

ADVANCE BOND
C. W. L. BROWN Paper

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

by

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ADVANCE BOND

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

INTRODUCTION

Highly efficient resource management is possible only when an inventory of the product to be managed has been made. This fact has been recognized in all phases of land management, whether the product is timber, grass, or water. In the field of forest management, inventory procedures have generally been restricted to stocking surveys, determination of stand volumes, or other measurements of the timber stand. Recently, however, an increasing number of forest managers have recognized the fact that although timber inventory surveys serve a useful purpose, they do not provide an adequate basis for sound management practices. As a result, greater attention is being focused on more basic inventories as provided by soil and soil-vegetation surveys.

The need for more basic information in addition to an inventory of the products under management arises from the fact that maximum production of the desired commodity can be attained only if the manager has an understanding of the productive capacity and the management limitations of each acre for which he is responsible. Problems to be resolved in forest management include such questions as whether or not an area is suited to the production of crop trees, the selection of tree species best suited to a given site, the selection of silvicultural practices which will result in adequate regeneration, whether or not

the chances for success in a tree planting operation justify the cost, and many more. Obviously, timber cruise data and the current forest type mapping methods do not provide answers to these questions and consequently more basic information concerning the forest environment is necessary. In the last analysis, the extent to which the manager can manipulate timber production is restricted largely by the characteristics of the soil and climate.

Since soils are partially the product of the climate under which they are formed, well-developed soils frequently reflect even relatively subtle changes in climatic conditions. However, many soils exhibit immature profile characteristics. These are soils developing on parent materials of relatively recent origin or in areas of extreme relief where profile development is retarded. Soils within this class have not yet reached equilibrium with their environment and therefore possess uniform profile characteristics over large areas. As a result, environmental changes of sufficient magnitude to cause significant differences in productive capacity may not be detected by a consideration of soil profile characteristics; often areas diverse with respect to microclimatic conditions may be remarkably uniform in soil depth, texture, and horizon sequence. Thus a soil survey alone in such an area would not be expected to provide the sort of stratification necessary for efficient intensive management. The added information derived from a vegetation survey made in conjunction with the soil survey is necessary to achieve the desired level of refinement.

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The mapping of vegetation in conjunction with soils has gained in popularity and many advantages of such an undertaking have been suggested. First of all, it supplies the land manager with an inventory of the vegetation existing at the time of mapping. Uses of such information may vary from aiding in the formulation of a range management plan to the delineation of areas of high shrub concentration posing problems in tree regeneration. Even if these were the only uses they would, in many cases, justify the cost of mapping vegetation. However, the survey information greatly increases in value if the vegetation mapping units are based on sound ecological interpretations. Failure to use such an approach in some vegetation surveys is probably attributable to a lack of a uniform and workable system of vegetation classification. As a result, vegetation mapping has often consisted of recording species lists or the delineation of artificial groupings which may or may not bear a relationship to natural units. Such procedures are in direct contrast to those employed in mapping soils; for soil delineations are made on the basis of sound taxonomic units of a well-established classification system. It is suggested that in order to be of maximum value, vegetation classification should be equally detailed. Ecological information of practical worth includes the classification of vegetation into fundamental interpretive units, or communities, and the development of an understanding of their successional relationships. With this knowledge the land manager is then in a position to gain a finer appreciation of the environmental framework with which he is dealing. This increased understanding stems

from the fact that significant environmental changes are denoted by shifts in species composition and plant density, or in other words, by different plant communities. Stated differently, each plant community is indicative of a different effective environment and consequently each may call for different management techniques. In some areas the existing vegetation units may be accompanied by significant changes in soil characteristics and, in the case of mature soils, there may be an almost perfect correlation between plant communities and soils at the series level. On the other hand, in areas of immature soils such correlations often do not exist. Here a knowledge of the distribution of plant communities is an indispensable requirement for the stratification of the management area on the basis of relative productive capacities.

The present study embodies investigations conducted following the completion of a soil-vegetation survey of 50,000 acres of predominantly ponderosa pine forestland in central Oregon. The general aim was to make the survey information more useful through the complete characterization of the basic units of both soil and vegetation, coupled with the investigation of relationships between them. Because the study area is located in a region of very immature pumice soils, it affords an unusual opportunity for the study of soil-vegetation relationships in an area where climatic rather than soil conditions are apparently the principal factors influencing plant distribution. Since these relationships would not be expected to involve large-scale changes in soil characteristics, it was necessary to design the study

in such a manner that even small differences in chemical and physical soil properties could be detected. In addition, an attempt was made to define the significance of several of the more important soil-vegetation units with respect to forest management practices.

Because very little previous work had been conducted in the central Oregon pumice region, emphasis, of necessity, was placed on the characterization of the soils and vegetation. It was necessary, for example, to first gain some understanding of pumice soil moisture relationships before the interpretation of data for soil moisture trends under different plant communities could be undertaken. Likewise, close attention to soil morphology and genesis would not have been necessary if this information had already been available. Such investigations of the basic properties of the soils and vegetation, although essential, developed into an unexpectedly large segment of the present study. Accordingly, it was not possible to explore relationships between soil and vegetation in as much detail as it was at first hoped. This thesis, therefore, constitutes a report of the results of preliminary investigations into the fundamental soil-vegetation relationships as they occur on pumice soils and in no sense does it exhaust the subject.

DESCRIPTION OF THE STUDY AREA

The field portion of this study was carried out in the Antelope Unit of Weyerhaeuser Company's Klamath Falls Tree Farm. The area of this unit is approximately 50,000 acres and is predominantly ponderosa pine (Pinus ponderosa)¹ forest land. It is situated on the Lake-Klamath County line immediately adjacent to the northern boundary of the Klamath Indian Reservation. Chemult, in Klamath County, is about 20 miles west of the western boundary of the unit and the town of Silver Lake (Lake County) is situated 11 miles to the east. The Antelope Unit is bounded on the south by the Klamath Indian Reservation and on the north, east, and west by the Fremont National Forest. Figure 1 shows the approximate location of the study area in relation to the surrounding territory.

At the time the field studies were conducted, the vegetation of the Antelope Unit had been subjected to very little logging disturbance. Although a small amount of sanitation-salvage logging had been carried on, such operations were largely restricted to the extreme southeastern portion of the Unit. Portions of the area, especially at the lower elevations, have been used for many years as a summer sheep range. Disturbance caused by the sheep is often locally severe and is especially noticeable in localities used as "bed grounds". In

¹ Source of common names of plants in the text is Standardized Plant Names by Kelsey and Dayton (41). All plant species mentioned are listed in the appendix by both common and scientific names.

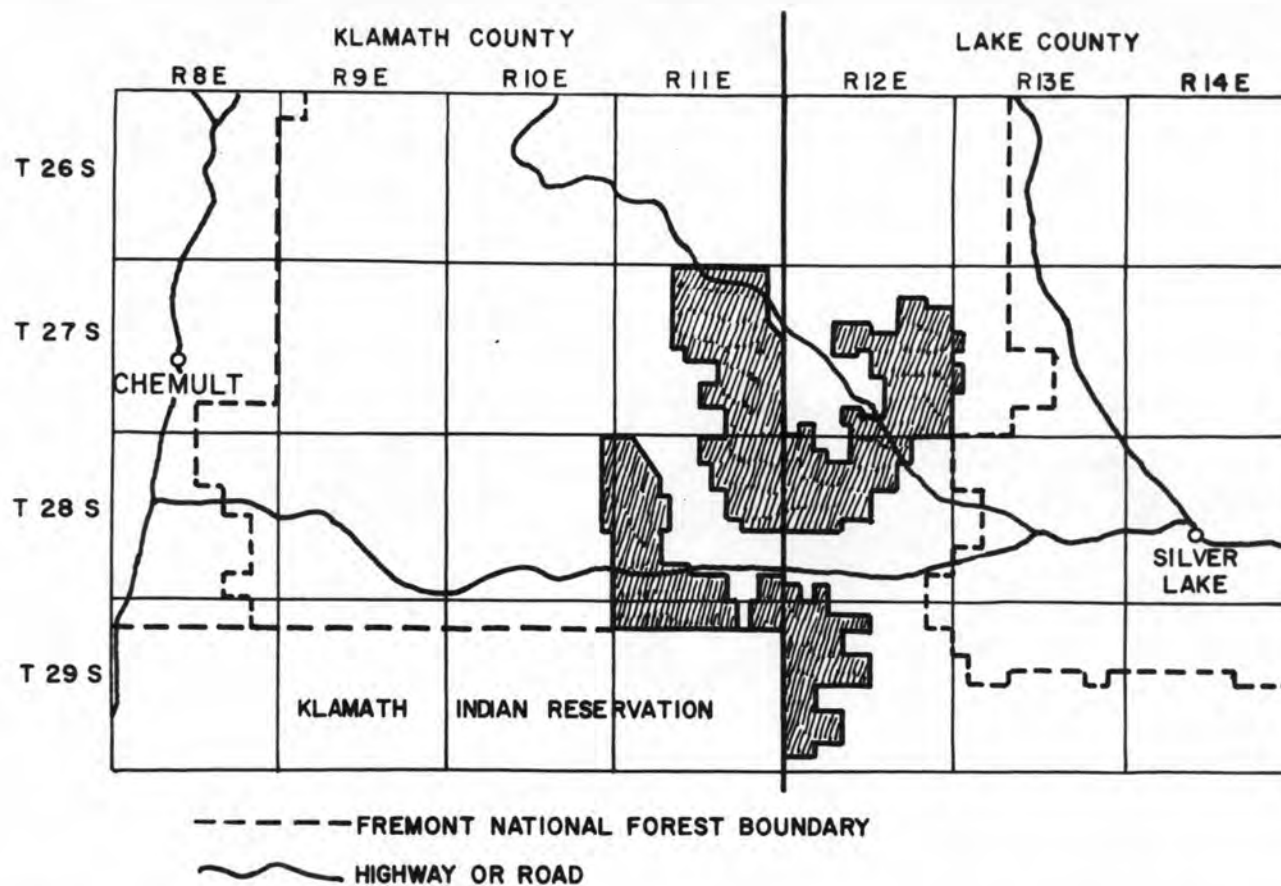


Figure 1. Location of the study area. Shaded area is Weyerhaeuser Company's Antelope Unit. Each inch represents approximately 5 miles.

addition, small numbers of cattle occasionally graze in areas supporting sufficient grass, however the animals use only a small portion of the available forage.

In common with most other areas in the ponderosa pine type, wild fires have been an important factor in the history of the Antelope Unit. Mature trees, almost without exception, exhibit fire scars. The frequency with which these fires occurred has not been determined. However, since 1900 the region has been relatively free of widespread wildfires and only one area of any size has been burned over in the last 30 years.

Topography and Geology

The Antelope Unit is located on a high plateau which extends eastward from the base of the Cascade Mountain Range. Elevations within the study area vary from 5,000 to approximate 6,300 feet above sea level. Immediately to the east there is an abrupt drop in elevation, with Silver Lake situated at 4,347 feet. This change is accompanied by decreased precipitation resulting in an abrupt transition from the ponderosa pine type to the juniper (Juniperus occidentalis)-sagebrush (Artemisia tridentata) type. According to Fenneman (22, pp. 226, 327), the study area lies very close to the boundary between the Harney section of the Columbia Plateau physiographic province and the Great Basin, a subdivision within the Basin and Range province.

The most conspicuous topographic features in the area are numerous volcanic cones or buttes. Several have associated lava flows but

the majority appear to have been formed independently of any secondary activity. Most of the cones have extensive deposits of volcanic cinders on their slopes, hence the local designation, "cinder cone". Generally these buttes are only 100 to about 500 feet in height, although one, Antelope Mountain, rises 1300 feet above the surrounding landscape. In addition to several smaller escarpments, there is one scarp in the western portion of the unit that extends in a north-south direction for a distance of almost 5 miles and averages approximately 300 feet in height. Broad, almost level areas and extensive basin-like depressions are common at the lower elevations. Commonly the level to gently rolling areas support a meadow type of vegetation from which trees are completely absent. These openings, locally termed "flats", vary in size from less than an acre to several sections (Figure 2).

The geologic history of the study area is related to that of the Cascade Mountains as well as to those portions of eastern Oregon and Washington covered by the extensive Columbia River basalt flows. Consequently, it is necessary to take both areas into consideration in order to arrive at an understanding of the geologic past of the region. Williams (102, p. 10) states that prior to the Eocene Epoch (early Tertiary) most of the present land area of western and central Oregon was covered by the sea. During the Eocene the shoreline retreated to the west as far as the vicinity of Roseburg and the previously submerged area was then a gently undulating plain. Towards the close of this epoch some volcanic activity began to occur locally. It was not



Figure 2. General view of Bear Flat, one of several large, almost level meadows within the study area. Elevation here is approximately 5,000 feet. The distant peak is Yamsay Mountain.

until the Miocene, however, that the major lava flows occurred. At this time the extensive sheets of basaltic lava, found in both the Columbia Plateau and Great Basin provinces, extruded out of innumerable fissures (98, pp. 21-22; 22, pp. 229-232; 70, pp. 79-80). Concurrently the Western Cascades were being built up, chiefly of andesites (102, p. 13). This uplift did not, as yet, constitute a formidable barrier to the supply of moisture from the west. As a result, the vegetation east of the Western Cascades consisted of more mesic species than those encountered today. During the Pliocene Epoch the major portion of the High Cascade Range was formed of olivine basalt and olivine-bearing andesites deposited mainly as quiet effusions. Most of the major peaks (e.g. Mt. Shasta and Mt. Mazama) are younger composite cones composed chiefly of hypersthene andesite and formed as a result of more violent eruptions during an early period of the Pleistocene. Although this marked the end of the major portion of volcanic activity, the eruption of basalt and andesite continued from numerous vents until as recently as several hundred years ago (102, p. 19).

Based on the available information, some of which has been briefly reviewed, it is only possible to reach tentative conclusions concerning the geologic history of the study area. It is safe to assume that the region is underlain by extensive basalt lava flows which were deposited during the Miocene Epoch. Very likely volcanic activity continued at least through the Pliocene, with the later eruptions resulting in the formation of the numerous volcanic cones

which are common in the area. Most of these cones are composed largely of basalt, although andesite is occasionally found. According to Russell (70, pp. 94-95), the andesitic cones are generally older than those composed of basalt. He also points out that the volcanic cones of Central Oregon vary greatly in age, ranging from early Tertiary to recent centuries. Some evidences of the faulting and folding which produced great scarps and block structures to the south and east are also present in the study area. Although some of the smaller escarpments in the unit are probably of erosional origin, one or two of the larger scarps appear to have resulted from faulting. According to Waring (98, p. 28), most of the deformation in Lake County occurred during the Pliocene Epoch.

Following the cessation of general volcanic activity, rock weathering and soil formation produced a shallow, stony soil over much of the area. Post-Pleistocene vegetation, as determined by pollen analysis, included many of the tree species which are today still common in the region (34, pp. 527-532). These conditions, however, were profoundly altered by the explosive culminating eruption of Mt. Mazama on the crest of the Cascade Range. The eruption included pumice showers and glowing avalanches that resulted in very extensive deposits of this material. The pumice fall, having a maximum depth of approximately 15 feet, is largely concentrated to the north and east of the crater, probably due to a prevailing southwest wind at the time of the eruption (102, p. 69). Pumice deposited in this manner is found more than 100 miles northeast of the source, while less than 10%

of the total volume of pumice fell west of the summit of the Cascade Range. Carbon-14 dating of a charred log excavated from a pumice avalanche deposit has placed the age of the pumice at approximately 6,500 years (47, pp. 118-119).

The Antelope Unit is situated within the region affected by the pumice-fall and virtually the entire area is covered by a layer of pumice. Depth of the deposit within the study area ranges from $4\frac{1}{2}$ feet to approximately 1 foot. Pumice depth varies with remarkable regularity, with the deepest deposits occurring in the northwestern portion of the Unit, and the shallowest to the southeast. Over large areas there are two more or less discrete layers which differ with respect to size of the component pumice particles. The lower layer, immediately above the buried soil, contains primarily sand-sized particles, while in the surface layer the pumice fragments tend to be considerably larger, with cobbles 3 to 4 inches in diameter not uncommon. Williams (102, p. 73) ascribes the prevalence of coarse pumice particles near the surface to an increase in the violence of the eruption prior to its termination.

The majority of the pumice fragments are approximately equidimensional; however some are spindle or disk-shaped. The vesicles within the particles are generally tubular and the fragments frequently have a fibrous appearance. Williams (102, p. 145) has identified it as a dacite pumice, or, more specifically, glassy hypersthene-augite dacite with accessory hornblende. Crystals are very common throughout the

deposits, either imbedded in the glassy matrix of the pumice particles or occurring separately. Williams estimated that the crystals comprise 10-15% of the total volume. He also determined the minerals occurring in crystalline form to be plagioclase, hypersthene, augite, hornblende, and magnetite, in that order of abundance.

Soils of the Area

During the summer of 1956 a soil-vegetation survey of the Antelope Unit was conducted for Weyerhaeuser Company with the Soil Conservation Service and Oregon State College cooperating. Of the 7 soil series mapped in the area, 6 were derived from an aeolian parent material consisting mainly of pumice sand and gravel from Mt. Mazama. The 6 soil series formed on pumice are all typified by relatively immature profiles and are therefore classified as Regosols. Knox (44, pp. 26-27) includes the study area in a region where, under the existing climatic conditions, the zonal upland soils would be expected to belong to the so-called "Western Brown Forest" great soil group.

Leighty (46), in 1946, was the first to classify pumice soils of the forested region of central Oregon. Although his work was centered in an area of shallower pumice near Lapine, the soil series which he described and mapped in an experimental survey were found to provide a generally applicable classification for the soils of the Antelope Unit as well. He divided the pumice soils of that area into three series considered as members of a soil catena. The well to excessively drained member, formed under ponderosa pine and white fir (Abies

concolor), was designated as Lapine; soils imperfectly to poorly drained supporting lodgepole pine (Pinus contorta) were included in the Wickiup series; and a very poorly drained meadow soil derived from pumice was established as the Dilman series. All three of these soils were mapped extensively in the Antelope Unit and are described briefly below.

The Lapine series, as it occurs in the study area, is generally found on gently to steeply sloping topography and is associated primarily with ponderosa pine timber stands. The main features of the soil profile include a thin accumulation of litter on the surface, a dark grayish brown (10YR 3/2 moist) loamy coarse sand or coarse sandy loam A₁ horizon 2 inches thick, a yellowish brown (10YR 5/6 moist) gravelly loamy coarse sand AC horizon 8-14 inches thick, a light yellowish brown (10YR 6/4 moist) medium and coarse pumice gravel C₁ horizon 8-16 inches in thickness, and a light gray (10YR 7/2 moist) coarse pumice sand and fine pumice gravel C₂ horizon about 12-36 inches thick which is underlain by the buried soil. At lower elevations and in nearly level positions the Lapine soil may be somewhat imperfectly drained and exhibit a seasonally high water table. Frequently in these cases the only indication of impeded drainage is slight mottling in the buried soil material (D horizon).

The poorly drained Wickiup soil occupies low topographic positions in basin-like depressions or in areas adjacent to intermittent streams. Generally this soil supports a very dense growth of lodgepole pine. It is characterized by a dark gray to grayish brown

(10YR 5/2, 2.5Y 5/2 moist) sandy loam or loam A₁ horizon, usually about 6 inches thick, underlain by a light gray to white (2.5Y 8/3-8/2 moist) C horizon composed of pumice gravels and sand. Depth to the buried D horizon which is generally of a sandy clay texture, varies from 20 to more than 50 inches. The perched water table is typically above the surface in May, after which it slowly falls during the summer to a depth of approximately 2 to 3 feet in September.

The numerous wet meadows in the Antelope Unit are consistently associated with soils belonging to the very poorly drained Dilman series. These sites are located only at the lowest elevations, or approximately 5000 feet, and are ordinarily adjacent to "lodgepole flat" areas possessing either the Wickiup or imperfectly drained Lapine soils. The Dilman soil profile most often consists of a surface horizon of black (10YR 2/1 moist) alluvium usually of silty clay loam texture, underlain by light gray (10YR 7/2 moist) pumice sands and gravels. The D horizon is conspicuously mottled and is a clay loam or clay. The perched water table is frequently within 2 feet of the surface throughout the growing season.

In certain areas of the Antelope Unit the pumice mantle has been thoroughly mixed, apparently by alluvial action, with finer sand and silt particles derived from basalt. During the 1956 survey the soil formed on this material was provisionally classified as Shanahan coarse sandy loam. Examples are most frequently encountered on nearly level to gently sloping uplands under stands of ponderosa pine. The

salient features of the Shanahan profile include a dark grayish brown (10YR 3/2 moist) coarse sandy loam A₁ horizon averaging 2 inches in thickness, and a dark brown (10YR 3/3 moist) coarse sandy loam AC horizon 12-24 inches thick over the buried soil. In the study area the buried soil usually consists of a dark brown (10YR 3/2 moist) loam A_p horizon approximately 10 inches thick over a dark reddish brown (5YR 3/4 moist) clay B_p horizon 6 to 10 inches in thickness which grades into weathered basalt. The Shanahan is considered to be moderately well-drained as internal drainage is impeded to a certain extent by the presence of the fine-textured buried soil.

During the 1956 survey a soil which was apparently an intergrade between the Lapine and Shanahan series was encountered frequently, especially in the eastern portion of the mapping area. Like the Shanahan, the pumice mantle was mixed with a considerable amount of fine sand and silt apparently from the D horizon. However, the soil still retained many characteristics of the Lapine, especially with regard to horizon sequence, size of pumice particles, and nature of the underlying buried soil. In the majority of cases the C horizon was considerably coarser-textured than that characteristic of the Shanahan and pockets of yellowish, unmixed pumice were not uncommon. Since the vegetation occurring on this soil also appeared to be an intergrade, it was thought advisable to keep it separate from the Lapine and Shanahan. Accordingly, it was classified as Bear Flat coarse sandy loam and mapped separately. This soil was not considered to be a discrete series, but rather a reoccurring, easily identified

intergrade. However, during a subsequent survey of an area south of the Antelope Unit it was found that this soil occupied a very large acreage and its separation was significant. Accordingly, a new series, the Longbell, was proposed for the soil although it had been mapped as an intergrade in the study area. According to the present concept, Lapine-like soils possessing C horizons in which more than 50% of the fresh, sand and gravel-sized pumice is mixed with finer materials are classed as belonging to the Longbell series. The Shanahan C horizon, on the other hand, contains no fresh, light-colored pumice particles and very few pumice gravels.

Vegetation of the Area

Plant distribution and species composition within the study area are apparently largely dependent on microclimatic conditions. Elevation is, of course, an important factor in causing changes in climate which are reflected in differences in the species present and their relative importance. In addition, vegetational distribution gives abundant evidence that temperature and effective moisture may also be considerably modified by other topographic characteristics, especially slope and aspect. Because the well-drained uplands possess a relatively uniform soil mantle, soil characteristics appear to play a relatively minor role in controlling plant distribution in these areas. At the lower elevations, however, the effect of soils on species composition is sometimes clearly expressed. Soils exhibiting permanent or fluctuating high water tables are always accompanied by specific

kinds of vegetation. Therefore, unlike the uplands, there tends to be a rather close correlation between vegetation and soil series or phase.

Numerous meadows are situated at the lowest elevations within the study area. These meadows, occurring on the very poorly drained Dilman soil, exhibit a mesic vegetation due to the subirrigation effects of a shallow water table. The principal grasses are bluegrass (Poa spp.), tufted hairgrass (Deschampsia caespitosa), bottlebrush squirreltail (Sitanion hystrix), as well as several other annual and perennial grass species. In addition, sedges such as meadow sedge (Carex praegracilis) and Nebraska sedge (Carex nebraskensis) are very common, as are rushes (Juncus spp.). Forb species differ appreciably from place to place due to varying amounts of grazing pressure; however two of the more common are longstalk clover (Trifolium longipes) and western buttercup (Ranunculus occidentalis).

