A Transition Coniferous Forest in the Cascade Mountains of Northern Oregon

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A 29 km transect was established in northern Oregon from near the summit of the High Cascades, eastward across Green Ridge, to the W rim of Fly Creek canyon. The gradual eastward slopes descend in the Cascades from 1770 to 825 m, and on Green Ridge from 1370 to 915 m. The area is geologically and physiographically simple. Precipitation averages over 150 cm annually in the W, 50 cm or less in the E.

This transition region possesses an unusually rich coniferous flora, with 19 species on or near the transect. The subalpine forest on the upper slopes of the High Cascades includes *Tsuga mertensiana, Abies lasiocarpa, Pinus albicaulis, Pinus contorta, Abies amabilis* and *Juniperus communis* var. *saxatilis*. The middle elevations of the Cascades and the crest of Green Ridge have forests of *Pinus ponderosa, Abies grandis, Pseudotsuga menziesii, Larix occidentalis, Picea engelmannii* and *Taxus brevifolia*. Found on the Cascades slope, but absent from Green Ridge, are *Pinus monticola, Tsuga heterophylla* and *Abies procera. Pinus ponderosa, Pseudotsuga menziesii* and *Libocedrus decurrens* are common to the lower altitudes on both the Cascades and Green Ridge slopes. The more xeric Green Ridge lower slope also has *Juniperus occidentalis* in quantity. In isolated, well-watered sites at low elevations a few *Pinus lambertiana* and *Thuja plicata* grow.

High elevation forests appear relatively stable in composition with the slow-growing *T. mertensiana, A. lasiocarpa* and possibly *A. amabilis* gradually increasing in proportion. Between 1050 and 1500 m on the Cascades, and between 1200 and 1370 m on Green Ridge, *A. grandis* is replacing the shade intolerant *Pinus ponderosa, Pseudotsuga menziesii* and *Pinus contorta. L. decurrens* is replacing *Pinus ponderosa* as the predominant species throughout much of the lower elevations. Only on the driest locations on the Cascades slope is regeneration adequate for *P. ponderosa* replacement. The lower eastern slopes of Green Ridge now appear to have a stable forest composition.

INTRODUCTION

Coniferous trees, present since the late Paleozoic and dominant during the Mesozoic (Sporne, 1965), are now largely confined to regions of middle to high latitudes. Important concentrations grow currently in the northern parts of Asia, Europe and North America,

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with much less extensive stands in Africa and South America. A major extension of range toward the equator occurs in western North America from southwestern Canada through western United States and into northern Mexico. These forests grow in, or are associated with, mountain ranges and are normally subjected to seasonal drought. They have been generally described by Harshberger (1911), Shreve (1917), Clements (1920), Livingston and Shreve (1921), Oosting (1956), Eyre (1963) and Kuchler (1964). Particularly relevant to this study are the descriptions of forests in the states of Oregon and Washington reviewed by Franklin and Dyrness (1969).

These forests have been variously divided to facilitate description. One useful scheme (Clements, 1920) recognizes three main forest types: (1) coastal forest, (2) montane forest and (3) subalpine forest.

The coastal forest, floristically the richest of the three, occupies the narrow heavily watered strip adjacent to the Pacific Ocean from southern Alaska to central California. The width varies with local topography, the eastern boundary usually formed by subalpine forest where high mountains are present, by montane forest at lower elevations in the N and by shrub or woodland vegetation in the rain shadows of the lower ranges in the S.

The most important species include *Thuja plicata* (western red cedar), *Tsuga heterophylla* (western hemlock), *Pseudotsuga menziesii* (douglas fir), *Picea sitchensis* (Sitka spruce) and *Pinus contorta* (lodgepole pine). Local modifications include, as additions or substitutes, *Tsuga mertensiana* (mountain hemlock) and *Chamaecyparis nootkatensis* (Alaska yellow cedar) in Alaska and British Columbia; *Abies grandis* (grand fir), *A. amabilis* (silver fir) and *Taxus brevifolia* (western yew) northward from W-central Oregon; and *Chamaecyparis lawsoniana* (Port Orford cedar) and *Sequoia sempervirens* (coast redwood), in southern Oregon and California (Preston, 1961).

The dryer inland belt in southern Oregon and California has *Pinus lambertiana* (sugar pine), *P. monticola* (western white pine), *P. ponderosa* (ponderosa pine), *P. attenuata* (knobcone pine), *Abies concolor* (white fir), *A. magnifica* (California red fir) and *Libocedrus decurrens* (incense cedar) among its important species. Northward into British Columbia moister conditions prevail so that, except for the substitution of *Picea engelmannii* (Engelmann spruce) for *P. nootkatensis,* the inland forest is similar to that of the coast.

The montane forest type, floristically less diverse, is located on the mountains between central British Columbia, southwestern South Dakota, western Texas and southern California. *Pinus ponderosa* and *Pseudotsuga menziesii* are the most characteristic species. *Pinus contorta, Abies concolor* and *Juniperus* spp. (junipers) are present in large segments of the region.

Of local importance are *Pinus albicaulis* (whitebark pine) and *Larix occidentalis* (western larch) in the NW; *Pinus lambertiana, P. jeffreyi* (Jeffrey pine), *Libocedrus decurrens* and *Sequoiadendron gigantea* (giant redwood) in the SW; *Pinus edulis* and *P. monophylla*

(pinyon pines) in the S; and *Pinus flexilis* (limber pine) and *Picea pungens* (blue spruce) in the E-central area (Preston, 1961).

The subalpine forests are found in cool, humid sites with short growing seasons from Alaska to New Mexico. These conditions occur near sea level in the N but are found only on mountain tops in the S; thus distribution is much less continuous southward. *Picea engelmannii* and *Abies lasiocarpa* (subalpine fir) are the characteristic species, and *Pinus contorta, Larix lyallii* (alpine larch) and *Juniperus communis* var. *saxatilis* (dwarf juniper) are also prevalent. Of more limited range are *Abies magnifica* in southern Oregon and California, *Pinus albicaulis* on the more westerly peaks; and *Pinus flexilis* toward the E (Preston, 1961).

Along the eastern boundary of the coastal forest in northwestern Oregon the ranges of the species from the northern and southern parts of the type overlap. The montane and subalpine forests also extend into this area along the Cascade Mountain summit, resulting in vegetation unusually rich in coniferous species. The study deals with this transition forest.

The area is in the northern part of the Deschutes National Forest in western Jefferson Co., Oregon (Fig. 1). A transect was established within T.12 S. of the Mt. Jefferson and Madras quadrangles, and extended through Sections 1-4 of R. 8E., Sections 1-6 of R. 9 E., Sections 1-6 of R. 10 E., and Sections 5-6 of R. 11 E. Latitude is 44° 33′N to 44° 34′N; longitude is 121° 30′W to 121° 47′W.

