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By

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SOIL-VEGETATION RELATIONSHIPS WITHIN THE PONDEROSA PINE TYPE IN THE CENTRAL OREGON PUMICE REGION

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Abstract. Six plant communities occurring within the ponderosa pine (*Pinus ponderosa*) and white fir (*Abies concolor*) zones were identified east of the Cascade Mountains in south-central Oregon. These units, listed in order of increasing effective moisture and increasing elevation, are as follows: (1) *Pinus ponderosa/Purshia tridentata,* (2) *Pinus ponderosa/Purshia tridentata/Festuca idahoensis,* (3) *Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana* var. *pinetorum,* (4) *Pinus ponderosa/Ceanothus velutinus-Purshia tridentata,* (5) *Pinus ponderosa/Ceanothus velutinus,* and (6) *Abies concolor/Ceanothus velutinus.*

The *Pinus/Purshia/Festuca* association is restricted to areas of Shanahan coarse sandy loam, while the remaining five units all occur on Lapine loamy coarse sand. Both series are Regosols developed on aeolian pumice deposits. Lapine profile characteristics influencing plant root distribution, such as thickness of the gravelly C1 horizon and amount of mixing of C2 material with the buried soil, showed some apparent correlations with plant communities. The Lapine soil under the *Pinus/Purshia* and *Pinus/Ceanothus-Purshia* communities had thickest C1 horizons and the smallest amounts of mixing in the C2. The soil associated with the *Pinus/Ceanothus* community had the thinnest C1 and a well-mixed C2 horizon. Roots were generally well distributed throughout the C2 horizon in the latter community, whereas in soils possessing a thick C1 and little mixing in the C2 roots are restricted largely to the A1, AC, and D horizons.

Soil-moisture measurements indicated that depth and time of onset of soil drought are important factors in controlling the distribution of plant communities in the study area.

The A1 horizon under *Pinus/Ceanothus* and *Abies/Ceanothus* communities contained appreciably greater quantities of available P, exchangeable Ca, and total N. Organic matter content of the Lapine A1 horizon was considerably higher under the more mesic communities. Carbon-nitrogen ratios of Lapine and Shanahan A1 and AC horizons were not correlated with plant groupings. C/N values were found to be very much higher than those encountered in surface horizons of zonal forested soils, probably due to slow rates of organic matter decomposition.

INTRODUCTION

The vegetation and soils of the pumice region of central Oregon have received little attention. Material published to date is devoted largely to discussions of factors controlling distribution of lodgepole (*Pinus contorta* Dougl.)[1] and ponderosa pine (*Pinus ponderosa* Laws.). Kerr (1913) was perhaps first to record several observations which are still often repeated. He pointed out that "on wide pumice flats there is an unbroken stand of lodgepole," while on every hill and slight rise in topography this species had a tendency to give way to ponderosa pine. Kerr suggested that ponderosa pine was excluded from level areas because of its intolerance to conditions of poor soil drainage. Munger (1914) attached far more importance to fire as the principal factor encouraging lodgepole pine. He felt that since many areas were burned over on the average of once every 30 years, lodgepole pine was definitely favored because of its much more prolific seeding habit. Tarrant (1947, 1953), in agreement with Kerr, has concluded that lodgepole is able to compete successfully with ponderosa pine on pumice soils having a permanent, fluctuating high water table. Youngberg and Dyrness (1959) studied the soils and understory vegetation associated with lodgepole pine stands of central Oregon in an attempt to develop guides for differentiating between seral and climax stands.

Forested pumice soils in central Oregon were first classified by Leighty (1947) during a soil survey of a portion of the Pringle Falls Experimental Forest near Lapine. Three soil series tentatively established at that time have since been mapped extensively in other areas. Pumice soil morphology and classification also received considerable attention during the course of a soil survey of the Klamath Indian Reservation (U. S. Bureau of Indian Affairs 1958). Most research

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[1] Common and scientific names of trees follow Little (1953).

on fundamental properties of pumice soils has been in New Zealand. Youngberg and Dyrness (1964) recently published on physical and chemical properties of pumice soils in Oregon.

This study was concerned with ecological interpretations following completion of a soil-vegetation survey of 50,000 acres of predominantly ponderosa pine forest land in central Oregon. The aim was to make the survey information more useful by completely describing basic units of both soil and vegetation and investigating relationships between them. In addition, an attempt was made to determine how some of the important soil-vegetation units affect forest management practices.

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Description of Study Area

Location and use

This study was carried out in the Antelope unit of Weyerhaeuser Co.'s Klamath Falls Tree Farm, located in south-central Oregon approximately 35 miles east of the Cascade Range summit and 65 miles north of Klamath Falls, adjacent to the northern boundary of the old Klamath Indian Reservation. The Lake-Klamath County line runs through the middle of the unit.

The Antelope unit is located on a high plateau which extends eastward from the base of the Cascade Range. Elevations vary from 5,000 to 6,300 ft above sea level. Topography includes broad, almost completely level areas, abrupt basalt escarpments and benches, and numerous cone-shaped buttes generally composed of basalt and volcanic cinders.

At the time of the study, vegetation of the Antelope unit had been subjected to very little logging disturbance. Portions of the area provided forage for sheep and a small number of cattle during summer months. However, severe animal disturbance was encountered only at lower elevations. In common with most other areas in the ponderosa pine type, fire has been an important factor in the past. Since 1900, however, the region has been relatively free of widespread wildfires, and only one area of any size has been burned in the last 30 years.

Geology

The region has a history of extensive and repeated volcanic activity. Available information indicates that the area is underlain by extensive basalt lava flows deposited during the Miocene epoch. Volcanic activity very likely continued at least through the Pliocene, with later eruptions forming numerous volcanic cones. During the Pleistocene, general volcanic activity subsided, allowing the formation of a shallow, stony soil over much of the area. Post-Pleistocene vegetation, as determined by Hansen (1942) through pollen analysis, included many of the tree species still common in the region. These conditions, however, were profoundly altered by the explosive, culminating eruption of Mount Mazama on the crest of the Cascade Range, resulting in the formation of Crater Lake. The eruption included pumice showers and glowing avalanches that left very extensive deposits. The pumice fall is largely concentrated to the north and east of the crater in layers up to 15 feet deep but is also found more than 100 miles from the source. Carbon-14 dating has placed the age of the pumice at approximately 7,600 years (Williams 1957).

The Antelope unit is within the region of the pumice fall and is covered by a layer of pumice ranging from 4½ feet to approximately 1 foot in thickness. The buried soil under the pumice mantle exhibits very little profile development. Williams (1942) has identified the pumice as a dacite or, more specifically, glassy hypersthene-augite dacite with accessory hornblende.

Climate

No temperature or rainfall records are available for the Antelope unit or any nearby comparable area. For this reason, climatic characteristics can be described in only a general manner. Annual precipitation very likely ranges from about 20 to 25 inches, depending on elevation. Crescent, Oregon, located approximately 25 miles to the northwest, receives an average of 19 inches annually. Inasmuch as the Antelope unit is situated some 500 ft higher than Crescent, total precipitation could be expected to be slightly higher in the study area. Annual precipitation undoubtedly decreases gradually towards the eastern border of the unit to a possible minimum of 15 inches. Generally, very little rain falls during the summer months and winter precipitation is largely snow. The study area has an extremely short frost-free season as a result of its relatively high elevation. Although daytime temperatures during July and August often reach 95°F or higher, nighttime frosts are common. Mean January and July temperatures at Silver Lake (11 miles to the east) are approximately 28° and 64°F, respectively.

Methods

Stands to be sampled were selected after extensive reconnaissance and only if they were representative of the entire community. Plots were placed in widely distributed stands in an attempt to secure an adequate estimate of geographic variation within a community, as it was apparent from reconnaissance data that variations in species composition, plant density, and other characteristics were greater among stands than they were within a single stand.

Other criteria used in selection of plot locations were: (1) homogeneity with respect to soil type and depth, (2) uniform relief, and (3) absence of extensive recent disturbance.

Vegetation sampling

Vegetation sampling was not undertaken until natural plant groupings of the area had been recognized. Accordingly, vegetation plot data characterized already recognized plant communities rather than aided in their original identification. Six distinctive plant communities were selected for study, with six plots each in five of the communities and five plots in the sixth, for a total of 35 plots.

The basic approach to vegetation sampling employed in this study was first fully developed by Daubenmire (1959). Percentage of canopy coverage was estimated for all species occurring within a series of small, two-dimensional plots. Plot size and layout procedure were essentially the same as outlined by Poulton and Tisdale (1961).

