. As indicated in Table 18, species-diversities do decrease along the moisture gradient in the mixed evergreen forests on diorite, and in a less clear-cut fashion on gabbro and serpentine. Species diversities increase, however, from the relatively humid and equable climates of the Coast toward the drier and more variable climates of the Interior. Even more striking is the increase in floristic diversity from the “normal” diorite to the “abnormal” serpentine soils. In relation to elevation, finally, it may be observed that the expected decrease in num-

bers of species toward higher elevations occurs among woody plants, but not herbs; and the diversity relations of the latter are such that total numbers of species increase into middle elevations before decreasing into the highest elevations sampled.

These data do not fit into any simple pattern of interpretation in relation to environmental favorableness. It is difficult to frame any definition of “favorableness” that does not amount to the observation that those environments are most favorable to high species-diversity where high species-diversities are encountered. Floristic diversity appears to occur as it occurs, a complex resultant of a number of influences which are at present scarcely understood. The limited interpretations which may be offered for the present material are as follows: (1) There is some correlation between species-diversity of a stratum and the extent of its development as expressed in coverage or biomass. This correlation, however, is conspicuously a partial one to which exceptions may be observed; one author (Yount 1956) has even suggested the reverse relation. (2) Diversity relations to environment are clearly different for different community fractions and groups of organisms (cf. Whittaker 1956:18). In the Siskiyou, a general inverse relation appears between diversities of tree strata and undergrowth. (3) In this vegetation the herb strata in all cases include half or more of the total vascular flora; and community diversity is in large part an expression of herb stratum diversity. (4) The conditions which are “favorable” for maximum diversity of herb strata, and thereby for community diversity, are not the conditions most favorable for development of the tree stratum and community biomass. Maximum herb-stratum diversities are encountered in the more open vegetations of drier climates and “atypical” parent materials, in which lower tree coverage permits greater development of the undergrowth. And, from low to middle elevations, herb-stratum and community diversity also increase as the density of tree cover (determined primarily by the density of sclerophylls) decreases.

Perhaps the most significant diversity trend encountered is that from maritime to continental climates. Average numbers of vascular plant species per sample increased inland from 15.4 in the Mill Creek redwood forests, to 33.7 in the mixed evergreen forests at Sturgis Creek. Biological meaning of this trend is quite uncertain. The greater variety of temporal niches, of life-history timings avoiding direct competition, in the more widely variable seasons of the continental climate may contribute to it, along with the more open structure of the inland forests. There is also a marked decrease in average amplitudes of species distributions along topographic moisture gradients, from the coast inland. The corollary of this decrease in species amplitudes is an increase in floristic differentiation of communities along the moisture gradient, from the coast inland. It is as if only one flora occupied the whole of the

moisture gradient in the redwood belt, but two or three floras in the inland environments. Because the distributions of species overlap more broadly in the maritime pattern, the community types there seem to intergrade and interpenetrate one another more broadly. Because of the narrower amplitudes in the continental climates, a larger number of distinguishable community-types appear along the moisture gradient, and these community-types seem more distinct.

The increasing species-diversities from the coast inland are thus the product of two phenomena—diversity of individual stands, and relative differentiation of vegetation patterns along topographic moisture gradients—, both increasing inland to produce the observed contrasts. The extent to which these contrasts characterize continental and maritime climates in general is unknown; but they are consistent with conditions of western Europe observed by Rübel (1927) and with the author's material on the central Siskiyou and the more strongly continental Great Smoky Mountains. The two phenomena involved suggest the need for distinguishing three aspects or levels of species-diversity in natural communities: (1) The richness in species of a particular stand or community, or a given stratum or group of organisms in a stand. Fisher's (1943) *alpha* index is one means of measuring this, which may be designated primary or "alpha" diversity. (2) The extent of change of community composition, or degree of community differentiation, in relation to a complex-gradient of environment, or a pattern of environments, which may be designated secondary or "beta" diversity. (3) The species-diversity of a number of community samples, for some range of environments, which have been combined, so that the diversity value is a resultant of both alpha and beta diversities of these samples. The transect diversities of Table 18 are of this tertiary or "gamma" diversity type, as are many of those for animal collections to which diversity measurements have been applied. The same types of measurements may be applied to "gamma" as to "alpha" diversity; "beta" diversity represents a different problem, to be discussed in the following section.

#### SAMPLE SIMILARITIES AND COENOCLINE DIFFERENTIATION

There are many possibilities for expressing the relative similarity or dissimilarity of two communities; but two most simple and direct ones have been most widely used—*coefficient of community* and *percentage similarity* (Whittaker & Fairbanks 1958). The coefficient of community, first used by Jaccard (1902a, 1902b, 1908, 1912, 1932; Koch 1957) is:

$$CC = \frac{\text{number of species in both samples or floras}}{\text{number of species in one or both}}$$

Percentage similarity, which, with variations, has been independently discovered and used by a num-

ber of authors (Gleason 1920, Kulezyński 1928, Renkonen 1938, Dyksterhuis 1949, Odum 1950, Whittaker 1952; Bray 1956, Curtis 1959) compares two samples in terms of percentage composition:

$$PS = 1 - 0.5 \Sigma |a - b| = \Sigma \min(a, b),$$

in which *a* and *b* are the percents which a particular species includes of the total samples A and B. The computation, and some of the limitations inherent in the measurement, have been discussed elsewhere (Whittaker 1952, Whittaker & Fairbanks 1958).

It has been observed that olivine gabbro is chemically intermediate to quartz diorite and serpentine, and correspondingly supports vegetation which is intermediate and connects the very anomalous serpentine communities with the "normal" ones of diorite. Physiognomically the gabbro vegetation is intermediate, but closer to that of diorite. It is consequently of interest to determine the underlying floristic similarities of these vegetation patterns, computing coefficients of community for lists of 81, 101, and 116 species in the transects. Resulting values were—diorite *vs.* gabbro 34.4%, gabbro *vs.* serpentine 38.2%, diorite *vs.* serpentine, 14.8%. The gabbro flora shares species in almost equal proportions with diorite and serpentine.

Percentage similarities also were used to compare the three vegetations in terms of quantitative composition of stands. The three comparison standards (see Part II) for mesic sites (ravines), intermediate slopes (open E-facing), and xeric slopes (open SW-facing) were compared in all possible combinations, with separate computations for the tree strata and undergrowth. Relations of interest in the resulting sample-association matrices include the following:

1) In general, the gabbro samples are clearly intermediate to the comparable samples from other parent materials; but in detail, complex interrelations appear. The gabbro ravine samples were more similar to serpentine than to diorite ravine samples in both strata; among E-slope samples gabbro was more similar to diorite than to serpentine; among SW-slope samples the gabbro undergrowth was equally similar to diorite and serpentine, but the tree stratum was closer to diorite. Averaging all three samples together, the undergrowth of gabbro was closer to serpentine (21%) than to diorite (15%), while the tree stratum of gabbro was closer to diorite (36%) than to serpentine (20%).

2) In general, the contrast between the different vegetation patterns increased from mesic sites to xeric ones. Averaging percentage similarities for the strata and parent materials (diorite *vs.* gabbro and gabbro *vs.* serpentine) gave: 30% for ravine samples, 27% for east slopes, and 13% for southwest slopes.

3) In all cases the SW-slope samples were more similar to E-slope than SW-slope samples of the next parent material in the series—diorite, gabbro, serpentine. This fact is to be correlated with the "shift toward the mesic" of species distributions (Part VII).

4) Although percentage similarities for the tree stratum and undergrowth are necessarily correlated, lack of any strict consistency of these is evident in the data. In extreme cases contrasts of these values were as high as 67 and 34, 30 and 8, 9 and 1%. This fact is consistent with what has already been observed on the lack of strong correlation between different strata and community-fractions.

A further problem to which such measurements may be applied is that of degree of differentiation of the communities along an environmental gradient. "Half-changes" in a rather crude form were suggested in a previous study (Whittaker 1956) as a basis of such measurement. A quite different approach has been suggested as the "index of biotal dispersity" of Koch (1957).