Immediately adjacent to the meadows and in low-lying drainages dense, pure stands of lodgepole pine occupy areas of the poorly-drained Wickiup and seasonally ponded Lapine soils. These soils are ponded in the spring, with the water table dropping to depths ranging from 2 to 6 feet in the summer. As a result of the very moist growing conditions the understory vegetation is characterized by many of the same species characteristic of the meadows. On these moist sites a plant cover of 100% is commonly maintained throughout the growing season. Bearberry (Arctostaphylos uva-ursi) is by far the most common

shrub, although occasional spiraea (Spiraea sp.) or bitterbrush (Purshia tridentata) plants are also encountered. Characteristic grasses are Idaho fescue (Festuca idahoensis), western needlegrass (Stipa occidentalis), bluegrass, timber danthonia (Danthonia intermedia), bentgrass (Agrostis scabra), and wheatgrass (Agropyron sp.). As in the meadows, sedges and rushes are also common. The common forbs are strawberry (Fragaria cuneifolia), longstalk clover, bedstraw (Galium sp.), aster (Aster campestris), geranium (Geranium sp.), false Solomonseal (Smilacina sessilifolia), and horsetail (Equisetum sp.).

Pure to nearly pure stands of lodgepole pine also occur on sites possessing an imperfectly drained phase of the Lapine soil; usually these are on very gently sloping topography and invariably at lower elevations, or approximately 5000 feet in the study area. The timber stand in these areas is generally not as dense and often includes scattered ponderosa pine. Inasmuch as the soil is only seasonally wet and dries out considerably in the summer, the understory vegetation is more scattered and comprised of species slightly less demanding in their moisture requirements. In these locations dominant shrubs are bitterbrush and currant (Ribes sp.). The most important grass species are Idaho fescue, western needlegrass, bottlebrush squirreltail, and Ross sedge (Carex rossii). The principal forb species include annuals such as Gayophytum diffusum, Collinsia parviflora, and Cryptantha affinis; and the perennial plants, tawny horkelia (Horkelia fusca), penstemon (Penstemon sp.), least lupine (Lupinus minimus), and

strawberry.

The principal tree species on well-drained sites at intermediate elevations is ponderosa pine. At elevations of 6000 feet and above, or considerably lower on steep north and east-facing slopes, substantial amounts of white fir occur. These more moist sites also commonly support small amounts of sugar pine (Pinus lambertiana). In addition, pure stands of lodgepole pine are occasionally situated in well-drained upland positions, apparently as a result of major disturbances. Except on the driest sites, lodgepole pine is also usually a minor component of those timber stands in which ponderosa pine or white fir is dominant. Vegetative characteristics of these well-drained uplands are more fully discussed in a subsequent section.

Climate

No temperature and rainfall records are available for the Antelope Unit or any area close by which would be comparable. For this reason, it is only possible to describe in a general manner the climatic characteristics of the region. Thornthwaite (83, pp. 654-655) includes south-central Oregon in a climatic province described as sub-humid, microthermal and with a marked summer deficiency of precipitation. Immediately to the east this province grades into the semiarid climatic type having precipitation deficiencies throughout all the year.

Annual precipitation very likely ranges from about 20 to 25 inches, depending on elevation. Crescent, Oregon, located approximately 25 miles to the northwest, receives about 19 inches annually

(88, p. 1077). Inasmuch as the Antelope Unit is situated some 500 feet higher than Crescent, total precipitation could be expected to be slightly higher in the case of the former. Annual precipitation undoubtedly decreases gradually towards the eastern border of the unit and may possibly approach 15 inches. A strong indication of this is the fact that Silver Lake, only 11 miles to the east, receives slightly less than 10 inches per year (88, p. 1077). Most of the precipitation comes during the fall, winter, and early spring, with very little occurring in the summer months. The rainfall during June, July, and August generally accompanies brief electrical storms and it is doubtful that it exceeds one inch for any one month. Much of the precipitation during the winter comes in the form of snow and annual snowfall in the area has been reported to average approximately 3 to 4 feet.²

The study area possesses an extremely short frost-free season as a result of its relatively high elevation (5,000 to 6,000 feet). Although day temperatures during July and August often reach 95°F. or higher, frosts during these 2 months are not uncommon. Most summer frosts are confined to low-lying pockets or depressions, probably due to the effects of temperature inversion and pronounced cold air drainage. The mean January and July temperatures at Silver Lake are

² Personal communication, Mr. T. L. Orr, Weyerhaeuser Co., Klamath Falls, Oregon.

approximately 28 and 64 degrees Fahrenheit respectively (88, p. 1077).

The climatic history of the area for the past 650 years has been partially determined by Keen (40, p. 188) through a study of ponderosa pine growth rings. His samples, collected from several locations throughout central Oregon, indicated that despite minor fluctuations, growing conditions have not changed greatly in the past six centuries. The pattern of growth, as recorded by the tree rings, consisted of a variable number of years of above average growth rate followed by an equally indefinite period of time when growth rate was below average. Since soil moisture is generally the limiting factor in the growth of ponderosa pine, these variations, outside of local defoliation and fire, largely reflect fluctuations in amounts of precipitation. On this basis, Keen was able to ascertain that a fairly severe drought occurred during the 1840's and early 1850's which was followed by 40 years of above average precipitation. Average growth during the period from 1900 to 1917 was equal to the general average for the entire record of 650 years. Beginning in 1917, however, a severe drought occurred in central Oregon, with the smallest amount of growth noted in the rings corresponding to the year 1924 and 1931. Following the second low, the trend was definitely toward a faster rate of growth.

REVIEW OF THE LITERATURE DEALING WITH SOIL-VEGETATION RELATIONSHIPS
WITHIN THE PONDEROSA PINE TYPE

The Central Oregon Pumice Region

The ecology and soils of the forested portion of central Oregon have received very little attention. Material published to date is devoted largely to discussions of factors controlling the distribution of lodgepole and ponderosa pine. In the majority of these papers the understory vegetation is either ignored or treated in a very superficial manner.

Forest succession in central Oregon, both before and after the advent of extensive pumice deposits, has been described by Hansen on the basis of the analysis of fossil pollen contained in peat profiles (30, 31, 33, 34). One peat profile in the pumice region was obtained from a bog 13 miles west of Bend and exhibited two separate layers of pumice, $2\frac{1}{2}$ meters apart (33, pp. 214-219). The upper layer has been dated at approximately 4,000 years and probably originated from Devil's Hill Volcano; and the pumice in the lower layer has been identified as Mt. Mazama pumice and is therefore about 6,500 years old.³ Results of pollen analysis showed that when sedimentation began at the close of the glacial period western larch (Larix occidentalis) was the predominant tree species. Within a very few centuries, however, lodgepole pine assumed dominance, only to be gradually replaced

³ Personal communication, Dr. H. P. Hansen, Oregon State College.

by ponderosa pine as the climate became progressively warmer and drier. This trend was abruptly reversed by the deposition of pumice from Mt. Mazama, following which lodgepole pine regained dominance. For the next 25 centuries the amount of ponderosa pine slowly increased, while there was a corresponding decrease in the occurrence of lodgepole pine. With the advent of the more recent pumice deposit the successional trend was again reversed and the growth of lodgepole pine favored. Evidence such as this led Hansen to state that the extensive pure stands of lodgepole pine occupying pumice soils at the present time have been able to persist only because of the absence of competition from species which would ordinarily constitute the climatic climax (31, p. 713). Hansen (31, pp. 727-732) has outlined broad climatic trends during the past 20 thousand years as shown by the analysis of fossil pollen: (1) 20-15 thousand years ago, cooler and more moist than at present; (2) 15-8 thousand years ago, a marked warming and drying trend; (3) 8-4 thousand years ago, maximum warmth and dryness; and (4) 4 thousand years ago to present, trend towards a cooler and more moist climate.

The earliest paper concerning the soils and vegetation of the central Oregon pumice region was published in 1913 by Kerr (42). He was perhaps the first to record several observations with regard to the distribution of lodgepole and ponderosa pine which are today still oft-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 the level areas because of its intolerance to conditions of poor soil drainage.

Munger (54), writing one year later, gave his interpretation of the process enabling lodgepole pine to gradually replace ponderosa pine in certain locations in central Oregon. He felt that since the area was burned over on the average of once every 30 years, lodgepole pine was definitely favored due to its much more prolific seeding habit. In the absence of fire, Munger contended that ponderosa pine would be expected to maintain dominance as a result of its much longer life. The pumice soils of the area were also discussed to a limited extent. He noted that although the surface layers dried out early in the growing season, soil only several inches below remained fairly moist.

More recently, Tarrant (78, 79) has reported on a study conducted at the Pringle Falls Experimental Forest near Lapine, Oregon. Based on observations made during a soil survey of a portion of the area it was concluded that ponderosa pine does not grow well on those pumice soils having a permanent or fluctuating high water table. Lodgepole pine, on the other hand, was apparently able to adjust its root system successfully and thrive under the same conditions. Leighty (46, p. 15), who conducted the survey, questioned whether fire had exerted much influence on the distribution of lodgepole and ponderosa pine in central Oregon: "In the area mapped no certain evidence was found that would indicate that fires have had a principal influence on the distribution of these two species."

Youngberg and Dyrness (105) have recently studied the soils and understory vegetation associated with lodgepole pine in an attempt to develop guides for differentiating between seral and climax stands. Three soil moisture situations and their associated understory vegetation are described and are proposed as lodgepole pine climaxes. These soils, the poorly drained Wickiup plus the seasonally ponded and seasonally wet phases of the Lapine, all possess a water table that is either permanently or seasonally high. They are confined to level or depressional areas at lower elevations. Lodgepole pine growing under these conditions is defined as a topo-edaphic climax. The authors state that climax lodgepole pine stands may also occur in areas of deep, well-drained Lapine soil. Here it is claimed that late spring frosts and cold air drainage during the growing season seriously limit the growth of ponderosa pine. In these situations lodgepole pine is considered a topographic climax species.

Synecological Studies Within the Ponderosa Pine Type

In 1917 Weaver (99) reported on an extensive study conducted in southeastern Washington and adjacent Idaho. The area receiving attention included plant communities within the prairie-plains, desert shrub, and Pacific Coast forest formations. Ponderosa pine was described as most commonly occupying sites shared by Douglas-fir (Pseudotsuga taxifolia) in what was termed a Pinus-Pseudotsuga associates. Common species of associated shrubs and herbs were also listed. Daubenmire (16, pp. 306-319) also studied the forest

vegetation of northern Idaho and eastern Washington but constructed a much more detailed classification. The highest categories of his classification scheme consisted of four main forested zones:

(1) Pinus ponderosa zone, (2) Pseudotsuga taxifolia zone, (3) Thuja plicata-Tsuga heterophylla zone, and (4) Picea engelmanni - Abies lasiocarpa zone. The understory associations characterized within the ponderosa pine zone were: (1) Agropyron spicatum, (2) Purshia tridentata, (3) Symphoricarpos rivularis, and (4) Physocarpus malvaceus, with amounts of available soil moisture increasing from (1) through (4). Daubenmire pointed out that quaking aspen (Populus tremuloides) is frequently seral to ponderosa pine on soils possessing a high water table.

McMinn (50) studied soil moisture trends during the 1950 growing season in seven plant associations of northern Idaho and southeastern Washington. Soil samples were collected weekly by one decimeter intervals to a total depth of one meter. The soil supporting the Pinus/Symphoricarpos association began to be depleted of available moisture by the third week in July; while the more moist Pinus/Physocarpus and Pseudotsuga/Physocarpus associations were located on sites which did not show signs of drought until the second and fifth weeks of August respectively. McMinn concluded that soil moisture levels exert considerable influence on the distribution of plant associations in the northern Rocky Mountains.

Rummell (69) studied the vegetation in two areas of the ponderosa

pine type in central Washington. The areas were similar except for the fact that one had been grazed, while the other was inaccessible to livestock. The understory vegetation, consisting largely of pinegrass (Calamagrostis rubescens) and elk sedge (Carex geyeri), had a density of 35% in the ungrazed condition as opposed to 14% for the grazed area. Rummell found numerous ponderosa pine seedlings in the grassy openings of the grazed study area, but very few to none in like positions in the ungrazed area. The ungrazed area averaged only 85 trees less than 4 inches in diameter per acre, while the corresponding figure for the area open to grazing was 3,291 trees.

Factors Influencing the Distribution of the Ponderosa Pine Type

Climate is generally considered to be the most important factor controlling the distribution of forest types. Pearson (61, p. 141), speaking of conditions in the southwest stated, "Soil is important, but when large differences in altitude are involved, the range in temperature and precipitation is so great that it usually overshadows differences in soil". The majority of studies of climatic and soil conditions within different forest types have been conducted in mountainous areas where the forest cover is varied due to the wide range in elevations. The question of which causes shifts in forest type with changing elevation, temperature or precipitation differences, is both old and oft-discussed. It is the opinion of Pearson (60, pp. 115-116) and Larsen (45, p. 671) that the upper altitudinal limit of a given forest type is set by some critical minimum temperature, while

the lower limit is governed by the minimum moisture requirement of the species. Bates (6, pp. 134-135), in disagreeing, has placed more emphasis on temperature by stating that in addition to low temperatures limiting the upward extension of a forest type, high temperatures are most important in limiting its downward extension. Daubenmire (17) has minimized tolerance of high soil surface temperature as an important factor in determining lower altitudinal limits of trees in the Rocky Mountains. He pointed out that, contrary to popular belief, ponderosa pine does not have a greater tolerance of high temperatures than Douglas-fir. According to Daubenmire, the ability to survive despite extended periods of soil drought is the primary factor enabling some tree species to extend their ranges to lower elevations.

The climatic requirements of ponderosa pine have been studied in some detail at several localities, notably in the Rocky Mountains and Arizona. Larsen (45, p. 671), after having studied the weather records from 13 northern Rocky Mountain Stations situated in the ponderosa pine type, concluded that the minimum requirements for the growth of ponderosa pine were a mean annual air temperature of between 44 and 50°F. and an annual precipitation within the range of 17 to 22 inches. Munger (53, p. 5), working in Oregon, emphasized that ponderosa pine attains its best growth in the heat and dryness which are characteristic of a continental climate. He also stated that ponderosa pine resisted drought better than any other commercial tree in the state. Pearson (60, pp. 22-34; 63, pp. 144-151) found that minimum temperatures in the ponderosa pine type of Arizona and New Mexico were

considerably lower than those in the Douglas-fir type due to the effects of cold air drainage. In addition, as a result of the high day temperatures in the ponderosa pine type, it exhibited the greatest diurnal temperature fluctuations. Pearson (60, p. 124) determined the following minimum requirements for the growth of ponderosa pine in northern Arizona: (1) a mean summer air temperature of 58°F., (2) a mean maximum summer air temperature of 70°F., and (3) 20 inches of annual precipitation. Bates (6, pp. 133, 138) studied the changes in climate which accompanied differences in elevation and timber type in the central Rocky Mountains. He found a temperature gradient of 2.8°F. for every change of 1000 feet in elevation, while the difference in precipitation for the same interval was 2.4 inches.

Pearson (59) compared the climate of four of the major regions supporting extensive stands of ponderosa pine. Although he found that mean monthly maximum temperatures were fairly similar in all regions, there were considerable differences in patterns of summer rainfall. Arizona has small amounts of rainfall in May and June, with a very sharp increase in July and August. The Black Hills area generally receives adequate amounts of rainfall during the entire summer. Northern California and eastern Oregon and Washington, on the other hand, receive very small amounts of rainfall in July and August. Pearson points out that these differences in rainfall may explain why ponderosa pine seed germination occurs in the spring in Oregon and Washington, but is deferred until July and August in Arizona.

Most workers attach considerable importance to soil characteristics in controlling the distribution of ponderosa pine. It is unfortunate, however, that the majority of soils investigations have largely consisted of reconnaissance observations of limited value. Munger (53, p. 6) stated that "In Oregon ponderosa pine grows on nearly every variety of soil" with the exception of cold and wet soils such as those adjacent to meadows. It was also noted that ponderosa pine is quite uncommon on broad, flat areas, but is rather, "distinctly a tree of the slopes". Dunnewald (20, pp. 577-578), working in the Big Horn Mountains, found the timbered soils to be shallow, stony, and yellow in color, while the meadow soils were considerably deeper and dark brown to black in color. Pearson (63, p. 156) found no correlation between timber type and the results of soil chemical analysis in Arizona. He concluded that availability of soil moisture was probably the most important soil factor. In another study (60, pp. 64-67) Pearson found that available moisture in the surface one foot of soil under ponderosa pine was usually exhausted by the latter part of June in Arizona. However, droughts in the Douglas-fir and Engelmann spruce types were rare. Bates (6, p. 139) claimed that soil moisture depletion under ponderosa pine was not serious in the Rocky Mountain area, since none of his soil moisture samples ever approached the permanent wilting percentage.

Pearson (60, p. 75; 61, p. 141) repeatedly emphasized the importance of soil texture in influencing the growth of ponderosa pine. He indicated that growth was usually best on the more sandy and gravelly

soils, while soils possessing a clay texture were virtually devoid of ponderosa pine regeneration unless modified by an admixture of stones in the soil matrix. According to Pearson, the best ponderosa pine growth was attained on granitic soils. He pointed out (61, p. 141) that at its lower elevational limits ponderosa pine occurred on sandy soils only, while the clay-textured soils supported the pinyon-juniper type exclusively. Pearson and Marsh (64, p. 16) investigated the behavior of ponderosa pine on cinder soils. They found seedling germination to be poor due to low moisture holding capacities and that underlying layers of clay or loam favored tree growth.

Bates (6, p. 134) reported a close correlation between timber type and the mean growing season soil temperature at a depth of one foot in the Rocky Mountains. Ponderosa pine became established where the mean growing season soil temperature was 58 to 62°F.; when temperatures were approximately 55 to 56°F. Douglas-fir reproduction began to occur with the pine; at temperatures of 52 to 53°F. Douglas-fir predominated; and when mean soil temperatures ranged from 44 to 48°F. Engelmann spruce began to come in under the fir. Pearson (60, pp. 43-48) investigated soil temperatures at a 6 inch depth under the ponderosa pine and Douglas-fir forest types. The temperatures under ponderosa pine in the summer were approximately 10°F. higher than those under stands of Douglas-fir. Conversely, in the winter temperatures were about 3 to 4°F. lower under the ponderosa pine type.

Howell (39) described the effect of a perched water table on the

distribution of lodgepole pine and ponderosa pine in California. A clay pan, found at a depth of 3 feet below patches of lodgepole pine, was completely absent from the soil supporting the ponderosa pine type. According to Howell, the clay pan caused a perched water table and accounted for the small areas of lodgepole pine in otherwise pure ponderosa pine stands.

Studies conducted by Thorp (86) and Spilsbury and Tisdale (73) provide good examples of that type of investigation which is concerned with broad soil-vegetation relationships over a large area, usually one with an extensive elevational range. Spilsbury and Tisdale studied the vegetation and soils of the Tranquille Range near Kamloops, British Columbia and identified 6 zones which were closely related to elevation. These zones, located within an elevational range of 1,100 to 6,100 feet, were as follows: (1) lower grassland and brown earth zone, (2) middle grassland and dark brown earth zone, (3) upper grassland and black earth zone, (4) montane forest and lower podzol zone, (5) subalpine forest and middle podzol zone, and (6) upper subalpine forest and upper podzol zone. Thorp, working in northern and northwestern Wyoming, separated the area into 6 zones starting at 4,500 feet and going up to 8,500 feet. Each zone was characterized by a distinct climate and vegetation type which ranged from desert to spruce-fir forest and also was associated with what he considered to be different great soil groups.

The Effect of Soil Characteristics on Ponderosa Pine Reproduction

The effects of various soil characteristics on the growth of ponderosa pine have been the subject of both experimentation and speculation for a considerable number of years. That some of the work carried out in this field is of doubtful validity may be attributed to the fact that it was undertaken by foresters with little knowledge of the basic facts and concepts of soil science. Nevertheless, their results may be of some interest and are included in the following short summary.

Haasis (28) studied the relationship between soil texture and the root form of ponderosa pine seedlings. He found roots were longest in clay-textured soil, but also were the least branched. Seedlings growing in cinders had roots showing the greatest amount of branching. In a similar experiment, Howell (38) grew ponderosa pine seedlings for 150 days in four kinds of soil material: pumice, sand, loam, and clay. Seedlings grown in pumice were by far the largest and best-developed. Total length of roots on seedlings grown in pumice was more than twice as great as the corresponding figure for roots developed in clay soil. The top-root ratio was 0.87 for seedlings grown in pumice, while in the case of the other soils it was never lower than 1 and most often between 2 and 4. Baker (5) investigated ponderosa pine seedling survival on several soils. Best rates of survival were noted for a very fine sandy loam, while a clay soil ranked second. Survival was poorest on a fine sandy loam which was very low in organic matter. Baker concluded that survival and

seedling growth was apparently correlated with the organic matter content of the soil.

Recently it has been reported that ponderosa pine is apparently unusual in its ability to obtain soil moisture held at relatively high tensions. Fowells and Kirk (24) found that ponderosa pine seedlings were able to become established and grow in a fine sandy loam soil maintained at only 2% above the permanent wilting percentage. In addition, the ponderosa pine seedlings did not show outward signs of moisture stress until 6 weeks after sunflowers growing in the same soil had wilted. Stone and Fowells (76) reported that dew occurring nightly definitely prolonged the life of ponderosa pine seedlings and also enabled them to more completely exhaust soil moisture supplies. Stone (75, pp. 420-421) found that ponderosa pine seedlings growing in clay soils died before soil moisture was depleted to the permanent wilting percentage. This was attributed to poor distribution of the roots within the soil mass as a result of their relatively unbranched habit. Perhaps this may at least partially explain why ponderosa pine is commonly observed to grow poorly on soils possessing a clay texture.

The nature of the most favorable seedbed for ponderosa pine seedling germination and survival has been the subject of considerable controversy. Sproat (74, p. 336) came to the conclusion that ponderosa pine seedlings survive better on undisturbed soil than on bare, disturbed soil. Baker (4, p. 402) holding exactly the opposite opinion, stated that at lower elevations in the Sierra Nevada the most favorable areas for reproduction have "recently disturbed mineral soil

free from root competition." Pearson (62, pp. 34-38), somewhere between the two extremes, maintained that although germination and survival were favored by loosening the soil, the removal of litter or vegetative cover was detrimental. He also presented data demonstrating that gravelly and rocky soils favor ponderosa pine regeneration in the Southwest. In rock outcrop areas there were an average of 367 seedlings per acre; very stony clay sites had 493 seedlings per acre; stony clay, 227 seedlings per acre; gravelly clay, 137 per acre; shallow clay, 64 per acre; and deep clay, 36 seedlings per acre. Meagher (51, p. 189) reached the conclusion that unsatisfactory ponderosa pine reproduction is most common on dry sites receiving very little summer rainfall. In these areas the two primary requisites for securing large number of established seedlings are above-average rainfall coupled with an unusually large seed crop. Munger and Westveld (55, p. 12) found that scattered slash apparently increased both germination and survival of ponderosa pine on pumice soils in central Oregon. Seedling survival was 37% on slash-covered areas, as compared with only 19% in areas where the slash was piled and burned.

REVIEW OF THE LITERATURE DEALING WITH PUMICE SOILS

Pumice soils, although of considerable extent especially in the Northwest, have received almost no attention from American soil scientists. As far as can be determined, nothing has been published dealing specifically with the nature and properties of pumice soils occurring in Oregon. This is somewhat surprising in view of the fact that well over two million acres of valuable forest land in central Oregon are situated on soils derived from Mt. Mazama pumice alone. Fortunately, a considerable amount of information has been supplied by workers in New Zealand, and some of their observations and experimental results may be applicable to pumice soils occurring in central Oregon. However, it should be borne in mind that both climatic conditions and mineralogical composition of the pumice differ appreciably between the two locations. The climate of the largest pumice soil region of New Zealand is described as humid-temperate. Precipitation ranges from 45 to 60 inches annually and is well-distributed throughout the year.⁴ In comparison, much of the pumice region of central Oregon receives only 15 to 25 inches of annual precipitation, with virtually no rain falling during July and August. In addition, the pumiceous parent material in New Zealand is classified as rhyolite, while in central Oregon the most widespread deposits contain pumice with the composition of dacite. Perhaps the one point of similarity

⁴ Personal communication, R. Q. Packard, New Zealand Soil Bureau.

of any importance is that in both regions frosts during the summer are not uncommon.