Macroplots for the sampling of understory vegetation were 50 by 100 ft. The long axis of the macroplots extended in the same direction as the slope. Four 50-ft transects extended parallel to the long dimension within each macroplot. The starting point for each transect was the coordinate of two random numbers: one number determining the distance up from the base line (the downslope boundary of the plot) to the origin, and the other corresponding to the horizontal distance from the right-hand, long boundary.

Ten 1- by 2-ft grass and herb observation plots were placed at equally spaced intervals along each transect with the aid of a 50-ft steel tape. An open-ended steel plot frame was used to delineate the boundaries of the plot. Percentage cover of each grass and herb species within the plot area was estimated with the aid of two wire estimating rings, one covering 5% and the other 2% of the total plot area. Ten 4- by 5-ft shrub and tree reproduction observation plots were also placed along each transect. Percentage crown cover of shrubs and tree seedlings and saplings occupying these plots was ocularly estimated and recorded in 1% increments up to 10% and 5% increments thereafter. In addition to cover estimates, tree seedlings and saplings and shrubs with their stems in the plot were counted and recorded by height class. The tree seedling class included all well-established individuals up to 3 ft in height and saplings were defined as 3-10 ft in height.

Diameter at breast height was determined and recorded by species for all trees in the macroplot larger than sapling size. Percentage of the total macroplot area covered by the crowns of each tree species was also estimated.

Three statistics were obtained for each plant species occurring within each macroplot: (1) percentage herbage cover, (2) percentage frequency, and (3) percentage constancy among macroplots. Where a species was encountered only within the macroplot boundaries and not on an observation plot, it was assigned a "trace" cover value. A constancy figure for a given species is defined as the percentage of the total number of macroplots within a single community containing at least one individual of that particular species.

Tree regeneration estimates were obtained by a milacre transect sampling method. Sampling transects were approximately 1,096 ft long and were situated 100 ft outside of and parallel to the macroplot boundaries. Each transect consisted of 166 contiguous milacre plots (6.6 ft square). The sampling procedure consisted of carefully inspecting a belt 6.6 ft wide, divided into milacre plots by means of marks every 6.6 ft on a 100-ft steel tape. Width of the belt to be sampled was determined by using a pole which, when held in a position perpendicular to the direction of the tape, extended 3.3 ft on each side. All stems of tree reproduction less than 10 ft in height occurring within each milacre section were counted and recorded by species and height class. In those cases where no stems of reproduction were encountered within a plot, the presence or absence of an overhead tree canopy was also noted and recorded. Milacre plots more than one-half covered by tree crowns, although containing no reproduction, were considered to be "occupied" by growing stock; and the number of these plots was subtracted from the total number (166) in the calculation of percentage milacre stocking. Accordingly, in this study, percentage stocking figures are termed percentage stocking in unoccupied milacres.

Soil sampling

Soil profiles were investigated to a minimum depth of 1 ft below the pumice, and a complete soil profile description was made for each macroplot location (U. S. Dept. Agriculture 1951). In addition, morphological features of each profile were sketched, with special attention given to any irregularities of horizon boundaries. After the profile was described, a sample of each horizon was obtained for laboratory analysis.

During the 1956 growing season, gravimetric soil-moisture samples were collected at weekly intervals from one plot (plot A) located within each of four plant communities. In 1957 these same four communities were sampled at two plots (plots A and B). Each horizon and the buried soil beneath the pumice were sampled separately with a King tube. Duplicate sets of samples were collected on each plot, one set collected in openings at least 4 ft from the closest shrub or tree and the other obtained directly beneath shrub plants. In addition, duplicate undisturbed core samples were collected with a modified Uhland sampler from each horizon at the eight sampling plots. Bulk density of each sample was used in calculating soil-moisture levels on a volume basis. Precipitation was measured in standard rain gages at each soil-moisture plot.

Permanent wilting percentages for sampled horizons were determined by the sunflower method. Amounts of moisture contained in samples collected the first week in May, soon after snowmelt, were used as an approximation of field capacity.

Soil particle-size distribution was determined by the pipette analysis procedure (Kilmer and Alexander 1949). Percentages of organic matter and total nitrogen in the two surface horizons were determined for all 35 profiles. In addition, the following determinations were carried out on selected samples: soil reaction, available P, exchangeable K, Ca, and Mg, and cation exchange capacity. Soil reaction was measured with a glass electrode pH meter using a 1:1 soil-paste. The sodium bicarbonate method of Olsen et al. (1954) was used to determine available P. Exchangeable K, Ca, and Mg were determined on a flame photometer after extraction with 1N ammonium acetate. Cation exchange capacity was determined by the ammonium acetate method of Schollenberger and Simon (1945).

RESULTS

Description of plant communities

The six plant communities chosen for study are listed in Table I, in order of increasing effective moisture. These six communities, their intergrades, and seral variants occupy virtually all of the study area that supports ponderosa pine or white fir as the climax-dominant tree species.

(1) *Pinus ponderosa/Purshia tridentata* association

The *Pinus/Purshia* association is restricted to the lower elevations immediately above the poorly drained wet meadows and areas of climax lodgepole pine. In the study area, it is situated on well-drained Lapine loamy coarse sand. It represents relatively xeric conditions as indicated by open, parklike timber stands including only small amount of advance regeneration (Fig. 1).

TABLE I. The six plant communities characterized by means of plot sampling

Plant community	Number of stands sampled	Elevational range of sample (feet)	Associated soil series
(1) *Pinus ponderosa/Purshia tridentata*....................	6	5,025–5,205	Lapine
(2) *Pinus ponderosa/Purshia tridentata/Festuca idahoensis*....	5	5,195–5,640	Shanahan
(3) *Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana* var. *pinetorum*................	6	5,300–5,400	Lapine
(4) *Pinus ponderosa/Ceanothus velutinus-Purshia tridentata*.....	6	5,190–5,500	Lapine
(5) *Pinus ponderosa/Ceanothous velutinus*.....................	6	5,560–6,050	Lapine
(6) *Abies concolor/Ceanothus velutinus*.....................	6	5,610–6,200	Lapine

FIG. 1. General view of a stand within the *Pinus ponderosa/Purshia tridentata* association.

Daubenmire (1952) has described a *Pinus ponderosa/Purshia tridentata* association occurring in northern Idaho and eastern Washington. The *Purshia tridentata* (Pursh) DC.[2] union is dominant. Others present are the *Agropyron spicatum* (Pursh) Scribn. & Sm. and *Poa secunda* Presl. Aside from sharing the *Purshia tridentata* and *Pinus ponderosa* unions, the association described by Daubenmire and the one occurring in the Antelope unit are floristically dissimilar. However, both are indicative of rather dry sites for the ponderosa pine type.

The majority of the herbaceous species present in the *Pinus/Purshia* association are found in all

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[2] Names of grasses, herbs, and shrubs follow Peck (1941) except where indicated.

TABLE II. Percentage cover, frequency, and constancy[1] of plant species occurring within six plant communities