The simplest measurement of beta diversity may be

the relation,  $\beta = \frac{\alpha}{\gamma}$ , in which  $\alpha$  is the diversity value

for an individual sample and  $\gamma$  that for the sample resulting from merging a number of individual samples from a community pattern or coenocline. Thus, comparing Fisher *alpha* measurements for average numbers of tree species and individuals in individual samples, with those for tree species and individuals in whole transects, gives "beta" diversities of 1.95 for diorite, 2.24 for gabbro, and 2.33 for serpentine at low elevations, and 1.60 for high-elevation forests (1920-2140 m) on diorite. An alternative approach, when a particular gradient is in question, is direct comparison of the extremes of the gradient by either coefficient of community or percentage similarity. Results have been found generally unsatisfactory; for such values are often zeroes, or so low as to permit no effective comparison. In the search for a more effective measurement, a number of transects from the Great Smoky and Siskiyou Mountains have been studied to determine the relations of percentage similarity and coefficient of community to distance along ecological gradients.

When these values on a logarithmic scale are plotted against distance along a gradient, the curves take the form illustrated in Fig. 18. The striking feature of the curves is the apparent straight-line relation between environmental gradients and log of sample similarities along much of the length of the gradients. Three qualifications of this straight-line relation must, however, be observed: (1) These straight lines, extrapolated back to zero intervals along the gradient, strike the ordinate not at 100% but at 70% or 80% (and values as low as 40% and as high as 95% have been obtained on other transects). This is consistent with the fact that coefficient of community and percentage similarity measurements for two samples from the same stand yield not 100%, but values of these magnitudes (cf. Whittaker 1952:12 on "internal association," Bray & Curtis 1957). (2) Beyond a certain point, the lower parts of the curves slope off with rapidly increasing steepness toward zero similarity. This also must be

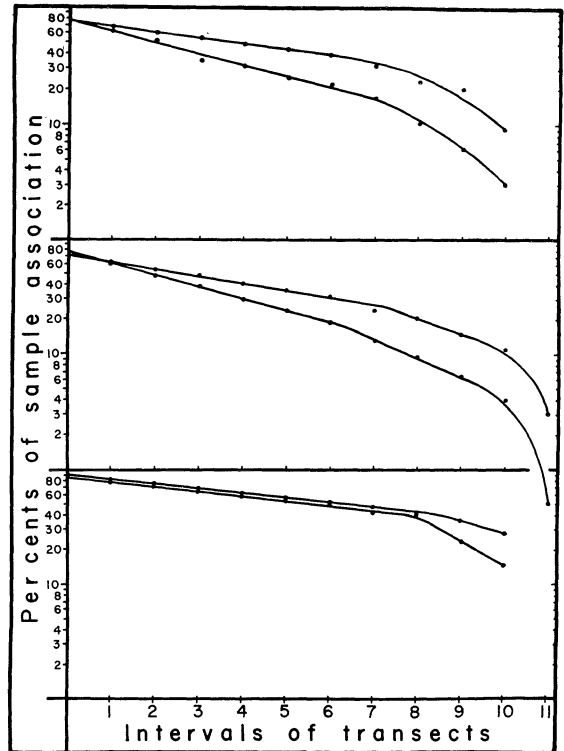


FIG. 18. Change in community composition, as measured by coefficients of community and percentage similarities for the tree strata, in relation to environmental gradients in transects. In each case the upper curve is for coefficients of community, the lower for percentage similarities; both these values are plotted on logarithmic scales. Top—along the elevation gradient in the Great Smoky Mountains; transect intervals are 400 ft (122 m). Middle—along the topographic moisture gradient between 460 and 760 m, Great Smoky Mountains. Bottom—along the topographic moisture gradient, 610-915 m on diorite, Siskiyou Mountains. Curves are smoothed by averaging values for given numbers of intervals along the transects; thus the first point plotted is an average of comparisons of samples one transect step apart, the second point an average of comparisons of transect steps two intervals apart, etc.

the case for, though species reach their limits gradually, one by one, along the gradient, a point is ultimately reached beyond which no species present in the first sample occurs. (3) In some curves of this type, steepness gradually increases beyond the first 2-3 intervals of the transect.

For the straight portions of the curves, change in community composition in relation to distance along an environmental gradient may be expressed in relatively simple form:  $y = ab^x$ , in which  $y$  is sample similarity (coefficient of community or percentage similarity),  $x$  is the number of intervals along the gradient,  $a$  is the value of  $y$  for zero distance, and  $b$  is the constant ratio which determines the slope of the line on log-linear plot and expresses rate of com-

munity change in relation to the scale of the x axis.

Or:  $y = ae^{-\lambda x}$ , in which  $\lambda$  also is a constant for slope in the form of the decay constant. This relation may provide, with due allowance for its limitations, a unit for "ecological distance" (Whittaker 1952, 1956)—relative distance along an environmental gradient, as expressed in change in community composition in response to that gradient. The "half-change" unit may be defined as the distance along an environmental gradient necessary to reduce sample similarity to one-half that of the zero distance.

When coefficient of community or percentage similarity values are available for a transect, the number of half-changes along the gradient may be determined:

$$z = a \times 2^{-\beta}$$

$$\beta = \frac{\log a - \log z}{\log 2}$$

in which  $\beta$  is the number of half-changes,  $a$  is the sample similarity at zero intervals, and  $z$  is the sample similarity for samples from the extremes. This measurement, however, gives a disproportionate weight to the sample comparison for the extremes. A measurement which better expresses community change along the gradient as a whole can be derived from the slope of the first, nearly linear portion of the curve. The line formed by this, extrapolated to the number of environmental intervals represented by the extremes of the transect, indicates a value of  $z$ , from which a value for  $\beta$  may be determined. Table 19 gives percentage similarity half-changes by both methods. From this, and the author's other ma-

terial on the Great Smoky and Siskiyou Mountains, the following observations are suggested:

1) Extent of change of community composition, or "coenocline differentiation," as measured in half-changes along the moisture gradient, increases from the diorite to the serpentine vegetation pattern. The lower coenocline differentiation on gabbro may reflect its location closer to the coast.

2) Extent of population change along the moisture gradient tends to increase from the tree, through the shrub, to the herb stratum (Table 19). This contrast in rates of change of different strata becomes conspicuous in some subalpine forests (Whittaker 1956).

3) There is some decrease in coenocline differentiation with increasing elevation in the forest vegetation of the Smokies and the central Siskiyou. This tendency does not apply equally to all strata and elevations, and is most marked in the tree strata of highest elevations.

4) There is a very impressive increase in coenocline differentiation in all strata from the Coast inland in the Siskiyou, as indicated above. Coenocline differentiation is still higher in the lower-elevation forests of the Great Smoky Mountains, in a more continental climate, than in any of the mixed ever-green forest areas.

5) Coenocline differentiation and numbers of species in individual stands, beta and alpha diversities, appear to increase and decrease in parallel over most of the range of environments represented in the study.

The results discussed do not fit into any very simple pattern of interpretation. The greater humidity and more equable temperatures of the maritime climate may imply smaller contrast of moisture-balance conditions in most xeric and most mesic sites, and therefore a smaller contrast of moisture-balance conditions along the topographic moisture gradient in a maritime, as compared with a continental, climate. The more open vegetation structure of serpentine, with greater exposure to insolation and evaporation, may imply greater contrast in moisture-balance conditions along the moisture gradient than on diorite.

In general, extent of change in community composition seems correlated with extent of environmental contrast along the topographic moisture gradient. Coenocline differentiation is not a direct expression of range of environments, however. In the Great Smoky Mountains there is striking contrast in the degree of change in tree-stratum composition between the *Picea-Abies* forests above 4500 feet on the one hand, and the mostly deciduous forests outside the range of spruce and fir at the same elevations, on the other. Coenocline differentiation may thus be affected by the kinds of communities that develop in a range of environments, as well as by that range of environments itself. Coenocline differentiation, like species-diversity of samples, is presumably a community characteristic complexly related to characteristics of environments and of the communities which

TABLE 19. Change in community composition (percentage similarities) along the topographic moisture gradient in low-elevation transects in the Siskiyou Mountains, by parent materials and strata.