Sections 3,4 and the NW one third of 2, R. 8E., are within the Mt. Jefferson Wilderness Area, and thus are free of present human disturbance. From this point eastward to Section 1, R. 10 E. (Fig. 2) at the top of Green Ridge, only salvage operations to remove dead or dying trees had affected the stand when the field work was done in 1959-60. This area has since been logged or is under contract to be
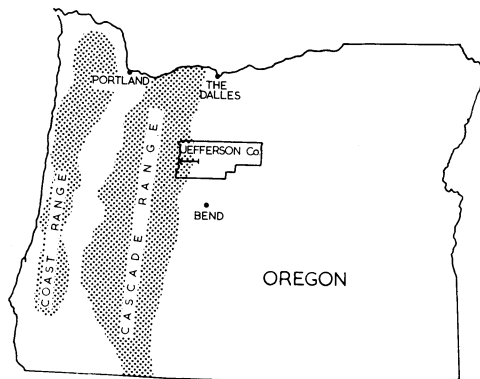

Fig. 1.—Location of Jefferson Co., Oregon. The horizontal line in
western Jefferson Co. shows the location of this study

logged, with up to 40% cut. East of the summit of Green Ridge, recent but limited logging had altered the forest in 1959-60.

GEOLOGY AND PHYSIOGRAPHY

The Cascade Mountain Sub-province, the most conspicuous feature in the relief of Oregon, is part of the Sierra-Cascade Province (Fenneman, 1931) extending from central California through western Oregon and Washington. The older component of two distinct physiographic divisions is the Western Cascades of Eocene-Miocene origin, the younger the High Cascades of Pliocene-Pleistocene development. The broad Western Cascades with the High Cascades imposed on its eastern flank results in a more gradual western incline and a short, steep eastern slope.

The thick volcanic rock strata of the Western Cascades result primarily from fissure eruptions (Williams, 1957). Though peaks such
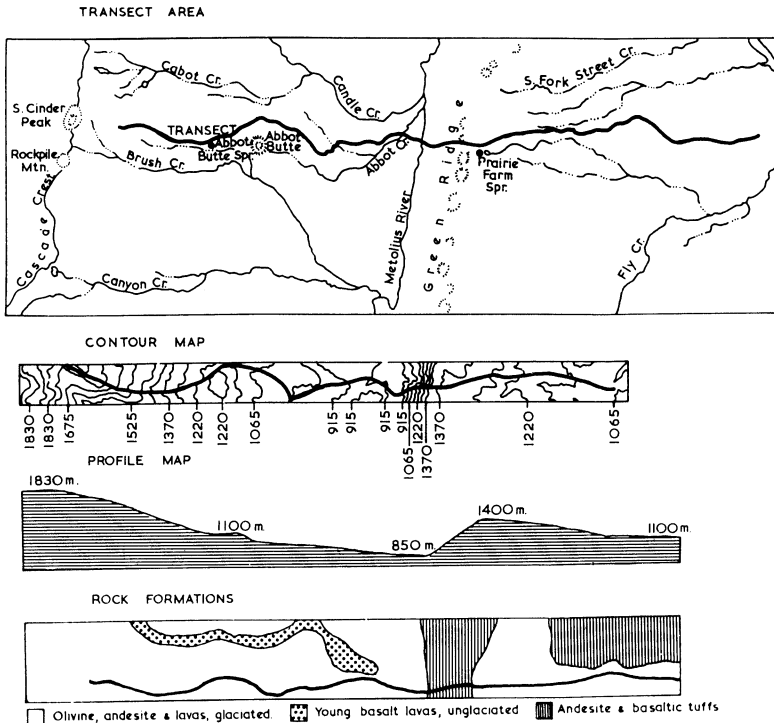

Fig. 2.—Coincident maps of the transect region. The transect is marked on the transect area, contour, and rock formation maps. The transect area map was adapted from the U.S. Forest Service map of Deschutes National Forest, Oregon. The contour and profile maps are adapted from the U.S.G.S. Mt. Jefferson, Oregon, Quadrangle. The rock formations map was adapted from Williams (1957)

as Mt. Jefferson and Mt. Washington result from explosive eruptions, the High Cascades are mostly the product of broad shield volcanoes.

The original smooth western slope of the Cascades has been dissected by streams carrying runoff from heavy orographic precipitation, so that deep canyons separate ridges of near equal height. The glaciated valleys of the younger and dryer eastern slope, however, are separated by broad, comparatively uneroded ridges. It was thus possible to locate a gently sloping tableland for this study, uncomplicated by N- and S-facing exposures and nowhere less than 2 km wide (Fig. 2, contour map).

The decrease in elevation from the W end of the transect to the Metolius River about 13 km away is a little over 900 m (Fig. 2, contour and profile maps). Abbot Butte, a major exception to an otherwise quite uniform E-facing slope (average slope angle, 7%) was detoured to the N.

Immediately E of the Metolius River the W-facing fault scarp of Green Ridge rises 520 m (average slope angle, 40%, Fig. 2, contour and profile maps). Because of a gentle eastern strata tilt, average slope angle on the E side is only 5%.

The study area is geologically simple; Williams (1957) designates only two formations (Fig. 2, rock formations). Everything except the well-bedded basaltic tuffs of Green Ridge's western slope is lava of olivine basalt and basaltic andesite, somewhat reworked by glacial activity and attendant meltwaters.

Soils

The soils along the transect are quite uniform with the exception of the Green Ridge escarpments where gravitational movement of the variously sized rock particles has prevented substantial soil deposition or development.

Derived from basic igneous rocks, all soils are loam and sandy loam (U.S.D.A. Soil Survey Manual, 1951) containing stones, larger and more abundant toward the W, up to 25 cm diam. Parent material, with some cinders but little pumice, has been transported probably as glacial outwash. Soft when dry and friable when moist, these slightly acid regosols are moderately well-drained to well-drained. The upper 45-64 cm are very porous and nearly structureless. A slightly decomposed organic layer up to 4 cm thick covers the surface.

Above 1200 m altitude soil moisture is higher with evidence of a fermented layer between litter and mineral soil. A dark reddish-brown layer (8-12 cm) rests on a slightly finer and more consolidated layer of different origin. The wetter soils of the W are redder than the characteristic brown, dryer soil to the E. The soils do not exhibit gradients approaching the magnitude of those shown by the vegetation.

Climate

The study area lies on the boundary between the maritime climate of the western part of Oregon and the continental climate of the E,

but the temperature extremes are those of the E, where highs may be 35 C and lows —18 C. Mean temperatures, however, are similar on both sides of the Cascades summit, typically 0 C in Dec.-Jan. and 18 C in July-Aug. (U.S. Weather Bureau, 1947-1968).

From a maximum at the summit, precipitation decreases eastward to the Metolius River (Fig. 2), the 50, 100, and 150 cm isohyets all crossing the transect (Fig. 3). Eastward from the Metolius vegetation character indicates that precipitation increases up the W slope and decreases down the E slope of Green Ridge. Precipitation is largely snow, particularly at higher elevations where roads above 1200 m are usually blocked for several winter months. Snow patches were still present at 1200 m on 1 June 1960 and at 1730 m on 12 July 1960.

METHODS

A 29 km transect was established from the High Cascades summit eastward across 18 sections to the W rim of Fly Creek Canyon in June 1959 (Fig. 2). Forest Service roads and trails were followed for most of this distance. Elevations ranged from 1770 m at the Cascade crest to about 825 m at the Metolius River (Fig. 2, contour and profile maps).