	Pinus/Purshia			*Pinus/Purshia/ Festuca*			*Pinus/Purshia-Arctostaphylos*			*Pinus/Ceanothus-Purshia*			*Pinus/Ceanothus*			*Abies/Ceanothus*		
Plant species	% Cover	% Freq.	% Const.	% Cover	% Freq.	% Const.	% Cover	% Freq.	% Const.	% Cover	% Freq.	% Const.	% Cover	% Freq.	% Const.	% Cover	% Freq.	% Const.
Overstory:																		
Pinus ponderosa	18			26			24			32			31			18		
Pinus contorta	Tr			Tr			4			2			3			6		
Abies concolor													3			28		
Pinus lambertiana													2			5		
Total	18			26			28			34			39			57		
Timber reproduction:																		
Pinus ponderosa	1.8	42	83	11.6	70	100	4.0	59	100	4.6	49	100	2.2	43	100	1.2	33	67
Pinus contorta	Tr+	3	33	Tr	—	20	1.4	27	50	Tr+	1	33	.4	8	100	1.0	10	67
Abies concolor													1.9	19	83	10.8	56	100
Pinus lambertiana													.1	5	17	.3	6	33
Total	1.8			11.6			5.4			4.6			4.6			13.3		
Shrubs:																		
Purshia tridentata	18.9	91	100	13.9	90	100	14.8	88	100	11.5	60	100	.2	12	50	Tr	—	17
Arctostaphylos parryana var. *pinetorum*	Tr+	1	33	Tr+	1	60	14.2	42	100	1.0	8	100	6.5	22	100	.5	5	67
Haplopappus bloomeri				Tr+	—		.1	3	67	Tr	—	17	Tr+	2	50			
Ceanothus velutinus							.7	8	50	25.4	53	100	33.0	67	100	26.5	60	100
Ribes viscosissimum							Tr	—	17							.1	2	33
Prunus emarginata																.1	1	17
Arctostaphylos nevadensis													Tr	—	17	2.8	8	50
Total	18.9			13.9			29.8			37.9			39.7			30.0		
Grasses:																		
Stipa occidentolis	5.2	71	100	2.6	47	100	4.2	60	100	1.5	21	100	1.9	23	100	.6	8	100
Carex Rossii	1.2	17	100	.7	14	100	1.2	16	100	2.5	14	100	1.2	13	83	1.0	10	100
Sitanion Hystrix	.5	12	100	.6	12	100	1.1	18	100	.9	10	100	.3	5	83	.1	2	83
Festuca idahoensis	Tr	—	17	14.1	74	100	.2	—	17									
Koeleria cristata				Tr	—	20												
Total	6.9			18.0			6.7			4.9			3.4			1.7		
Herbs:																		
Gayophytum diffusum	1.1	65	100	.2	20	80	.5	23	100	.5	16	100	.3	20	100	Tr+	5	83
Cryptantha affinis	.3	24	83	.1	8	100	.2	13	100	.2	10	100	.1	9	83	Tr+	3	67
Collinsia parviflora	.2	11	100	.2	14	100	Tr+	2	67	Tr+	2	83	Tr+	1	50	Tr+	4	67
Viola purpurea	.5	48	100	.2	16	100	.1	6	100	Tr+	2	100	Tr+	3	67	Tr	—	33
Lactuca sp.	.1	3	17				.1	3	50	Tr	—	17	.3	4	67	Tr+	1	17
Senecio integerrimus	1.3	38	67	.1	4	60							Tr	—	17			
Lomatium triternatum	.2	4	33	.1	4	100				Tr	—	17						
Mentzelia albicaulis	Tr+	2	50				Tr+	—	17									
Arabis rectissima	Tr+	1	67	Tr+	1	20	Tr+	—	17	Tr+	2	83	Tr+	—	33			
Madia minima	.1	15	67	.2	14	80												
Microseris nutans	Tr+	1	17	.2	3	60												
Linanthus sp.	Tr	—	17															
Linanthus ciliatus				Tr+	3	40												
Agoseris sp.				.3	5	20												
Achillea lanulosa				1.4	23	100												
Horkelia fusca				.2	3	20												
Delphinium Menzeisii				Tr+	1	20												
Ranunculus occidentalis				Tr	—	20												
Paeonia Brownii				Tr	—	20												
Taraxacum officinale				Tr	—	20												
Antennaria corymbosa				Tr+	1	40				.1	1	17						
Eriophyllum lanatum				Tr+	1	40	Tr	—	17									
Phacelia heterophylla	Tr+	—	33	Tr	—	20	.1	3	100				Tr+	—	33			
Fritillaria atropurpurea							Tr	—	17									
Lupinus caudatus				.1	2	100	.1	2	83				Tr+	1	17	Tr+	—	17
Phlox gracilis				.1	9	80	Tr+	1	33									
Fragaria cuneifolia				.2	3	100	2.4	32	100	Tr	—	17	.8	17	100	.6	11	67
Antennaria Geyeri				.1	2	80	.2	5	83	Tr+	1	67	Tr+	—	33	Tr	—	17
Epilobium angustifolium							.3	4	100	.2	2	33	.6	14	100	.6	13	100
Hieracium cynoglossoides							Tr	—	17	.1	3	50	Tr+	1	33	Tr+	1	33
Pyrola picta							Tr	—	17				Tr	—	67	Tr+	2	83
Chimaphila umbellata										.2	3	67	Tr	—	50	.1	2	100
Apocynum androsaemifolium										.4	10	100	Tr	—	50	.1	3	100
Total	3.8			3.7			4.0			1.7			2.1			1.4		
Total understory cover	31.4			47.2			45.9			49.1			49.8			46.4		
Total cover	49.4			73.2			73.9			83.1			88.8			103.4		

[1] % frequency = number of observation plots the species occurred in/the total number of observation plots X 100.
% constancy = number of macroplots the species occurred in/the total number of macroplots X 100.
Tr + = the species occurred in trace amounts (less than 0.1% cover), but was encountered in at least one observation plot.
Tr = the species occurred in trace amounts and was encountered outside of the observation plots, but within at least one macroplot.

the communities, but presence alone is not a strong criterion of phytosociological differentiation. When relative species dominance is considered, some of these widespread herbs take on indicator significance. Annuals such as *Gayophytum diffusum* T. &. G. and *Cryptantha affinis* (Gray) Greene, although widely distributed in the study area, are most abundant in the *Pinus/Purshia* association (Table II). *Stipa occidentalis* Thurb. occurred in greater quantities in this community than in any other, with an average herbage cover of 5.2% and a frequency of 71%.

The arborescent layer of the *Pinus/Purshia* association is generally composed of widely spaced mature to nearly mature ponderosa pine with very little advance regeneration. The tree canopy covered an average of only 18% of the total area of the macroplots located within this habitat-type[3] (Table II). Ponderosa pine reproduction occurred primarily in small, widely spaced patches (Table III). The densest clumps of ponderosa pine seedlings and saplings were generally located in "snag patches" or other openings in the stand. This suggests that competition for soil moisture is possibly the limiting factor in establishment and development of ponderosa pine seedlings and that, unless gaps appear in the stand either through natural mortality or logging, available moisture is almost completely exhausted by the larger trees.

Although large lodgepole pines are fairly common in *Pinus ponderosa/Purshia tridentata* stands, lodgepole reproduction averaged only 11 stems per acre. These data suggest that lodgepole pine is a seral species in this community and is declining in importance. However, extensive tree cutting in this community sometimes results in the establishment of lodgepole pine as a seral dominant.

(2) *Pinus ponderosa/Purshia tridentata/Festuca idahoensis* association

The *Pinus/Purshia/Festuca* association is found on Shanahan coarse sandy loam, a soil series which supported this community exclusively within the study area. Shanahan soil has a finer texture than Lapine and, with its associated vegetation, is restricted largely to gentle slopes at elevations lower than 5,700 ft. The presence of numerous dense patches of ponderosa pine seedlings and saplings presents a marked contrast to the open nature of the *Pinus ponderosa/Purshia tridentata* association. Grass cover, featured by vigorous stands of Idaho fescue (*F. idahoensis* Elm.), is lush by comparison with the *Pinus/Purshia* association (Fig. 2).

FIG. 2. General view of a representative stand within the *Pinus ponderosa/Purshia tridentata/Festuca idahoensis* association.

The adaptability of Idaho fescue to the Shanahan soil is clearly demonstrated by the fact that isolated bunches were encountered in only two stands representative of other communities (Table II). Appreciable quantities of *Stipa occidentalis, Carex Rossii* Boott., and *Sitanion Hystrix* (Nutt.) J. G. Sm. were also noted in all study plots. The *Pinus/Purshia/Festuca* association is also characterized by a comparatively large number of perennial herb species. Some of the more diagnostic are *Agoseris* sp. Raf., *Achillea lanulosa* Nutt., *Paeonia Brownii* Dougl., and *Eriophyllum lanatum* (Pursh) Forbes. Of those herbs with 100% constancy, *Cryptantha affinis, Collinsia parviflora* Dougl., and *Viola purpurea* Kell. apparently possess extremely wide ecologic amplitudes and therefore are of almost no indicator value. Herbs, characteristic of this association, although not necessarily diagnostic, are *Madia minima* (Gray) Keck,[4] *Microseris nutans* Schultz, *Lupinus caudatus* Kell., *Phlox gracilis* (Hook.) Greene,[5] *Fragaria cuneifolia* Nutt., and *Antennaria Geyeri* Gray.

Ponderosa pines within the *Pinus/Purshia/Festuca* association are frequently of very low quality. Larger trees tend to have short, stubby boles and light-colored, scanty foliage. Low vigor is reflected by a high susceptibility to bark beetle (*Dendroctonous brevicomis*) attack and beetle-killed trees are much in evidence. Advance regeneration of ponderosa pine is generally dense and trees of sapling size are frequently grouped in almost impenetrable, stagnated stands. In marked contrast to the other communities, there were almost three times as many ponderosa sap-

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[3] The term "habitat-type" as used here is the same as proposed by Daubenmire (1952).

[4] Taxonomy per Hitchcock et al. (1955).

[5] Taxonomy per Abrams (1951).