Transect	Estimated percentage similarity for zero transect steps	Percentage similarity for transect steps 1 and 10	Indicated half-changes	Percentage similarity of transect steps 1 & 10 from extrapolation of straight line	Indicated half-changes
Diorite					
Trees.....	90	17.8	2.5	43	1.1
Shrubs.....	90	14.2	2.7	22	2.0
Herbs.....	82	5.8	3.7	15	2.4
Gabbro					
Trees.....	73	27.9	1.4	40	.86
Shrubs.....	72	25.0	1.5	38	.92
Herbs.....	-70	14.3	2.3	24	1.6
Serpentine					
Trees.....	80	7.0	3.5	23	1.8
Shrubs.....	72	7.0	3.4	21	1.8
Herbs.....	70	3.8	4.2	18	2.0

TABLE 20. Geographic Relations of Floras.

	PARENT MATERIAL AND ELEVATION IN THE CENTRAL SISKIYOU MTS.						EAST-WEST CLIMATIC TRANSECT OF THE SISKIYOU MT.: AT LOW ELEVATIONS						
	Low-Elevation Forests			High-Elev. Forests		Summits		West. . . . . Coastal			East Continental		
	Quartz diorite	Olivine gabbro	Serpentine	Quartz diorite	Serpentine	Quartz diorite	Serpentine	Mill Creek	South Fork	Siskiyou Fork	Sturgis Creek	Beaver Creek	Emigrant Creek
Total nos. of spp. in transect floras. . . . .	84	101	116	81	87	54	48	41	58	56	93	102	81
Floristic Groups (per cent of transect floras)													
Siskiyou Endemic. . . . .	1	7	16		5	2	8	2	2	2	1		
Klamath Endemic. . . . .		3	9	4	6	7	10		2		1	3	
Sierran. . . . .	4	9	10	6	10	7	6	2	3	2	3	8	6
Sierra-Cascadian. . . . .	8	5	3	7	2	7	2		7	9	6	5	6
Cascadian. . . . .	1	1	6	5	6	6	6	2	2	2	1	3	
Sierra-Coastal. . . . .	6	13	9	1	7	4	2	2	3	5	6	5	4
Coastal. . . . .	12	20	15	6	11	6	6	7	9	11	11	10	5
Coastal-Northern. . . . .	17	9	5	6	2	2		39	28	27	12	11	7
Western. . . . .	36	25	21	38	34	46	48	27	34	30	39	37	48
Nearctic. . . . .	15	10	11	25	17	13	10	17	10	12	19	19	23
Floristic Vectors													
Tree: North. . . . .	3.4	3.1	3.0	4.2	2.9			3.6	3.5	3.3	3.4	3.5	4.0
East. . . . .	2.3	2.3	2.3	2.8	2.7			2.4	2.4	2.2	2.5	2.9	2.8
South. . . . .	3.0	3.4	3.3	2.2	3.4			2.2	3.0	2.8	3.2	3.5	3.8
Total. . . . .	8.7	8.8	8.6	9.2	9.0			8.2	8.9	8.3	9.1	9.9	10.6
Shrub: North. . . . .	3.7	2.6	1.5	3.0	2.2	3.0		4.1	4.6	4.0	3.2	3.4	3.2
East. . . . .	2.5	2.0	1.6	2.8	2.5	2.8		1.8	2.5	2.4	2.6	2.8	3.2
South. . . . .	2.6	2.6	2.1	2.0	3.3	3.0		2.4	2.5	2.7	2.7	2.6	3.2
Total. . . . .	8.8	7.2	5.2	7.8	8.0	8.8		8.3	9.6	9.1	8.5	8.8	9.6
Forb: North. . . . .	3.6	2.5	1.9	3.6	2.5	2.8	2.1	4.3	3.6	3.8	3.4	3.2	3.4
East. . . . .	2.9	2.2	1.9	3.4	3.0	3.0	2.7	3.2	2.8	3.0	3.2	3.2	3.2
South. . . . .	2.8	2.5	1.8	2.5	2.3	2.4	2.0	3.1	2.9	2.9	2.8	2.5	3.0
Total. . . . .	9.3	7.2	5.6	9.5	7.8	8.2	6.8	10.6	9.3	9.7	9.4	8.9	9.6
Graminoid: North. . . . .	4.4	3.4	3.3	4.6	4.1	3.5	3.6	4.6	4.0	3.3	4.0	4.5	4.2
East. . . . .	4.2	3.3	3.8	4.6	4.4	3.8	4.1	2.8	2.3	3.3	5.1	4.6	4.9
South. . . . .	2.9	2.6	2.9	3.2	3.1	3.5	3.4	2.0	2.3	2.7	3.1	2.7	2.8
Total. . . . .	11.5	9.3	10.0	12.4	11.6	10.8	11.1	9.4	8.6	9.3	12.2	11.8	11.9
All together: North. . . . .	3.6	2.7	2.1	3.8	2.7	2.9	2.3	4.1	3.8	3.8	3.5	3.5	3.6
East. . . . .	2.8	2.3	2.2	3.5	3.1	3.1	2.9	2.7	2.6	2.7	3.2	3.3	3.5
South. . . . .	2.8	2.7	2.1	2.6	2.6	2.6	2.3	2.6	2.8	2.8	2.9	2.7	3.1
Total. . . . .	9.2	7.7	6.4	9.9	8.4	8.6	7.5	9.4	9.2	9.3	9.6	9.5	10.2
Maximum extents (per cent of transect floras)													
North. . . . .	45	29	21	37	22	22	10	56	47	45	34	33	30
East. . . . .	13	10	15	23	22	22	25	17	9	12	20	18	18
South. . . . .	13	27	23	9	20	19	12	12	12	14	16	12	15
Indeterminate	29	35	41	31	37	37	52	15	33	29	30	37	37

develop in those environments, and may be very differently expressed in different strata and groups of organisms in the same communities.

GEOGRAPHIC RELATIONS OF FLORAS

Another approach to analysis of relations of plant life to environments in the Siskiyou Mountains is possible, that dealing with geographic relations of floras. The comparisons given in Table 20 are based on transect floras; data are given also for species in 6 samples of high-elevation serpentine vegetation ranging from *Abies nobilis* forest to *Pinus jeffreyi* woodland at elevations between 1900 and 2100 m on Big Red and Little Red Mountains and Observation Peak. Summit lists are based on collections from

four of the high peaks on acid or intermediate rocks (Lake Mtn., Mt. Elijah, and Grayback Peak, and Mt. Ashland) and two high peaks of serpentine (Big Red Mtn. and Observation Peak).

Geographic relations of all species, and subspecies and varieties, were codified in two ways. All were classified first by areal types on the basis of statements of distribution in floristic manuals (primarily Peck 1941, Abrams 1940-51, Jepson 1923-5). Areal types in relation to plant communities have been much less studied in North America than in Europe (cf. Hansen 1930, Böcher 1938, 1954, Meusel 1939, 1943, Schmid 1950, Ellenberg 1950, Walter 1954), and the information on which to base them is less adequate; but a system was developed with the fol-

lowing major types: (1) Siskiyou Endemics—species (or, when distinguished, subspecies or varieties) restricted to the narrower area of the Siskiyou Mountains, (2) Klamath Endemics—restricted to the larger Klamath Region, (3) Sierran—extending south from the Klamath Mountains and having the principal area of occurrence in the Sierra Nevada, (4) Cascadian—extending northward and having the principal area of occurrence in the Cascade Range, (5) Sierra-Cascadian—extending both north into the Cascades and south into the Sierra Nevada, (6) Sierra-Coastal—extending south from the Klamath Region both in the Sierra Nevada and the Coast Ranges, (7) Coastal—extending along the California and Oregon coasts (including coastal mountains), but not north along the coast to Washington, (8) Coastal-Northern—extending northward along the coast to Washington and beyond with extensive occurrence in the area of mesophytic forests surrounding Puget Sound, (9) Western—widespread in the western Interior, especially the Great Basin and interior mountain ranges, (10) Nearctic—of wide distribution in North America, extending eastward beyond the Rocky Mountains.