Quadrats 9.75 x 9.75 m (32 x 32 ft) divided into eight subplots 2.44 x 4.88 m (8 x 16 ft) each (total sampling units 1488), were placed at 15.25 m (50 ft) altitudinal intervals along the transect. The interval was lengthened to 23 m on the partially logged eastern slope of Green Ridge, and to 61 m on the steep and unstable western face of Green Ridge. Altitudes were determined by combinations of U.S.G.S. topography maps, section line markers, vehicular odometer and Taylor altimeter. Slope angle averaged 7% on the Cascades' eastern slope, 40% on Green Ridge's W slope, and 5% on Green Ridge's E slope.
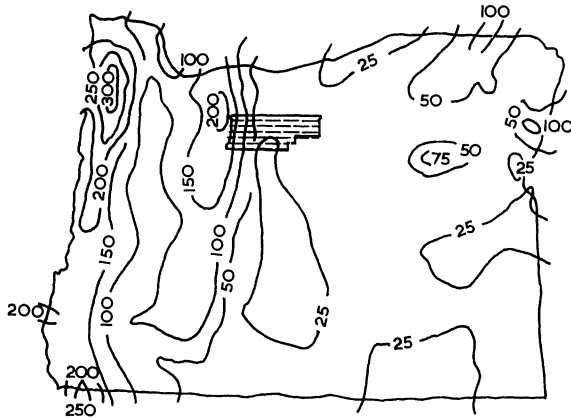

Fig. 3.—Mean annual precipitation (cm) of Oregon, Jefferson Co. Adapted from the U.S.D.A. yearbook, *Climate and Man* (1941)

The quadrats were located 50 paces N and 50 paces S of designated points on the transect, with the distance increased to 100 paces in open stands. If logging disturbance or large rock outcrops were met at the basic distance, 50 pace increments were added until undisturbed, well-developed vegetation was found, an adjustment necessary in 57 of the 186 quadrats established.

All trees over 3 dm in height were recorded by species within each subplot. Specimens over 3 m tall were measured for diam at breast height. One or two increment cores were taken from selected trees in each quadrat.

Associated species of shrubs and herbs were recorded in each quadrat, and voucher specimens of common species are filed in the Oregon State University Herbarium. Nomenclature follows Hitchcock, *et al.* (1955-1969). The list of shrubs and herb species is available from the author.

The nearby areas of the High Cascades summit between Rockpile Mountain and South Cinder Peak, burned areas near Canyon Creek and Brush Creek, the S wall of Cabot Creek canyon, the lower canyon of Candle Creek, the valley of the Metolius River several km N and S of the transect, and the head of the South Fork of Street Creek were reconnoitered for supplementary observations (Fig. 2).

Frequency, relative density, relative dominance and number of trees per hectare were calculated. Computations followed these formulae (Curtis and McIntosh, 1950; Phillips, 1959):

1) Frequency $= \dfrac{\text{number of subplots containing the species}}{\text{total number of subplots}} \times 100$

2) Relative density $= \dfrac{\text{number of individuals of the species}}{\text{number of individuals of all species}} \times 100$

3) Relative dominance $= \dfrac{\text{total basal area of the species}}{\text{total basal area of all species}} \times 100$

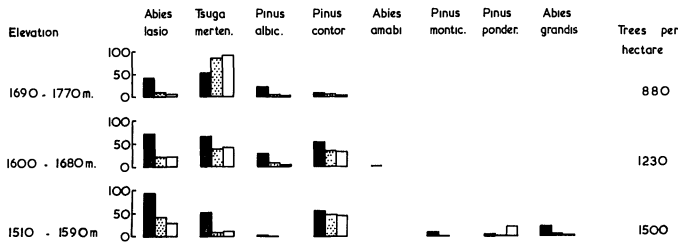Frequency, relative density and relative dominance for each tree

Fig. 4.—Frequency (solid), relative density (dotted), relative dominance (clear), and trees/ha for the species recorded in 1510 to 1770 m altitude on the Cascades' eastern slope. Data from 112 subplots (2.44 x 4.88 m) are included in the histograms for each set of altitudinal ranges

TABLE 1.—Relative densities of saplings (0.3-3.0 m)/trees (>3.0 m)

Elevation (m)	*A. lasiocarpa*	*T. mertensiana*	*P. albicaulis*	*P. contorta*	*A. amabilis*	*P. monticola*	*P. ponderosa*	*A. grandis*	*P. menziesii*	*P. engelmannii*	*L. occidentalis*	*L. decurrens*	*J. occidentalis*
East slope of Cascades													
1690-1770	44/11	38/78	17/5	1/6	---	---	---	---	---	---	---	---	---
1600-1680	50/21	30/39	8/7	12/33	<1/	---	---	---	---	---	---	---	---
1510-1590	65/41	9/8	<1/	17/44	---	1/2	<1/1	8/4	---	---	---	---	---
1420-1490	45/27	6/1	---	5/30	---	1/	<1/7	43/35	---	---	---	---	---
1330-1400	8/2	1/	---	1/3	---	---	/5	90/90	---	---	---	---	---
1240-1310	1/	<1/	---	/1	---	---	/2	95/90	3/5	/2	<1/	---	---
1140-1230	---	---	---	/<1	---	---	13/3	78/65	8/32	<1/	/1	1/<1	---
1050-1130	---	---	---	---	---	---	12/9	33/41	12/40	---	/1	43/9	---
960-1040	---	---	---	---	---	---	36/36	2/8	6/27	---	/3	56/29	---
840- 950	---	---	---	---	---	---	27/75	<1/	3/12	---	---	70/10	---
West slope of Green Ridge													
820- 950	---	---	---	---	---	---	15/43	---	8/43	---	---	77/14	---
1000-1130	---	---	---	---	---	---	40/67	---	5/19	---	---	55/14	---
1190-1310	---	---	---	---	---	---	30/70	28/	33/15	---	---	6/15	---
East slope of Green Ridge													
1300-1370	---	---	---	---	---	---	24/50	73/50	3/	---	---	---	---
1210-1280	---	---	---	---	---	---	30/36	41/48	7/7	---	---	22/9	---
1120-1190	---	---	---	---	---	---	63/45	/5	18/30	---	---	19/20	<1/
1030-1100	---	---	---	---	---	---	68/63	---	3/7	---	---	27/23	3/7
920-1010	---	---	---	---	---	---	69/76	---	---	---	---	12/5	19/19

species appear in the histograms of Figure 4 and Figures 8-11. Frequency is used primarily to indicate dispersal, relative dominance to indicate tree size, and relative and absolute density to indicate prevalence of each species.

Relative density was determined separately for saplings (plants 0.3-3.0 m tall) and trees (plants over 3 m tall) (Table 1). When read as ratios, the highest ratio indicates most effective reproduction.

FOREST DESCRIPTION

The study area was chosen for its transitional nature; hence, boundaries between discrete plant assemblages are unusually difficult to draw. The extreme diversity is so unwieldy, however, that description requires division of the data. The eastern slope of the Cascades can be separated into three descriptive units, using as basis the predominance of *Abies grandis* at the middle elevations. None of these three "types" is homogeneous, though each has a number of distinctive qualitative and quantitative features. Figures 4 and 8-11 demonstrate the transitional nature of the forest along the transect, while simultaneously showing the dissimilarities on which the descriptions are based.

The W slope (Fig. 10) and E slope (Fig. 11) of Green Ridge are less complex, and are not further divided for description.

1. Upper elevation forest (1500-1770 m).— The upper limits of the transect is imposed by the sharp, exposed rim of Brush Creek canyon

Fig. 5.— Clump of small *Tsuga mertensiana* exhibiting "black body" radiation effect, resulting in earlier snow-melt next to established trees

(Fig. 2), 200 m below timberline, which occurs at about 1980 m on the peaks of the Three Sisters 50 km to the S (Van Vechten, 1960).