The most extensive deposits of pumice in New Zealand are located in the central plateau region of the North Island. Baumgart (7, p. 17; 8, p. 466) reports that approximately 1,700 years ago a major volcanic eruption resulted in the deposition of what is commonly known as the "Taupo ash shower". The majority of investigations of New Zealand pumice soils are concerned with soils derived from Taupo ash.

The soils formed on Taupo ash material are included in the Yellow-Brown pumice soil group of New Zealand (7, p. 18; 81, p. 12). Grange (26, pp. 391-393) and Baumgart (7, p. 18) report that podzolized pumice soils are frequently formed under a podocarp forest cover. Packard⁵ describes these soils as consisting of a distinct A₂ horizon 2 to 4 inches in thickness, underlain by a yellowish-brown B horizon 6 to 10 inches thick. Wherever shrubs have replaced forest trees as a result of repeated fires, the A₂ horizon is quickly lost and its place taken by a black-colored layer, generally "sandy silt" or sand in texture. Taylor (82, pp. 195-201), in 1933, observed that podzolization tended to be the dominant soil-forming process in deposits of rhyolitic ash and lapilli, while in more basic andesitic material latosolization was apparently active. Taylor theorized that coarse rhyolitic ash, such as was deposited in the Taupo shower,

⁵ Personal communication, R. Q. Packard, New Zealand Soil Bureau.

affords more opportunity for downward percolation of water and hence also translocation. Therefore the first products of mineral weathering would be expected to be quickly transported downward in the profile. Andesitic ash, on the other hand, is deposited in intermittent and quiet eruptions and is therefore much finer-textured. Also, due to its more basic composition, the andesitic material decomposes more quickly. Taylor states that under these conditions the clay could possibly reach the allophane stage before it was moved downward.

Approximately one-half million acres of New Zealand's North Island pumice region are occupied by plantations of exotic conifers. According to van't Woudt (92), the species planted most commonly is Monterey pine (Pinus radiata). During the course of planting and managing the stands certain soil factors were noted to have important effects on tree growth and these were described by van't Woudt in 1953. In certain low-lying areas poor tree growth was apparently caused by frost damage. The adverse microclimatic effects were most pronounced in localities where soil conditions were unfavorable and these areas were invariably denoted by the presence of a certain understory plant species. Hard pans, or "pumice pans", were frequently encountered on level to gently sloping sites. Apparently they are formed by the blocking of subsoil pore spaces with finer material leached down from the surface soil. Packard⁶ reports that these pans are frequently a

⁶ Personal communication, R. Q. Packard, New Zealand Soil Bureau.

formidable barrier to plant roots, and that 30 years may elapse before Monterey pine roots are able to penetrate a pan 3 feet thick.

In 1952 Birrell and Fieldes (10), working in New Zealand, reported the presence of allophane in both andesitic and rhyolitic ash on the basis of evidence gained through differential thermal analysis and X-ray diffraction. They pointed out that these soils should be dispersed in an alkaline medium as acid treatment is likely to cause partial decomposition of the allophane. Fieldes (23, p. 349) proposed a weathering sequence for volcanic ash clay minerals which consisted of a gradual transition with increasing age through 3 forms of allophane, meta-halloysite, to kaolinite as the end product. He analyzed 7 soils, each representing a different stage of weathering, and found all members of the sequence with the exception of kaolinite. Gradwell and Birrell (25, p. 108) have suggested that allophane exerts an important effect on soil physical properties for two principal reasons: (1) its extremely small "particle size", and (2) the fact that it is a very slowly reversible gel of high water content.

Van't Woudt (91, 93), working with Taupo pumice soils in New Zealand, noted a marked variation in productivity with position on slopes. For example, the growth of pasture grasses would often improve greatly from the top to the bottom of moderately steep slopes. This he attributed to down-slope transport of nutrients by surface runoff and subsurface flow. A series of soil analysis showed that contents of organic matter, nitrogen, and silt were greater at the

foot of the slope than at the top. According to van't Woudt, subsurface downslope water movement occurs in pumice soils as a result of three main factors: (1) When rain falls on a dry pumice soil the surface layer readily becomes wetted, while the soil beneath tends to be resistant to wetting. (2) The B horizon of the Taupo soil is usually far less permeable than the A, therefore water has a tendency to move laterally on the surface of this layer. (3) The usual horizon sequence in Taupo pumice soils consists of a fine-textured surface layer overlying a much more coarse-textured subsoil. It has been found that the boundary between two such layers presents an effective barrier to the penetration of water.

Until recently, the lack of information on the physical properties of pumice soils has been a serious limitation. Packard (57), in 1957, published some of the first information concerning the physical properties of Taupo pumice soils in New Zealand. His study had two principal aims: (1) To compare the physical properties of coarse-textured pumice soils located near the pumice source with those of finer-textured soils found at the fringes of the pumice shower, and (2) To compare the properties of pumice soils under different vegetation types. The properties investigated were particle size distribution, bulk density, particle density, and macro-porosity. He reported an unusual amount of difficulty in obtaining adequate dispersion for mechanical analysis. This difficulty was attributed to incomplete organic matter oxidation and the presence of allophane, a mineral notoriously resistant to dispersion. To check mechanical analysis

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results, clay content was also estimated by the determination of surface area through use of the method devised by Brunauer, Emmett, and Teller (12). By the use of this method the percentage of clay contained in a typical sample was calculated to be 11.6, while conventional mechanical analysis gave a figure of 2%. Thus, in this particular case, incomplete dispersion was strikingly demonstrated. Most of the samples Packard analyzed possessed a sandy texture. As he points out, however, pumice soil textures are often misleading because other physical properties commonly more closely resemble those of a silt loam. Bulk density studies indicated a very close relationship between this soil property and vegetation type. For example, in one set of samples the bulk density of soil under forest was 0.47 g./cc., while the corresponding figure for pasture conditions was 0.71 g./cc. The greater density of pasture soil was attributed to compaction caused by the trampling of livestock.

Packard also studied the moisture relationships of Taupo pumice soils. Initially he was concerned with establishing moisture constants for the soils under consideration. In order to determine field capacity he flooded a 6 x 6 foot plot and allowed it to drain for 3 days. This moisture value and that obtained for moisture in the same soil under a tension of 0.19 atmospheres were in good agreement. Permanent wilting percentage values determined by both the sunflower and pressure membrane methods were also found to be approximately the same. When calculated on the basis of weight, pumice soils were found

to have 2 to 3 times more available water than a normal mineral soil of silt loam texture. In order to discover the effect of organic matter on moisture holding capacity, Packard compared results of moisture determinations before and after treatment with hydrogen peroxide. It was found that although removal of organic matter noticeably reduced amounts of available moisture, this reduction was not great and apparently the porous nature of the pumice itself was largely responsible for the unusual moisture relations of the soils tested. Packard repeatedly emphasized the point that pumice soil moisture content should be expressed on a volume basis, especially if comparisons with other soils are to be made. The favorable effect of compaction on moisture properties was demonstrated by the fact that pasture soils were found to contain almost twice the amount of available moisture as soils under forest. In an earlier study, Packard (58) found that the movement of water in an unsaturated pumice soil was 7 or 8 times slower than that in ordinary mineral soils. However, soil moisture conditions were apparently favorable throughout the year for plant growth, as 23 separate moisture samplings over a 2 year period failed to find an area where soil moisture had been depleted to the permanent wilting percentage.

Although generally speaking the Taupo pumice soils are only slightly weathered, several workers (19, p. 20; 93, p. 168) have stated that their present rate of weathering may be considered quite rapid. This fast rate of decomposition is generally attributed either to the relatively large exposed surface area of the pumice particles

(93, p. 168), or to the absence of resistant crystal faces (19, p. 20). As van't Woudt (93, p. 169) points out, the rather rapid rate of pumice breakdown becomes especially important in view of the inherent low fertility of pumice soils of rhyolitic composition. Thus the release of nutrient elements by means of pumice weathering allows at least some plant growth on a soil which would otherwise be virtually sterile.

A summary of the nutrient status of the New Zealand Tapuo soils has been presented by Dixon and Jackman (19). They report that although on the basis of base saturation considerations pumice soils are apparently low in Ca, very little agricultural lime is applied because investigators have failed to obtain plant responses by the use of this soil amendment. Exchangeable K is present in sufficient amounts in uncultivated soils, but usually becomes deficient after several years of cropping. Amounts of Fe and Al were generally low, thus indicating only a slightly weathered soil. Analyses showed 200 ppm of Na, an amount which the authors considered low. Amounts of Mn, Mo, and Cu were all adequate, being 140, 2.2, and 40 ppm respectively. The authors give no figures for S and B content, which is unfortunate as these elements have been found to be scarce in certain soils derived from volcanic materials.

Most of the workers who have studied pumice soils in New Zealand apparently agree that supplies of available phosphorus are too low for optimum plant growth, even in uncropped areas. Aston (2, p. 377), in 1912, suggested that, "Improvement of pumice soils must depend largely

on increasing the store of humus and by application of phosphatic fertilizers." Taylor (80, p. 403) prescribed the regular application of 300 pounds of superphosphate fertilizer per acre for optimum crop production. Grange (26, pp. 391, 393) pointed out that podzolic pumice soils although low in general fertility, are especially deficient in phosphorus. Only one author showed any concern for the nitrogen fertility of Taupo pumice soils. Aston (2, p. 376) suggested planting leguminous plants and plowing them under. However, even this practice was aimed more at building up soil humus than correcting any nitrogen deficiency.

Van't Woudt (92) has described the difficulties in soil fertility encountered in the practice of forestry on pumice soils. He states that signs of serious leaching are often found under young stands of Pinus radiata. This excessive leaching is attributed to an incomplete canopy of vegetation. The nutrient loss, coupled with the removal of essential elements in wood products, led van't Woudt to question whether it would be possible to grow many tree crops on short rotations without the addition of fertilizers. It was also noted that local variations in site quality were frequently due to differences in the degree of weathering of the pumice particles. Invariably highly productive sites were correlated with a soil in which the pumice had undergone considerable weathering. Van't Woudt attributed this relationship to the fact that as weathering proceeds quantities of nutrients are constantly made available. On the basis of another study (93, pp. 168-170), van't Woudt concluded that crop production

on a relatively unweathered pumice soil is largely dependent on:

(1) amount of nutrients already made available by weathering, (2) rate of weathering at the present time, and (3) total amount of nutrients the parent material is capable of supplying. Pumice weathering is especially important in the release in available forms of such elements as potassium, calcium, and magnesium. However, the rate of liberation of these elements through mineral breakdown apparently fails to keep pace with plant use under farming conditions in New Zealand and, especially in the case of phosphorus, additional amounts must be added in the form of fertilizers.

Bailey (3), working with Taupo pumice soils, found their organic matter content to be consistently higher than that of ordinary mineral soils formed under the same conditions of climate and vegetation. He concluded that the buildup of organic matter was due to slower rates of decomposition in the pumice soil. This was borne out by the fact that certain fractions such as cellulose, ordinarily only partially resistant to decomposition, comprised a considerably larger proportion in pumice soils than in conventional mineral soils. Bailey expressed considerable surprise that organic matter decomposition should be retarded in a soil which would appear to provide nearly optimum conditions for microbiological activity. Dixon and Jackman (19, pp. 20-21) found that plowing led to faster rates of decomposition, as evidenced by carbon-nitrogen ratio data. Their figures show a carbon-nitrogen ratio of 24 for an undisturbed topsoil and a corresponding value of 12 for a soil plowed for a period of 19 years. However,

despite the accelerated rate of decomposition, amounts of organic carbon and nitrogen remained appreciably higher than that characteristic of most zonal soils. Values given as representative were for pumice soils: 9.8% organic carbon and 0.81% total nitrogen, and for a zonal soil: 5.4% organic carbon and 0.34% total nitrogen. Both Bailey and Dixon and Jackman offered possible explanations for the unusual behavior of organic matter in pumice soils. Bailey (3, p. 420) suggested that since liming was only seldom practiced, perhaps a calcium deficiency limited the activity of both bacteria and earthworms. The theory developed by Dixon and Jackman (19, p. 21) attributed slow decomposition rates to the stabilizing effect of clay-humus bonding. They pointed out that although amounts of clay in pumice soils are generally small, the predominant clay mineral is allophane which possesses a relatively high cation exchange capacity.

As yet, very little is known concerning the amounts and activities of macro- and micro-organisms in pumice soils. Smith and Griggs (72) studied the microflora present in 18-year old volcanic ash in the Valley of Ten Thousand Smokes in Alaska. They found an average of only 140,000 micro-organisms per gram of soil and a complete absence of actinomycetes. Experiments failed to demonstrate any measurable nitrogen fixation. Rose (68), investigating soils derived from Taupo Shower material in New Zealand, found that soil samples from level areas generally contained larger quantities of bacteria, fungi, and actinomycetes than did samples collected from hilltops or slopes. Representatives were found of virtually all the physiological groups

of organisms, such as nitrosoifiers, nitrifiers, cellulose decomposers, and nitrogen fixers. Thornton et al. (84) report that although only a few species of earthworms have become established in the pumice region of New Zealand, they have a very widespread distribution owing to a lack of competition. However, all species are confined to the topsoil and litter. They also studied the soil protozoan population and found their growth was encouraged more by high organic matter contents than any other single factor.

Published material pertaining to pumice soils is very largely descriptive except for that coming from New Zealand. Harada (35) has described some volcanic ash and pumice soils occurring in Japan. Hardy and Rodrigues (36) reported on azonal soils formed on volcanic ejecta in the Lesser Antilles. Pumice soils occurring in the Netherlands Indies have been described by Mohr (52, pp. 212-218).

Lowermilk and Bailey (48) visited Paricutin, Mexico soon after the volcano erupted early in 1943. They found spectacular erosion occurring in the ash deposits, with gulleys frequently up to 25 feet in depth. Where the ash beds were shallow and the residents could plow through them into the underlying soil, crop yields were increased.

FIELD METHODS

Vegetation Plots

The basic approach to the sampling of vegetation employed in this study was first fully developed by Daubenmire (15). Essentially the procedure consists of the estimation of canopy coverage for all species occurring within a series of small, two-dimensional plots. The underlying assumption is that adequacy of sampling is more easily achieved by increasing the number of plots rather than their size. Daubenmire recommends six rather broad cover classes and maintains that relatively precise averages are obtained while, at the same time, personal error is minimized. He found 40 plots, 20 by 50 cm. in size, gave an adequate estimation of the cover of herbaceous and shrubby vegetation within a single stand.

Eckert (21), in collaboration with Poulton (65) together with Tisdale and Hironaka of the University of Idaho,⁷ developed the basic sampling procedure which was tested and used with minor modifications in this study. In brief, this procedure consisted of the placement of several 50 by 100 foot plots at representative and homogeneous sites within each vegetation type selected for study. Sampling of forbs, grasses, and shrubs for the purpose of obtaining cover and frequency statistics was done along four 50 foot transects randomly located within each plot. At each plot location soil profile

⁷ Work conducted under regional research project W-25, Ecology and Improvement of Brush Infested Ranges.

descriptions were made and soil samples collected by horizon for laboratory analysis.

In this investigation understory vegetation plots were established within stands representing 6 distinctive plant communities which were selected for study. The stands to be sampled were carefully selected after an extensive reconnaissance and only if they were representative of the entire community. Every attempt was made to avoid placing plots in stands that were a complex of more than one plant grouping. The plots were placed in widely distributed stands in an attempt to secure an adequate estimation of the variation within a community, as it was felt that the variations in species composition, plant density, and other characteristics were greater among stands than they were within a single stand. In addition to vegetation considerations, other criteria used in the selection of plot locations were homogeneity with respect to soil type and depth, uniform relief, and the absence of extensive recent disturbance. Six plots were established in 5 of the communities and 5 plots in the sixth, for a total of 35 plots. The number of replications per plant community was considered adequate to describe their modal characteristics. Eckert (21, p. 35) concluded that a minimum of 4 plots within each community was needed for the sage-bunchgrass vegetation of the high desert region.

The success or failure of such a procedure with respect to plot placement is obviously dependent on the investigator's understanding of the ecological relationships within the area under consideration.

Fortunately, the writer had an opportunity to become acquainted with plant-soil-topography relationships of the area prior to the initiation of the study through participation for 3 months in the soil-vegetation survey. Furthermore, the pattern presented by the vegetational mosaic is, in the region under discussion, fairly clear-cut and easily recognized, largely as a result of the small number of plant species present.

The macroplots were 50 x 100 feet in size. This plot size was found to be adequate for the sampling of understory vegetation and was not meant to provide a sufficient sample of the timber stand. Eckert (21, p. 37) reports that, based on species-area determinations, 50 x 100 foot plots are entirely adequate for the range-lands of central Oregon. The macroplots were located in such a manner that the long axis of the plot extended in the same direction as the slope. In the few cases where relief was negligible the long axis of the plot was oriented in a north-south direction.

Four 50 foot transects were randomly located within the macroplot, each one extending parallel to the long dimension of the plot. The starting point for each transect was determined by the selection 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 distance from the reference corner along the base-line. In order to insure plot coverage, 2 of the transects were started within 25 feet of the base-line and 2 from 25 to 50 feet.

Ten 1 x 2 foot grass and forb observation plots were placed at equally spaced intervals along each transect. These microplots were located with the aid of a 50-foot steel tape and were situated on the reference corner side of the tape beginning at the 1 foot mark. An open-ended steel plot frame was employed to delineate the boundaries of the plot. The herbage cover of each grass and forb species within the plot area was estimated and recorded. An estimation was also made of the percentage of the ground surface within the observation plot occupied by litter, bare ground, and stones. Two wire estimating rings, one covering 5% and the other 2% of the total plot area, were used as an aid in the determination of percent cover.

Ordinarily frequency information was automatically obtained with herbage cover estimates. However, if an individual plant, although contributing herbage cover, was rooted less than half within the plot, a notation was made and it was not included in frequency determinations. In order to provide a complete species list for constancy data the entire macroplot was carefully examined and species not encountered in the observation plots were recorded.

Ten 4 x 5 foot shrub and tree observation plots were also placed along each transect. A 5-foot segment of the steel tape constituted one boundary and the plot extended to a point 4 feet from the tape on the reference corner side. The crown cover of shrubs and tree seedlings and saplings occupying these plots was ocularly estimated and recorded in 1% increments up to 10%, with 5% increments thereafter. Spaces within a shrub crown with no foliage or live branches and

having a diameter of one foot or more were not included in the estimation of shrub cover. In addition to cover estimates, trees and shrubs rooting within the plot were counted and recorded by size class. The size classes employed are as follows: for small shrubs (e.g. bitterbrush) (1) 0-6 inches, (2) 6-12 inches, and (3) over 12 inches in height; for larger shrubs (e.g. snowbrush) (1) 0-12 inches, (2) 12-36 inches, and (3) over 36 inches in height; and for tree reproduction (1) 0-3 feet in height (seedlings), (2) 3-10 feet in height (saplings). In addition, dead shrub plants occurring in the plot were also noted and recorded by species.

In an attempt to assess the effect of shrubs on tree reproduction the number of seedlings and saplings falling within 3 shrub-influence classes was determined for each 4 x 5 foot plot. Trees belonging to the first class were those growing out in the open, several feet away from the nearest shrub plant. The second class included those seedlings and saplings which, although not rooted directly under or within a shrub clump, were none the less growing in close proximity to a shrub plant and therefore may have been affected by some side-shade and root intermingling. The remaining class included only those stems of tree reproduction rooted directly under a shrub crown.

The diameter at breast-height was determined and recorded by species for all trees rooted in the macroplot which were taller than 10 feet. The percentage of the total macroplot area covered by the crowns of each tree species was also estimated.

Specimens were collected of all grass and forb species occurring on the macroplots in order to facilitate identification.

Tree Reproduction Transects

Early in the study the writer concluded that data collected on understory macroplots provided an inadequate sampling of tree reproduction and therefore a larger sample was necessary. No generally accepted sampling procedure was available and choice of a method proved somewhat of a problem because of the patchy pattern of advance regeneration characteristic of ponderosa pine stands. After considering several alternatives, a milacre transect method was adopted as offering the most efficient means of gaining a fairly reliable estimate, while still holding the sample size to a minimum. Sampling transects were approximately 1,096 feet long and were situated 100 feet outside of, and parallel to, the vegetation macroplot boundaries. Each transect consisted of 166 contiguous milacre plots (6.6 feet square). Thus observations were made in an area totaling slightly more than one-fourth acre at each plot site.

The sampling procedure consisted of carefully inspecting a belt 6.6 feet wide, divided into milacre plots by means of marks every 6.6 feet on an 100 foot 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 feet on each side. All stems of tree reproduction less than 10 feet in height occurring within each milacre section were counted and recorded by species and

size class. The size classes were the same as those used on the macroplots. Only well-established seedlings at least 6 inches in height were counted.

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 therefore the number of these plots was subtracted from the total number for the 1,096 feet in the calculation of percent milacre stocking. Accordingly, percent stocking figures are, in this study, termed percent unoccupied milacre stocking. For example, if in the area sampled, 80 out of the total 166 plots contained at least one seedling or sapling the conventional percent milacre stocking figure would be $80/166 \times 100$, or 48%. However, if 25 of those plots devoid of timber regeneration were situated directly under a tree canopy, the percentage of unoccupied milacre stocking would be $80/(166-25) \times 100$, or 57%.

Soil Profile Description and Sampling

A soil pit was excavated at each vegetation macroplot location. Pits were located in areas free of large concentrations of shrubs and small trees and were within 3 feet of the macroplot boundary. The soil profile was investigated to a minimum depth of one foot below the pumice. At this depth large basalt boulders commonly restricted further excavation. A complete soil profile description was made

following the procedure as outlined in The Soil Survey Manual (89). In addition, a sketch was made of the morphological features of each profile, with special attention given to any irregularities of the horizon boundaries. Following description of the profile, samples from each horizon were carefully removed and placed in paper sacks. Several samples were often taken from different areas of a single horizon if its morphology varied appreciably.

Soil Moisture Studies

During the summer of 1956 gravimetric soil moisture samples were collected at weekly intervals from plots located within 4 plant communities. Three plots were situated on Lapine soil and one on the Shanahan soil. 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 consisting of samples collected in openings at least 4 feet from the closest shrub or tree, and the other made up of samples obtained directly beneath shrub plants. During the 1957 growing season one additional plot within each of the 4 understory communities was sampled besides those previously established, thus making a total of 8 soil moisture plots. The sampling procedure followed was the same as that used in 1956.

Duplicate undisturbed core samples were collected from each horizon at the 8 sampling sites by use of a modified Uhland Sampler. The bulk density of each sample was determined and this figure used in the calculation of soil moisture levels on a volume basis.

A rain gauge was placed in each of the 8 soil moisture plots at the beginning of the 1957 field season. These gauges, placed on the ground in openings well removed from tree crowns, were constructed from number 10 cans and aluminum foil following a method suggested by Berry and Berg (9). The amount of precipitation contained by the gauges was determined each week by the use of a calibrated plastic cylinder capable of measuring one-hundredth of an inch of rainfall.

LABORATORY METHODS

Soil Moisture Determinations

Soil moisture samples were placed in air-tight cans in the field and weighed on a trip balance the same day they were collected. After drying for 2 days in a 105°-110°C. oven, the samples were reweighed and the percentage of moisture on an oven-dry basis calculated for each sample. Because of the very low weight per unit volume of pumice soils, percent moisture by weight offers a poor basis for the comparison of pumice soil moisture characteristics with those of a conventional mineral soil. Accordingly, it was thought advisable to convert the moisture data from a weight to volume basis. Packard (57, p. 286), in New Zealand, has strongly emphasized this point by stating that moisture properties of pumice soils are only seen correctly when expressed on a volume basis. The weight-volume relationship necessary for conversion of the moisture data was supplied by the bulk density value for each horizon of the 8 soil moisture plots. Bulk density was obtained by determining the oven-dry weight of undisturbed soil contained in a cylinder of known volume.