The second approach was through actual extent of species areas in a given direction—north (and west to Alaska), east, and south. Because of the difficulty of translating statements of distribution in floristic manuals into numbers of km, arbitrary 7-point scales were used to express distances of extent, not beyond: 0—the Siskiyou Mountains themselves in a given direction; 1—the Klamath Region north and south, and the Cascades east; 2—the Oregon-Washington border northward, the Oregon-Idaho border and central Nevada eastward, and middle California (Monterey) southward; 3—the Washington-British Columbia border northward, the Idaho-Wyoming border and central Utah eastward, and southern California (Los Angeles) southward; 4—Prince Rupert, British Columbia northward, eastern Wyoming and the Colorado Front Range eastward, northern Baja California southward; 5—the north-south border of Alaska and Yukon territory and its projection to the coast northward, west-central Kansas and Nebraska (100th meridian) eastward, Guaymas southward; 6—the Alaska Peninsula and Bering Sea northwestward, the Mississippi River eastward, Mexico City southward; 7—northwestward into Siberia, eastward to the Atlantic Ocean, southward into Central America or beyond.

Representation of areal types in the low-elevation floras of the three parent materials in Table 20 is very significantly different. There are few narrowly endemic species in the diorite flora (*Tauschia kelloggii* is the only such species in the list); but the number of species endemic to the Siskiyou Mountains and the Klamath Region increases to 10% of the gabbro and 25% of the serpentine floras. The three parent materials show marked differences also in the decreasing representation of Coastal-Northern species and increasing importance of a southern or "Californian"

grouping including the Sierran, Coastal, and Sierra-Coastal species from diorite to serpentine. These relations seem interpretable on the basis that the gabbro and serpentine vegetation is more open and more xerophytic in appearance, with greater exposure of the undergrowth to light and evaporation. A larger proportion of the species of the closed forests on diorite extend into the relatively dense mesophytic forests to the north of the Siskiyou; a larger proportion of the gabbro and serpentine floras extend into the more open and xerophytic communities of California (Whittaker 1954b). The data suggest that different parent materials in the same climate may not only have marked effects on extent of narrow endemism in their floras, but may act as differential filters, admitting different proportions of species from the whole spectrum of geographic relations into their floras.

Various trends in floristic relations appear when floras of low-elevation forests on diorite and serpentine are compared with those of high-elevation forests and high summits on these same parent materials. The proportion of narrow endemics is higher in the higher-elevation floras on diorite, and representation of wide-spread Western species (of interior mountains, primarily) increases toward higher elevations, especially on serpentine. The contrast between serpentine and diorite floras decreases toward higher elevations, though it is by no means absent at the highest elevations available for study. This trend is consistent with the more general observation that floristic distinctiveness of serpentine is less in far-northern environments (and especially glaciated areas) than in warm-temperate and tropical ones (Whittaker 1954b).

Floristic trends in the east-west climatic transect include: (1) Decreasing proportions of coastal species, in the broad sense, toward the interior. (2) Among the different coastal groups, the Coastal-Northern species decline in numbers into the drier climates of the interior, but the Coastal and Sierra-Coastal species increase in numbers from Mill Creek to Sturgis Creek. There is no paradox in this increase of "Coastal" species toward the interior since most of them are species of the California Coast Range mountains, rather than the more narrowly maritime environments of the coast itself. (3) Representation of Sierran and Sierra-Cascadian species increases toward the interior. (4) Representation of the widespread Western and Nearctic species also increases inland. These trends seem clearly correlated with climates; for the more mesophytic species of the Coastal-Northern grouping decrease toward the interior while species of the somewhat drier and more continental climates of the California mountains and the interior increase. Representation of narrowly endemic species is small throughout; for representation of these is generally high on special parent materials, moderate at high elevations on any parent material, but low on the more "normal" parent materials at low elevations.

The data on floristic "vectors," or relative extents in different directions, are compiled in two forms in Table 20. Distance values for the different directions have been averaged for species within growth-forms, and for whole floras; and numbers of species with greatest extent in a given direction, according to the scale values, are tabulated also for whole floras. Direction of greatest extent is determined in this case by the largest of the three values for directional extent. "Indeterminate" species are those in which the two highest scale values were equal; and many of the narrow endemics are included among these.

A very marked decrease in average extent of species areas appears in the series of floras from diorite through gabbro to serpentine. This decrease applies, in essentially parallel fashion, to the shrub and forb groupings; but it does not apply to trees and graminoids; for the conifers and grasses of serpentine are predominantly widespread Western or Nearctic species. In directions of maximum extent also, the diorite and serpentine floras are in contrast. A high proportion of species have maximum extent to the north in the former, maximum extent to the south in the latter. On both soils average distances of extent appear to increase from low-elevation into high-elevation forests, but to be lower in the summit floras, with their greater representation of alpine endemics, than in the high-elevation forests.

Other approaches to floristic generalization were experimented with. Correlations of geographic relations and topographic moisture gradients were studied. On diorite and gabbro some correlation in the expected direction appeared; average extents toward the north were greater, and a higher proportion of species had maximum extents toward the north, in mesic sites than in xeric. No such correlation was observed in the more strongly endemic serpentine flora. Analysis of dispersion values for the distances of extent, as an approach toward measurement of relative floristic heterogeneity, was attempted. No significant differences were obtained, apart from those resulting from degree of endemism. Measurements of relative difference in extent to the north and the south were attempted as an approach to measurement of the degree to which the different floras were intraneous or extraneous to the Klamath area. Again, no significant differences appeared which did not result from the proportion of narrow endemics. These and other approaches to floristic abstraction encounter a fundamental limitation in the fact that all floras are mixtures of species with heterogeneous, "individualistic" relations to climate and geography. Yet the different communities within a limited area do differ significantly in geographic relations of their floras; and these differences are systematic and interpretable, and subject to measurement.

## VII. RELATIONS OF SPECIES POPULATIONS TO THE THREE SOILS

The results of the study which remain to be discussed are autecological—the manner in which species

populations are distributed in relation to the three soils.

### TREES

*Pseudotsuga menziesii* is the major tree species of low elevations; and on all three soils it extends along most or all of the moisture gradient with apparently bimodal populations (Fig. 20). Average densities of *Pseudotsuga* stems are considerably lower on gabbro and serpentine; densities of stems from the 1-in. class up per hectare were 177, 60, and 78 on the three soils. Effects of serpentine and gabbro are more striking when numbers of large stems are compared; densities of stems 37 cm (15 in.) dbh and over on the three soils were 88, 19, and 23. The ratio between the two density values, expressed as numbers of stems 37 cm and over among 100 stems over 1 cm dbh, provides an indication of slope of the stem number-diameter curve (Part IV), and average survival of trees into larger size classes. These values for diorite, gabbro, and serpentine were 49.7, 32.6, and 6.0, indicating an appreciable reduction of average *Pseudotsuga* size on gabbro, as compared with diorite, and a striking reduction on serpentine. Increment borings are available for diorite and serpentine; the lower rate of diameter growth on the latter is illustrated in Fig. 19 (see also Fig. 14).

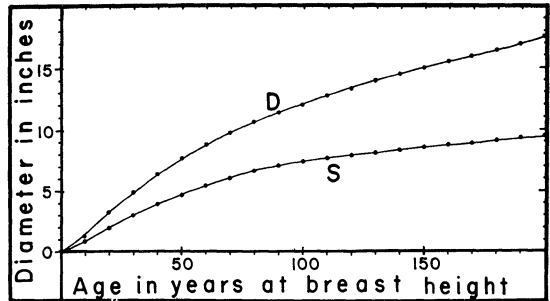


FIG. 19. Growth in diameter in relation to age for *Pseudotsuga menziesii* on diorite (D) and serpentine (S), based on 11 increment borings for low elevations on diorite, 7 increment borings from serpentine, chosen to represent all sites and average out site differences on a given parent material.