TABLE III. Average numbers of tree seedlings and saplings within six plant communities

Plant community	Seedlings per acre	Saplings per acre	Total stems per acre	Stocking of unoccupied milacres (%)
Pinus ponderosa/Purshia tridentata:				
Pinus ponderosa	267	246	513	32.5
Pinus contorta	6	5	11	1.3
Total	273	251	542	33.5
Pinus ponderosa/Purshia tridentata/Festuca idahoensis:				
Pinus ponderosa	750	2,067	2,817	72.6
Pinus contorta	1	7	8	1.2
Total	751	2,074	2,825	72.6
Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana:				
Pinus ponderosa	812	974	1,786	65.0
Pinus contorta	90	131	221	13.8
Total	902	1,105	2,007	67.8
Pinus ponderosa/Ceanothus velutinus-Purshia tridentata:				
Pinus ponderosa	1,208	865	2,073	74.7
Pinus contorta	50	52	102	7.8
Total	1,258	917	2,175	76.5
Pinus ponderosa/Ceanothus velutinus:				
Pinus ponderosa	1,355	1,033	2,388	67.7
Pinus contorta	52	104	156	11.7
Abies concolor	228	296	524	24.3
Pinus lambertiana	4	3	7	.8
Total	1,639	1,436	3,075	78.7
Abies concolor/Ceanothus velutinus:				
Pinus ponderosa	541	533	1,074	45.5
Pinus contorta	145	184	329	20.5
Abies concolor	967	907	1,874	60.3
Pinus lambertiana	130	39	169	10.2
Total	1,783	1,663	3,446	85.0

lings as there were seedlings in the area sampled (Table III). This complete reversal of the usual size distribution is difficult to explain. Apparently conditions were more favorable for ponderosa pine regeneration 30 to 40 years ago.

(3) *Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana* var. *pinetorum* association

This association is confined largely to areas of Lapine loamy coarse sand on gentle-to-moderate slopes. In the study area, it is situated at slightly higher elevations than the *Pinus/Purshia* association, averaging approximately 5,300-5,500 ft depending on aspect. The *Pinus/Purshia-Arctostaphylos* association is characterized by considerably more tree reproduction, a larger component of seral lodgepole pine, slightly less grass cover, and a more dense tree canopy (28% vs. 18% directly over the macroplots) than the *Pinus/Purshia* association.

Many herbaceous species characteristic of the *Pinus/Purshia* association are also present in this community, although an additional nine species, indicative of greater effective moisture, were encountered (Table II). Three diagnostic species are *Phacelia heterophylla* Pursh, *Fragaria cuneifolia,* and *Epilobium angustifolium* L.

The shrub element of this association is made up largely of *Purshia tridentata* and *Arctostaphylos parryana* var. *pinetorum* (Rollins) Wies. and Schr.[6] accompanied by very small amounts of *Ceanothus velutinus* Dougl. and *Haplopappus bloomeri* (Gray) H. M. Hall[7] (Table II).

Both total number of stems of tree reproduction per acre and percentage stocking of unoccupied milacres are approximately twice as high in the *Pinus/Purshia-Arctostaphylos* association as in the *Pinus/Purshia* habitat-type (Table III). The position of these seedlings and saplings relative to shrub clumps is also quite different. Whereas only about 35% were rooted directly under shrub plants in the *Pinus/Purshia* habitat-type, almost 60% of ponderosa pine seedlings and saplings were in this position in the *Pinus/Purshia-Arctostaphylos* type. Lodgepole pine, as shown by regeneration figures, occupies a more important position. Lodgepole pine, however, is best characterized as

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[6] Taxonomy per Wieslander and Schreiber (1939).

[7] Taxonomy per Hitchcock et al. (1955).

a seral subordinate in all six communities covered by this study.

(4) *Pinus ponderosa/Ceanothus velutinus-Purshia tridentata* community

The *Pinus/Ceanothus-Purshia* community is restricted to Lapine soil in the study area and generally occupies sites having gentle slopes. It was most often located on benches at elevations ranging from 5,200 to 5,500 ft. The shrub component differs from that of the *Pinus/Purshia-Arctostaphylos* in the occurrence of large amounts of snowbrush (*Ceanothus velutinus*) and the relative absence of manzanita (*Arctostaphylos parryana* var. *pinetorum*) (Table II). Growing conditions are more moist, as indicated by greater amounts of advance tree reproduction and occasional patches of willow (*Salix* sp.).

Characteristic herbaceous plants include *Stipa occidentalis, Carex Rossii,* and *Sitanion Hystrix* (Table II), occurring widely over the entire study area. None of the individual herb species contributed an average herbage cover greater than 0.5%, and total herb cover was a low 1.7%. Thus, it is rather difficult to single out diagnostic species. *Apocynum androsaemifolium* L., although totaling only 0.4% cover, was present in 10% of the 1- by 2-ft grass and herb observation plots and was therefore the most common perennial herb. Other characteristic perennial herbs are *Chimaphila umbellata* (L.) Nutt. and *Hieracium cynoglossoides* Arv.-Touv.

The *Pinus/Ceanothus-Purshia* community includes abundant and well-distributed advance regeneration (Table III). Almost 60% of the trees within seedling and sapling size classes were rooted directly under shrubs, usually snowbrush. Although lodgepole pine cover on the macroplots totaled 2%, only 102 stems per acre were tallied on the timber reproduction transects. Pole-sized ponderosa pines in these areas are apparently quite susceptible to needle blight (*Elytroderma deformans*). In some locations almost all the ponderosa pines in the younger age classes were infected; however, the disease was seldom noted in the other communities.

It is difficult to determine the successional status of the *Pinus/Ceanothus-Purshia* community. It is probably best interpreted as representing an early successional stage within the *Abies concolor/Ceanothus velutinus* habitat-type. The absence of white fir and related species may be due to greater amounts of disturbance coupled with insufficient elapsed time for the successional changes to have occurred in *Pinus/Ceanothus-Purshia* stands.

(5) *Pinus ponderosa/Ceanothus velutinus* community

The *Pinus/Ceanothus* community is interpreted as a more advanced successional stage within the *Abies/Ceanothus* habitat-type. The most noticeable effect of current succession is a tendency towards replacement of the seral dominant, ponderosa pine, by the climax tree species, white fir (*Abies concolor* Lindl.). Although it is similar in some respects to the climax *Abies/Ceanothus* association, the *Pinus/Ceanothus* community is described separately for two main reasons. First, plant density and species composition are sufficiently distinct to warrant separate treatment. The most logical reason for differences between the two groupings is that succession has proceeded more slowly in areas supporting the *Pinus/Ceanothus* community, perhaps due to the effects of fire. Second, although seral, ponderosa pine attains its best growth in this community.

Characteristics setting this community apart from those already discussed include substantial amounts of white fir reproduction, smaller quantities of grasses and herbs, and denser crown canopy. In the study area, the elevational distribution of the type averages about 5,800 ft and ranges from approximately 5,600 to 6,000 ft. It is found on Lapine loamy coarse sand of varying depth. The understory vegetation occurs in a characteristic pattern of dense patches of shrubs, dominantly snowbrush, between which are fairly large openings almost devoid of vegetation (Fig. 3). Although white fir is climax, mature and nearly mature individuals of this species only occur in scattered positions.

Perennial herbs are restricted largely to areas

FIG. 3. General view of a representative stand in the *Pinus ponderosa/Ceanothus velutinus* plant community. The shrubs are predominantly snowbrush with some manzanita.

occupied by shrub clumps. *Chimaphila umbellata* and *Pyrola picta* Smith, despite their scattered occurrence, seemed to have considerable diagnostic value. In the openings between shrub clumps were scattered stems of *Carex Rossii* and *Stipa occidentalis* and occasionally a small number of annual plants (e.g., *Gayophytum diffusum* and *Cryptantha affinis*). Prevalence of serious frost heaving may explain the fact that these openings supported so little vegetation. In the spring the soil surface was exceedingly soft and spongy, indicating repeated freezing and thawing. Despite its patchy distribution, total understory cover was higher than for any other community studied.

Successional relationships of the tree species in this community are indicated in Tables II and III. A comparison of crown cover for trees larger than 10 ft in height shows 10 times more ponderosa pine than white fir. Regeneration figures, however, demonstrate a marked increase in relative importance of white fir. Sampling indicated that both ponderosa pine and white fir seedling survival may be affected by shrub cover. An average of 68% of all ponderosa pines less than 10 ft in height were rooted directly within shrub clumps, while 60% of the white fir seedlings and saplings occupied the same position.