The vegetation above 1670 m is a mosaic of forest, meadows and dry cinder flats resulting in low frequencies and densities. The higher frequency and density figures between 1500 and 1670 m reflect an essentially closed forest canopy (Fig. 4).

A. *Discontinuous forest (1670-1770 m).*—*Tsuga mertensiana* is the most abundant tree above 1670 m, diminishing in importance with lower elevation. Old trees live to at least 280 years and reach 106 cm dbh, but trees over 30 cm dbh usually suffer from heart rot so that maximum age was unobtainable.

Above 1650 m trees are often in clumps of three to eight stems (Fig. 5). The "black body effect" (Geiger, 1950) produces an available seed bed earlier than in adjacent treeless areas, and vegetative reproduction by layering may also contribute to this clumping (Lutz, 1930; Cooper, 1931).

In the extensive pure stands found in protected locations the forest floor is covered by a compact, feltlike layer of hemlock litter up to 5 cm thick. Decomposition fungi are active in this litter only when it is moist, and it dries and cracks into plates 5-30 cm in diam soon after the snow melts in early summer. The only plants evident in the litter are a few dwarfed saplings of *T. mertensiana* and *Abies lasiocarpa* and some nonreproducing specimens of the herbaceous *Lupinus* and *Luzula* (Fig. 6). Seedling establishment in this substrate must be exceedingly difficult. Thus, while *T. mertensiana* reproduces throughout the upper

Fig. 6.—Closed stand of *T. mertensiana,* with very heavy litter layer

140 m of sampled altitude, its most vigorous seedlings and saplings are outside the closed canopy forest.

Mature trees of other species grow at the margins of the *T. mertensiana* forest or as isolated specimens within it, but their low relative dominance values demonstrate their comparative unimportance (Fig. 4). *Abies lasiocarpa, Pinus albicaulis* and *Pinus contorta* here were measured to 45, 29 and 31 cm dbh, respectively.

Table 1, Line 1 indicates effective regeneration of *A. lasiocarpa, T. mertensiana* and *P. albicaulis*. The disproportionately high relative density of *A. lasiocarpa* and *P. albicaulis* saplings is caused primarily by invasion of currently treeless areas. Neither is making significant inroads into mature *T. mertensiana* forest. *A. lasiocarpa* is generally considered a shade tolerant tree (Baker, 1949), but it does not here effectively compete with *T. mertensiana* where the latter forms a closed canopy. This has been observed in other parts of the Cascades by Franklin and Mitchell (1967).

The better-drained treeless areas are slowly being invaded by *Abies amabilis* and the four recorded species (Fig. 4), which germinate at the margins of melting heavy snowpack in summer. The coarse soils provide a harsh environment for the growth of young trees, however, and establishment is a rare event. For example, a very heavy seedfall but no germination by *Tsuga* and *Abies* on a moist site recently freed from snow was observed on 3 July 1960. On July 12 the soil had dried to a depth of 5 cm, and although some germination had occurred on a shaded forest border, most of the seeds had disappeared.

Intense frost heaving also prevents seedling establishment. Between September 1959, and July 1960, large numbers of taprooted perennial herbs had been lifted enough to expose root crowns and kill the plants.

Fig. 7.—A developing "timber atoll," with *Abies lasiocarpa, Tsuga mertensiana* and *Juniperus communis* var. *saxatilis*. The "lagoon" is not yet mature, but the density is lower there than at the periphery

Taprooted tree seedlings are subjected to the same forces. Once established, seedlings and saplings on sloping sites are subjected to strong shearing forces from snowpack, and breakage of stems is common in all but the supple *T. mertensiana*.

Two other coniferous species occur in the immediate area but did not appear in the 1670-1770 m quadrats. *Juniperus communis* var. *saxatilis* grows in sunny exposed sites (Fig. 7). *Abies amabilis* grows in profusion N of Cabot Lake (Fig. 2) and is scattered throughout the forest near the transect above 1600 m. The trees near the study area are small, indicating recent establishment. In British Columbia Schmidt (1957) found that the effective seed dispersal range of *A. amabilis* is very limited so the species is a slow invader.

Across the head of Brush Creek canyon towards South Cinder Peak (Fig. 2) the cinder flats increase. Forest is there restricted to low, rocky ridges or outcrops not covered by cinders. Many of these patches of trees are similar to the "timber atolls" in the Rocky Mountains (Griggs, 1938). The stand illustrated in Figure 7 is at 1860 m altitude and is composed of *A. lasiocarpa, P. albicaulis, T. mertensiana* and *J. communis* var. *saxatilis*. It appears to result from the initial establishment of one or a few trees, with centrifugal expansion occurring under the protective influence of the pioneers. The trees in the center have not yet died, so the atoll is immature, but the density at the margin is considerably higher than at the center.

B. Continuous forest (1500-1670 m).—The forest below 1670 m is also dominated by *T. mertensiana* to about 1620 m (Fig. 4). Individual trees are smaller with decreasing elevation, however, and litter accumulation is less. *Abies lasiocarpa* density increases as the *Tsuga* decreases, particularly in the sapling and small tree sizes. The very narrow excurrent crown of *A. lasiocarpa* creates a comparatively open stand in spite of high density and a frequency of 93% at 1500-1600 m. A pattern of clumping appears in *A. lasiocarpa* here at about the same elevation that it disappears in *T. mertensiana*. The presence of smaller satellite trees around large individuals and adventitious roots at the bases of living branches buried in decomposing litter suggest that layering may have caused the pattern.

The importance of *P. albicaulis* also diminishes with decreasing elevation, and it is absent below 1500 m. Very intolerant of shade (Baker, 1949), it is confined to gaps in the canopy. *Pinus monticola* first appears at 1570 m, slightly overlapping the range of *P. albicaulis*, as noted by Klyver (1931) in the California Sierra Nevada. There are a few cone-bearing *P. monticola* at about 1500 m, but the only extensive stand, as well as the only *Abies procera,* was seen one km N centered at around 1225 m on the S wall of Cabot Creek Canyon.

Pinus ponderosa was sampled at 1570 m as saplings in well-lighted locations. The most conspicuous specimens, however (at 1525 m measuring 129 cm dbh), grow as isolated individuals as high as 1700 m along the canyon rim S of the transect.

A few saplings of *A. amabilis* grow within this zone, but they are

not common. *A. grandis* is established up to around 1550 m, but the trees are small and of marginal vigor.

Charred wood and fire scars indicate a destructive fire a century ago at what is now a major vegetative discontinuity. Here a dense stand of mature, 100-year-old (dbh to 38 cm), nonreproducing *Pinus contorta* is found. Shrubby understory is nearly absent in this stand. The low-growing *Arctostaphylos nevadensis*, confined to the best-lighted sites, and considerable dead and dying *Arctostaphylos patula* are the most common and are undoubtedly remnants of the brush fields which grew up following the fire.

2. *Abies grandis forest (1150-1500 m).*—*Abies grandis* dominates the forest within these elevational limits (Fig. 8). Mature trees are common only between 1250-1400 m but young trees and saplings are abundant throughout (Table 1). The tree reproduces well even in deep shade. One 2.44 x 4.88 subplot containing the largest tree measured (98 cm dbh) also supported four saplings.