*Chamaecyparis lawsoniana* was of about equal abundance on diorite and serpentine but less abundant in the gabbro transect. The reduction in tree size on serpentine which is so evident in *Pseudotsuga* did not appear in *Chamaecyparis*, which is in consequence a smaller tree than *Pseudotsuga* on diorite, but a larger one on serpentine. Whereas the densities of *Pseudotsuga* and *Chamaecyparis* were lowest in the gabbro transect, that of *Pinus lambertiana* was highest there. Relative survivals into larger size classes were similar on all three soils, but *P. lambertiana* showed very different relations to the moisture gradient on the different soils (Fig. 20). On diorite the population is highest in xeric sites, on gabbro in subxeric ones (significance of the mesic population peak is doubt-

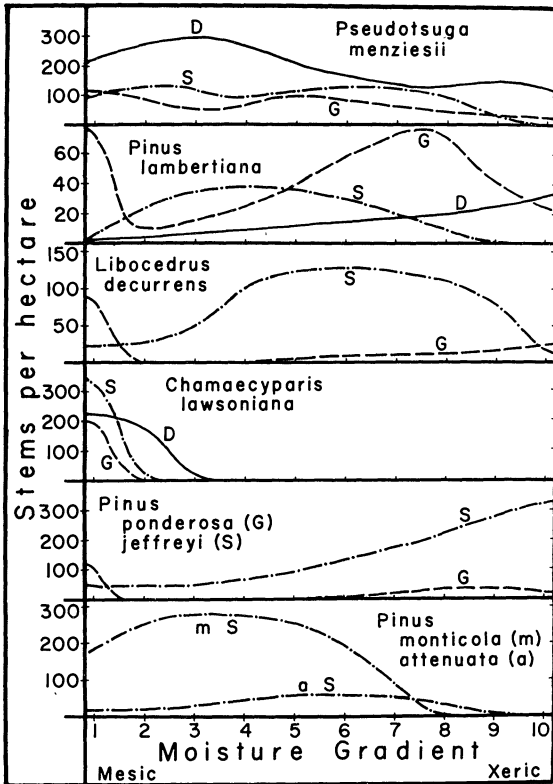


FIG. 20. Population distributions of conifers in relation to topographic moisture gradients at low elevations on diorite (D), gabbro (G), and serpentine (S). In this and following figures, populations on diorite are represented by continuous lines, those on gabbro by broken lines, and those on serpentine by dot-and-dash lines.

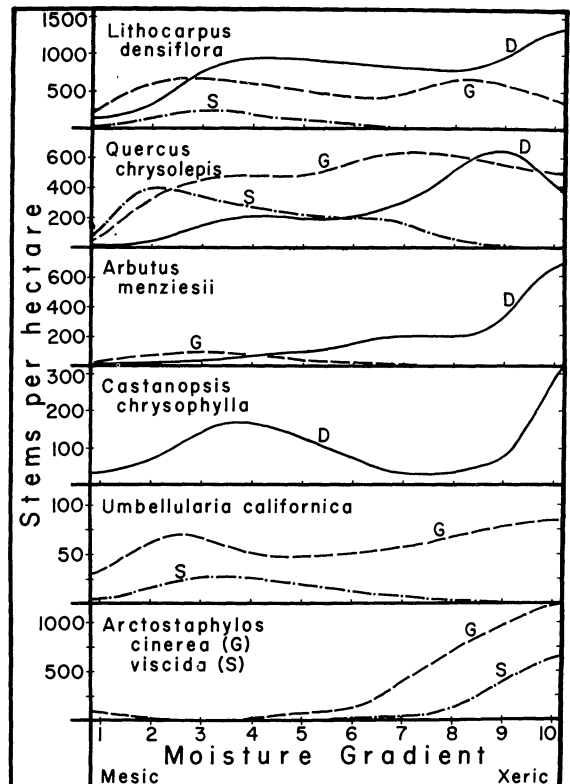


FIG. 21. Population distributions of sclerophylls on diorite (D), gabbro (G), and serpentine (S).

*californica* is almost absent from diorite; it is an abundant small tree on gabbro and a common shrub, with habitus very different from that on gabbro, on serpentine.

#### UNDERGROWTH SPECIES

Figs. 22-25 summarize distributional relations for a number of major undergrowth species. Almost all show the shift toward the mesic, though there are a few exceptions (e.g. *Whipplea modesta* from diorite to gabbro, Fig. 23) presumably implying occurrence of ecotypic populations with greater drought tolerance on the more mafic soils. In some undergrowth species, as in a number of trees, there is evidence of genetic complexity in population bimodality along the moisture gradient. The last four species, in Fig. 25, are bimodal in relation to the parent-material gradient, with higher populations on diorite and serpentine, lower on the intermediate gabbro.

ful), on serpentine in submesic ones. Through the series of soils the population center or mode is displaced progressively toward the mesic end of the gradient. Such "shifts toward the mesic," as they will be called, are a most general feature of the population relations to be discussed.

Among the sclerophyllous trees, both *Lithocarpus densiflora* and *Quercus chrysolepis* have apparently bimodal populations on both diorite and gabbro (Fig. 21). Both species are represented on serpentine by shrubby varieties with submesic modes (*Lithocarpus densiflora* var. *echinoides* and *Quercus chrysolepis* var. *vaccinifolia*). *Castanopsis chrysophylla* occurs on diorite with a large and apparently bimodal population; its occurrence on the other soils is scattered and irregular, but the serpentine population again is predominantly shrubby (*Castanopsis chrysophylla* var. *minor*). *Arbutus menziesii* occurs on diorite, with an apparently bimodal population centered in more xeric sites, and on gabbro with a lower population centered in submesic sites; there is no shrubby form on serpentine, where the species is represented by trees of uncommon and irregular occurrence. *Umbellularia*

Further complexities appear in *Polystichum munitum* and *Trientalis latifolia* (Figs. 23 and 25). *P. munitum* var. *munitum* is an important mesic population on diorite, with an apparent secondary mode in subxeric sites. The population on gabbro (predominantly var. *imbricans*) is centered in submesic sites; allowing for the shift toward the mesic this may correspond to the subxeric-xeric population on diorite (in which var. *imbricans* or its characteristics appear



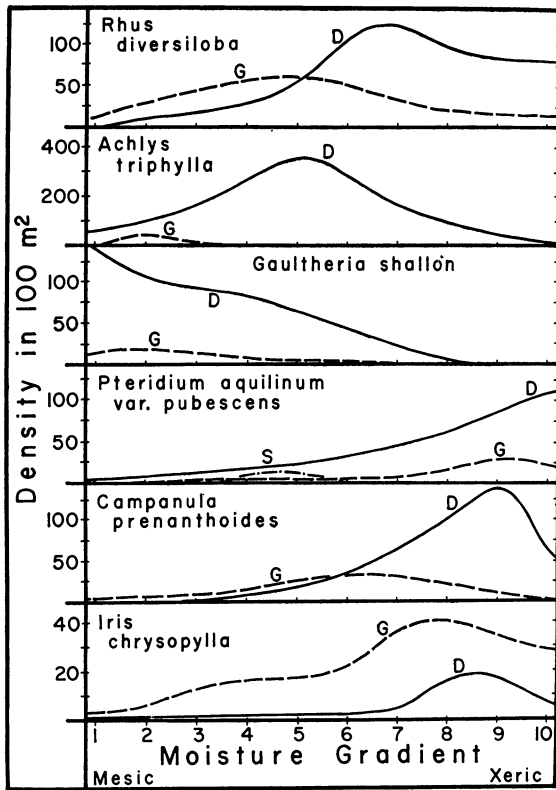


FIG. 22. Population distributions of undergrowth species on diorite (D) and gabbro (G).