The determination of moisture constants necessary for the interpretation of soil moisture data presented several problems. First of all, there has been very little experience in the use of conventional procedures on pumice soils for determining the range of available moisture. Secondly, the availability to plants of moisture contained in the pore spaces of larger pumice particles was questioned, even

though the water may be held at tensions lower than 15 atmospheres. In order to resolve the latter difficulty, permanent wilting percentages for the horizons sampled were determined by the use of the sunflower method instead of the more empirical pressure membrane extraction procedure. Soil samples collected from the various horizons were placed in tin containers with a volume of 750 cc. Sunflowers were raised from seed and, in order to insure thorough root penetration, allowed to grow until they reached a height of approximately 18 inches. At this time irrigation was terminated and the soil surface sealed off by melted paraffin. When the sunflower plants reached permanent wilting, as evidenced by a flaccid condition of the lower leaves and their failure to regain turgidity in a saturated atmosphere, the soil was removed and its moisture content determined. The determination was replicated twice for each horizon. Four of the C horizon samples were incapable of supporting satisfactory sunflower growth without the addition of nutrient elements. Consequently, it was necessary to periodically apply a nutrient solution containing N, P, K, Ca, and Mg to the deficient soils. The effect of these applications on the osmotic concentration of the soil solution was believed to be minor, as relatively small quantities of nutrient salts were used.

Preliminary investigations disclosed that moisture equivalent values were considerably lower than field capacity as approximated by early spring sampling. The Buchner funnel method of approximating moisture equivalent, described by Veihmeyer and Hendrickson (94, pp.

76-77), also gave low values, although higher than those obtained with the centrifuge method. Since there is apparently no laboratory method capable of supplying a reliable estimate of field capacity for pumice soils, field values were considered to offer the closest approximation. For this reason, the amounts of moisture contained in samples collected the first week in May, soon after the snow-melt, are considered as approximate field capacity values for the purpose of this study.

Determination of Soil Particle Size Distribution

Soil samples were first passed through a 2 mm. sieve and percentage by weight of gravels determined. Determination of size distribution for soil particles smaller than 2 mm. in diameter was accomplished by means of a modification of the pipette analysis procedure described by Kilmer and Alexander (43, pp. 21-23). The most important changes in the procedure were as follows: (1) the analysis was made on a 20 gm. rather than a 10 gm. sample because of the generally small amounts of silt and clay present. (2) The extremely small quantities of organic matter found in the C horizons and the buried soil made it unnecessary to treat samples from these horizons with hydrogen peroxide. (3) The step involving the removal of dissolved minerals by filtration was eliminated. The soil samples contained very small amounts of dissolved salts and preliminary tests showed that greater amounts of clay were obtained if the sample had not been filtered. (4) The samples were dispersed on a reciprocating

shaker for 30 minutes only instead of the prescribed 12 hours.

McDonald (49) found that dispersion on a shaker for periods longer than 1/2 hour resulted in the breakdown of pumice sand particles.

Soil Chemical Determinations

Percentage of organic matter and total nitrogen contained in the 2 surface horizons were determined for all 35 profiles. In addition, the following determinations were carried out on selected samples: (1) soil reaction, (2) amount of available P, (3) amount of exchangeable K, (4) amount of exchangeable Ca, (5) amount of exchangeable Mg, and (6) cation exchange capacity. Percent organic matter was determined by use of the Walkley-Black method (97). Total nitrogen content was determined by the Kjeldahl method. Measurement of soil reaction was accomplished using a 1:1 soil-water paste and a glass electrode pH meter. The sodium bicarbonate method as outlined by Olsen et al. (56) was employed for the determination of available P. Exchangeable K, Ca, and Mg were determined on the flame photometer after extraction with 1 N ammonium acetate. Cation exchange capacity was determined by the ammonium acetate method introduced by Schollenberger and Simon (71).

RESULTS AND DISCUSSION

VEGETATION STUDIES

Introduction

The concepts and approaches involved in the consideration of naturally occurring plant groupings are far from standardized. For example, many different systems for the classification of plant communities have been suggested, both in this country and in other parts of the world. Accordingly the ecologist is faced with the necessity of choosing the particular approach which is most applicable to the type of vegetation with which he is working. In view of the confusion stemming from the existence of such a varied array of approaches to community ecology, a brief discussion of the fundamental concepts serving as a basis for vegetation interpretation in this study may be of value.

A question of prime importance bearing on the present study is whether or not recognizable plant communities actually exist. Although the majority of ecologists have answered this question in the affirmative, several have claimed communities are only abstractions which have no basis in actual fact. Representative of the latter view is the following statement made by Curtis and McIntosh (14, p. 488), "The tree species found form a continuous series, with overlapping ranges but distinct conditions for optimum development of each species. No discrete groupings of species are apparent; rather, the entire assemblage forms a continuum." Findings such as this prompted

the conclusion that discontinuities in natural vegetation do not exist except in conjunction with abrupt environmental changes. The view held by Clements (13, pp. 273-283) is at the opposite end of the scale. He conceived of plant communities as being very real entities analogous to living organisms. The ability of each species to survive, for example, was thought to be increased by means of the interactions among the many species comprising the community.

A more or less intermediate position, and the one upon which this study is predicated, holds that plant communities consist of groups of species that tend to have similar environmental requirements. Although each plant species attains maximum development only in a certain characteristic environment (e.g. amounts of precipitation and sunlight, and type of soil), other species are also able to thrive under the same conditions because their requirements overlap. Therefore, wherever the same set of environmental conditions reoccurs equivalent plant communities would exist or tend to develop. Species with wide ecological amplitudes (i.e. tolerant to a fairly wide range of soil, rainfall, and other environmental characteristics) may, therefore, be encountered in several different communities, while a species with a narrower range of tolerances may be restricted in its occurrence to a single community. Thus the species present and their relative dominance in the stand may be used as an index of site or effective environment.

If plant species tend to grow together in reoccurring groups as a result of their overlapping environmental ranges; why then have

some workers failed to detect discrete communities? Perhaps this is at least partially attributable to their sampling methods and interpretation of the vegetation. The work of Whittaker (100) in the Smoky Mountains provides an interesting example. His data, derived from counts of plant populations along a transect, showed a series of population curves with each species possessing its own center of distribution away from which it declined either rapidly or gradually. He therefore concluded that the species he studied were not organized into discernable units. There are several possible reasons why this study failed to produce evidence for the existence of plant communities. First, the sole statistic employed was frequency which was obtained by population counts. In other words, the only measure of the importance of a given species was the number of times it occurred along the transect. This information alone provides insufficient evidence for the determination of the role of a plant species with respect to permanency, dominance, and other important criteria. For example, frequency data may be misleading when the plant is present only as a single generation accidental or when it occurs in an impoverished condition because it is approaching its tolerance limits. Some measure of dominance, generally obtained by cover estimations, is essential for determining which species exert the major influence on the habitat. This information is necessary before plant communities can be delimited. Secondly, single species were considered rather than species groups. Whenever this is done evidence for a continuum is obtained. This may be attributed to the fact that plant species

do not generally possess exactly the same ecological amplitudes. Accordingly, plant communities must be recognized by the combinations of plants which are the result of overlapping ranges of the individual species. This fact must not be lost sight of if discrete communities are to be seen. Finally, portions of the transect were undoubtedly located in transitional zones between adjacent plant communities. Since the plant species present in these areas would include those characteristic of both communities, their inclusion within the sample would show the transition and thus emphasize the continuum nature of the vegetation. This would not completely mask the existence of recognized, real communities, but it does make their initial recognition more difficult.

How then is one to sample vegetation in such a way that information concerning plant communities may be gained? Probably the most important consideration is that intergrade areas or transition zones should not be sampled. All stands selected for study should be as representative as possible of the entire community and yet still exhibit a normal amount of variability. In like manner, in the characterization of soil series, sampling and description are conducted at representative "modal profiles", intergrades generally receiving little attention. Naturally if one follows this procedure a portion of the vegetation will remain unsampled. However, the extent of the area thus neglected is usually minor, for, as Greig-Smith (27, p. 120) points out, "The fact that an area is recognized subjectively as distinctive and not transitional is evidence that it represents a

significant portion of the total vegetation of a region." Another point, already mentioned, is that species should never be considered singly, but always in relation to the others present. In order to fully understand the relative importance of all the species, some estimation of dominance is essential.

Assuming therefore that plant communities do exist and can be recognized, how are these groupings to be classified with respect to succession? Perhaps the most familiar class is designated by the term "climax". This term, although of common usage, has been the subject of many different definitions and interpretations. Daubenmire (16, p. 302) states that a climax community is one in which the species are apparently self-regenerating and there is no concrete evidence that it is followed by a different subsequent community. This definition contains probably the most important single concept in the poly-climax viewpoint. Obviously, not all plant communities are climax, many are transitory since the species comprising them are constantly being replaced. These are commonly termed seral communities and each may be considered a successional stage leading to a climax state if succession is allowed to progress unhindered. Seral and climax communities are most often differentiated by a consideration of size or age class distributions of the species present. For example, if a community includes several shade-tolerant tree species occurring predominately as seedlings, it may then be inferred that they will eventually replace one or more species which at present hold dominant positions. Since succession is apparently still underway, this community would

therefore be classed as seral. In order to avoid confusion, the term "association" is reserved for communities comprised of climax vegetation.

A scheme for the classification of climax communities has been suggested by Tansley (77) and Daubenmire (16). The system is based on the assumptions that several different environmental factors may be responsible for the termination of plant succession and that these "limiting factors" vary from place to place. If an association is situated on a zonal, well-drained soil occupying undulating topography it is concluded that climate is the principal factor limiting further shifts in species composition. Therefore climax communities in these positions are termed climatic climaxes. However, other factors in the environment besides climate may exert a great influence on the characteristics of the stable climax vegetation. In areas of extreme topography climax communities are found to differ to some degree from the climatic climax, largely due to differences in insolation. Accordingly, it is helpful to denote this difference by labelling associations on steep terrain topographic climaxes. Extremes in soil characteristics, such as those encountered in immature soils, also cause considerable changes in successional trends and the end product, or climax, is characterized by species which may be considerably different from those on an adjacent, well-developed soil. These are edaphic climaxes, a term which may be applied to the associations discussed in the present study. Man himself often influences the composition of stable communities through, for example, silvicultural

practices which are designed to enable him to produce the maximum amount of the desired tree species. The attempt to perpetuate the production of Douglas-fir in some areas of the Northwest by means of special cutting practices is an example of this. Similarly, grazing often considerably modifies the plant community. If, in both cases, species composition and plant density are relatively constant despite interference by man or animals, the resultant association is termed a biotic climax. In a like manner, vegetation which has reached an equilibrium with reoccurring fires may still be considered climax and is classed as a fire climax. Frequently two factors may control the end product of plant succession. In those cases a binomial term is utilized in their classification, e.g. topo-edaphic climax.

"The collective area which is occupied by a single plant association or will come to be occupied by that association as succession advances" is denoted by the term habitat type. This term, introduced by Daubenmire (16, p. 303), is especially useful because it provides a means of designating geographic areas having equivalent effective environments regardless of the stage of plant succession. It is implicit in this concept that the division of all portions of a landscape into its natural habitat types involves a knowledge of successional patterns, as well as the nature of the climax communities. Obviously the task is less difficult if the communities present are climax or representative of later successional stages. It should be pointed out, however, that the identification and characterization of habitat types is also an essential prerequisite to the understanding

of seral vegetation. For these reasons, initial ecological investigations are most often centered in representative stands of climax vegetation. The habitat type is designated by the name of its accompanying association. It should be borne in mind, however, that the two terms are not synonymous, as one habitat type may include several seral communities as well as the climax association.

Six distinct plant communities were found to occur within the ponderosa pine and white fir zones in the study area. They are listed in order of increasing effective moisture in Table 1. As may be seen, each was studied at a minimum of five different locations. These six communities, their intergrades, and seral variants occupy virtually all of that portion of the study area which supports ponderosa pine or white fir as the climax tree species.

Five of the communities investigated are associated with Lapine loamy coarse sand, while the remaining one, the Pinus ponderosa/Purshia tridentata/Festuca idahoensis, is confined to finer-textured soils belonging to the Shanahan series (Table 1). Such a situation should certainly not be considered unusual in an area possessing regosolic soils exhibiting very few profile differences despite major changes in climatic conditions. A close correlation between vegetation and soils at the series level is usually to be expected only in areas where the soils are approaching maturity and therefore reflect with some degree of precision the environmental conditions under which they were formed. In the present study changes in species composition and

Table 1. The six plant communities occurring in the study area which were characterized by means of plot sampling

Community	No. of Stands Sampled	Elevational Range of Sample (feet)	Associated Soil Series
(1) <u>Pinus ponderosa/Purshia</u> <u>tridentata</u>	6	5025-5205	Lapine
(2) <u>Pinus ponderosa/Purshia</u> <u>tridentata/Festuca</u> <u>idahoensis</u>	5	5195-5640	Shanahan
(3) <u>Pinus ponderosa/Purshia</u> <u>tridentata-Arctostaphylos</u> <u>parryana var. pinetorum</u>	6	5300-5400	Lapine
(4) <u>Pinus ponderosa/Ceanothus</u> <u>velutinus-Purshia</u> <u>tridentata</u>	6	5190-5500	Lapine
(5) <u>Pinus ponderosa/Ceanothus</u> <u>velutinus</u>	6	5560-6050	Lapine
(6) <u>Abies concolor/Ceanothus</u> <u>velutinus</u>	6	5610-6200	Lapine

plant density are not always accompanied by important differences in morphological characteristics of the soil. Rather, relations between soil and vegetation appear to involve less obvious soil properties such as soil moisture availability and fertility.

There is a fairly clearly defined correlation between the communities and elevation (Table 1). Aspect also exerts considerable influence, especially on the steeper slopes. For example, the Abies concolor/Ceanothus velutinus association, which at higher elevations constitutes an edaphic climax, is frequently a topographic climax on north or east-facing slopes at lower elevations.

(1) Pinus ponderosa/Purshia tridentata Association

The Pinus ponderosa/Purshia tridentata 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. The fact that it represents relatively xeric conditions is indicated by the very open "park-like" timber stand which includes only small amounts of advance regeneration (Figure 3).

Daubenmire (16, pp. 307-308) has described a Pinus ponderosa/Purshia tridentata association occurring in northern Idaho and eastern Washington. Other unions⁸ present were the Agropyron spicatum and

⁸ Daubenmire defines a union as a group of species that are closely similar in their micro-environmental requirements and phenology and which may share the same growth form.



Figure 3. General view of a stand within the Pinus ponderosa/Purshia tridentata association. Note the lack of pine regeneration.

Poa secunda, however Purshia tridentata was the most dominant. The association occurred on alluvial soils which were described as being both drouthy and fertile. 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.

On the Antelope Unit summer sheep grazing occurs primarily in the Pinus ponderosa/Purshia tridentata habitat type. The disturbance caused by sheep was sufficiently widespread to necessitate the location of several plots in stands showing evidence of moderate sheep use. Perhaps the most noticeable change brought about by this use is the large amount of bare soil exposed (Figure 4). In addition, intensive shrub browsing is often indicated by pronounced hedging. Only 36% of the bitterbrush plants sampled were taller than 12 inches, while for the Pinus ponderosa/Ceanothus velutinus-Purshia tridentata association, in which there is almost no livestock use, the corresponding figure was 54%.

The floristic composition of the Pinus ponderosa/Purshia tridentata association is rather unusual in that the majority of the forb species present in any appreciable quantity are more or less ubiquitous. However, Table 2 shows that annuals such as Gayophytum diffusum and Cryptantha affinis, although widely distributed in the study area, are most abundant in the Pinus ponderosa/Purshia



Figure 4. Close-up view showing ground detail in the Pinus ponderosa/Purshia tridentata association. Note the incomplete covering of litter and the very small amounts of grasses and forbs.

Table 2. Cover, frequency, and constancy of plant species occurring within 6 plant communities

	Pinus/Purshia			Pinus/Purshia/ Festuca			Pinus/Purshia- Arctostaphylos			Pinus/Ceanothus- Purshia			Pinus/Ceanothus			Abies/Ceanothus		
	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
	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	0.4	8	100	1.0	10	67
Abies concolor													1.9	19	83	10.8	56	100
Pinus lambertiana													0.1	5	17	0.3	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	0.2	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	0.5	5	67
Haploppapus bloomeri				Tr +	-		0.1	3	67	Tr	-	17	Tr +	2	50			
Ceanothus velutinus							0.7	8	50	25.4	53	100	33.0	67	100	26.5	60	100
Ribes viscosissimum							Tr	-	17							0.1	2	33
Prunus emarginata																0.1	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 occidentalis	5.2	71	100	2.6	47	100	4.2	60	100	1.5	21	100	1.9	23	100	0.6	8	100
Carex rossii	1.2	17	100	0.7	14	100	1.2	16	100	2.5	14	100	1.2	13	83	1.0	10	100
Sitanion hystrix	0.5	12	100	0.6	12	100	1.1	18	100	0.9	10	100	0.3	5	83	0.1	2	83
Festuca idahoensis	Tr	-	17	14.1	74	100	0.2	-	17									
Koeleria cristata				Tr	-	20												
Total	6.9			18.0			6.7			4.9			3.4			1.7		

Table 2, continued

	Pinus/Purshia			Pinus/Purshia/ Festuca			Pinus/Purshia- Arctostaphylos			Pinus/Ceanothus- Purshia			Pinus/Ceanothus			Abies/Ceanothus		
	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
	Cover	Freq.	Const.	Cover	Freq.	Const.	Cover	Freq.	Const.	Cover	Freq.	Const.	Cover	Freq.	Const.	Cover	Freq.	Const.
Forbs																		
Gayophytum diffusum	1.1	65	100	0.2	20	80	0.5	23	100	0.5	16	100	0.3	20	100	Tr +	5	83
Cryptantha affinis	0.3	24	83	0.1	8	100	0.2	13	100	0.2	10	100	0.1	9	83	Tr +	3	67
Collinsia																		
parviflora	0.2	11	100	0.2	14	100	Tr +	2	67	Tr +	2	83	Tr +	1	50	Tr +	4	67
Viola purpurea	0.5	48	100	0.2	16	100	0.1	6	100	Tr +	2	100	Tr +	3	67	Tr	-	33
Lactuca sp.	0.1	3	17				0.1	3	50	Tr	-	17	0.3	4	67	Tr +	1	17
Senecio																		
integerrimus	1.3	38	67	0.1	4	60							Tr	-	17			
Lomatium triternatum	0.2	4	33	0.1	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	0.1	15	67	0.2	14	80												
Microseris nutans	Tr +	1	17	0.2	3	60												
Linanthus sp.	Tr	-	17															
Linanthus ciliata				Tr +	3	40												
Agoseris sp.				0.3	5	20												
Achillea lanulosa				1.4	23	100												
Horkelia fusca				0.2	3	20												
Delphinium																		
menzeisii				Tr +	1	20												
Ranunculus																		
occidentalis				Tr	-	20												
Paeonia brownii				Tr	-	20												
Taraxacum																		
officinale				Tr	-	20												
Antennaria																		
corymbosa				Tr +	1	40				0.1	1	17						
Eriophyllum																		
lanatum				Tr +	1	40	Tr	-	17									
Phacelia																		
heterophylla	Tr +	-	33	Tr	-	20	0.1	3	100				Tr +	-	33			

Table 2, continued

	Pinus/Purshia			Pinus/Purshia/ Festuca			Pinus/Purshia- Arctostaphylos			Pinus/Ceanothus- Purshia			Pinus/Ceanothus			Abies/Ceanothus		
	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
	Cover	Freq.	Const.	Cover	Freq.	Const.	Cover	Freq.	Const.	Cover	Freq.	Const.	Cover	Freq.	Const.	Cover	Freq.	Const.
Fritillaria							Tr	-	17									
autrepurpurea							0.1	2	83				Tr +	1	17	Tr +	-	17
Lupinus caudatus				0.1	2	100	Tr +	1	33									
Phlox gracilis				0.1	9	80												
Fragaria																		
cuneifolia				0.2	3	100	2.4	32	100	Tr	-	17	0.8	17	100	0.6	11	67
Antennaria geyeri				0.1	2	80	0.2	5	83	Tr +	1	67	Tr +	-	33	Tr	-	17
Epilobium																		
angustifolium							0.3	4	100	0.2	2	33	0.6	14	100	0.6	13	100
Hieracium																		
cynoglossoides							Tr	-	17	0.1	3	50	Tr +	1	33	Tr +	1	33
Pyrola picta							Tr	-	17				Tr	-	67	Tr +	2	83
Chimaphila																		
umbellata										0.2	3	67	Tr	-	50	0.1	2	100
Apocynum																		
androsaemilifolium										0.4	10	100	Tr	-	50	0.1	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		

% 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

tridentata association. This may be due partially, however, to decreased competition resulting from the utilization of perennial forbs and grasses by sheep. Stipa occidentalis occurred in greater quantities in this community than in any other, with an average herbage cover of 5.2% and a frequency of 71%. Two perennial forbs, Senecio integerrimus and Lomatium triternatum, were absent from the majority of grazed stands. However, on 2 plots located in the northwestern portion of the Unit which have been relatively free from livestock use in recent years, S. integerrimus was present in substantially greater amounts and L. triternatum, absent in grazed areas, was encountered for the first time.

The climax status of Purshia tridentata in the sampled stands is demonstrated by its size class distribution (Table 3). Inasmuch as the number of plants in each size class approximates one-third of the total, the shrub is successfully completing its life-cycle and thus may be expected to maintain dominance despite browsing by livestock. Recently, the bitterbrush plants in several areas within this habitat type have been subjected to severe infestations by tent caterpillars (Malacosoma plumiale). During the summers of 1956, '57, and '58 infestations were of such severity that frequently all bitterbrush plants over several acres were completely defoliated by the second week of July. Investigations conducted by the Pacific Northwest Forest and Range Experiment Station (90, p.55) have shown that the shrub is capable of producing a second crop of foliage later in the growing season and exhibits very little permanent injury. Plant

Table 3. Size class distribution of shrub species occurring in 6 plant communities

	Pinus/Purshia		Pinus/Purshia/ Festuca		Pinus/Purshia- Arctostaphyles		Pinus/Ceanothus- Purshia		Pinus/Ceanothus		Abies/Ceanothus	
	Total No.	%	Total No.	%	Total No.	%	Total No.	%	Total No.	%	Total No.	%
<u>Purshia tridentata</u>	634		499		597		228		31			
0 - 6 in.	196	30.9	72	14.4	125	20.9	38	16.7	13	41.9		
6 - 12 in.	157	24.8	125	25.0	242	40.5	60	26.3	16	51.6		
12 in. +	229	36.1	251	50.3	195	32.7	123	53.9	1	3.2		
Dead	52	8.2	51	10.2	35	5.9	7	3.1	1	3.2		
<u>Arctostaphyles parryana</u> var. <u>pinetorum</u>	3		2		60		16		19		5	
0 - 12 in.	1	33.3	1	50	5	8.3	1	6.2	1	5.3	1	20
12 - 36 in.	1	33.3	-	-	20	33.3	2	12.5	2	10.6	2	40
36 in. +	-	-	-	-	26	43.3	5	31.2	14	73.7	1	20
Dead	1	33.3	1	50	9	15.0	8	50.0	2	10.6	1	20
<u>Haplopappus bloomeri</u>			2		10				3			
0 - 6 in.			1	50	4	40			-	-		
6 - 12 in.			-	-	4	40			3	100		
12 in. +			1	50	2	20			-	-		
Dead			-	-	-	-			-	-		
<u>Ceanothus velutinus</u>					13		42		90		56	
0 - 12 in.					4	30.8	-	-	-	-	3	5.4
12 - 36 in.					6	46.2	12	28.6	40	44.4	14	25.0
36 in. +					1	7.7	29	69.0	46	51.1	33	58.9
Dead					2	15.4	1	2.4	4	4.5	6	10.7
<u>Ribes viscosissimum</u>											2	
0 - 6 in.											-	-
6 - 12 in.											1	50
12 in. +											-	-
Dead											1	50

Table 3, continued

	Pinus/Purshia		Pinus/Purshia/ Festuca		Pinus/Purshia- Arctostaphylos		Pinus/Ceanothus- Purshia		Pinus/Ceanothus		Abies/Ceanothus	
	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%
	No.		No.		No.		No.		No.		No.	
<u>Prunus emarginata</u>												
0 - 12 in.											5	
12 - 36 in.											1	20
36 in. +											2	40
Dead											2	40
											-	-

vigor, however, is reduced by defoliation and it has been noted to cause an increase in the number of dead branches.