The best *A. grandis* forest is a nearly pure stand at about 1300 m growing in deep soil just W of Abbot Butte Spring (Fig. 2). Trees to 100 cm dbh are common here, and some of the largest show basal fire scars. Since *A. grandis* is not very resistant to fire damage, particularly as a young tree, and small- to medium-sized individuals are plentiful, this site is unlikely to have had a hot fire within the past 200 years.

A few widely scattered saplings of *A. lasiocarpa, A. amabilis* and *T. mertensiana* within the mature *A. grandis* stand do not form a significant part of the forest (Fig. 8).

At the margins of the pure stand there are substantial numbers of very large *P. ponderosa* and a few dead or moribund *P. contorta*. These pines generally occur on slightly raised, rocky sites and are regenerating only in the occasional canopy gap.

With increasing elevation above the pure stand, *A. grandis* compete with the shade-tolerant *A. lasiocarpa* and, to a lesser extent, with *T. mertensiana* (Fig. 8 and Table 1). The position of the final border between the two *Abies* species will be determined by long-term climatic
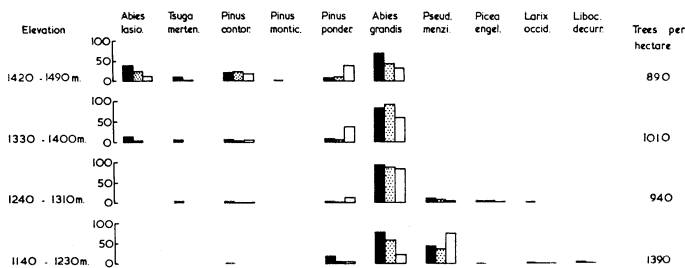

Fig. 8.—Frequency (solid), relative density (dotted), relative dominance (clear), and trees/ha for species recorded 1140-1490 m altitude on the Cascades' eastern slope. Data from 112 subplots (2.44 x 4.88 m) are included in the histograms for each set of altitudinal ranges

trends. *A. grandis* is a taller tree at maturity and needs less soil moisture than *A. lasiocarpa*. Haig *et al.* (1941) suggest that heavy snowpack is a limiting factor for *A. grandis*. Heavy winter precipitation with an accompanying shorter growing season would thus favor *A. lasiocarpa*.

Pinus monticola is mostly confined to the 1400-1600 m level. Although it is the most shade tolerant of the native pines, it does not compete effectively with maturing *Abies* species. Barring fire or other serious disturbance, *P. contorta, P. monticola* and *P. ponderosa* will all be confined eventually to the few sites whose topographic or edaphic features preclude development of closed canopy *Abies* forest.

Between about 1100 and 1200 m altitude mature trees are *Pseudotsuga menziesii* and a few *Pinus ponderosa* (Fig. 8). Some of the *Pseudotsuga* grow to 160 cm dbh, and their size is reflected in the high relative dominance value for the species at these elevations. The *A. grandis* here is smaller, from saplings to small trees of 30 cm dbh. Near 1200 m almost all the small trees are *A. grandis*, but *P. menziesii* appears increasingly as the 1150 m level is approached. The absolute density of these young stands may be very high—as many as five trees (10-20 cm dbh) and six saplings in a single subplot.

There are a few small trees of *Larix occidentalis* in the better-lighted sites of the lowest 100 m (Fig. 8), and a few large ones were observed near the transect line. The highest outliers of *Libocedrus decurrens* in the quadrats and occasional large nearby seed trees are found at about 1175 m.

At the eastern margin of the pure *A. grandis* stand begins the upper end of the 300 m long, shallow valley of Abbot Butte Spring (Fig. 2), whose lower end flattens into a hectare of outwash flat. The spring course occupies only the lower 75 m of this E-W-oriented valley and only there do the valley walls reach 40% slope.

This valley is particularly rich in coniferous species. Along the stream occurs a small stand of *Tsuga heterophylla*, its only occurrence near the transect. Here the tree size ranges from seedlings to cone-producing individuals 30 cm dbh. Here also are a few pole-sized *Larix occidentalis*, cone-bearing *P. monticola* and many *Picea engelmannii*. The outwash flat is vegetated by very large specimens of *A. grandis, P. ponderosa, L. occidentalis, P. menziesii* and *P. engelmannii*, the latter 50 cm dbh.

3. *Low elevation forest (840-1150 m).*—The overstory forest here is chiefly an open-grown stand of *P. ponderosa*, up to 124 cm dbh, obscured in many places by a dense understory of small- and medium-sized trees (Fig. 9, Table 1). In descending order of abundance after *P. ponderosa* in the upper 200 m of elevation are: open-grown *Pseudotsuga menziesii*, to 83 cm dbh, *Libocedrus decurrens*, to 98 cm dbh, and *L. occidentalis*, to 58 cm dbh.

P. ponderosa is being replaced. Its saplings and small trees are common only below 1100 m elevation, and it is not the majority sapling even there (Table 1). Although the absolute numbers of *P. ponderosa*

saplings increase with decreased altitude, the percentage of the total remains low throughout.

A. grandis, a recent invader, is the most shade tolerant tree, but is common only in moister, cooler sites at higher elevations, with no sampled trees larger than 29 cm dbh. Its saplings are common above 1050 m and various tree sizes are found in small, shallow, N-to-S drainages. Below 1050 m it is confined to the few gradual, N-facing slopes.

Trees and saplings of *P. menziesii* and *A. grandis* often occupy the same subplots, *Pseudotsuga* increasing in importance as *Abies* decreases with lower elevation. At 1050-1150 m *Abies* saplings are 2½ times as common as *Pseudotsuga*, but below that, *Pseudotsuga* saplings are the more abundant and dead saplings of *Abies* suggest a marginal habitat for the species here.

The shade-intolerant *Larix occidentalis* (Baker, 1949) has low frequency at these elevations (Fig. 9) and seems restricted to unusually moist locations. *Libocedrus decurrens*, on the other hand, is a very effective competitor, particularly in the lower two-thirds of this forest (Fig. 9). It is the most common sapling throughout the entire 300 m of elevation and makes up 70% of all saplings between 840 and 950 m (Table 1). Its absolute density is extremely high in places, up to 238 saplings (deer- or sheep-browsed but vigorous) in a single quadrat at 930 m.

4. *Stream-bottom vegetation.*—The mesic conditions afforded by streams have produced several notable modifications from the forest typical of the adjacent uplands. The N-flowing Metolius River is the largest of these, but Abbot Creek, Candle Creek and Canyon Creek also support species not otherwise found in the region (Fig. 2).

The upland forest, where the transect crosses the Metolius, is almost totally dominated by *P. ponderosa* and *L. decurrens*, with
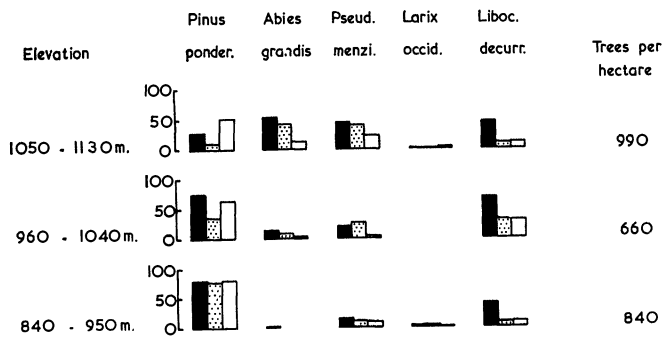

Fig. 9.—Frequency (solid), relative density (dotted), relative dominance (clear), and trees/ha for species recorded 810-1130 m altitude on the Cascades' eastern slope. Data from 112 subplots (2.44 x 4.88 m) are included in the histograms for 960-1040 m and for 1050-1130 m; 128 subplots are included in those representing 840-950 m

scattered *P. menziesii* in the protected sites only. The river bottom-land, too, is dominated by large *P. ponderosa* and *L. decurrens*, but there are also numbers of small- and medium-sized *P. menziesii* and *A. grandis*. Southward near the mouth of Canyon Creek is a substantial stand of *L. occidentalis*, including some very large individuals.