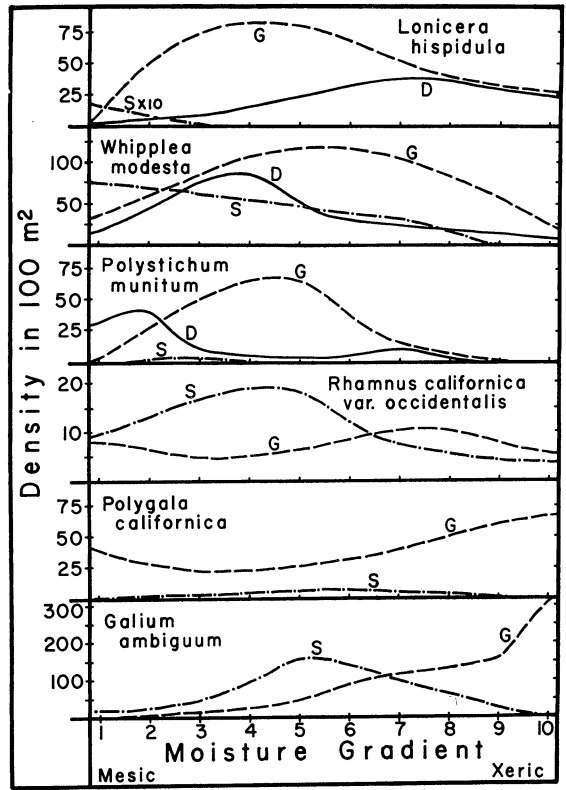


FIG. 23. Population distributions of undergrowth species on diorite (D), gabbro (G), and serpentine (S).

exceptionally). Only var. *imbricans* appears on serpentine, with a shift toward the mesic compared with the gabbro population. *Trientalis*, with two modes in relation to moisture on diorite and a third on serpentine, has a triangular pattern of population centers in relation to the moisture and parent-material gradients. *Trientalis* is also one of a number of undergrowth species (*Rosa gymnocarpa*, *Symphoricarpos rivularis*, *Whipplea modesta*, *Apocynum pumilum*, *Smilacina racemosa*, *Senecio bolanderi*) showing evidence of population bimodality in relation to elevation (Tables 13 and 14).

GENERAL RESULTS

The shift toward the mesic is one of the general features emerging from such study: In general, a species population which is observed on two or more soils of the diorite-gabbro-serpentine series in the same climate, will show a shift of its population distribution toward more mesic sites on the more mafic soil. Comparable shifts in relation to climate are more familiar. In transects of different elevation belts on diorite, high-elevation species shift toward the mesic as their populations are followed down into the warmer and drier climates of lower elevations; and low-elevation species show parallel shifts toward the xeric toward higher elevations. Shifts of the same

nature are observed along the east-west gradient from humid to drier climates (Part IV). The interrelation of local topographic and broader climatic distributions of species, with the tendency of topographic distributions to shift in such a manner as to compensate for differences in climate, has twice been formulated as a distributional "law"—the law of geoeological distribution of Boyko (1945, 1947) and the law of relative site constancy of Walter & Walter (1953).

The three parent materials studied are in similar general climates. To the extent that the shift may represent a response to climate, it is a response not to general climate outside communities, but to microclimates within communities as affected by the kinds of vegetation developing on the three soils. Equivalence of moisture-balance conditions in such different ecosystems, with different relations between soil moisture and evaporative conditions, as these three soils may be very difficult to define. The average magnitudes of the shifts toward the mesic, measured in terms of steps of the ten-step transects, may indicate something of what equivalent moisture-balance conditions on the three soils are. Among sets of 8 species which could be compared on two of the three soils, the average shift toward the mesic was 3.0 transect steps from diorite to gabbro, 4.2 transect

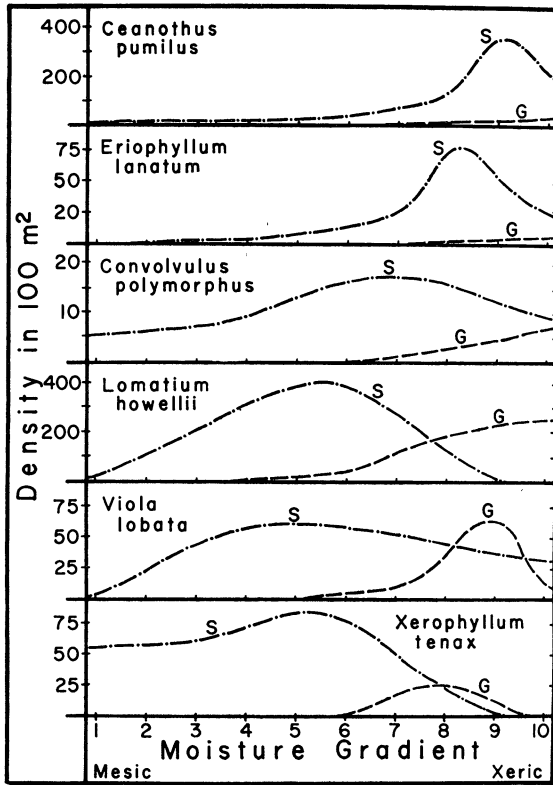


FIG. 24. Population distributions of undergrowth species on gabbro (G), and serpentine (S).

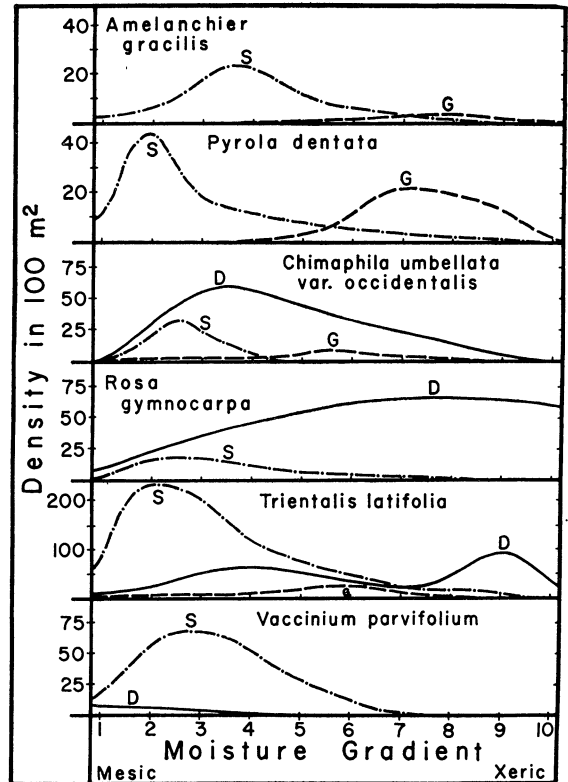


FIG. 25. Population distributions of undergrowth species on diorite (D), gabbro (G), and serpentine (S).

steps from gabbro to serpentine. Among 8 species compared from diorite to serpentine, several showed the 7.0 to 7.5-step displacement suggested by these values; the average was 6.5.

A second generalization suggested by the data is the individuality in species responses to the sequence of soils. Different species show all possible patterns of distributional response or "preferences" among the three parent materials. The only relations to the three soils which were not observed were the ideal ones which an ecologist might like to expect—sets of ecologically equivalent varieties or congeners replacing one another at comparable population levels on the three soils, or sets of clearly "associated" species with closely similar distributional relations to the three soils. The principle of species individuality (Ramensky 1924, Gleason 1926, 1939), which is familiar in application to geographic areas of species and distributional relations to moisture and elevation gradients, also appears clearly in relations to soil parent-materials in the Siskiyou.

A third conclusion suggested is the general occurrence of differences in stature or morphology when species populations occur on more than one of the soils—especially serpentine and non-serpentine soils. The phenomenon of "serpentinomorphism," the occurrence of morphologically distinctive forms on serpentine in species which also occur on non-serpen-

tine soils, has been described in the European literature (Vilhelm 1925, Pichi-Sermolli 1936, 1948, Rune 1953, Ritter-Studnička 1956). It has been observed that most woody species occurring both off and on serpentine are of reduced stature on serpentine, or are represented there by smaller varieties. Even casual observation of herb species occurring on serpentine and non-serpentine soils permits recognition of serpentinomorph differences in leaf size, texture, and color, in pubescence, in stature and branching pattern—differences which in most cases suggest those which would be expected in a drier or more open environment. The environments on serpentine are in fact more open; a species whose population shifts toward the mesic 7 transect steps from diorite to serpentine is still in a community of less tree coverage and greater exposure to sunlight and evaporation on the latter. Genetic differentiation of serpentine ecotypes is known to be frequent among species occurring both on and off serpentine (Kruckeberg 1951, 1954).