The arborescent layer of the Pinus ponderosa/Purshia tridentata association is generally composed of widely spaced mature to nearly mature ponderosa pine with very little advance regeneration. Table 2 shows that the tree crown canopy covered an average of only 18% of the total area of the macroplots located within this habitat type. Although there was an average of 513 stems of ponderosa pine reproduction per acre in the stands investigated, these young trees occurred primarily in small, widely spaced patches (Table 4). Their spotty distribution is illustrated by the low figure of 32.5% for unoccupied milacre stocking. It was repeatedly noted that the most dense clumps of ponderosa pine seedlings and saplings were generally located in snag patches or other openings in the stand (Figure 5). This would suggest that competition for soil moisture is possibly the limiting factor in the establishment and development of ponderosa pine seedlings; and that unless gaps appear in the stand either through natural mortality or logging, supplies of available moisture are 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 at present declining in importance.

Based on the data presented, there appears to be very little evidence for any hypothesis suggesting that the Pinus ponderosa/

Table 4. Average amounts of tree seedlings and saplings within 6 plant communities

	Seedlings/ Acre	Saplings/ Acre	Total Stems/Acre	% unoccupied milacre stocking
<u>Pinus ponderosa/Purshia tridentata</u>				
Pinus ponderosa	267	246	513	32.5%
Pinus contorta	6	5	11	1.3%
TOTALS	273	251	542	33.5%
<u>Pinus ponderosa/Purshia tridentata/Festuca idahoensis</u>				
Pinus ponderosa	750	2,067	2,817	72.6%
Pinus contorta	1	7	8	1.2%
TOTALS	751	2,074	2,825	72.6%
<u>Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana</u>				
Pinus ponderosa	812	974	1,786	65.0%
Pinus contorta	90	131	221	13.8%
TOTALS	902	1,105	2,007	67.8%
<u>Pinus ponderosa/Ceanothus velutinus - Purshia tridentata</u>				
Pinus ponderosa	1,208	865	2,073	74.7%
Pinus contorta	50	52	102	7.8%
TOTALS	1,258	917	2,175	76.5%
<u>Pinus ponderosa/Ceanothus velutinus</u>				
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	0.8%
TOTALS	1,639	1,436	3,075	78.7%
<u>Abies concolor/Ceanothus velutinus</u>				
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%
TOTALS	1,783	1,663	3,446	85.0%



Figure 5. Ponderosa pine seedlings and saplings growing in an area formerly occupied by mature ponderosa pine. Note that the foreground is almost completely devoid of tree regeneration. (Pinus ponderosa/Furshia tridentata association)

Purshia tridentata community will be replaced in the foreseeable future. Therefore it must be concluded that this vegetation is in stable equilibrium with its environment or, more simply stated, is representative of the climax. It is quite certain, however, that the zonal climatic climax would differ to some extent from this community in so far as the individual species and perhaps also total plant density are concerned. In view of the very immature nature of the Lapine soil, it is safe to assume that a large part of this difference is attributable to limitations imposed by soil characteristics. Accordingly, the term edaphic climax is probably the most appropriate designation for this community.

The importance of past fires in determining the characteristics of the Pinus ponderosa/Purshia tridentata association, and the other five communities as well, is very difficult to assess. It is true that the vegetation within the study area is at least partially the product of an adjustment to a long history of periodic disturbance by fire. However, it is not possible to tell with the evidence at hand if fire has played a major role in controlling succession or whether its importance has been relatively minor. It is the writer's opinion that plant distribution in the study area has been influenced more by climate and soil conditions than by periodic disturbances; and although fire should be given due consideration as an important environmental factor, its activity has not prevented a high degree of equilibrium between vegetation and other site factors such as temperature and soil moisture. Another interpretation, perhaps equally valid, is

that effects of fire have shared importance with soil characteristics in the shaping of the Pinus ponderosa/Purshia tridentata association and it is therefore a pyro-edaphic climax.

(2) Pinus ponderosa/Purshia tridentata/Festuca idahoensis Association

The Pinus ponderosa/Purshia tridentata/Festuca idahoensis association is unique among the six studied in that it is associated with a soil series which, within the study area, supported this community exclusively. This soil, Shanahan coarse sandy loam, has a somewhat finer texture than the Lapine. The soil and its associated vegetation are restricted largely to gently sloping topography at elevations lower than 5700 feet. The general aspect of this type presents a marked contrast to the open nature of the Pinus ponderosa/Purshia tridentata association due to the presence of numerous dense patches of ponderosa pine seedlings and saplings. In addition, grass growth in the Pinus ponderosa/Purshia tridentata/Festuca idahoensis association is lush by comparison as a result of a vigorous stand of Idaho fescue (F. idahoensis) as shown in Figure 6.

The dominant herbaceous plant is Idaho fescue, with an herbage cover of 14.1% and a frequency of 74% (Table 2). Its preference for the Shanahan soil is clearly demonstrated by the fact that isolated bunches were encountered in only two stands representative of other communities. Appreciable quantities of Stipa occidentalis, Carex rossii, and Sitanion hystrix were also noted in all study plots. The Pinus ponderosa/Purshia tridentata/Festuca idahoensis association is



Figure 6. General view of a representative stand within the Pinus ponderosa/Purshia tridentata/Festuca idahoensis association.

also characterized by a comparatively large number of perennial forb species. Several are restricted primarily to this association and therefore may serve as diagnostic species. Some of the more important are Agoseris sp., Achillea lanulosa, Paeonia brownii, and Eriophyllum lanatum. Although a total of 24 annual and perennial forb species were present in sampled stands, only 7 were found in all five macro-plots and herbage cover of forbs averaged only 3.7% (Table 2). Of those forbs with 100% constancy, Cryptantha affinis, Collinsia parviflora, and Viola purpurea apparently possess extremely wide ecologic amplitudes and therefore are of almost no indicator value. Forbs which are characteristic, although not necessarily diagnostic, of this association are Madia minima, Microseris nutans, Lupinus caudatus, Phlox gracilis, Fragaria cuneifolia, and Antennaria geyeri.

There are striking differences between this association and the Pinus ponderosa/Purshia tridentata with regard to the condition of the soil surface. Whereas the Pinus ponderosa/Purshia tridentata/Festuca idahoensis habitat type had an average of 95.0% of the total ground surface covered by litter (Figure 7), the sampled areas in the Pinus ponderosa/Purshia tridentata type averaged only 76.9% litter cover. Although this difference may be partially attributed to heavier grazing pressure in areas of Pinus ponderosa/Purshia tridentata, the significantly larger amount of total understory cover in the Pinus ponderosa/Purshia tridentata/Festuca idahoensis association would also be expected to have some effect.



Figure 7. Ground detail in the Pinus ponderosa/Purshia tridentata/Festuca idahoensis association showing the almost complete litter cover and vigorous stand of Idaho fescue.

The ponderosa pines within the Pinus ponderosa/Purshia tridentata/Festuca idahoensis association are frequently of very low quality. The larger trees tend to have short, stubby boles and crowns exhibiting light-colored, scanty foliage. This low vigor is reflected by their high susceptibility to bark beetle (Dendroctonus brevicornis) attack and beetle-killed trees are much in evidence (Figure 8). Advance regeneration of ponderosa pine may be described as 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 saplings as there were seedlings in the areas sampled (Table 4). This complete reversal of the generally encountered size distribution is rather difficult to account for. It is, however, obvious that conditions were more favorable for ponderosa pine regeneration 30 to 40 years ago; and it is possible this may have been brought about by decreased grass competition due to heavier grazing at that time. The figure for percent unoccupied milacre stocking shows that ponderosa pine seedlings in this habitat type are fairly well distributed.

The climax nature of the Pinus ponderosa/Purshia tridentata/Festuca idahoensis grouping is strongly indicated by the close association of this community with a unique soil series. Such a correlation would not be expected in the case of seral vegetation, for it presupposes a high degree of equilibrium between vegetation and environment. Since the Shanahan soil, like the Lapine, is classified as a Regosol, this association may be interpreted as an edaphic climax.



Figure 8. Timber stand in the Pinus ponderosa/Purshia tridentata/Festuca idahoensis association. Note the poor crown form and the beetle-killed trees.

Observations in nearby areas, however, suggest that, of all units studied, the Pinus ponderosa/Purshia tridentata/Festuca idahoensis association most nearly approaches climatic climax vegetation for the zone. Except for the presence of certain plants absent on pumice soils (e.g. Balsamorhiza sagittata), most of the species common on zonal soils situated near the study area are also important in this community.

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

This association is confined largely to areas of Lapine loamy coarse sand on gently sloping to moderately sloping topography. In the study area it is situated at slightly higher elevations than the Pinus ponderosa/Purshia tridentata association, averaging approximately 5300 to 5500 feet depending on aspect. The Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum association is characterized by considerably more tree reproduction, a larger component of seral Pinus contorta, slightly less grass cover, and a more dense crown canopy (18% vs. 28% directly over the macroplots) than the Pinus ponderosa/Purshia tridentata association. Figure 9 shows a general view of the Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum association.

Many herbaceous species which are characteristic of the Pinus ponderosa/Purshia tridentata association are also present in this community, however an additional 9 species not found in the lower elevational habitat type were encountered (Table 2). Among them are



Figure 9. General view of a representative stand within the Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum association.

Fragaria cuneifolia, Antennaria geyeri, and Epilobium angustifolium, species which occur in considerable quantities and appear to be indicative of greater effective moisture. Forb species present in all stands sampled were the widely occurring Gayophytum diffusum, Cryptantha affinis, and Viola purpurea, plus three diagnostic species: Phacelia heterophylla, Fragaria cuneifolia, and Epilobium angustifolium. Grass and sedge cover totaled 6.7% and consisted almost entirely of Stipa occidentalis, Carex rossii, and Sitanion hystrix.

The shrub element in this association is made up largely of Purshia tridentata and Arctostaphylos parryana var. pinetorum accompanied by very small amounts of Ceanothus velutinus and Haploppapus bloomeri (Table 2). The size class distribution found for Purshia tridentata (Table 3) appears to substantiate the hypothesis that this particular species occupies a climax position. However, Table 3 indicates that only 5 Arctostaphylos parryana var. pinetorum seedlings smaller than 12 inches in height were encountered on the observation plots. Ordinarily this would indicate that the shrub is failing to maintain its place in the community. However, it was repeatedly observed that in the study area this shrub reproduces vegetatively more often than by seed. Although Wieslander and Schreiber (1961, pp. 46-47) have pointed out that this variety of manzanita does not ordinarily sprout from adventitious buds, it is frequently propagated by the layering of lower branches. Consequently a single manzanita clump would often be composed of several stems, all of different ages. Despite the fact each stem is undoubtedly capable of existing

independently of the others, each clump was considered a single plant for sampling purposes.

The successional status of manzanita in central Oregon has been the subject of considerable speculation. It has often been stated or implied that stands of manzanita denote areas which have recently been burned-over, while those sites that have not been disturbed are characterized by other shrubs, such as bitterbrush. There is some evidence that on pumice soils this may not be the case and that although fire may aid in its original establishment, its ultimate fate is dependent on other environmental factors. As nearly as could be determined, none of the sample stands located in Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum areas had been subjected to burning within the last 50 years. Furthermore, there was apparently no reason to believe that this habitat type had been exposed to wildfires any more frequently or with any greater degree of severity than, for example, the Pinus ponderosa/Purshia tridentata type. Therefore, it is the writer's opinion that manzanita plants are present in these areas not because of differences in amounts of disturbance, but rather as a result of a microenvironment in these locations which is suited to the requirements of the species. Some evidence for this is the presence of occasional young and dead manzanita plants in Pinus ponderosa/Purshia tridentata stands. This would seem to indicate that despite opportunity for encroachment the species is unable to complete its life cycle in this drier habitat type.

The tree component in the Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum association is considerably different from that found in the Pinus ponderosa/Purshia tridentata. Table 4 shows that both the total number of stems of tree reproduction per acre and the figure for percent unoccupied mlacre stocking are approximately twice that obtained in the Pinus ponderosa/Purshia tridentata habitat type. The position of these seedlings and saplings relative to shrub clumps is also quite different, as indicated in Table 5. Whereas only about 35% were rooted directly under shrub plants in the Pinus ponderosa/Purshia tridentata habitat type, almost 60% of ponderosa pine seedlings and saplings were in this position in the Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum type. Lodgepole pine, as shown by the regeneration figures, occupies a more important position in this community. However, this species is best interpreted as being a seral subordinant in all communities with which this study is concerned.

Available evidence seems to indicate that the Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum community is largely comprised of climax vegetation. Accordingly, because it also is situated on the regosolic Lapine soil, this association constitutes an edaphic climax.

(4) Pinus ponderosa/Ceanothus velutinus-Purshia tridentata Association

The Pinus ponderosa/Ceanothus velutinus-Purshia tridentata community is restricted to the Lapine soil and generally occupies sites

Table 5. The location of tree seedlings and saplings with respect to shrub plants in 6 plant communities

	Seedlings and saplings having no shrub influence		Seedlings and saplings sufficiently close to shrub plants for side shade and root intermingling		Seedlings and saplings directly under shrub plants	
	%	No.	%	No.	%	No.
<u>Pinus ponderosa/Purshia tridentata</u>						
Pinus ponderosa	37.5	67	27.9	50	34.6	62
Pinus contorta	22.25	2	22.25	2	55.5	5
<u>Pinus ponderosa/Purshia tridentata/Festuca idahoensis</u>						
Pinus ponderosa	49.5	155	30.6	96	20.0	63
<u>Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana</u>						
Pinus ponderosa	13.8	45	29.1	95	57.1	186
Pinus contorta	17.5	20	36.0	41	46.5	53
<u>Pinus ponderosa/Ceanothus velutinus-Purshia tridentata</u>						
Pinus ponderosa	17.8	59	24.5	81	57.7	191
Pinus contorta	100	2	---	---	---	---
<u>Pinus ponderosa/Ceanothus velutinus</u>						
Pinus ponderosa	14.3	30	18.1	38	67.6	142
Pinus contorta	50.0	8	6.2	1	43.8	7
Abies concolor	30.8	24	9.0	7	60.2	47
Pinus lambertiana	22.2	2	11.1	1	66.7	6
<u>Abies concolor/Ceanothus velutinus</u>						
Pinus ponderosa	26.0	39	24.0	36	50.0	75
Pinus contorta	54.5	12	22.75	5	22.75	5
Abies concolor	51.6	149	13.8	40	34.6	100
Pinus lambertiana	33.3	4	16.7	2	50.0	6

having gently sloping topography. In the study area it was most often located on benches at elevations ranging from 5200 to 5500 feet. The shrub component of this association differs from that of the Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum in the occurrence of large amounts of snowbrush (25.4% cover) and the relative absence of manzanita (1.0% cover). The more moist growing conditions are reflected by greater amounts of advance tree reproduction, as well as the occurrence of occasional patches of willow (Salix sp.). Figure 10 shows a typical stand within the Pinus ponderosa/Ceanothus velutinus-Purshia tridentata habitat type.

Characteristic herbaceous plants include Stipa occidentalis, Carex rossii, and Sitanion hystrix (Table 2), three species which occur widely over the entire study area. The ubiquitous Gayophytum diffusum, Cryptantha affinis, and Viola purpurea were also present in each of the 6 stands investigated. None of the individual forb species contributed an average herbage cover greater than 0.5%, and the figure for total forb cover was a very low 1.7%. Thus it is rather difficult to single out diagnostic species. However, Apocynum androsaemilifolium, although totaling only 0.4% cover, was present in 10% of the 1 x 2 foot grass and forb observation plots and was therefore the most common perennial forb. Other characteristic perennial forbs are Chimaphila umbellata and Hieracium cynoglossoides. Fragaria cuneifolia, contributing 2.4% cover in the Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum association, was



Figure 10. General view of a representative stand within the Pinus ponderosa/Ceanothus velutinus-Purshia tridentata association.

almost nonexistent in the sampled stands.

The successional status of the shrubs in this habitat type presents a problem which is both interesting and controversial. Apparently bitterbrush may be considered a member of the climax community on the basis of the number of seedlings present and the unusually high proportion of plants larger than 12 inches in height (Table 3). Although a total of 16 manzanita plants were encountered in sample plots, exactly one-half were dead. On the basis of this small sample, it is suggested that the importance of manzanita may at present be decreasing in these areas. Table 3 shows that no snowbrush plants which could be considered in the seedling size class were present in the sampled areas. However, this species, like manzanita, reproduces vegetatively causing considerable difficulty in the detection of trends. It is possible that snowbrush may need some disturbance to become established, but once established and providing conditions are favorable, is able to maintain its place in the community by vigorous vegetative reproduction.

The Pinus ponderosa/Ceanothus velutinus-Purshia tridentata community includes abundant and well distributed advance tree regeneration (Table 4). Sampling indicated that almost 60% of the trees within the seedling and sapling size classes were rooted directly under shrubs, usually snowbrush (Table 5, Figure 11). Although lodgepole pine cover on the macroplots totaled 2%, only 102 stems per acre of this species were tallied on the timber reproduction transects. The pole-sized ponderosa pines in these areas are apparently quite



Figure 11. Ponderosa pine seedlings and saplings rooted beneath a dense clump of snowbrush (Ceanothus velutinus).

susceptible to needle-blight (Elytroderma deformans). In some locations within this habitat type almost all the ponderosa pines in the younger age classes were infected; however, the disease was seldom noted in the other communities.

The Pinus ponderosa/Ceanothus velutinus-Purshia tridentata community presents a rather difficult problem with regard to its proper classification. The species composition of the understory vegetation indicates that perhaps it may be related successionally to the most mesic habitat type in the study area. For example, both Chimaphila umbellata and Apocynum androsaemilifolium are common in the Abies concolor/Ceanothus velutinus association as well as in the community under discussion. In addition, snowbrush is the dominant shrub species in both communities. Based on these considerations, one valid interpretation might be that this community represents a seral stage developing toward a climax association in which white fir is the dominant tree species and snowbrush the dominant shrub. However, the complete lack of white fir seedlings and saplings along sampling transects as shown in Table 4 is rather difficult to explain if this were the case. If white fir constituted the climax species in these areas, one would expect to find at least a sprinkling of "pioneer" invaders. Lack of seed source would not seem to provide a logical explanation since stands of white fir were nearby in every case; and even several mature trees, devoid of progeny, were noted within the community. Largely on the basis of the observed absence of vigorous

white fir from the Pinus ponderosa/Ceanothus velutinus-Purshia tridentata community, it is the writer's opinion that it constitutes a separate habitat type. Apparently the association occupies sites which fail to meet the moisture requirements of white fir by only a small margin. The writer realizes, however, that the first suggested interpretation may very possibly be borne out by further work.

(5) Pinus ponderosa/Ceanothus velutinus Community

The Pinus ponderosa/Ceanothus velutinus community is best interpreted as an earlier successional stage within the Abies concolor/Ceanothus velutinus habitat type. The most noticeable effect of current succession is the tendency towards the replacement of the seral dominant, ponderosa pine, by the climax tree species, white fir. Despite the fact that this community occupies the same habitat type as the climax Abies concolor/Ceanothus velutinus association, it 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 the differences between the two groupings is that succession has proceeded more slowly in areas supporting the Pinus ponderosa/Ceanothus velutinus community, perhaps due to the effects of fire. Second, ponderosa pine attains its best growth in this community, in spite of its seral position. However, careful management may be necessary if ponderosa pine is to remain as the dominant tree species.

Characteristics which set this community apart from those already

discussed include substantial amounts of white fir reproduction, smaller quantities of grasses and forbs, and increased crown canopy density. In the study area the elevational distribution of the type averages about 5800 feet and ranges from approximately 5600 to 6000 feet. 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 (Figure 12). Although white fir is climax in this community, mature and nearly mature individuals of this species only occur in scattered positions.

Perennial forbs are restricted largely to areas occupied by shrub clumps. Several of the more important species are Chimaphila umbellata, Pyrola picta, Epilobium angustifolium, and Fragaria cuneifolia. Although only the latter two occurred in all stands sampled, both Chimaphila and Pyrola, despite their scattered occurrence, appeared to have considerable diagnostic value. In the openings between shrub clumps occur scattered stems of Carex rossii and Stipa occidentalis and occasionally a small number of annual plants (e.g. Gayophytum diffusum and Cryptantha affinis). The fact that these openings support so little vegetation may be due partially to the prevalence of serious frost heaving. It was noted in the spring that the soil surface in these areas was exceedingly soft and spongy, indicating repeated freezing and thawing. Despite its patchy distribution, total understory cover averaged 49.8%, which is higher than the corresponding figure for any other community studied.



Figure 12. General view of a representative stand within the Pinus ponderosa/Ceanothus velutinus plant community. Tree sapling in the foreground is a white fir and shrubs are predominantly snowbrush with some manzanita.

Data presented in Tables 2 and 4 illustrate rather clearly the successional relationships of the tree species in this community. A comparison of figures for crown cover of trees larger than 10 feet in height shows 31% for ponderosa pine and only 3% for white fir. Values for regeneration, however, demonstrate a marked increase in the relative importance of white fir. An average of 24.3% of milacre plots unoccupied by mature trees contained at least one white fir seedling or sapling, while the corresponding figure for ponderosa pine was 67.7%. Sampling indicated that both ponderosa pine and white fir seedling survival may be affected by shrub cover. Table 5 shows that an average of 68% of all ponderosa pines less than 10 feet in height were rooted directly within shrub clumps, while 60% of the white fir seedlings and saplings occupied the same position.

In the western portion of the study area there appeared to be a rather close correlation between the occurrence of the Pinus ponderosa/Ceanothus velutinus community and dwarf mistletoe (Arceuthobium sp.) infestation. Whether this relationship holds in other areas is not known.

(6) Abies concolor/Ceanothus velutinus Association

This association represents a more advanced successional stage within the Abies concolor/Ceanothus velutinus habitat type. Although the replacement of ponderosa pine by white fir is not yet complete in the sampled stands, the latter species has gained dominance. Crown cover over the macroplots averaged 28% for white fir, as compared to

18% for ponderosa pine (Table 2). Total tree canopy cover was 57%, or 18% higher than that found for the Pinus ponderosa/Ceanothus velutinus community. Seral tree species present include lodgepole pine and sugar pine in addition to ponderosa pine. Thus it appears that further shifts in composition may be expected, assuming, of course, 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. It would, for example, be expected that the degree of crown closure would remain more or less constant and, as a result, understory vegetation would also not be subject to major change. Therefore, although there is abundant evidence that succession has not been halted completely, it is the writer's opinion that this community is representative of climax vegetation in most of its characteristics.

The Abies concolor/Ceanothus velutinus association is generally found at the highest elevations in the study area (6100 to 6200 feet), although stands are located as low as 5600 feet on north and east-facing slopes. The lower elevational stands provide excellent examples of topographic climaxes where vegetation, normally found at higher elevations, extends downslope due to the ameliorating influence of aspect. Like the Pinus ponderosa/Ceanothus velutinus community, this association is located on Lapine soil. Figure 13 illustrates the greater density of vegetation characteristic of the Abies concolor/Ceanothus velutinus association.



Figure 13. General view of a representative stand within the Abies concolor/Ceanothus velutinus association. The majority of the larger trees are white fir.

Table 2 shows that the forb species present are largely the same as those occurring in the Pinus ponderosa/Ceanothus velutinus community. Fragaria cuneifolia and Epilobium angustifolium both possessed an average herbage cover of 0.6%, with 0.1% being the highest figure for any other forb species. Grass cover totalled only 1.7%. This is much lower than the corresponding figure for the other five communities. The amount of manzanita found within this association was considerably smaller than that encountered on ponderosa pine dominant sites (Table 2). It is probable that the scarcity of this particular species is due partially to the more dense tree canopy. The occurrence of manzanita was almost entirely limited to locations beneath larger openings in the canopy, thus suggesting that this species may be largely excluded because of its relatively high light requirement. Snowbrush cover, on the other hand, remained at a fairly high level despite the heavier shade. Other shrub species which are only common within stands representative of this association are indicative of a comparatively moist habitat; they are Ribes viscosissimum, Prunus emarginata, and Arctostaphylos nevadensis. As may be noted in Table 2, bitterbrush was present in only one of the six stands sampled.