The forest N along the river, where elevation drops slightly and canyon walls steepen, has a different character. Frequent large *P. menziesii* and *A. grandis* and some *P. engelmannii* are found as conditions become increasingly mesic. Six km N of the transect the canopy closes and although scattered, moderate-sized *P. monticola* and cone-bearing *P. lambertiana* appear, young trees are the shade-tolerant *A. grandis* and *P. engelmannii*.

The banks of Candle Creek (900-950 m) support a mixed, old-growth stand of *P. engelmannii*, *T. heterophylla*, *T. plicata*, *P. monticola*, *P. menziesii* and *A. grandis*. Further upstream (1050 m) there is considerable *T. heterophylla* and *Taxus brevifolia*. The Recent lava flow (Fig. 2, rock formations map) just N of Candle Creek has a sparse stand of *P. ponderosa* and *P. menziesii*.

Along Abbot Creek (915-1000 m) are limited stands of the moisture-requiring *P. engelmannii*, *T. brevifolia* and *T. heterophylla*. Large *A. grandis* and *P. menziesii* are also prevalent here, with lesser numbers of *P. ponderosa* and *L. occidentalis*. The adjacent uplands are dominated by *P. ponderosa*, with *L. decurrens*, *P. menziesii* and *A. grandis* encroaching.

The banks of Canyon Creek at 1100 m are particularly rich in species composition. Growing here are *T. plicata*, *T. heterophylla*, *T. brevifolia*, *L. occidentalis*, *A. grandis*, *P. menziesii*, *P. ponderosa* and the deciduous *Sorbus sitchensis* (mountain ash) and *Populus trichocarpa* (black cottonwood).

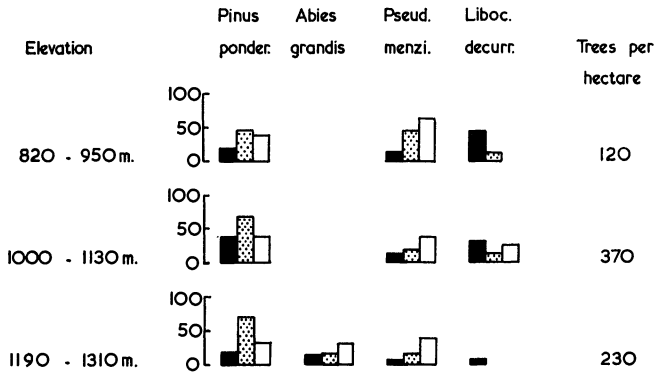   5. *West slope of Green Ridge (840-1310 m)*.—This fault scarp

Fig. 10.—Frequency (solid), relative density (dotted), relative dominance (clear), and trees/ha for species recorded 820-1310 m altitude on the W slope of Green Ridge. Data from 48 subplots (2.44 x 4.88 m) are included in the histograms for each set of altitudinal ranges

is steep (Fig. 2, contour and profile maps) and relatively barren, with rock outcrops and unstable sliding substrate limiting the available tree habitat. Its western exposure subjects it to severe desiccation, making tree establishment difficult.

P. ponderosa is the most common tree, with all ages present (Fig. 10). Mature trees are not as large as those at comparable elevations across the Metolius River—the largest measuring 75 cm dbh at 950 m. Low frequency of all species indicates the open nature of the canopy.

Other species of importance are *P. menziesii* and *L. decurrens*. The largest trees on the slope are *P. menziesii,* sampled at 1300 m at 89 cm dbh. The species is not reproducing well here, probably because of the limiting effect of drought on seedling survival. An occasional large specimen of *L. decurrens* is found, one measured at 76 cm dbh.

Near the top of the ridge where soil depth is greater and slope angle decreases to 15%, both density and frequency of trees increases. Old-growth *P. ponderosa* and *P. menziesii* dominate the forest physiognomy, but only the latter is reproducing very effectively. *A. grandis* shows moderate sapling frequency (Table 1) in the uppermost 100 m, but *L. decurrens* is less important in these cooler, moister conditions. Near the base of the western slope are a few small *J. occidentalis*.

6. *East slope of Green Ridge (920-1370 m)*.—This gradual eastward slope is a physiographic duplicate of the E slope of the Cascades (Fig. 2, contour and profile maps). The rain shadow effect of the Cascades, however, is apparent in the forest of Green Ridge, since
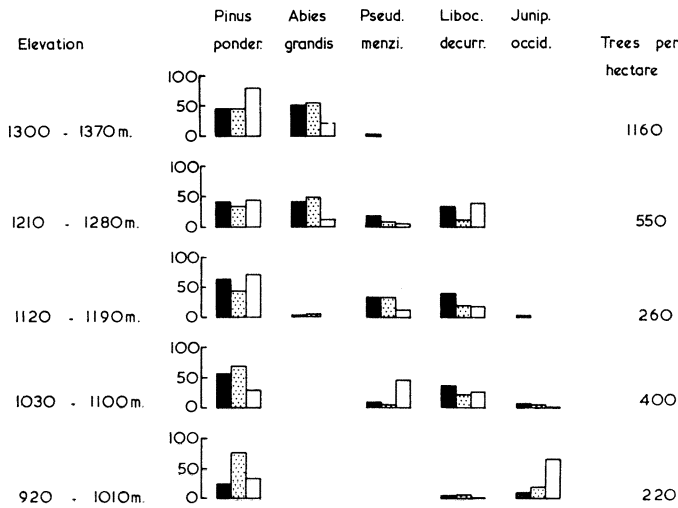
Fig. 11.—Frequency (solid), relative density (dotted), relative dominance (clear), and trees/ha for species recorded 920-1370 m altitude on the E slope of Green Ridge. Data from 80 subplots (2.44 x 4.88 m) are included for the histograms for 920-1010 m; all others are based on 64 subplots

the forest at the top of the ridge is most similar to that at a point 200 m lower on the Cascades' eastern slope.

The forests of the two eastern slopes have in common substantial proportions of *P. ponderosa, A. grandis, P. menziesii* and *L. decurrens*. They differ in the near absence of the moisture-requiring *P. engelmannii* and *L. occidentalis* from the slopes of Green Ridge, and the presence of the drought-resistant *J. occidentalis* on the lower two thirds of Green Ridge's leeward side.

The Green Ridge forest changes from a dense, closed canopy stand at the crest, to a savannah 13 km eastward at the rim of Fly Creek Canyon. *P. ponderosa* is the only species that is common throughout, although its role changes from W to E. Above 1200 m and particularly above 1300 m its very high dominance and only moderate frequency and relative density suggest the impending replacement by *A. grandis* (Fig. 11). *P. ponderosa* is the most abundant sapling below 1200 m, however, and will continue to be important here unless there is a drastic climatic change or other disturbance. The largest pine sampled was 102 cm dbh at the ridge top. This area had been selectively logged before the time of the study, so there had undoubtedly once been larger specimens present.