#### RARE SPECIES AND SERPENTINE INDICATORS

Restriction to special soil materials is relative; Siskiyou species may be arranged in a continuous sequence from those observed on only one soil to those with substantial populations on all three. Expansion of the field of observation further illustrates the rela-

tiveness of parent-material restriction. Among species which might be thought "serpentine species" from their occurrence in the low-elevation transects, a whole series appear on diorite at higher elevations (*Pinus monticola*, *Arctostaphylos nevadensis*, *Quercus garryana* var. *breweri*, *Eriophyllum lanatum*, *Silene campanulata* var. *orbiculata*, *Eriophyllum lanatum*, *Erysimum capitatum*, *Monardella odoratissima* var. *glauca*, *Epilobium paniculatum*, *Habenaria sparsiflora*, *Gilia capitata*, *Phlox diffusa*, *Eriogonum umbellatum*, *Holodiscus dumosus*, *Castilleja mimata*, *Angelica arguta*, *Lomatium macrocarpum*). Most of these occur on diorite in high-elevation meadows or on rocky summits, in communities as open and well-lighted as serpentine vegetation, rather than in forests. Conversely, a few low-elevation "diorite species" appear in the denser serpentine stands of higher elevations (*Arenaria macrophylla*, *Hieracium albiflorum*, *Iris chrysophylla*). Others of the "serpentine species" could be observed on soil materials (quartzite and argillite) that had little to do with serpentine and gabbro, but which supported vegetation somewhat more open and xerophytic-looking than that of diorite (*Silene campanulata* var. *orbiculata*, *Crepis pleurocarpa*, *Eriophyllum lanatum*, *Convolvulus polymorphus*, *Erysimum capitatum*, *Monardella odoratissima* var. *glauca*, *Lotus crassifolius*, *Calochortus tolmiei*, *Gilia capitata*, *Eriogonum umbellatum*, *Polystichum munitum* var. *imbricans*, *Galium ambiguum*, *Lomatium macrocarpum*). Still other species largely restricted to serpentine within the study area occurred on non-serpentine soils in other parts of the Siskiyou (*Vancouveria chrysantha*, *Balsamorhiza deltoidea*, *Eriophyllum lanatum*, *Hieracium cynoglossoides* var. *nudicaule*, *Arctostaphylos viscida*, *Rhododendron occidentale*, *Calochortus tolmiei*, *Epilobium paniculatum*, *Phlox speciosa*, *Ceanothus cuneatus*, *Rhamnus californica* var. *occidentalis*, *Galium ambiguum*, *Lomatium triternatum*, *Perideridia ore-gana*, *Polygala californica*). For such species relative serpentine restriction, like relative community-type fidelity, is clearly dependent on extent of the field of observation of the species' distribution.

When these are eliminated from the list of "serpentine species" there remain a good number which both were rarely or never observed off serpentine, or serpentine and gabbro, and are fairly abundant and widely distributed in the main serpentine area (*Horkelia sericata*, *Balsamorhiza platylepis*, *Iris bracteata*, *Lomatium howellii*, *Epilobium rigidum*, *Calochortus howellii*, *Antennaria suffrutescens*, *Cordylanthus viscidus*, *Erigeron foliosus* var. *confinis*, *Aster brickelliioides*, *Schoenolirion album*, *Tauschia glauca*, *Sanicula peckiana*). Almost all these are endemic to the Siskiyou or Klamath Mountains. These and other species largely restricted to, but less widely distributed on, serpentine are truly rare species in the sense of restricted occurrence.

It has been suggested by Griggs (1940, cf. Rune 1954a) that rare species tend to occur in unstable, successional communities rather than climax. The

serpentine communities of the Siskiyou are climax in the sense of stability or self-maintenance (Whittaker 1954b), and are very old. Serpentine communities have existed in the Klamath Region through the Cenozoic, and the rich floras of these communities represent the product of millions of years of species evolution into and in climax communities on serpentine. Rare species occur in most varied circumstances; they occur where, according to the population characteristics of and environmental limitations for particular species, they occur. So far as concentrations of considerable numbers of rare species are concerned, however, the Siskiyou material is in accord with the hypothesis of Detling (1948a, 1948b) that concentrations of narrow endemics are correlated with concentrations of environmental extremes, and the emphasis by Mason (1946a, 1946b) of edaphic factors. In relation to succession and climax, it is suggested that such concentrations may be associated not with unstable successional communities, but with relatively stable or climax communities of environments which are distinctive or "extreme" and spatially restricted.

The group of species largely restricted to serpentine, but widely distributed on it, form a nucleus of "characteristic" serpentine species which might serve as indicators of serpentine soil. In practice, observing serpentine outcrops scattered through the Siskiyou Mountains, they were found to have little indicator value. Stands containing several of them were usually within the major serpentine areas and obviously serpentine vegetation; stands of smaller and sometimes unmapped outcrops, for which serpentine indicators were most needed, might contain one or two of these species, but usually none. The most useful indicators were found to be some of the stratal dominants of serpentine (*Pinus jeffreyi*, *P. attenuata*, *P. monticola*, *Quercus chrysolepis* var. *vaccinifolia*, *Xerophyllum tenax*, *Ceanothus cuneatus*, *Arctostaphylos nevadensis*) and other species of more frequent occurrence in smaller serpentine areas (*Galium ambiguum*, *Pyrola dentata*, *Lomatium macrocarpum*, *Cheilanthes siliquosa*, and in wetter sites *Rhododendron occidentale* and *Darlingtonia californica*). *Xerophyllum tenax* seems the most useful single indicator for small serpentine outcrops. Most of these are species of extensive occurrence on non-serpentine soils. In other areas they are wholly meaningless as serpentine indicators but within the Siskiyou their presence may suggest, though not indicate, serpentine soil.

## VIII. CONCLUSION

One object of the present study was the analysis and description of a pattern of vegetation of much intrinsic interest; another was the further development of techniques for quantitative analysis of vegetation patterns. In the study as it has been developed in the preceding sections, various aspects of community relations have been brought into a system of quantitative treatment. In some cases the quantita-

tive analysis may seem only to provide numerical expressions for relations which an observant ecologist would detect without them, and yet may be well worth while for the additional clarity with which these relations are expressed. In other cases relations are revealed which are impossible to determine by field observation. Quantitative techniques can, when ineptly or mechanically used, obscure important ecological relations (Braun 1956). They can never substitute for effective observation, judgment, intuition, and scope of understanding; for only these can suggest which quantitative analyses are worth undertaking and provide evaluation and interpretation of the relations which emerge. Yet, in those studies for which the time-consuming sampling and analysis are feasible, techniques of gradient analysis may be productive for problems of both species autecology and community relations.

A central concept of the treatment in this work is the community-gradient or "coenocline" in relation to the topographic moisture gradient; these community-gradients are the units of comparison from one climate or parent material to another. It is felt that for some uses this approach has significant advantages over those centered on climatic climaxes or community classification. Any "system" for the study of natural communities is an integration of selected aspects of species and community relations, which can be investigated through a given, coherent set of concepts, to the neglect of other relations which cannot, and is necessarily more appropriate and productive in some circumstances than others. The limitations inherent in any approach or system may suggest the desirability of applying more than one approach to a given study when this is feasible—of supplementing a study in gradient analysis with consideration of classification as in the present work, a study based on classification with consideration of gradient relations.

Differentiation in relation to topography, and patterning in relation to patterns of topographic and other environmental gradients, are general characteristics of vegetation; and the concept of such patterning should be part of the ecologist's approach to interpretation of a present vegetation or a fossil flora. The terms *ecocline* and *coenocline* are suggested, not to name the obvious, but because of the need for these gradient-conceptions in the interpretation of relations of natural communities to environment. The vegetation of the Siskiyou can be conceived in terms of climax regions and vegetation units. One may regard the Mixed Evergreen Forests as forming a vegetational matrix for lower elevations in the central Siskiyou, a prevailing climax type in which the serpentine and other localized communities are dispersed, and which is replaced toward higher elevations by Montane Forest and Subalpine Forest climaxes, toward the west by Coast Forest, and toward the east by Oak Woodland, climaxes. But it is profitable also to conceive of the vegetation in terms of coenoclines changing in composition, physiognomy, and floristic relations in relation to climates and parent materials,

as a multi-dimensional pattern of vegetational gradients in relation to these environmental gradients. Thus the distributional relations of species, floristic groups, and community-types, and the interrelations of communities may be conceived through an abstract, conceptual "pattern" which is not simple, but brings into comprehensible form much of the still greater complexity of the vegetation itself.