(6) *Abies concolor/Ceanothus velutinus* association

This association represents the climax vegetation within the *Abies/Ceanothus* habitat-type. Although replacement of ponderosa pine by white fir is not yet complete in the sampled stands, the latter species has gained dominance (Table II). Total tree canopy cover was 18% higher than that found for the *Pinus/Ceanothus* community. Seral tree species present include lodgepole pine and sugar pine (*Pinus lambertiana* Dougl.) in addition to ponderosa pine. Thus, it appears that further shifts in composition may be expected if the area remains free from major disturbances. These successional changes, however, appear relatively minor when viewed in the light of those that have already occurred. The degree of crown closure will probably remain more or less constant, and as a result understory vegetation also may not be subject to major change. Although there is abundant evidence that succession has not been halted completely, this community appears representative of climax vegetation in many of its characteristics.

The *Abies/Ceanothus* association was generally found at the highest elevations in the study area (6,100-6,200 ft), although stands are located as low as 5,600 ft on north- and east-facing slopes. Like the *Pinus ponderosa/Ceanothus velutinus* community, this association is on Lapine soil.

Herb species present are largely the same as those occurring in the *Pinus/Ceanothus* community (Table II). Grass cover is much lower than the corresponding figure for the other five communities. Less manzanita was found than on sites dominated by ponderosa pine, probably the result of a denser tree canopy. Other shrub species common only within stands representative of this association are indicative of a comparatively moist habitat.

The *Abies/Ceanothus* association has the most tree reproduction (Table III). Percentage stocking in unoccupied milacres for ponderosa pine and white fir was 45.5 and 60.3, respectively. Because of differences in growth habit, however, a given number of white fir seedlings and saplings occupy much more area than an equal number of ponderosa pines. Therefore, insofar as the impact of these two species on the habitat is concerned, differences between them are even wider than frequency figures or stem counts would seem to indicate.

Soil morphology

All sampled stands of vegetation occurred on either Lapine or Shanahan soils. Of the two, Lapine is the more widespread and in the study area supported five out of the six communities

FIG. 4. Lapine soil profile. Note the dark-colored A1 and AC surface horizons, the lighter-colored gravelly C horizons, and the abrupt boundary to the underlying buried soil.

studied. The *Pinus/Purshia/Festuca* association was restricted to areas of Shanahan soil.

The Lapine series is a Regosol with a shallow, immature profile developing in aeolian pumice deposits from Mount Mazama. It is well drained with a horizon sequence as follows: 01, A1, AC, C1, C2, and D (Fig. 4). The A1 horizon averages 2 inches in thickness and is loamy coarse sand or coarse sandy loam in texture. Structure of the A1 is generally weak medium or fine granular and its moist color a very dark brown (10 YR 2/2). The AC horizon is characteristically variable in thickness, with frequent narrow tongues extending deep into the C horizon. Its approximate mean thickness ranges from 5 to 13 inches, the most frequently encountered value being 10 inches. The AC horizon is single grained with a loamy coarse sand texture. Moist colors range from dark brown (10 YR 4/3) to dark yellow brown (10 YR 4/4).

The transition from the weathered AC horizon into the relatively unweathered and gravelly C1 is surprisingly abrupt. This transition is accompanied not only by abrupt changes in degree of weathering and color, but also by an equally noticeable change in the occurrence of plant roots. Roots, abundant in the A1 and AC horizons, are virtually absent from the C1. The C1 horizon is composed largely of gravel and sand-sized pumice which, even to the casual observer, are noticeably fresh and virtually unweathered. In profiles examined, C1 horizons ranged from 3 to 16 inches in thickness, with an average of approximately 8 or 9 inches. In some areas, the C1 was found to be discontinuous and in others, completely absent. In the latter case, this coarse-textured pumice layer had apparently been wholly incorporated into the AC horizon. The C1 material has a gravelly coarse sand texture. Color in this horizon varies considerably, but the predominant moist colors are yellow (10 YR 7/8, 8/8, 8/6, or 7/6), white (10 YR 8/2), and very pale brown (10 YR 8/3). Below a rather thin transition zone lies the C2 horizon which, although resembling the C1 in being relatively unweathered, is somewhat finer textured. Most of the pumice particles are very coarse to medium sand-sized (0.25-2 mm) although fine gravel content may range as high as 25%.

Lapine C2 horizons often exhibit considerable local variability in morphological characteristics. Most striking differences occur in the amount of mixing of the relatively unweathered pumice with dark-colored silt and fine sand particles. All gradations in amounts of mixing may be encountered in profiles from almost complete mixing with only occasional pockets of pure pumice to layers exhibiting dominantly pure pumice with small, discrete areas of mixed material. Largest amounts of mixing were generally found in the shallowest soils. However, some pockets of mixed C2 occur even in the deepest Lapine soils. The mixed zones appear to offer a more favorable environment for root growth; roots were generally quite plentiful in these portions of the profile even though they were almost completely absent from the pure, unmixed C2 horizon.

Unmixed portions of the C2 horizon exhibit a yellow (10 YR 8/6, 8/8, 7/8, or 7/6) and/or white (10 YR 8/2) color when moist. Areas of mixed C2 are characterized by considerably less coarse sand and larger amounts of silt and fine sand. In these mixed zones, yellow and white colors of pumice particles are interspersed with varying amounts of brown (10 YR 3/3, 5/3) and dark yellowish brown (10 YR 3/4, 4/4, 5/4). Field observations and mechanical analyses indicate that the finer, dark-colored soil material mixed with the C2 pumice has been transported up from the D horizon in a manner not yet completely understood. Many of the larger zones of mixing may result from the action of windthrown trees. However, in many instances pockets of mixing are quite small and round in cross section. Whatever the cause, mixing has a very sporadic pattern, and local variability in amounts of C2 disturbance is large.

The buried soil (D horizon) beneath the pumice mantle is characterized by little or no profile development and the presence of large quantities of basalt stones. The texture ranges from fine sand to fine sandy loam, and basalt gravels, cobbles, and boulders generally comprise at least 25% of the total volume. Moist color is commonly brown (10 YR 4/3), dark yellowish brown (10 YR 3/4), or dark brown (10 YR 3/3). Plant roots are common except where pumice depth exceeds 4 or 5 ft.

Two Lapine soil features which apparently exert most influence on plant growth are thickness of the C1 horizon and amount of mixing of C2 pumice with buried soil material. Lapine soils with very little mixing and a thick C1 horizon are characterized by root growth which is restricted largely to the A1, AC, and D horizons. On the other hand, plant roots are usually quite plentiful in C horizons which have undergone extensive mixing, and are often conspicuously present in even small mixed zones in an otherwise unmixed horizon.

The Lapine profile features vary greatly between the plant communities occurring on this soil (Table IV). In addition, plant-soil relationships are further obscured by a correlation between depth of the pumice mantle and amount of mixing in the

TABLE IV. Morphological characteristics of Lapine soil in relation to five plant communities

Plant community	Thickness of Al+AC (inches)	Thickness of C1 (inches)	Depth to D (inches)	Mixed in C2 (%)
Pinus/Purshia:				
Mean..............	9.7	7.0	31.7	18.3
Range..............	7-12	6-11	17-49	5-60
Pinus/Purshia-Arctostaphylos:				
Mean..............	11.7	5.8	30.2	48.3
Range..............	10-13	0-13	13-33	5-80
Pinus/Ceanothus-Purshia:				
Mean..............	10.5	10.5	38.8	18.5
Range..............	8-12	5-14	32-47	5-30
Pinus/Ceanothus:				
Mean..............	10.8	3.3	21.7	75.0
Range..............	9-12	0-8	18-26	40-95
Abies/Ceanothus:				
Mean..............	12.0	8.8	32.3	56.6
Range..............	9-15	4-16	20-43	20-90

C2 horizon and thickness of the C1. As the pumice mantle increases in depth, mixing in the C2 generally becomes less extensive and the C1 horizon tends to become thicker. Some exceptions to this relationship occur in the soil profiles within the *Pinus/Purshia* association. With the exception of one plot location, these soils exhibited very little mixing in the C2 horizon regardless of the depth of the pumice mantle. In addition, the C1 horizon was found to be relatively thick, especially in comparison with the C1 under the *Pinus/Ceanothus* community. Reconnaissance observations also indicate that the AC horizon tends to be noticeably thinner in areas supporting the *Pinus/Purshia* association.

Less modification of the pumice mantle under *Pinus/Purshia* vegetation would be expected because this association represents the most xeric conditions encountered. Uprooting of large trees by windthrow is probably one of the most important factors causing the mixing of buried soil material with C horizon pumice. Possibly ponderosa pine did not become established on these sites until long after pumice deposition. Thus, the smaller amounts of mixing in comparison with the more moist sites may be partially due to a shorter history of tree growth. Shallower depth of weathering in these areas may be largely ascribed to lower density of vegetation and consequent smaller amounts of organic matter and less extensive root penetration.