A. grandis density is highest in the upper 150 m of altitude; it is the major sapling above 1300 m and is common down to 1200 m. (Table 1). Its lower altitudinal limit is 200 m higher than on the Cascades' eastern slope, reflecting decreased precipitation. But while frequency and relative density are high above 1225 m, relative dominance is low (Fig. 11), and the largest tree measured was only 36 cm dbh.

L. decurrens is important here, and at 1100 m measured to 82 cm dbh. Its sapling density (Table 1) is about 20% of total saplings between 1030 and 1280 m.

P. menziesii occurs primarily at 1000-1200 m but significant numbers of saplings are found only in the lower 100 m on mesic, slightly N-facing irregularities of terrain. (Fig. 11, Table 1). The largest measured specimen was 111 cm dbh.

At the eastern end of the transect only *P. ponderosa* and *J. occidentalis* occur in any quantity. Saplings of both species are uncommon (Fig. 11). *J. occidentalis* is of low frequency but with dbh to 98 cm. *P. ponderosa* at these lower elevations is severely infected with dwarf mistletoe and suffers considerable bark damage by porcupines.

Like the trees, those shrubs and herbs common to the E slopes of both the Cascades and Green Ridge range lower on the Cascades' flank, presumably in response to the decreased E side precipitation (Table 2). Heavy litter under the closed canopy pine and fir stand on the ridge top supports few living plants, but dead, precanopy-closure, *Arctostaphylos patula,* remains in places. In more open, middle elevation stands dense *A. patula* and *Ceanothus velutinus* have developed, the former as low as 1000 m, the latter absent below

1125 m. *Chrysothamnus nauseosus* is important at lowest elevations, and *Purshia tridentata* increases in abundance to the eastern terminus of the transect. The only shrub common here but absent on the Cascades' E slope is the decumbent *Ceanothus prostratus*.

Discontinuities in the generally smooth transition from forest into savannah include Prairie Farm Spring and Prairie Farm (Fig. 2), a nearly treeless area of 15-20 ha, formerly the site of an early sawmill. It does not now appear to have been forested, although there are stumps of very large pines (probably *P. ponderosa*) on the few low ridges that intrude into the opening and a few *P. ponderosa* with poor vigor along an intermittent stream. Grass competition now seems adequate to prevent tree invasion of these well-drained surfaces.

A former livestock watering pond impounded by an earthern dam across the eastern end of the opening is surrounded by *Populus tremuloides* (quaking aspen) and *Pinus contorta*.

Around the Prairie Farm Spring drainage basin are *P. engelmannii*, *T. brevifolia, L. occidentalis, P. ponderosa, A. grandis* and *P. menziesii*. Toward the head of the South Fork of Street Creek (Fig. 2) is a mixed open stand of *P. lambertiana, P. ponderosa* and *P. menziesii*, the largest *P. lambertiana* over 150 cm dbh.

DISCUSSION

Aside from such conventional components of the physical environment as precipitation and temperature, the most pervasive influence in these forests has been fire. Circumstantial evidence for a history of burning is commonplace; *e.g.*, even-aged stands of *P. contorta* and isolated, open-grown specimens of *P. menziesii* towering over an understory of young *A. grandis*. More direct evidence is provided by charred bark and basal fire scars on many of the large trees, particularly *P. ponderosa*. Weaver (1959) cut and examined cross sections of mature *P. ponderosa* on the Warm Springs Indian Reservation, just N of this transect. He found one 316-year-old tree that has been fire-damaged 18 times, averaging once each 11 years, though the interval between fires varied from three to 49 years. Soeriaatmadja (1965), also on the Warm Springs Indian Reservation, determined average intervals be-

TABLE 2.—Occurrence of shrubs and herbs on the E slopes
of the Cascades and Green Ridge

	Cascades E slope	Green Ridge E slope
Chimaphila umbellata	above 1150 m	above 1350 m
C. menziesii	above 1050 m	above 1350 m
Castanopsis chrysophylla	above 1100 m	above 1200 m
Lathyrus bijugatus	above 1050 m	above 1250 m
Trientalis latifolia	950 - 1250 m	above 1150 m
Ceanothus velutinus	above 900 m	above 1150 m
Symphoricarpos albus	above 900 m	above 1300 m
Holodiscus discolor	above 850 m	above 1200 m
Purshia tridentata	below 1050 m	below 1300 m
Balsamorhiza sagittata	below 1050 m	above 1150 m

tween fires of 14.2 and 30.2 yrs for two locations within the pine forest.

Fires have been much less common in this region in the twentieth century (Weaver, 1959). Deliberate burning no longer occurs, and accidental fires are extinguished with all possible haste. Thus, a forest that has grown up in the presence of fire is not now usually subject to its effects. Fire protection is not complete, however, since the combination of summer drought and occasional electrical storms with little or no accompanying rainfall still exists. Extensive fires have occurred within the last 30 years at the upper ends of Brush Creek and Canyon Creek (Fig. 2).

The species whose performance is most intricately responsive to fire is *P. ponderosa*. Cooper (1960) has described its interaction with fire in Arizona, and its response is certainly similar here. Mature trees have thick, fire-resistant bark and crowns elevated well above the ground surface. Young trees with thin bark and low crowns are much more fire-susceptible. Thus when fire sweeps through a forest every few years, young trees are often killed but mature trees are seldom seriously damaged.

The usual fire in pine forests burns along the ground, since the widely spaced mature trees with high crowns are not conducive to a crown fire. Since fire burns hottest where the fuel supply is greatest, and in a frequently burned forest, fuel will accumulate in needles, cones and branches under large trees, young trees in this area will almost certainly be killed when the next fire occurs. Dense thickets of small trees are also susceptible, particularly if enough time has elapsed since the last fire to permit litter accumulation. Those young trees most likely to survive are the isolated ones growing in sites with little fuel on the ground. The result is a fire-maintained open, "park-like" forest with little undergrowth and with reproduction confined to gaps in the overstory. While actual enhancement of *P. ponderosa* growth by burning has not been conclusively demonstrated (Woold-ridge and Weaver, 1965), it certainly does benefit from the reduction of competing species.

When a population regulator is no longer operative, the status of the controlled species must change. *P. ponderosa* has such broad ecological tolerances that it is unlikely to behave the same way throughout its range, not only because different factors may be limiting at the range extremes, but because it meets so many different competing species. Indeed, its response to the absence of fire does vary considerably along this transect.

One reason for the success of *P. ponderosa* is its reliable seed production and germination (U.S.D.A. Forest Service, 1965). Seeds normally are released in autumn, germinating in the spring in Oregon and points N, but at the time of release in the southwestern U.S.A. Cooper (1960) observed seedling densities of 30-40 per 930 sq cm in the White Mountains of Arizona in September 1957.

Once established, dense stands of seedlings, saplings and young trees may persist for a long time. Cooper (1960) found that natural

mortality of established small trees of 2.5 cm dbh probably did not exceed 2% annually. Even the clumps of seedlings resulting from the germination of uneaten rodent caches appear to persist little diminished for a season or two. The highest density measured in this study was at 880 m elevation on the Cascades' lower slope, with 40 trees (6-22 cm dbh) growing within one quadrat. Obviously, density-dependent regulation of the population size in the absence of fire is here sluggish at best.