As might be expected, the Abies concolor/Ceanothus velutinus association was accompanied by the largest amounts of tree reproduction. The averages for all species were as follows: 3,446 seedlings and saplings per acre and 85% unoccupied milacre stocking (Table 4). Percent milacre stocking figures for ponderosa pine and white fir were 45.5 and 60.3 respectively. However, because of differences in growth

habit, a given number of white fir seedlings and saplings tend to occupy much more area than an equal number of ponderosa pines. Therefore, in so far as their impact on the habitat is concerned, the differences between these two species is even wider than frequency figures or stem counts would seem to indicate.

SOIL MORPHOLOGY

Morphology of the Lapine Series

The Lapine soil series occupies the majority of the area within the Antelope Unit and supports a wide variety of vegetation. Of the six plant communities studied, all but one occur on soils belonging to the Lapine series. Only the Pinus ponderosa/Purshia tridentata/Festuca idahoensis community was associated with a soil series other than the Lapine.

In the central Oregon pumice region as a whole, the Lapine series is without doubt the most common soil developed on deposits of Mazama pumice in upland positions. It has been mapped at the southern extremity of the pumice mantle in the Klamath Indian Reservation (87, pp. 159-164) and far to the north in the Pringle Falls area, about 10 miles northwest of Lapine (46). The estimated total acreage of Lapine soils in the Klamath Indian Reservation alone is one-half million acres, or approximately half the total land area of the Reservation (87, p. 159). Leighty (46, p. 3) reported that Lapine soil occupied approximately 91% of the area mapped in a detailed survey of 4 sections on the Pringle Falls Experimental Forest.

The Lapine is a well to excessively drained soil occurring in a variety of topographic positions. Despite the fact that the buried material exerts considerable influence on tree roots, the solum as recognized has developed in the aeolian pumice mantle only. Consequently soil depth is a function of the depth of the pumice deposit, which in turn is largely dependent on the distance from the pumice source, Mt. Mazama. In areas where depth of the pumice deposit was originally less than 18 to 24 inches the pumice particles are usually found to be mixed to some extent with residual soil material. This condition is represented in the Antelope Unit by Shanahan sandy loam, a soil formed on pumice which has been mixed with buried soil material, possibly by alluvial action. Where the pumice layer was originally 6 inches or less in depth, the pumice particles have become thoroughly mixed with the residual soil and apparently exert very little influence on soil properties (102, p. 70). Generally Lapine soils are developed in relatively undisturbed deposits of pumice fall material. However, in some areas within the Klamath Indian Reservation the pumiceous parent material of the Lapine has apparently been redeposited by water (87, p. 159). The Lapine soil is classified as a Regosol since the profile lacks both textural development and structural change with depth. The sequence of horizons is as follows: A₀₀, A₁, AC, C₁, and C₂. Because the underlying buried material is unrelated to the solum, it is designated as a D horizon.

The A₀₀ horizon is generally quite thin and discontinuous. Its

maximum thickness in the study area is 1 1/2 inches at the higher elevations; however in the majority of cases it is approximately 1/2 inch in depth. It most often consists of the current year's litter, or usually ponderosa pine needles and twigs. An A₀ horizon is occasionally encountered, but even under rather dense stands of white fir the layer is of sporadic occurrence.

The A₁ horizon averages 2 inches in thickness, with a range of approximately 1 1/2 to 2 1/2 inches. Its lower boundary is most often abrupt or clear and smooth. The textural class is loamy coarse sand or coarse sandy loam and the content of gravel-sized pumice particles varies from about 15 to 25%. The structure is generally weak medium or fine granular; however, a marked tendency towards platiness is noted in some places. This soil material is very soft when dry, very friable when moist, and nonplastic and very slightly sticky when wet. The moist color of the A₁ horizon is most commonly very dark brown (10YR 2/2), although a very dark gray brown color (10YR 3/2) is not unusual. Dry colors are gray brown (2.5Y 5/2) or dark gray brown (2.5Y 4/2). As would be expected, plant roots are very abundant in this horizon.

The AC horizon is characteristically variable in thickness. Very commonly narrow tongues of the AC extend deep into the C horizon, while only a short distance away the layer may be unusually shallow. As a result of this irregular lower boundary, it was sometimes difficult to estimate the average depth of the horizon. However, its approximate mean thickness ranged from 5 to 13 inches, with the most

frequently encountered value being 10 inches. The boundary between the AC and C horizons may be described as abrupt and irregular to wavy. Texture of this horizon is uniformly a loamy coarse sand, and pumice gravel content varies from approximately 20 to 30%. Individual pumice particles range up to 4 cm. in diameter and many are weathered to such an extent that they crumble readily under pressure. The soil in this horizon is virtually single-grained, although a weak tendency towards blocky structure is noted in some profiles. The most common moist colors are dark brown (10YR 4/3) and dark yellow brown (10YR 4/4), while the dry soil color is generally pale brown (10YR 6/3). Abundant plant roots are well-distributed throughout the entire horizon.

The transition from the weathered AC horizon into the relatively unweathered and gravelly C₁ is surprisingly abrupt (Figures 14 and 15). 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. In those instances where several plant roots extended a short distance into the C₁ horizon it was found that the pumice gravels immediately adjacent to the roots invariably exhibited considerable weathering. Thus it appears that plant roots may play a most important role in the weathering of the pumiceous parent material. The difference between the C₁ and AC horizons with respect to degree of weathering is demonstrated by the fact that the AC is considerably finer textured than is the C₁.



Figure 14. Lapine soil profile. Note the darker-colored A₁ and AC surface horizons, the lighter-colored gravelly C horizons, and the abrupt boundary to the underlying buried soil.

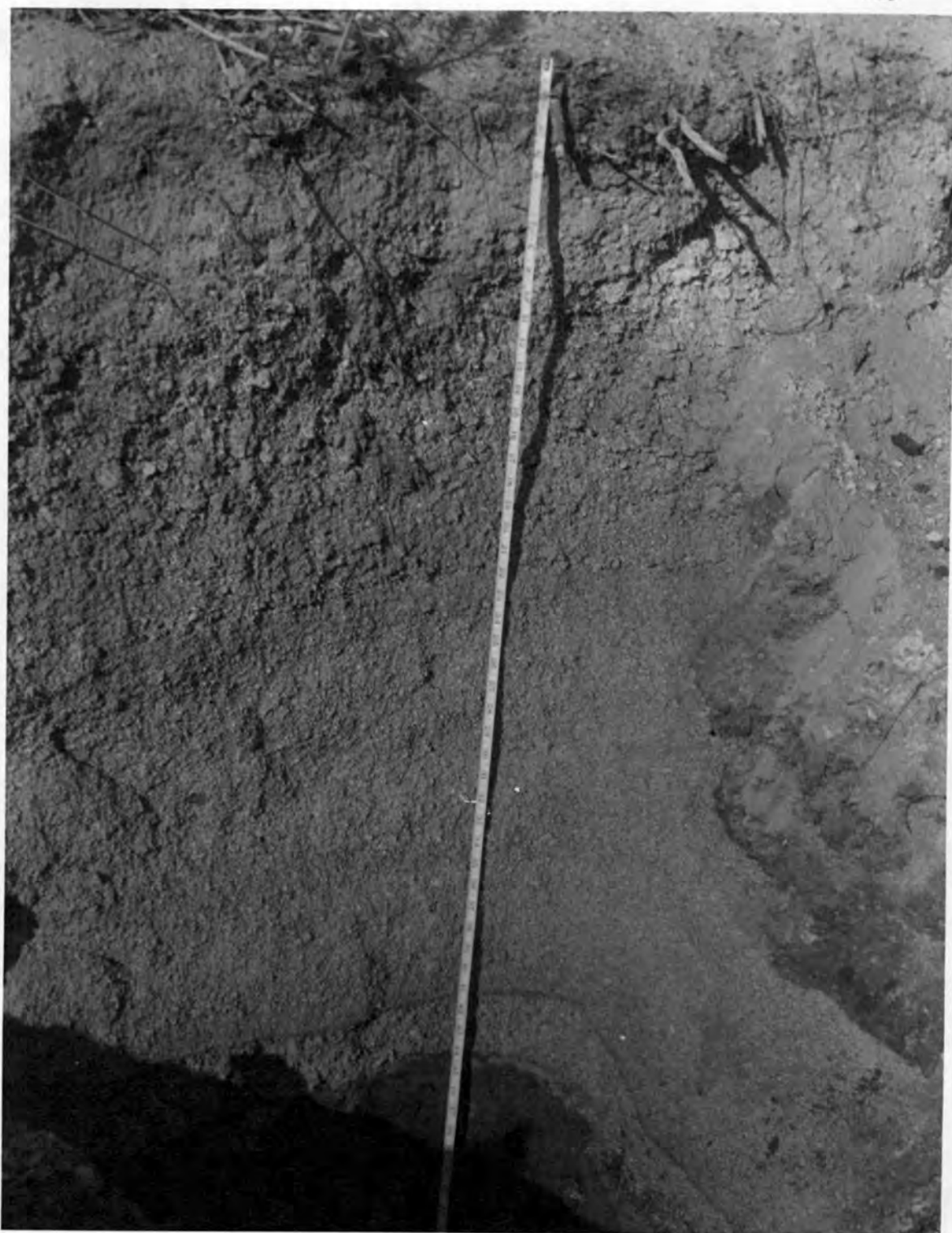


Figure 15. Closeup view of a Lapine soil profile. Note the abrupt boundaries between the AC and C₁ horizons and C₁ and C₂. The C horizons are comprised of pure, unweathered pumice and show almost no mixing.

On the basis of the foregoing observations it may be concluded that the general course of Lapine soil formation is apparently from the surface downward. This is not surprising since the surface of a fresh pumice deposit, being exposed to the atmosphere, would be expected to exhibit the most rapid rate of weathering. The resultant finer textured surface layer would subsequently extend progressively deeper into the pumiceous material, largely as a result of the addition of organic matter originating from plant roots and litter. Apparently the Lapine resembles Taupo pumice soils in New Zealand with regard to its main weathering sequence. Van't Woudt (93, p. 169), in describing the development of Taupo soils, stated that, "A topsoil, initially only a few inches thick, gradually extends in depth and in a number of years a finer top layer, one foot thick or more, comes to lie on coarser subsoil material."

The C₁ horizon is composed largely of pumice of gravel and sand-sized particles which, even to the casual observer, are noticeably fresh and virtually unweathered. In the profiles examined the horizon ranged from 3 to 16 inches in thickness, with the average being 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 incorporated in its entirety into the AC horizon. In other instances, however, only tongues of the AC had obliterated the layer, and bright, fresh C₁ material appeared between these maximum extensions of the weathered horizon. The boundary between the C₁ and C₂ horizon below is

generally clear and smooth. The C₁ material falls into the gravelly coarse sand textural class and pumice gravels up to 10 cm. in diameter total 50 to 70% by weight. As a general rule the diameter and abundance of pumice gravels increases from east to west in the study area, probably as a result of a decrease in distance to the pumice source. Coarse and medium sand-sized crystals of plagioclase, hypersthene, augite, and hornblende are also present and usually comprise approximately 10% of the total volume. The horizon is strikingly single grained and plant roots are almost nonexistent except near the transition to the AC horizon. The color of this horizon varies considerably and even a single pumice particle may exhibit spots of 2 or 3 distinct colors. The predominant moist colors are yellow (10YR 7/8, 8/8, 8/6, or 7/6), white (10YR 8/2), and very pale brown (10YR 8/3). The dry colors most frequently encountered are white (10YR 8/2), yellow (10YR 8/6), and very pale brown (10YR 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. The majority of the pumice particles are coarse and medium sand-sized; and although gravel content ranges from 15 to 30% in this layer, few individual particles are more than 5 mm. in diameter. Williams (1962, p. 73) has attributed this abrupt change in particle size distribution to a sudden increase in the violence of the eruption in conjunction with a shift in the prevailing winds from west to southwest. This layer ranges from 7 to 27 inches in thickness within the study area and attains its maximum depth in the

northwestern portion of the Unit.

Early in the course of describing Lapine soil profiles it was noted that the C horizons, and especially the C₂, often exhibited considerable local variability in morphological characteristics. The most striking differences concerned the amount of mixing of the relatively unweathered pumice with dark-colored silt and fine sand particles. Although the C₂ horizon was commonly composed almost entirely of pumice sands and gravels, it was also common to find the pumice mixed to some extent with the finer material. All gradations in amounts of mixing were encountered: from the majority of the horizon mixed with only occasional pockets of pure pumice, to layers exhibiting dominantly pure pumice with small, discrete areas of mixed material (Figure 16). Generally the largest amounts of mixing were 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 the growth of roots, inasmuch as roots were generally quite plentiful in these portions of the profile even though they were almost completely absent from the pure, unmixed C₂ horizon. Because mixing was a common profile feature and one which very likely exerted considerable influence on plant growth, the zones within the C₂ horizon exhibiting mixing were described and sampled separately. The percentage of the total cross-sectional area of the horizon showing some mixing was also estimated and recorded. In addition, a sketch was made of each profile, showing the location and relative size of the pure and mixed zones, as well as root distribution and nature of the

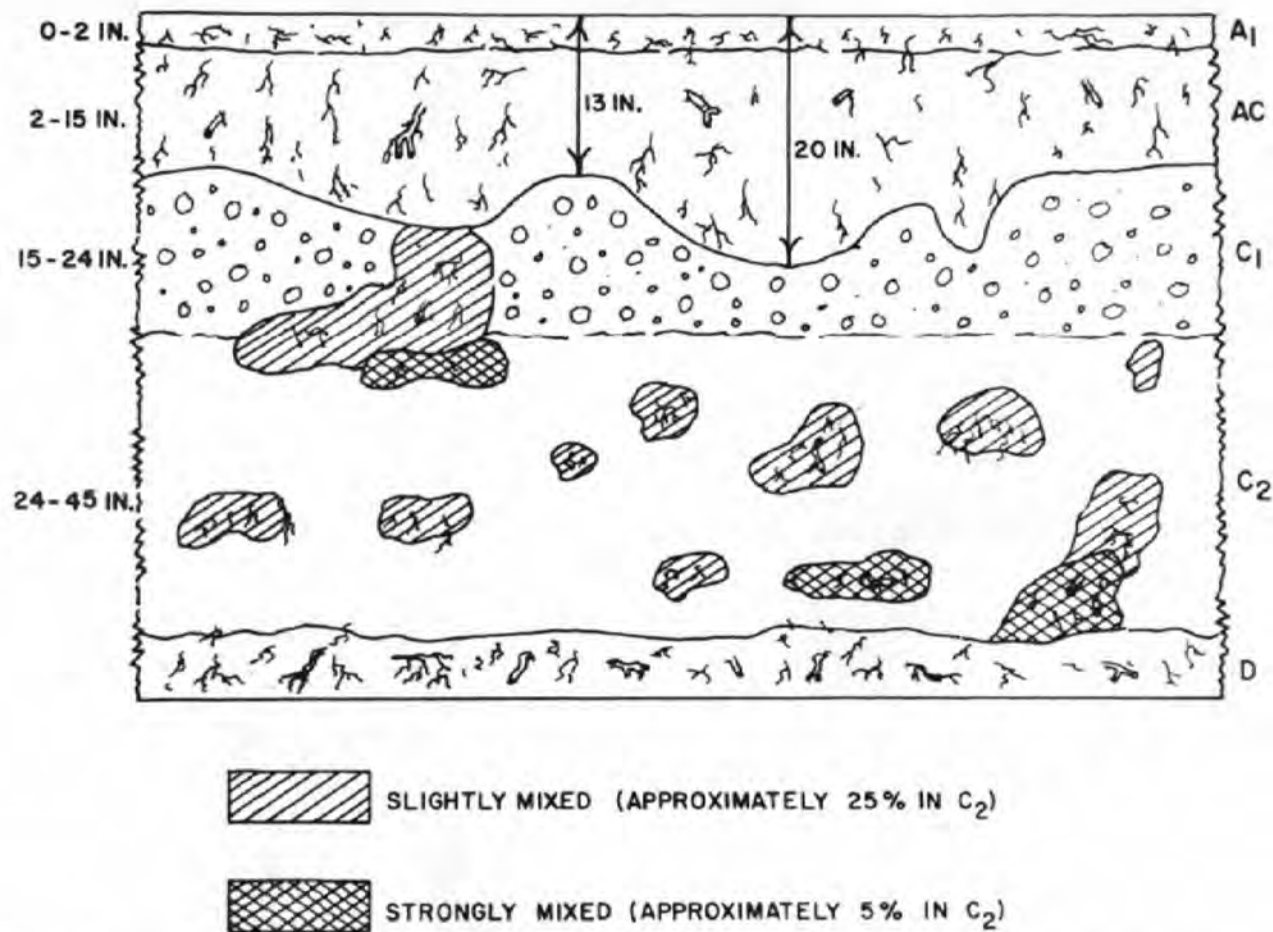


Figure 16. Sketch of a Lapine soil profile showing the distribution of plant roots and zones of mixing. Note that plant roots are virtually absent from unmixed portions of the C₁ and C₂ horizons.

horizon boundaries.

Three different degrees of mixing were recognized in the C₂ horizon of Lapine soils. The first class, unmixed and probably the most common, consists of pure, relatively unweathered pumice composed mainly of coarse and medium sand-sized particles. Portions of the C₂ horizon within this class exhibit a yellow (10YR 8/6, 8/8, 7/8, or 7/6) and/or white (10YR 8/2) color when moist. The second condition was termed slightly mixed and is characterized by considerably less coarse sand and larger amounts of silt and fine sand. The moist colors of these zones are dominantly yellow (10YR 8/6, 8/8) and white (10YR 8/2), accompanied by very prominent flecks of brown (10YR 3/3, 5/3) and dark yellowish brown (10YR 3/4, 4/4, 5/4). These zones commonly are either coarse sand or gravelly coarse sand in texture and may also contain larger quantities of pumice gravels than the adjacent, unmixed material. The third degree of mixing, which is mainly found in small pockets, is designated as strongly mixed. When in this condition the soil is composed of approximately 50% C₂ pumice material and 50% dark-colored sand and silt particles. The moist color of these zones is dominantly brown (10YR 4/3), dark yellowish brown (10YR 3/4, 4/4), or reddish brown (5YR 3/4), and the individual pumice particles contained in this matrix appear as flecks of yellow (10YR 8/6, 8/8, 7/6). A sketch of a profile showing typical arrangement of mixed zones is presented in Figure 16.

Throughout the investigation of Lapine soil profiles it became increasingly apparent, largely by means of comparisons of general

particle size and color of the mixed zones with the buried soil, that the finer particles had been transported up from the D horizon. Results of mechanical analyses of mixed C₂ material bears out this observation. As can be seen in Figure 17, cumulative particle size distribution curves for the three classes of mixing in a single horizon and the D horizon below plainly indicate that the buried soil is the primary source of fine particles in the mixed zones. The manner in which this mixing has been accomplished is, as yet, not completely understood. Many of the larger zones of mixing may be the result of the action of wind-thrown trees. The up-rooting of trees has been shown to have an important effect on soil formation in the Northeast (18, pp. 55-66). However, in many instances the pockets of mixing are quite small and round in cross-section. These appear to have had their origin as animal burrows or root channels. Thorp (85) has emphasized the importance of burrowing animals in changing soil texture. In one area in Colorado he found that sufficient coarse-textured material had been deposited near the surface of the Rago soil to cause a loam texture, despite the fact that the surface mantle consisted of 8 feet of wind-blown silt. Whatever the cause, the mixing has a very sporadic pattern, and local variability in amounts of C₂ disturbance are large. It was commonly observed that whereas one profile pit would reveal considerable mixing in the C₂, another pit only a short distance away would show almost no mixing.

Four Lapine soil profiles out of the total of 30 investigated possessed a uniform subsoil which showed no clear stratification into

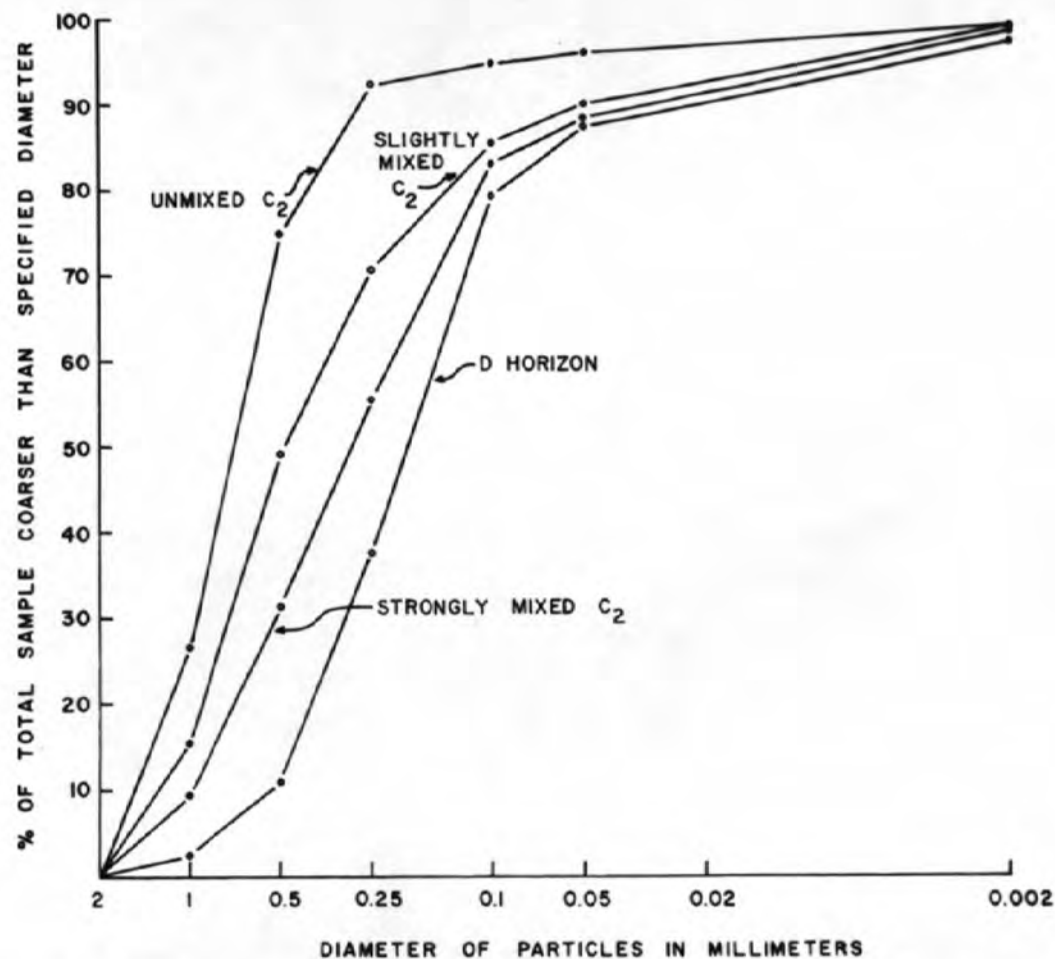


Figure 17. Cumulative particle size distribution curves for unmixed, slightly mixed, and strongly mixed portions of the Lapine C_2 horizon and the D horizon.

distinct C₁ and C₂ horizons. This condition was found only in areas where the pumice mantle was relatively shallow. In each case the C horizon was only 8 or 9 inches in thickness. Generally this layer consists largely of slightly mixed pumice with only occasional pockets of pure, unmixed pumice. Textures of the C horizon vary from a loamy coarse sand to a gravelly sand. Predominant moist colors range from brown or pale brown (10YR 4/3, 5/3, or 6/3) in mixed zones to yellow (10YR 8/6) in pockets of pure pumice. During the soil-vegetation survey of 1956 these soils were commonly classified as Bear Flat sandy loam and were considered to be an intergrade between Shanahan sandy loam and Lapine loamy coarse sand. Recently a new series, the Longbell, has been proposed which would include these soils. However, because the classification was not as refined at the time of the field investigations, soils having uniform C horizons of slightly mixed pumice are included in the Lapine series in this report.

The boundary between the pumice mantle and underlying buried soil is commonly marked by a thin layer of light gray, silty material. In the 12 profiles in which it was found it varied from 1/4 inch to 1 inch in thickness. Its particle size distribution is most often that of a fine sandy loam and in laboratory samples the maximum content of silt was 43%. When moist, both the finer textured layer and a 1/4 to 1/2 inch layer of pumice sands immediately above are either white (2.5YR 8/0) or light gray (10YR 6.5/1) in color.