The Lapine soil associated with the *Pinus/Ceanothus* community generally possesses a relatively deep AC horizon. As a result of the extension of the weathered layer, the C1 horizon is correspondingly thinner and frequently discontinuous. In some cases, portions of the C1 horizon—in one instance, the entire layer—were noticeably altered and appeared to represent a condition midway between the C1 horizon and the modal AC.

Although there are wide variations in profile characteristics within a single plant community (Table IV), the amount of alteration of the Lapine pumice mantle apparently increases with increasing effective moisture and plant density. Final definition of existing relationships awaits more intensive sampling.

Shanahan soil, associated with the *Pinus/Purshia/Festuca* community, is commonly found on very gently sloping to nearly level topography and is either moderately well or well drained. It is classified as a Regosol and is developed on a predominantly pumiceous parent material. Although the pumice originally was aerially deposited as a uniform mantle, Shanahan parent material has been reworked, perhaps by water. In all cases, extensive mixing with buried soil material has occurred, so that contamination of the pumice is much more widespread than in the case of Lapine soil.

Most Shanahan soil areas have a fairly thick covering of litter over the mineral soil. The 01 horizon averages about 1 inch in thickness and is predominantly composed of fresh and partially decomposed pine needles. The A1 horizon averages 2 inches in thickness and has a coarse sandy loam or a loamy coarse sand texture. It possesses weak fine or medium granular structure and the most frequently encountered moist color is dark gray brown (10 YR 3/2 or 4/2).

The soil mantle beneath the A1 horizon is generally quite uniform with respect to texture. The most noticeable change is a decreasing amount of organic matter with depth accompanied, in some cases, by a change in structure. Without exception, an AC horizon is found below the A1 and, depending on profile depth, may extend uninterrupted to the D horizon. Thickness of the AC horizon varies from approximately 5 to 20 inches. Texture of this horizon is a loamy coarse sand, and structure is weak medium subangular blocky. Moist soil color is generally dark yellowish brown or yellowish brown (10 YR 4/4, 5/4).

Total depth of the Shanahan soil profile above the D horizon is commonly less than 24 inches and only rarely extends as deep as 35 inches. Accordingly, the C horizon, completely absent in the shallower pumiceous deposits, is seldom more than 12 inches thick. Texture of the C horizon is loamy coarse sand and the horizon is structureless. Its moist color is generally yellowish brown (10

YR 5/4 to 5/6), with single pumice grains exhibiting a brownish yellow color (10 YR 6/6).

Unlike the substratum beneath Lapine soil, the buried soil under Shanahan has considerable profile development. Thus the D horizon material consists of two distinct layers, a buried A horizon (D1) and a very much finer textured buried B (D2). The D1 horizon, or Ab, ranges from approximately 5 to 20 inches in thickness and varies in texture from loam to sandy loam. This horizon is generally very stony, and three-fourths of the volume may be occupied by basalt fragments. The D2 (Bb) horizon is generally about 5-15 inches thick and possesses either a loam or clay loam texture. Basalt fragments are common and constitute 25-90% of the volume. This horizon grades into weathered basalt.

The ability of the Shanahan soil to support vigorous stands of Idaho fescue and other plant species virtually excluded from Lapine soils may be largely due to differences in root distribution within the two soils. Plant roots are very abundant in the Shanahan A1, AC, C, and D1 horizons, while they become less numerous in the fine-textured D2. On the other hand, very few roots extend into the C horizons of the Lapine unless considerable mixing with buried soil material has occurred. As a result, maximum depth for roots of grass and herb species growing on Lapine soil is usually equal to the depth of the AC horizon, which averages approximately 12 inches. For Shanahan soil, however, effective rooting depth for herbaceous plants averages 30-40 inches and may be considerably greater in areas where roots are able to enter the D2 horizon.

Soil physical properties

Particle-size distribution was determined for Lapine soil samples collected at the 30 plots primarily to ascertain whether rates of pumice weathering differ among plant communities. Since it was assumed that each plant grouping is indicative of a slightly different microclimatic regime, it seemed possible that these differences might be associated with shifts in particle-size distribution, at least in the surface horizons.

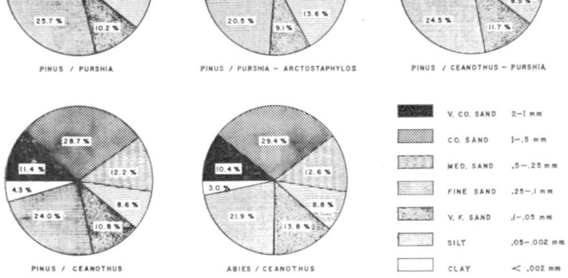

FIG. 5. Soil particle-size distribution of the Lapine A1 horizon under five plant communities.

Differences in particle-size distribution among the five plant communities are very small and inconsistent (Fig. 5), but in some cases differences are apparent. For example, the silt content of the A1 horizon within the *Pinus/Purshia-Arctostaphylos* association appears lower than amounts found in the remaining four types. This difference and others similar to it are comparatively small, especially in view of the appreciable variability among observations. However, the uniformity of the means for the A1 horizons within the various plant communities is much more striking than are any of the apparent differences.

We can tentatively conclude that although variations in particle-size distribution of the Lapine A1 and AC may be of considerable magnitude, these variations do not appear to be significantly correlated with vegetation in the types studied. Apparently either rates of pumice weathering are about constant regardless of climatic differences or insufficient time has elapsed to allow shifts in particle-size distribution to be detected, at least with a limited number of observations.

Soil moisture is generally considered to be the most important factor in limiting the growth of ponderosa pine, as well as in determining the distribution of associated understory species. This should be especially true in an area such as the Antelope unit, since it is situated close to the boundary between the ponderosa pine and juniper-sagebrush zones. The importance of soil moisture in regulating plant distribution is also suggested by the fact that several plant communities occupy sites with equivalent soils, different only in elevation or aspect.

Soil-moisture measurements were made during the summers of 1956 and 1957 in the following plant communities: (1) *Pinus/Purshia,* (2) *Pinus/Purshia/Festuca,* (3) *Pinus/Purshia-Arctostaphylos,* and (4) *Pinus/Ceanothus.* Time limitations prevented soil moisture sampling in the *Pinus/Ceanothus-Purshia* and *Abies/Ceanothus* groupings. Moisture depletion was considerably more rapid in 1957 than in 1956 (Fig. 6). Replenishment of soil moisture during July resulting from heavy rains is indicated by a marked upswing in the curves for 1956. On the other hand, the 1957 depletion curves are fairly smooth and uninterrupted due to the occurrence of only small amounts of precipitation which in no case totaled more than 0.3 inch per week. Weather records

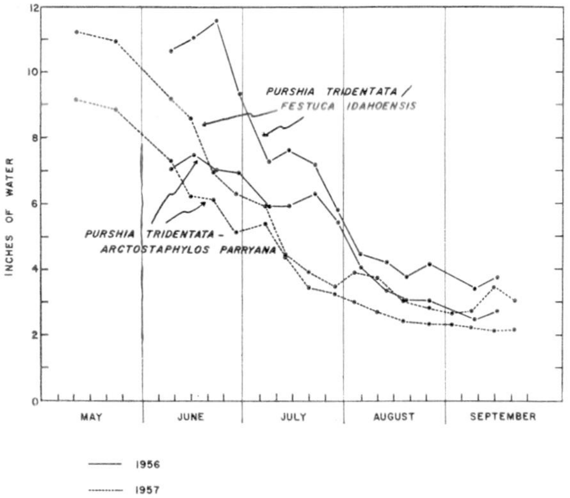

FIG. 6. Soil-moisture depletion under the *Pinus ponderosa/Purshia tridentata/Festuca idahoensis* and *Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana* var. *pinetorum* associations during the 1956 and 1957 growing seasons. Moisture values are for the entire profile and represent the average for conditions under shrubs and in the open.

for Chemult (Weather Bureau 1957), 20 miles to the west, show 2.26 inches of rainfall for July 1956, as opposed to a long-term average of only 0.71 inch. For this reason soil-moisture levels during the 1956 growing season were likely atypical. Thus, most emphasis is placed on 1957 data.