The fact that the Southern Appalachians and Klamath Mountains bear comparable "central" relations to eastern and western forests has been commented on. One other parallel between these two mountain areas may be observed—their combination of unusual geological and biological interest with relatively undisturbed conditions. The Klamath Mountains are now, as the Southern Appalachians were some decades ago, relatively remote and little known. Partly because they are remote, extensive areas remain which are wild and natural. Both areas have exceptional scenic attraction; in the Klamath Region the coast of southern Oregon and northern California, the Rogue and other canyons, and some of the mountain landscapes themselves deserve to be more widely known—and, to the extent that is feasible, protected. Because the Klamath Region is not well known, it may be appropriate to observe that this is an area of biological interest as great as that of the Southern Appalachians: a comparable center of survival of ancient, Arcto-Tertiary forms in the Coastal Redwood and Mixed Evergreen Forests, an even greater concentration of rare species and remarkable floras, together with an unusually diverse range of floras and communities within a limited distance from the Coast inland, and as dramatic an expression of relations of natural communities to geological formations as is to be found anywhere in the world. There are many areas of biological and scenic value in the West, but among these the over-all interest of the Klamath Region is high, and suggests continued thought on long-range policies of utilization and preservation.

## SUMMARY

### I. Introduction

The Klamath Mountain Region, lying between the southern Cascade Mountains and Pacific Coast in northern California and southern Oregon, is an area of great climatic, geological, and vegetational diversity. One major range of the Region, the Siskiyou Mountains along the California-Oregon border, was chosen for a study of relations of mountain forests to climates and parent materials.

For reasons of vegetational history, the age of the Klamath Mountains, and the diversity of habitats in them, the Klamath Region is a "center" for forest floras and forest vegetation of the West.

### II. Procedure

An area of quartz diorite in the central Siskiyou Mountains was chosen for intensive study of elevation

and moisture-gradient relations of vegetation on a more typical parent material. Low-elevation vegetation of olivine gabbro and serpentine was compared with that of diorite to study effects of parent materials. The change of vegetation from the humid coastal forests inland at low elevations, and serpentine vegetation at all elevations, were studied less intensively.

Gradient analysis techniques were applied to relations of species and communities to major environmental gradients. Within each 1000-foot elevation belt, or parent material, 60 vegetation samples representing all parts of the topographic moisture gradient were taken. Three techniques for arrangement of these samples into composite transects—by topographic classes of sites, by weighted averages of community composition, and by comparison with standards representing mesic, intermediate, and xeric sites—were used and evaluated. The weighted-average technique gave best results in this study.

### III. Vegetation Description

Low-elevation diorite vegetation gradates from *Chamaecyparis lawsoniana*-*Pseudotsuga menziesii* forests in mesic sites, through *Pseudotsuga* forests with sclerophyll trees in intermediate sites, to sclerophyll forest with scattered *Pseudotsuga* in xeric sites. Low-elevation gabbro vegetation gradates from more open *Chamaecyparis*-*Pseudotsuga* stands, through more open sclerophyll-*Pseudotsuga* stands, to open, xeric *Pinus*-*Pseudotsuga*-*Quercus*-*Arctostaphylos* stands. Low-elevation serpentine vegetation gradates from still more open *Chamaecyparis*-*Pinus monticola*-*Pseudotsuga* mesic stands, through very distinctive forest-shrub stands with several conifers and two-phase undergrowth of sclerophyll shrubs and grass, to *Pinus jeffreyi* woodlands.

Toward higher elevations on diorite, the forests of *Pseudotsuga* and sclerophylls gradate into montane forests dominated by *Pseudotsuga* and *Abies concolor* above about 1200 m, and these into subalpine forests dominated by *Abies nobilis* and *Tsuga mertensiana* above 1800 m. Mosaic charts (Figs. 11 and 12) show relations of vegetation to elevation and topography on both diorite and serpentine.

### IV. Climax Interpretation

All low- and most high-elevation vegetation of the Siskiyou Mountains has been affected by fires. Evidence from stand-curve analysis suggests, however, that the effect of frequent, less severe fires during the past century has been to reduce stand density without changing essential character of most stands. Different patterns of climax vegetation develop on diorite, gabbro, serpentine, and other parent materials in the Siskiyou Mountains. Any significant difference in parent material may imply difference in climax vegetation.

For a gradient of environmental complexes the term *complex-gradient* has been suggested; for the corresponding community-gradient the term *coeno-*

*cline* is here suggested; for the gradient of ecosystems comprising both of these the term *ecocline* may be used. The principal basis of the study was the comparison of moisture-gradient patterns, or coenoclines, from different climates and parent materials. Along a gradient from humid, maritime climates near the Coast to drier and more continental ones inland, the character of low-elevation coenoclines changes from *Sequoia sempervirens* and coastal *Pseudotsuga* forests, through mixed evergreen forests in the central part of the range, to a pattern of *Pseudotsuga* forest, oak woodland, and valley grassland in the Interior.

### V. Problems of Classification

Formations, dominance-types, sociations, associations, and unions in the Siskiyou vegetation are discussed. The Mixed Evergreen Forests of conifers and sclerophylls are a prevailing climax of the Klamath Region and north California Coast Ranges. These forests are regarded as a major community-type of the West, and interpreted as a formation connecting the coniferous Coast and Montane Forests with the California broad-sclerophyll vegetation.

### VI. Floristic Comparisons

Arcto-Tertiary forest remnants from opposite sides of North America, the Mixed Mesophytic and Mixed Evergreen Forests, have very similar life-form spectra, approximating: P 34, C 8, H 33, G 23, and T 2 per cent. The transformations of such "mid-temperate mesophytic" spectra along gradients of parent material, elevation, topographic moisture, and east-west climatic change in the Siskiyou are tabulated and discussed. The principal effect of the maritime-continental climatic gradient is in decreasing representation of evergreen forms.

Species diversities of plant communities increase markedly from maritime into continental climates, increase from diorite to serpentine, decrease along the topographic moisture gradient on diorite, and increase, then decrease, toward higher elevations on diorite. Such relations are not simply interpreted on the basis of environmental "favorableness." In the Siskiyou, community diversities tend to be higher in the more open communities, with more highly developed herb strata, of drier sites and climates and special parent materials.

Three aspects of species-diversity may be distinguished: richness in species of individual stands, degree of floristic change of communities along environmental gradients, and species-diversity of a community pattern or broadly defined community-type which results from both of these. Measurements of "coenocline differentiation" along the topographic moisture gradient, as one approach to the second of these, are discussed and applied. Coenocline differentiation increases from maritime to continental climates in the Siskiyou.

Measurements (coefficients of community and percentage similarities) show that the vegetation of

gabbro is floristically intermediate to that of diorite and serpentine, though physiognomically closer to the former.

Geographic relations of floras were studied through two approaches—representation of areal types, and average extents of distribution in different directions. Marked correlations of these geographic relations with local environments within the Siskiyou appear. The serpentine flora has a much higher representation of endemics, smaller average extent in all directions, but stronger southern or Californian affinity than the diorite vegetation.

#### VII. Relations of Species Populations to the Three Soils

Some Siskiyou species show evidence of population bimodality in relation to the topographic moisture gradient or elevation. Most species show a "shift toward the mesic," or displacement of their distributions toward less xeric sites, from diorite to gabbro and gabbro to serpentine. Rare species in this area are concentrated in stable or climax communities on special parent materials, especially serpentine.

#### VIII. Conclusion

Quantitative techniques of gradient analysis permit this complex vegetation to be analyzed and understood as a multi-dimensional pattern in relation to topographic moisture gradients, climates, and parent materials. The biological interest and scenic appeal of the Klamath Region equals that of the eastern center of vegetational and floristic diversity, the Southern Appalachians, and suggests further consideration of preservation of parts of the region for the future.

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## ERRATA

Two errors were introduced into the paper on "Vegetation of the Siskiyou Mountains, Oregon and California" by R. H. Whittaker by incorrect entry of galley proof corrections:

1) Pages 289-290. The paragraph beginning "These results..." on page 290 should follow the first paragraph on page 289 ending "...on serpentine—34.9, 32.2, 34.7" and precede the section on "Transect Tables."

2) Page 321. The equation in the second paragraph should read,  $\beta = \frac{\gamma}{\alpha}$

A note from the author on uncertain taxonomic status of the population designated *Arctostaphylos cinerea* on gabbro was not received in time for inclusion.