Most observers have been of the opinion that the material comprising this light gray layer is probably volcanic ash. Available

evidence seems to indicate that the ash material was deposited sometime before the advent of the Mazama pumice fall. Williams⁹ states that just prior to its culminating eruption, Mt. Mazama was the source of a small amount of volcanic ash which was deposited to the north and east. That this deposition was very likely the source of the silty layer in the profiles examined is borne out to some extent by cumulative particle size distribution curves (Figure 18). Because the mechanical composition of this layer much more closely resembles that of the D horizon than the C₂, it seems reasonable to assume that it is the product of a prior and completely separate deposition. The influence of the D horizon is also demonstrated by the fact that the particle size distribution of the gray layer is not constant for all profiles, but shifts with small changes in the texture of the D horizon. This is logically explained inasmuch as some mixing of the thin volcanic ash deposit with the paleosol would be expected in the interim between its deposition and the main pumice fall.

The buried soil, or D horizon, situated beneath the Lapine pumice 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. The soil particles are generally arranged into weak medium subangular blocky structure, but a massive condition is not uncommon. Moist colors are

⁹ Remarks made by Dr. Howell Williams during the course of an address made on the Oregon State College campus, May, 1959.

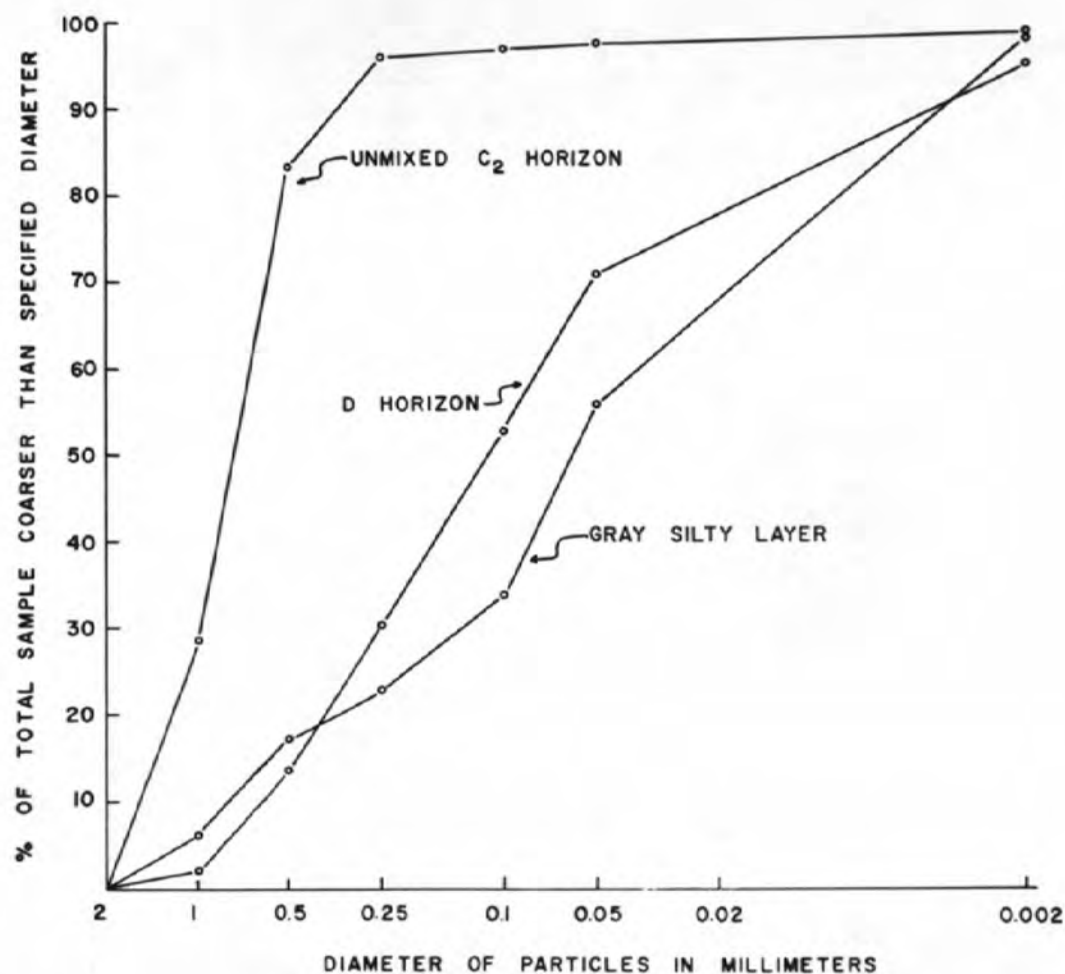


Figure 18. Cumulative particle size distribution curves for a typical Lapine C₂ horizon, D horizon, and a thin, gray, silty layer located on the surface of the D.

most often brown (10YR 4/3 or 7.5YR 4/4), dark yellowish brown (10YR 3/4), or dark brown (10YR 3/3). In several instances indistinct mottles of yellowish brown (10YR 5/6) or brownish yellow (10YR 6/6) were noted. Most commonly encountered dry colors are pale brown (10YR 5.5/3) and yellowish brown (10YR 5/4). Plant roots are generally common in this horizon, except in areas where pumice depth exceeds 4 or 5 feet. Near the surface of the horizon pockets of almost pure pumice are fairly common. Apparently pumice from the C₂ horizon filters down into the channels remaining after the decay of larger roots. Alexander (1, p. 3) has described the downward movement of sandy material through old root channels in Ruston sandy loam in Louisiana.

The genesis of the Lapine D horizon occurring in the study area is difficult to reconstruct. The presence of large quantities of basalt fragments would immediately suggest the possibility that the soil has been formed through the weathering of this rock material. However, there are dominantly two considerations which would indicate that such may not be the case. The first is the surprising uniformity of soil texture, structure, and color with depth. Secondly, basalt stones and outcrops have hard, fresh surfaces and there is no evidence that rock breakdown has occurred in the past or is occurring at the present time. These conditions would not be expected in a soil which has been formed in place through rock weathering; rather, they would seem to indicate an unconsolidated, uniform parent material, probably of aeolian origin. This material may possibly be volcanic ash deposited

as a result of volcanic activity which predated the eruption of Mt. Mazama.

Relationships Between Lapine Soil Morphology and Associated Plant Communities

Several features of the Lapine soil manifestly exert considerable influence on plant growth and therefore merit special attention. Two of the most important are the thickness of the C₁ horizon and the amount of mixing of the C₂ pumice with buried soil material. As previously mentioned, repeated observations have indicated that 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. In one area within the Pinus ponderosa/Purshia tridentata association the root systems of ponderosa pine saplings up to 40 years of age were found to be confined entirely to the A₁ and AC horizons, or, in this case, the surface 12 inches of soil. The Lapine soil in this area possessed a 15 inch thick C₁ horizon and exhibited almost no mixing in the C₂. When roots did occur in the C horizons, they were largely primary tap roots exhibiting very little branching. However, within the D horizon tree roots again showed abundant proliferation. Consequently, mature ponderosa pines were found to possess a pronounced "two-storied" root system in this and similar areas. 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 (Figure 16). As yet, the reasons for this unusual root distribution pattern are not fully understood; however several factors which may be of importance are discussed in a later section.

Some of the more important and variable Lapine profile features and their relation to the plant community supported by the soil are given in Table 6. It is at once apparent that these characteristics are extremely variable and that the number of profiles investigated is inadequate for the drawing of any final conclusions. In spite of these difficulties, it is possible to tentatively point out some correlations between vegetation and the condition of the C horizons which may be generally valid. These relationships are obscured, however, by another more obvious correlation between depth of the pumice mantle and amounts of mixing in the C₂ horizon as well as thickness of the C₁. The information presented in Table 7 demonstrates rather clearly that as the pumice mantle increases in depth, mixing in the C₂ becomes less extensive and the C₁ horizon tends to become thicker. However, some exceptions to this relationship may be seen in the data presented for the soil profiles examined within the Pinus ponderosa/Purshia tridentata association. With the exception of plot 1, 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 ponderosa/Ceanothus velutinus community. Another relationship which was borne out by reconnaissance observations is that in areas supporting the Pinus ponderosa/Purshia tridentata association the AC

Table 6. Morphological characteristics of the Lapine soil in relation to 5 plant communities

Community and Plot No.	Thickness of A ₁ & AC(in.)	Thickness of C ₁ (in.)	Depth to D(in.)	% Slightly Mixed in C ₂	% Strongly Mixed in C ₂
<u>Pinus ponderosa/Purshia tridentata</u>					
1	9	-	17	55	5
2	9	7	29	15	-
12	7	7	28	5	-
13	9	11	49	5	-
14	12	11	42	10	-
31	12	6	25	15	-
MEAN	9.7	7.0	31.7	17.5	0.8
<u>Pinus ponderosa/Purshia tridentata - Arctostaphylos parryana var. pinetorum</u>					
3	10	-	18	80	-
4	11	13	13	45	5
15	12	-	25	80	-
16	12	8	32	50	5
17	12	8	33	5	-
32	13	6	28	35	5
MEAN	11.7	5.8	30.2	45.8	2.5
<u>Pinus ponderosa/Ceanothus velutinus - Purshia tridentata</u>					
21	12	11	43	30	-
22	11	9	37	20	-
23	11	12	39	-	10
24	12	5	35	23	2
25	9	14	47	5	-
26	8	12	32	20	1
MEAN	10.5	10.5	38.8	16.3	2.2
<u>Pinus ponderosa/Ceanothus velutinus</u>					
7	10	8 ¹	26	80	-
8	9	-	18	90	5
18	11	5	24	90	-
19	12	3	23	50	5
20	11	-	19	90	-
23	12	4 ¹	20	38	2
MEAN	10.8	3.3	21.7	73.0	2.0
<u>Abies concolor/Ceanothus velutinus</u>					
27	9	7 ¹	23	75	5
28	9	5 ¹	20	75	5
29	13	13	43	18	2
30	15	8	41	47	3
34	12	4 ¹	26	90	-
35	14	16 ²	41	18	2
MEAN	12.0	8.8	32.3	53.8	2.8

1 Discontinuous

2 Mixed

Table 7. Variation of Lapine profile characteristics
with total depth of the pumice mantle

Depth Class (inches)	No. of Profiles	Average C ₁ Thickness (inches)	Average % Slightly Mixed in C ₂
12-18	3	--	75
19-24	6	4.0	70
25-30	7	5.4	46
31-36	4	8.2	24
37-42	5	11.2	19
43-49	5	12.4	17

horizon tends to be noticeably thinner.

The more unaltered nature of the pumice mantle under Pinus ponderosa/Purshia tridentata vegetation would be expected in view of the fact that this association represents the most xeric conditions encountered. As previously mentioned, the up-rooting of large trees by wind-throw 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 a considerable number of years had passed following the pumice deposition. Thus the smaller amounts of mixing in comparison to the more moist sites may be partially due to a shorter history of tree growth. Hansen (31, pp. 727-732) states that at the time of the eruption of Mt. Mazama the climate of central Oregon may have been somewhat warmer and drier than it is at present. This would suggest that perhaps the distribution of ponderosa pine has become more widespread during the last 6,000 years, since the climatic trend has been toward cooler and more moist conditions. The shallower depth of weathering in these areas may be largely ascribed to the less dense vegetation and consequent smaller amounts of organic matter and less extensive root penetration.

The Lapine soil associated with the Pinus ponderosa/Ceanothus velutinus community generally possesses a relatively deep AC horizon. As a result of the extension of this weathered layer the C₁ horizon is correspondingly thinner and frequently discontinuous. In addition, it was noted that plant roots are not uncommon in the C₁ and unmixed

zones of the C₂ horizon, possibly indicating a greater degree of pumice weathering than is characteristic of the drier sites. In some cases portions of the C₁ horizon, and in one instance (plot 35) the entire layer, were noticeably altered and appeared to represent a condition midway between the C₁ horizon and the modal AC.

Although the data presented in Table 6 show wide variations in profile characteristics within a single plant community, it may be concluded that the amount of alteration of the pumice mantle apparently increases with increasing effective moisture and plant density. Unfortunately, changes in the status of soil formation among the various plant communities are somewhat obscured by the influence of concomitant differences in the depth of the pumice deposit. Another difficulty in the interpretation of data is caused by the extreme variability of Lapine soil morphology within a small area. Thus a very large number of observations are necessary before any general conclusions may be reached.

Relationships Between Lapine Particle Size Distribution and Associated Plant Communities

A summary of the results obtained from the mechanical analysis of approximately 150 Lapine soil samples is presented in Table 8. The primary purpose in performing these determinations was to ascertain whether or not rates of pumice weathering differ among plant communities. Since each plant grouping is indicative of a slightly different climatic regime, it was felt that perhaps these differences might be

Table 8. Particle size distribution in the Lapine soil by horizon and plant community

Plant Community And Soil Horizon	No. of Samples	% Gravel larger than 2 mm	Average % of Particles Finer Than 2 mm and Range of Values							Textural Class
			V. Co. Sand 2-1 mm	Co. Sand 1-.5 mm	Med. Sand .5-.25 mm	Fine Sand .25-.1 mm	V. Fine Sand .1-.05 mm	Silt .05-.002 mm	Clay finer than .002 mm	
<u>Pinus/Purshia</u>										
A ₁	6	15.5 ¹ 14.5-18.3 ²	11.0 18.6-13.3	26.4 25.4-28.0	11.3 9.3-13.2	11.6 7.7-17.3	10.2 6.1-13.2	25.7 18.9-30.0	3.8 2.4-4.7	Sa. Lo. Sa.Lo.-Lo.S.
AC	6	24.2 18.4-29.9	13.1 10.2-16.4	34.0 29.2-37.7	14.1 12.3-16.5	12.4 7.1-18.6	7.4 5.5-11.0	17.7 16.3-19.0	1.3 0.2-2.4	Lo.Sa. Lo.Sa.
C ₁	5	59.5 56.7-67.4	35.6 31.1-40.9	47.4 43.5-49.2	5.8 5.0-6.8	2.2 1.3-3.2	1.9 0.9-2.6	6.6 4.3-7.8	0.6 Tr-0.8	Gr.Sa. Gr.Sa.
C ₂	6	27.0 15.4-40.8	23.8 21.3-28.1	52.4 45.5-56.4	15.2 11.4-18.7	2.9 1.3-7.5	1.7 1.2-3.2	3.5 2.4-5.3	0.6 0.2-0.8	Gr.Sa. Gr.Sa.-Sa.
D	6		2.9 1.3-6.0	9.7 3.4-13.9	15.1 7.8-22.4	37.0 20.8-50.3	14.6 12.2-20.0	17.7 11.4-28.0	3.0 1.6-5.9	Lo.Sa. Sa.-Sa.Lo.
<u>Pinus/Purshia-Arctostaphylos</u>										
A ₁	6	18.9 13.7-25.5	11.4 9.9-13.7	28.8 24.9-32.0	13.0 11.4-16.2	13.6 8.7-20.2	9.1 5.2-10.5	20.5 19.5-22.1	4.0 2.4-5.0	Lo.Sa. Lo.Sa.
AC	6	22.6 17.0-28.0	12.4 11.3-14.3	31.8 26.5-35.4	14.6 12.7-17.7	14.9 8.9-21.6	8.2 5.0-10.4	16.4 14.8-19.4	1.7 1.1-2.8	Lo.Sa. Lo.Sa.
C ₁	4	55.7 53.2-58.4	34.0 29.5-38.8	48.6 45.5-50.5	7.4 6.2-8.9	2.6 1.3-4.4	1.9 1.3-3.0	5.1 4.0-6.6	0.4 Tr-0.8	Gr. Sa. Gr.Sa.
C ₂ -Unmixed	3	17.7 16.7-19.0	24.6 22.1-26.6	50.3 48.1-54.3	18.2 17.7-18.7	2.9 2.2-3.5	0.7 0.5-0.8	2.4 1.6-5.6	0.3 0.1-0.5	Sa. Sa.
C ₂ -Sl.Mixed	2	14.9 13.8-16.0	13.4 11.1-15.6	27.7 21.4-34.0	17.0 12.8-21.2	24.8 15.0-34.5	7.8 4.4-11.2	8.4 7.7-9.2	0.9 0.5-1.3	Sa. Sa.
D	6		1.8 0.5-4.1	5.2 1.3-9.5	13.9 5.5-27.5	47.5 20.5-64.5	14.8 8.8-22.4	14.1 5.8-31.9	2.8 1.7-5.1	Lo.Sa. Sa.-Sa.Lo.
<u>Pinus/Ceanothus-Purshia</u>										
A ₁	6	23.4 21.7-27.1	9.8 8.3-11.3	28.9 24.6-31.5	11.7 10.2-13.9	9.5 7.5-12.1	11.7 9.4-15.5	24.5 20.6-28.5	3.9 2.2-6.1	Sa.Lo. Lo.Sa.-Sa.Lo.
AC	5	28.5 25.0-33.0	12.8 10.6-14.9	35.6 32.8-37.2	13.7 13.0-14.5	9.4 8.3-11.7	9.5 7.2-11.5	16.6 13.4-20.2	2.5 2.0-3.5	Lo.Sa. Lo.Sa.
C ₁	6	54.7 29.5-73.4	30.8 14.8-41.6	46.9 41.9-49.7	7.8 4.0-14.6	3.5 1.3-8.6	3.6 1.8-7.5	5.9 3.6-10.6	1.6 1.1-2.2	Gr.Sa. Gr.Sa.
C ₂ -Unmixed	5	31.0 27.7-38.4	22.1 15.0-29.3	54.4 51.1-58.0	17.1 12.8-26.9	2.5 1.1-4.1	1.3 0.7-2.3	1.8 0.6-3.3	0.9 0.5-1.6	Gr.Sa. Gr.Sa.

Table 8, continued

Plant Community And Soil Horizon	No. of Samples	% Gravel larger than 2 mm	Average % of Particles Finer Than 2 mm and Range of Values							Textural Class
			V. Co. Sand 2-1 mm	Co. Sand 1-.5 mm	Med. Sand .5-.25 mm	Fine Sand .25-.1 mm	V. Fine Sand .1-.05 mm	Silt .05-.002 mm	Clay finer than .002 mm	
C ₂ -Sl.Mixed	4	29.3	15.0	39.0	14.9	12.2	8.6	8.7	1.7	Gr.Sa.
		24.6-37.5	12.1-17.9	35.3-45.4	14.0-16.1	8.6-16.8	7.6-10.0	7.2-10.8	0.7-2.7	Gr.Sa.
C ₂ -Str.Mixed	2	23.6	6.2	20.6	20.0	28.8	11.8	9.4	3.1	Gr.Sa.
		17.8-29.4	6.1-6.4	19.5-21.8	19.3-20.6	21.7-35.9	8.9-14.7	6.3-12.6	2.6-3.6	Gr.Sa.-Lo.Sa.
D	6		2.2	9.1	17.2	32.4	17.4	17.9	3.8	Lo.Sa.
			1.2-2.9	5.9-12.9	8.4-21.6	23.0-45.4	11.0-26.4	9.0-25.1	2.5-4.9	Sa.-Sa.L.
<u>Pinus/Ceanothus</u>										
A ₁	6	20.2	11.4	28.7	12.2	8.6	10.8	24.0	4.3	Sa.Lo.
		15.6-22.7	8.9-14.2	26.6-30.4	10.8-13.4	7.1-10.2	7.9-12.8	20.3-27.2	3.5-5.2	Sa.L.-Lo.Sa.
AC	6	25.3	12.2	34.2	14.6	9.5	9.8	18.1	1.5	Lo.Sa.
		20.5-29.3	10.5-15.4	28.5-37.1	13.4-15.8	8.0-11.2	6.2-12.8	14.0-23.0	1.2-2.3	Lo.Sa.
C ₁	4	41.8	27.0	48.0	10.8	3.4	3.7	6.5	0.6	Gr.Sa.
		33.2-46.5	24.2-32.3	46.6-49.1	8.6-13.5	2.3-4.0	2.1-5.3	4.4-8.2	0.3-1.1	Gr.Sa.
C ₂	4	16.4	15.0	43.9	18.8	7.6	6.8	7.4	0.6	Sa.
		14.7-19.5	13.8-16.9	40.0-46.2	17.9-19.6	6.0-9.6	4.4-7.8	6.0-9.3	Tr-1.3	Sa.
D	6		3.4	8.0	6.2	22.4	26.2	28.2	4.2	F.Sa.Lo.
			1.4-4.4	3.9-12.2	4.3-8.6	18.9-24.8	19.5-36.7	23.8-32.5	3.9-5.7	F.Sa.Lo.
<u>Abies/Ceanothus</u>										
A ₁	6	20.6	10.4	29.4	12.6	8.8	13.8	21.9	3.0	Lo.Sa.
		18.6-25.1	9.5-11.5	27.6-30.7	11.6-13.7	8.2-10.2	11.8-17.3	19.2-25.6	0.8-5.2	Lo.Sa.
AC	6	27.4	11.4	35.3	16.2	9.2	11.3	15.1	1.7	Lo.Sa.
		24.7-30.4	9.4-13.6	32.0-37.8	14.4-16.9	7.6-10.6	8.4-17.3	13.8-16.2	0.8-2.3	Lo.Sa.
C ₁	5	54.7	28.2	50.1	9.5	2.7	3.4	4.9	1.2	Gr.Sa.
		49.0-60.2	23.8-31.2	48.9-51.4	7.5-11.7	2.1-3.5	2.7-4.4	4.2-5.6	1.1-1.3	Gr.Sa.
C ₂ -Unmixed	4	15.2	18.5	51.1	22.3	3.6	1.7	2.1	0.6	Sa.
		8.4-20.6	15.6-20.2	47.2-54.8	19.0-24.1	3.2-4.5	0.8-3.2	1.8-2.3	Tr-1.1	Gr.Sa.-Sa.
C ₂ -Sl.Mixed	4	23.5	13.6	41.0	19.1	7.9	8.2	8.9	1.1	Gr.Sa.
		17.4-35.8	8.4-17.0	35.0-46.6	17.3-21.3	6.2-9.7	3.9-14.8	5.4-12.9	0.1-1.9	Gr.Sa.-Sa.
D	6		3.9	8.3	6.5	18.9	27.7	30.4	4.3	F.Sa.Lo.
			3.0-4.3	5.6-10.2	3.9-8.8	16.6-21.4	19.5-39.6	21.4-35.7	1.8-6.0	Sa.Lo.-Lo.Sa.

- 1 Mean
2 Range of values

reflected in shifts in the particle size distribution of at least the surface horizons. Just how well this hypothesis survived analytical data is indicated below.

As table 8 shows, the variability in particle size distribution for a horizon, even within a single plant community, is quite great. For example, on the basis of 6 samples collected under Pinus ponderosa/Purshia tridentata vegetation the average value for silt in the A₁ horizon is 25.7%. However, the individual values ranged from 4.3% above the mean to 6.8% below. Because of such variations, conclusions derived from these data must necessarily be tentative.

When the mean values alone are considered some apparent differences between plant communities may be seen. For example, the silt content of the A₁ horizon within the Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum association apparently was lower than amounts found in the remaining four types. However, this difference and others similar to it are comparatively small, especially when the variability among observations is considered. On the contrary, the uniformity of the means for a given pumiceous horizon within the various plant communities is much more striking than are any of the apparent differences. Accordingly, the only conclusion which can be drawn is that the particle size distribution of the Lapine A₁, AC, and C horizons varies, and the variations may be of considerable magnitude. However, on the basis of the results of a limited number of analyses these variations do not appear to be significantly correlated with vegetation. Thus it appears that

either rates of pumice weathering are more or less constant regardless of climatic differences, or else insufficient time has elapsed to allow shifts in particle size distribution to be detected, at least with a limited number of observations.

Surprisingly, the particle size distribution of the D horizon, consisting of buried soil material, shows more correlation with vegetation than any other horizon. Both the Abies concolor/Ceanothus velutinus and the Pinus ponderosa/Ceanothus velutinus communities are apparently associated with a D horizon containing almost twice the amounts of silt and very fine sand than the D horizons occurring under the other three vegetation types. This shift in particle size distribution is undoubtedly due to influences active prior to the deposition of the pumice mantle.