Despite weekly fluctuations, main trends in the pattern of soil-moisture depletion within the four plant communities are readily apparent (Figs. 7 and 8). Amounts of rainfall were small, so soil moisture was depleted at a more or less constant rate until the permanent wilting percentage was approached. Comparison of Fig. 7 with Fig. 8 shows that the two plots located within the same plant community exhibit similar patterns of moisture use. The trend of moisture depletion at the two *Pinus/Purshia-Arctostaphylos* plots very closely resembles that for the *Pinus/Purshia/Festuca* habitat-type. In both plant associations, depletion proceeded at a fairly constant rate until almost no moisture remained available for plant use after the second or third week in August. In the *Pinus/Ceanothus* community, supplies of available moisture were depleted less rapidly, thus indicating more mesic conditions.

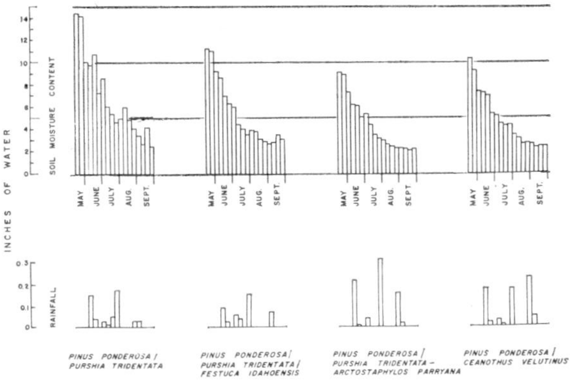

FIG. 7. The trend of soil-moisture depletion and accretion by rain in four plant communities (A plots) during the 1957 growing season. Moisture values are for the entire profile and represent the average for conditions under shrubs and in the open.

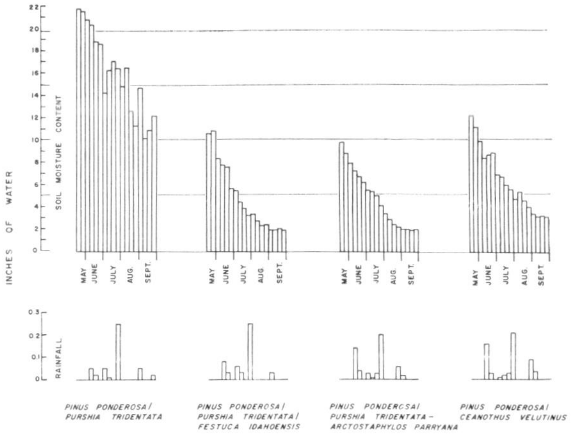

FIG. 8. The trend of soil-moisture depletion and accretion by rain in four plant communities (B plots) during the 1957 growing season. Moisture values are for the entire profile and represent the average for conditions under shrubs and in the open.

Although the moisture content of the A1 and AC horizons under *Pinus/Purshia* vegetation was reduced to permanent wilting percentage by July 13 at plot A and August 3 at plot B, the C horizon still contained available moisture at the end of the growing seasons (Figs. 9 and 10). This apparent anomaly is explained by the paucity of roots in the C horizon, as explained in the section on soil morphology. On the other hand, roots were well distributed throughout the soil profile at the sampling plots situated within the *Pinus/Purshia-Arctostaphylos* and *Pinus/Ceanothus* communities. The C horizon in these locations was in every case mixed to some extent with silt and fine sand from the D. Apparently the pattern of root distribution in the *Pinus/Purshia* habitat-type causes a rapid depletion of soil moisture contained in A1, AC, and D horizons, while only small amounts are removed from the C horizon.

The *Pinus/Purshia/Festuca* association, on Shanahan soil, utilized all available soil moisture by the last week in August and the first week in September, respectively (Figs. 9 and 10). A progressively deepening zone of soil-moisture depletion at *Pinus/Purshia-Arctostaphylos* plot B presents an interesting pattern. Permanent wilting percentage had been reached in the A1 and AC horizons by the last week in July. This, in turn, was followed by the exhaustion of available moisture supplies in the C horizon 2 weeks later. After an interval of 3 more weeks, the upper 12 inches of the D horizon was also at the permanent wilting percentage. An almost identical pattern occurred at *Pinus/Purshia-Arctostaphylos* plot A, except that soil-moisture content of the D horizon remained above the permanent wilting percentage. Only in the soil at plot B within the *Pinus/Ceanothus* community did all horizons, except the A1, still contain available moisture at the end of the sampling period.

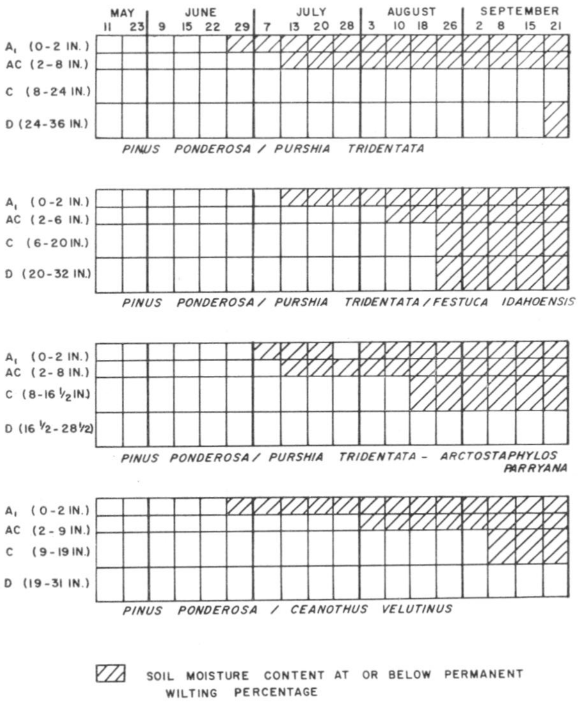

FIG. 9. Dates soil moisture content of the various horizons under four plant communities (A plots) was at or below permanent wilting percentage (1957).

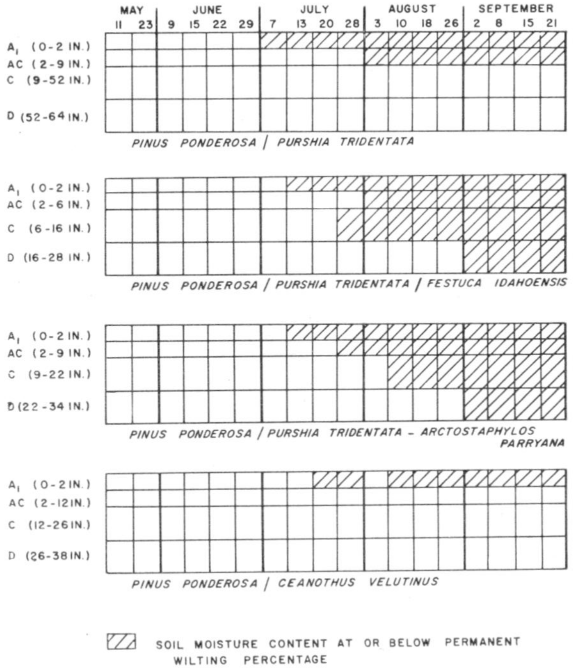

FIG. 10. Dates soil moisture content of the various horizons under four plant communities (B plots) was at or below permanent wilting percentage (1957).

These results indicate that soil moisture is important in controlling the distribution of plant communities in the Antelope unit. If the 1957 growing season was typical with respect to moisture conditions, soil drought evidently becomes less severe with increasing elevation. This is especially noticeable in the case of the *Pinus/Ceanothus* community, where soil-moisture depletion at Plot A was delayed until late in the growing season and soil moisture at plot B was apparently never limiting. Conclusions reached here are in accord with those of McMinn (1952), who concluded that distribution of plant associations in the northern Rocky Mountains was definitely influenced by differing amounts of soil drought.

Soil chemical properties

When the pumice mantle on which Lapine soil has developed was deposited, it was undoubtedly fairly uniform in its chemical composition. Since then, differences in amounts and availability of soil nutrients have developed. These changes have been caused largely by two factors having a dominating influence on soil-fertility relationships. The first, possibly of more importance in pumiceous soil than in any other type, is rate of weathering of the parent material. Although Mount Mazama pumice is dominantly SiO_2 (approximately 69%), it also contains 2.5% K_2O, 2.4% CaO, 0.8% MgO, and 0.1% P_2O_5 (Williams 1942). These essential elements are released in available forms at fairly constant rates by weathering processes. The importance of weathering in the release of nutrient elements from pumiceous material has been stressed by van't Woudt (1952). A second factor, which is undoubtedly of importance in influencing the fertility of the Lapine soil, is the addition of organic matter. Both quantity of organic matter and its source exert considerable influence on the relative quantity of nutrient elements available for plant growth.