When fire is excluded, the fuel in an area of high density *P. ponderosa* saplings is cumulative, and consequent reduction in population size by burning is likely to be catastrophic. Mortality would be greatest in the event of wildfire, since this would occur only in the season when fuel is near maximum flammability and after many years of litter buildup.

The problem of excessive *P. ponderosa* reproduction is not constant throughout its range. The histograms of Figs. 4, 8-11, and the comparative relative densities for saplings and trees of Table 1 demonstrate clearly that in many areas with mature *P. ponderosa,* the species is not regenerating effectively. Shade tolerant species capable of establishing in heavy litter, particularly *A. grandis* and *L. decurrens,* have higher frequency and relative density than does *P. ponderosa* throughout much of the latter's range. The lack of adequate *P. ponderosa* reproduction has been noted also on the W slope of the Sierra Nevada in Stanislaus National Forest, Calif. (Fowells and Schubert, 1951; Stark, 1965), and on the Warm Springs Indian Reservation, Ore. (Weaver, 1959).

The inability of *P. ponderosa* to regenerate in heavy litter and shade is well documented (Fowells and Schubert, 1951; Stark, 1965; Pearson, 1950). Since the decay-resistant needle litter of pines does not compact well, it seems likely that pine seeds would often be prevented from reaching a germination site that remained continuously moist long enough for seedlings to take root, except adjacent to emergent stones (Haasis, 1921). Even then, the limited shoot growth during the first growing season might prevent the foliage from emerging through the litter to obtain sufficient light for photosynthesis. Seedling damage by fungi and insects is more likely under the protective influence of litter as well (Fowells, 1940).

Larson (1967) found a constant temperature of 23 C was optimum for *P. ponderosa* seedling growth, and it is probable that seed germination occurs earlier on a mineral soil bed. Hulbert (1969) and Old (1969) have shown that higher temperatures are reached earlier in the season on denuded or burned surfaces, and the effect on early seed germination could be crucial in an area of characteristic summer drought.

A number of interspecific competition experiments have demonstrated the importance of relative starting dates for growth (*e.g.,* Williams, 1964). Fowells (1941) showed phenological differences in established coniferous trees in California. *P. ponderosa* began height

growth about May 13, continuing 81 days; *L. decurrens* on May 24, continuing 91 days; and *Abies concolor,* similar in ecology to *A. grandis,* was the last to commence spring growth. Assuming that germinating seed growth is similar, the delay in germination caused by slow warming of litter-covered soil would be important. When it is considered that *P. ponderosa* must compete with shrubs and herbs as well as other tree seedlings, the advantage of advanced germination date becomes obvious.

Both intra- and interspecific interaction are in part responsible for the suggested impending decline of *P. ponderosa* in these forests. *Abies grandis* appears to be its successor in the moister part of its range (Table 1, Lines 4-8, 14, 15). *A. grandis* can tolerate annual precipitation as low as 50 cm and grows more rapidly under moderate shade (U.S.D.A. Forest Service, 1965). Increment cores taken at 1100 m elevation on the Cascades' E slope near the soil drought limit of *A. grandis* indicate the effects of the *A. grandis-P. ponderosa* interaction. In a young, nearly closed stand, a pine 10 m tall and 15 cm dbh was 58 years old; while an adjacent fir 12 m tall and 20 cm dbh was only 34 years old. A few meters away an open-grown pine in similar soil and moisture conditions was 12 m tall, 22 cm dbh and 49 years old.

A. grandis normally grows more slowly than many of its competitors (U.S.D.A. Forest Service, 1965) in full sunlight, and its seedlings are susceptible to heat injury. Since Stark (1965) reported that *P. ponderosa* was the fastest growing tree in regenerating forests following logging in the Stanislaus National Forest, Calif., *A. grandis* would seem to require the shade produced by larger trees for optimum regeneration and growth.

P. menziesii, while fairly common at the middle elevations, is not the most important component among the sapling assemblage anywhere along the transect. It is less shade tolerant than either *A. grandis* or *L. decurrens,* and these two species completely overlap the range that *P. menziesii* can occupy. *P. menziesii* will no doubt maintain itself as a minority species on the more xeric sites within the general range of *A. grandis* and the more mesic locations in the range of *L. decurrens.* It would increase at the expense of *L. decurrens,* assuming adequate seed trees, if the climate becomes wetter. It requires mineral soil for effective seedling establishment, however, so it cannot remain important without occasional fires (U.S.D.A. Forest Service, 1965).

L. decurrens is near the northeastern limit of its natural range (Preston, 1961), so it is possible that some yet unrecognized tolerance limit may exercise control. Short of that, however, it may increase at the expense of *P. ponderosa.* A prolific seeder (U.S.D.A. Forest Service, 1965) whose seedlings and saplings are shade tolerant when young (Mitchell, 1918) and can persist for considerable time in the sapling stage, it has been found to have the longest growing season among trees on the cutover land of California's Stanislaus National Forest (Fowells and Schubert, 1951). It is a common sapling below

1100 m on the E slope of the Cascades and everywhere on Green Ridge except in the closed stand on top (Table 1). Although it may be severely browsed (U.S.D.A. Seed Manual, 1948), such damage here does not appear to cause much mortality. Young trees are very fire-susceptible but in the absence of fire they will apparently continue to prosper.

The behavior of *Picea engelmannii* in this area is at variance with that in much of the rest of its range. In the Rocky Mountains and in the North Cascades of Washington it is an alpine and subalpine species. Here it is a middle elevation species, occurring as low as about 800 m along the Metolius River N of the transect and not located higher than about 1400 m. It is confined to moist bottomland sites, though there is not always a permanent stream present.

Although species composition of a given spot may change, the forest above the range of *A. grandis* (1500 m) will remain relatively constant. *A. lasiocarpa* and *T. mertensiana* are the most shade tolerant and the latter, particularly, can exclude other species. However, the climate and snowpack are so severe that continuous forest is unlikely to persist. Gaps in the canopy remain where the shade-intolerant *P. albicaulis, P. contorta, P. ponderosa* and *J. communis* var. *saxatilis* can survive.

If the forest is destroyed by fire, the shade-intolerant species will be temporarily favored. The Brush Creek burn, which occurred in 1945, illustrates the likely sequence following fire. As often occurs in the discontinuous forest of high elevations, the fire skipped a number of areas, leaving islands of seed trees supporting *T. mertensiana, A. lasiocarpa, A. grandis, P. monticola, P. contorta* and *P. ponderosa* dispersed unevenly within the burned area.

Although the burned area had grown up with shrub species, particularly *Arctostaphylos patula, Ceanothus velutinus* and *Holodiscus discolor*, saplings of *P. contorta* and *P. ponderosa* were just appearing over the shrub canopy in 1960. In spite of the apparent availability of seeds from all or most of the species native to the area, these two pines appeared first. The other species may reappear later.

Succession, then, is still in progress throughout the area crossed by the transect, with only the high-elevation *T. mertensiana* and the mid-elevation *A. grandis* stands approaching climax status. The rate of succession is slow; thus, unpredictable environmental change can affect the sequence. Assuming continuation of present conditions, however, *T. mertensiana* at highest elevations, *A. grandis* at mid-elevations, *L. decurrens* in the moister low elevations and *P. ponderosa* in the xeric low elevations are likely to be the preponderant species.

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