Since both pumice weathering and addition of organic matter are largely centered in the surface layers of the Lapine soil, broad differences in fertility should be discerned most easily in the A1 and AC horizons. Two samples of these hori-

TABLE V. Fertility of the Lapine A1 horizon under five plant communities (averages of two values)

Plant community	pH	Available P (ppm)	Exchangeable K (meq/100 g)	Exchangeable Ca (meq/100 g)	Exchangeable Mg (meq/100 g)	Cation exchange capacity (meq/100 g)	Organic matter (%)	Total nitrogen (%)
Pinus/Purshia	6.2	11.75	0.48	2.35	0.40	13.97	6.41	0.135
Pinus/Purshia-Arctostaphylos	6.4	8.75	.46	3.60	.67	13.58	5.36	.105
Pinus/Ceanothus-Purshia	6.0	15.00	.44	3.50	.58	15.61	6.87	.160
Pinus/Ceanothus	5.8	18.70	.53	4.25	.60	19.54	9.54	.165
Abies/Ceanothus	6.2	19.50	.46	6.10	.65	19.28	8.84	.230

zons from each of the five vegetation types were analyzed in order to determine whether differences in soil fertility exist among the plant communities. Results show that differences in soil fertility among plant associations are generally minor (Table V). As might be expected, the greatest range in nutrient levels occurs in the A1 horizon. A1 samples collected under the *Pinus/Ceanothus* and *Abies/Ceanothus* communities contained somewhat greater amounts of available P, exchangeable Ca, and total N than did the A1 in the remaining three communities. These differences can be largely attributed to more abundant organic matter deposition and the fact that *Ceanothus* litter contains relatively large amounts of these elements (Wollum and Youngberg 1964, Youngberg and Dyrness 1964).

Fertility of the AC horizon apparently remains fairly uniform regardless of the associated plant community, the greatest difference being the higher level of available P within the *Abies/Ceanothus* association.

The amount of organic matter incorporated into pumice soils, or in any soil, is of utmost importance, not only for its nutrient-supplying role, but also for its activity in hastening weathering and soil development. For these reasons, the organic matter of soils at all vegetation plots was investigated thoroughly.

Carbon-nitrogen ratios of the A1 horizon do not differ greatly among the six plant communities, but amounts of incorporated organic matter are apparently greater in the more mesic communities (Table VI). For example, mean organic matter content of the A1 horizon under the *Abies/Ceanothus* association was 8.97%, almost twice the amount found in the *Pinus/Purshia/Festuca* habitat-type. There is also a corresponding increase in amounts of nitrogen present in the A1 horizon with increasing effective moisture. In the case of the AC horizon, the plant communities do not appear to be accompanied by changes in organic matter content. Nitrogen levels of the AC horizon under the various vegetation types show some minor and insignificant differences. Carbon-nitrogen ratios of the Lapine and Shanahan soils seem unusually high when they are compared to values for nonpumiceous soils. Unpublished data in the Department of Soils, Oregon State University, indicate that surface horizons of forested soils in Oregon possess carbon-nitrogen ratios ranging from approximately 10 to 25. The mean ratio, based on 48 determinations involving 10 soil series, was found to be 17. The surprisingly wide carbon-nitrogen ratios indicate that organic matter decomposition is slow, although soil reaction, nitrogen level, and aeration appear to be favorable for microbiological activity. Workers in New Zealand have reported a similar situation with respect to organic matter decomposition in Taupo pumice soils. Bailey (1953) attributed the unusually large amounts of organic matter in pumice soils to very slow rates of decomposition and likened the process to that occurring under anaerobic conditions.

TABLE VI. Organic matter, total nitrogen, and carbon-nitrogen ratios under six plant communities[1]

Plant community	% Organic matter	% Total nitrogen	C/N ratio
Al horizon:			
Pinus/Purshia	5.85	0.120	28.8
Pinus/Purshia/Festuca	4.89	.107	25.7
Pinus/Purshia-Arctostaphylos	6.54	.118	31.9
Pinus/Ceanothus-Purshia	6.79	.151	26.3
Pinus/Ceanothus	7.57	.158	27.5
Abies/Ceanothus	8.97	.200	26.9
AC horizon:			
Pinus/Purshia	1.31	.031	24.5
Pinus/Purshia/Festuca	1.30	.039	18.8
Pinus/Purshia-Arctostaphylos	1.28	.032	24.6
Pinus/Ceanothus-Purshia	1.25	.043	17.2
Pinus/Ceanothus	1.31	.041	19.3
Abies/Ceanothus	1.35	.032	24.4

[1] Mean values, based on the results of six determinations with the exception of the *Pinus/Purshia/Festuca* habitat-type where each mean represents five values.

DISCUSSION

The *Pinus/Purshia, Pinus/Purshia/Festuca, Pinus/Purshia-Arctostaphylos,* and *Abies/Ceanothus* associations are classified as edaphic climaxes. The overwhelming influence of the pumice soil becomes apparent when one moves out of the pumice area in the same climatic region. In these areas of residual soil a completely different type of understory vegetation is associated with ponderosa pine.

Amounts of herbaceous plant cover tend to be extremely low on these pumice soils. In addition, only a limited number of herbaceous species are present. For this reason, it was necessary to carry mean cover values to the nearest 0.1% and attach some significance to the occurrence of several species which seldom were present in more than trace amounts. Distribution of shrub species in the study area is such, however, that their relative abundance generally offers a fairly reliable means of identifying the various communities. Herbaceous indicators, however, lend support to vegetation classification decisions.

Soil-plant relationships in the Antelope unit are not always clear cut and easily defined, perhaps because of the immaturity of the soils. As a result, it is unreasonable to expect a close correlation between vegetation and soils, at least at the series level. In addition, there are substantial variations in soil characteristics within a small area, especially in the Lapine series. It is extremely difficult to precisely define correlations between soil properties and associated plant communities, because local variations may be of greater magnitude than differences over wide areas. Soil features which varied markedly within a small area are thickness of weathered surface soil, amount of mixing in the C2 horizon, soil fertility, and soil-moisture content. Indeed, the heterogeneity of the Lapine soil may well be its outstanding characteristic, which is surprising in view of the uniformity of its parent material.

Another factor obscuring soil-plant relationships was the limited number of observations. In some cases, sample size was undoubtedly too small for existing trends to become apparent. In addition, the study was confined to 60,000 acres, and although it is believed to be representative of a large portion of the central Oregon pumice region, variations in vegetation and soils are to be expected.

One of the most important conclusions drawn from this study is that the identification, characterization, and mapping of vegetation units in conjunction with standard soil surveys are especially important in areas of immature soils. Soils, such as comparatively young pumice soils, tend to exhibit little change over large areas in those soil characteristics serving as a basis for taxonomic classification. As a result, extensive areas are frequently included within the same soil mapping unit, in spite of the fact that there may be marked differences in temperature, precipitation, and other important environmental factors. In these areas, a soil map alone does not furnish an adequate basis for the stratification of land necessary in intensive forest management. Consequently, understory vegetation assumes a most important role inasmuch as it serves as a more sensitive indicator of changes in the many interacting variables regulating tree growth.

A map showing location of the various plant communities in the Antelope unit has been prepared. This information is currently being used by Weyerhaeuser Co. as a basis for forest inventory and as an aid in formulating management plans. For example, amount of advance reproduction was found to be an important timber stand characteristic that varies with plant communities. Since the volume of timber which can be safely removed in logging depends to a large extent on amounts of young growing stock present, plant communities provide a basis for broad stratification of cutting intensities.

In addition, the clumpwise pattern of regeneration in the *Pinus/Purshia* habitat-type has provided a valuable clue to the type of cutting needed in these areas in order to obtain prompt restocking. In this habitat-type, harvest cuts must open up the stand sufficiently to permit the establishment of reproduction but, at the same time, must not be heavy enough to overexpose the site and cause severe microenvironmental conditions. In contrast, cutting in the *Pinus/Purshia-Arctostaphylos, Pinus/Ceanothus-Purshia,* and *Pinus/Ceanothus* types can remove all but the fast-growing trees without any danger of overexposing the site. Adequate advance regeneration is already present in these types. The problems involved in maintaining ponderosa pine are more difficult in the *Abies/Ceanothus* type than in the others, and different cutting practices will be necessary.

A knowledge of the relationships between vegetation and soil properties is also of practical value to the forest manager. It might be expected, for example, that survival of planted seedlings would be poorer in the *Pinus/Purshia* habitat-type than in areas of *Pinus/Ceanothus* vegetation because of the higher rates of soil-moisture depletion in the surface soil.

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