Morphology of the Shanahan Series

The Shanahan soil, which is associated with the Pinus ponderosa/Purshia tridentata/Festuca idahoensis community, is largely restricted to the southeastern portion of the Unit. The soil is commonly found on very gently sloping to nearly level topography and is generally considered to be either moderately well drained or well drained. The Shanahan soil is classified as a Regosol and is developed on a predominantly pumiceous parent material. Although originally the pumice was aerally deposited as a uniform mantle, the Shanahan parent material appears to have been reworked by water. In all cores some mixing with the buried soil material has occurred, so that

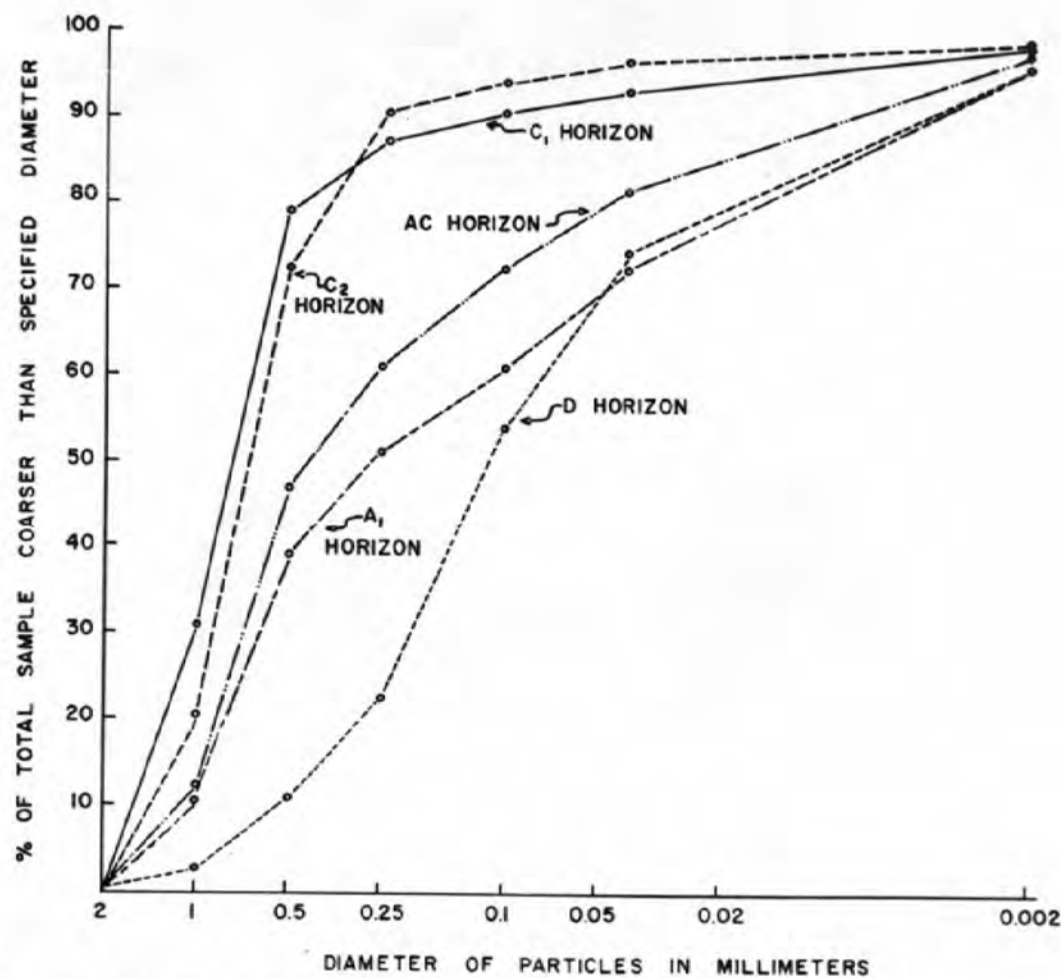


Figure 19. Cumulative particle size distribution curves based on average values for the Lapine A₁, AC, C₁, C₂, and D horizons.

contamination of the pumice is much more widespread than in the case of the Lapine soil.

The Shanahan soil occupies approximately one-fourth of the total land area of the Antelope Unit and also has been mapped extensively in the Klamath Indian Reservation. In the report on the soil survey of the Klamath Indian Reservation (87, p. 192) it is stated that within the survey area this soil occurred most commonly over diatomite, however it was pointed out that for the Reservation as a whole the most common occurrence would be over basalt or andesite.

In most Shanahan soil areas there is a fairly thick covering of litter over the mineral soil. The A_{00} horizon in the profiles investigated averaged about 1 inch in thickness and was predominantly composed of fresh and partially decomposed pine needles. The L and F layers grade abruptly into the A_1 horizon and no H layer (A_0) was noted. The A_1 horizon averages 2 inches in thickness and was found to possess a lower boundary ranging from clear and smooth to diffuse and wavy. Textures are either a coarse sandy loam or a loamy coarse sand. Pumice gravel is generally present in fairly large quantity and may constitute over 20% of the total mass of the horizon. The A_1 possesses weak fine or medium granular structure and consistence is loose when dry and very friable when moist. The most frequently encountered moist colors are very dark gray brown (10YR 3/2), dark gray brown (10YR 4/2), and dark brown (10YR 3/3). Dry colors are gray brown (2.5YR 5/2) and gray (10YR 5/1).

The soil mantle beneath the A_1 horizon is generally quite uniform

with respect to texture, the most noticeable changes involving decreasing amounts of organic matter with depth and, in some cases, a change in structure. An AC horizon is without exception found below the A₁ and, apparently largely depending on profile depth, may extend uninterrupted to the D₁ horizon. In many of the deeper soils the lowest portion of the pumice mantle is split out as a C horizon, largely on the basis of a shift in structure from weak subangular blocky to single grain.

The AC horizon varies from approximately 5 to 20 inches in thickness. When grading into a C horizon the boundary is gradual and irregular with tongues of AC material commonly extending far into the C. The texture of this horizon is a loamy coarse sand, with pumice gravel content at approximately 20% by weight. In addition, basalt fragments of gravel or cobble size may be present, especially if this horizon is situated in close proximity to the buried soil. Soil structure is weak medium subangular blocky and consistence is very friable when moist and slightly sticky and nonplastic when wet. Moist soil color is generally dark yellowish brown or yellowish brown (10YR 4/4, 5/4) and the dry color is light brownish gray (10YR 6/2).

The total depth of the Shanahan soil profile above the D horizon is commonly less than 24 inches and only rarely extends as deep as 36 inches. Accordingly, the C horizon, completely absent in the shallower pumiceous deposits, is very seldom more than 12 inches in thickness. The boundary between the C and D₁ horizons is diffuse and irregular as a result of the intermingling of the two layers. The

texture of the C horizon is loamy coarse sand and both pumice and basalt gravel is common. The horizon is structureless and very loose when dry or moist. Its moist color is generally yellowish brown (10YR 5/4 to 5/6), with single pumice grains exhibiting a brownish yellow color (10YR 6/6).

Unlike the substratum occurring beneath the Lapine soil, the buried soil under the Shanahan possesses a considerable amount of profile development. Thus the D horizon material is found to consist of two distinct layers, a buried A horizon (D_1) and a very much finer textured buried B(D_2). The D_1 horizon, or A_b , 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 up to three-fourths of the volume may be occupied by basalt fragments. The structure is commonly weak or moderate medium subangular blocky. When moist the color of the D_1 horizon is dark brown (10YR 4/3, 3/3 and 7.5YR 4/4, 3/2) and when dry, light brownish gray (10YR 6/2). The D_1 grades abruptly into the D_2 horizon (B_b) which, in turn, grades into weathered basalt with increasing depth. The D_2 horizon is generally from about 5 to 15 inches thick and possesses either a loam or clay loam texture. Basalt fragments are common and constitute 25 to 90% of the volume. This horizon generally has a strong fine and medium angular blocky structure. The color of the D_2 horizon is a dark brown (7.5YR 4/4) or dark reddish brown (5YR 3/4) when moist.

Particle size distributions for the various Shanahan soil horizons are presented in Table 9 and average values are portrayed

Table 9. Particle size distributions for the Shanahan soil by horizon. Associated plant community is the Pinus ponderosa/Parshia tridentata/Festuca idahoensis.

	No. of Samples	% Gravel larger than 2 mm	Average % of Particles Finer Than 2 mm and Range of Values							Textural Class
			V. Co. Sand 2-1 mm	Co. Sand 1-.5 mm	Med. Sand .5-.25 mm	Fine Sand .25-.1 mm	V. Fine Sand .1-.05 mm	Silt .05-.002 mm	Clay finer than .002 mm	
A ₁	5	19.4 ¹ 16.3-21.1 ²	11.3 9.3-13.6	29.5 25.7-33.4	10.9 9.0-11.8	9.5 7.1-13.0	14.6 13.3-17.2	20.3 18.3-24.0	3.8 1.8-5.2	Lo. Sand Sa. Loam- Lo. Sand
AC	5	22.2 20.9-24.3	12.6 10.3-15.2	31.9 27.8-34.2	12.0 10.5-13.1	9.8 7.5-14.2	13.7 11.0-16.4	17.7 15.4-20.6	2.3 0.8-3.2	Lo. Sand Lo. Sand
C	2	18.0 15.6-20.4	13.7 12.4-15.0	36.6 35.4-37.8	13.0 12.8-13.1	9.1 7.8-10.4	11.4 9.8-12.9	15.0 15.0-15.1	1.3 1.1-1.5	Lo. Sand Lo. Sand
D ₁ (A _b)	5		4.0 3.4-4.4	9.3 7.2-12.3	5.8 4.3-8.0	19.3 14.7-23.9	24.5 22.3-26.6	29.9 21.3-38.7	7.2 5.0-9.4	Sa. Loam Loam-Sa. Loam
D ₂ (B _b)	5		4.4 2.8-6.3	7.6 4.3-9.8	5.4 3.3-8.3	11.1 6.0-18.0	11.6 6.8-19.0	29.9 22.3-34.1	30.0 7.4-42.7	Clay Loam Clay-Sa. Loam

¹ Mean

² Range of values

graphically in Figure 20. It is interesting to note the small but consistent change in the amounts falling in the various size fractions with increasing depth in the soil profile. The percentages in the coarse sand fractions noticeably increase from the A₁ to C horizon, while amounts of fine sand, silt, and clay decrease proportionally in the same sequence of 3 horizons. Such a shift in particle size distribution is probably best explained by postulating differences in the degree of weathering of an originally uniform parent material. Undoubtedly, the pumice as it was first aerally deposited was stratified to a certain extent with regard to particle size. Such a condition can be seen in more or less undisturbed deposits such as the Lapine is formed in. However, in areas of Shanahan soil and at least in so far as the Antelope Unit is concerned, the entire pumice mantle was reworked and mixed with residual soil material already present.

The ability of the Shanahan soil to support vigorous stands of Idaho fescue and other plant species which are virtually excluded from Lapine soils may be largely due to differences in root distribution within the two soils. Plant roots are commonly 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, the maximum rooting depth for grass and forb species growing on Lapine soil is usually equal to the depth of the AC horizon, which averages approximately 12 inches. In the case of the Shanahan soil, however, the effective

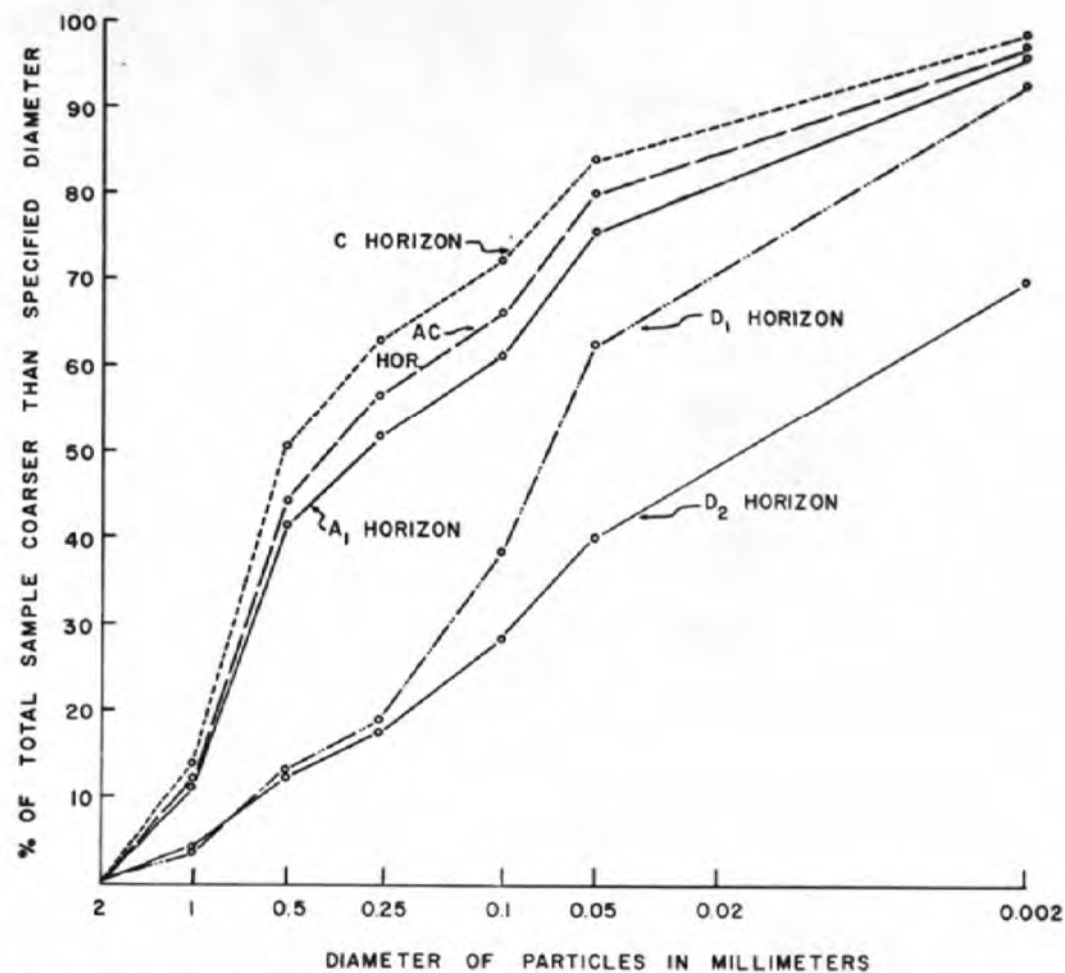


Figure 20. Cumulative particle size distribution curves based on average values for the Shanahan A₁, AC, C, D₁ and D₂ horizons.

rooting depth for herbaceous plants averages from 30 to 40 inches and may be considerably greater in areas where the roots are able to enter the D₂ horizon.

SOIL MOISTURE

Relationships Between Soil Moisture and Four Plant Communities

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 in close proximity to the transition area separating the ponderosa pine and juniper-sagebrush vegetation zones. The dominant influence of soil moisture in regulating plant distribution is also indicated by the fact that several plant communities occupy sites with equivalent soils, with the only difference being their location with respect to elevation or aspect.

Soil moisture measurements were made during the summers of 1956 and '57 in the following plant communities: (1) Pinus ponderosa/Purshia tridentata, (2) Pinus ponderosa/Purshia tridentata/Festuca idahoensis, (3) Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum, and (4) Pinus ponderosa/Ceanothus velutinus. A comparison of soil moisture values obtained during the two growing seasons shows that moisture depletion was considerably more rapid in 1957 than in 1956. Figure 21 compares the trend of soil moisture use under Pinus/Purshia/Festuca and Pinus/Purshia-Arctostaphylos vegetation

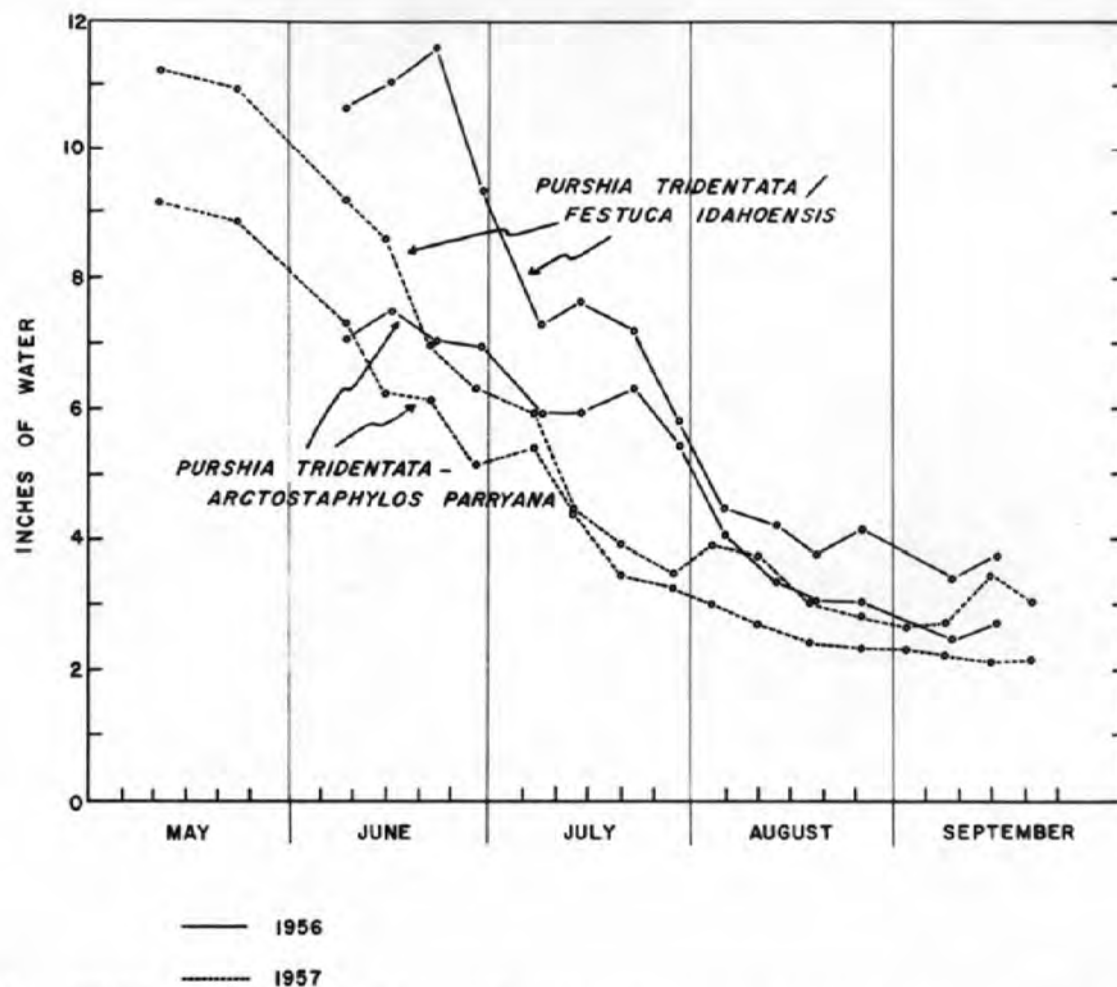


Figure 21. Soil moisture depletion under the *Pinus ponderosa*/*Purshia tridentata*/*Festuca idahoensis* and *Pinus ponderosa*/*Purshia tridentata*-*Arctostaphylos parryana* var. *pinetorum* associations during the 1956 and '57 growing seasons. Moisture values are for the entire profile and represent the average for conditions under shrubs and in the open.

throughout the two sampling periods. A replenishment of soil moisture during July as a result of 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. Soil moisture trends for 1956 were influenced not only by abnormally abundant summer rainfall, but also by an unusually wet spring. For these reasons soil moisture levels during the 1956 growing season were very likely atypical. Since climatic conditions during the 1957 growing season were apparently more nearly representative, more emphasis will be placed on the soil moisture trends for this period.

Soil moisture trends for the summer of 1957 are illustrated in Figures 22 and 23. These graphs show total amounts of water in the entire profile, extending from a 12 inch depth in the D horizon to the soil surface. In some cases the soil moisture content varied markedly from week to week and increases in the total supply of water were not always attributable to additions by rainfall. A great amount of variability in soil moisture values is especially noticeable in the case of the sampling plots located in the Pinus ponderosa/Purshia tridentata habitat type (Figures 22 and 23). As previously indicated, the Lapine soil exhibits a considerable amount of profile variability, especially with respect to the nature of the C horizon. Since these variations are accompanied by differences in root distribution, the soil moisture content might also be expected to vary appreciably,

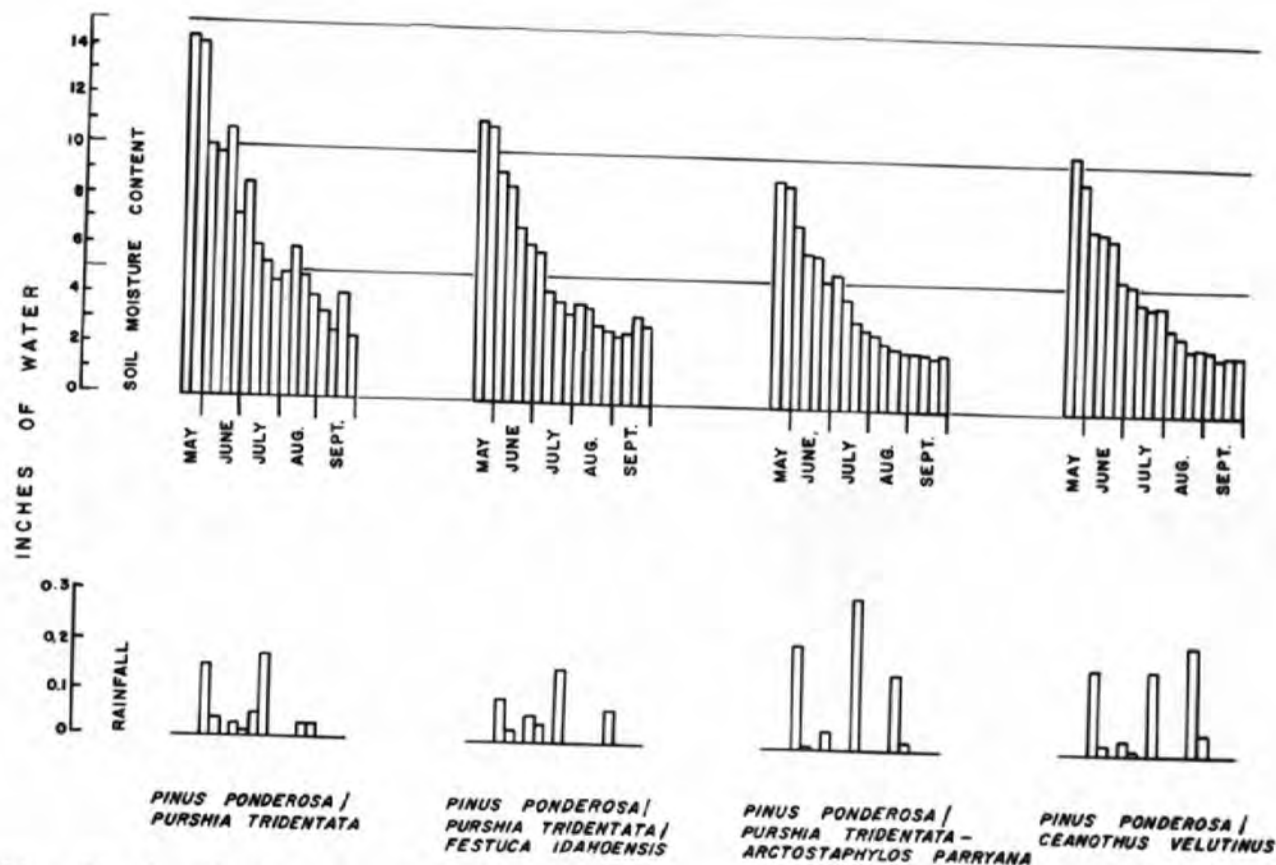


Figure 22. The trend of soil moisture depletion and accretion by rain in four plant communities (A plots) during the 1957 growing season. Moisture values are for the entire profile and represent the average for conditions under shrubs and in the open.

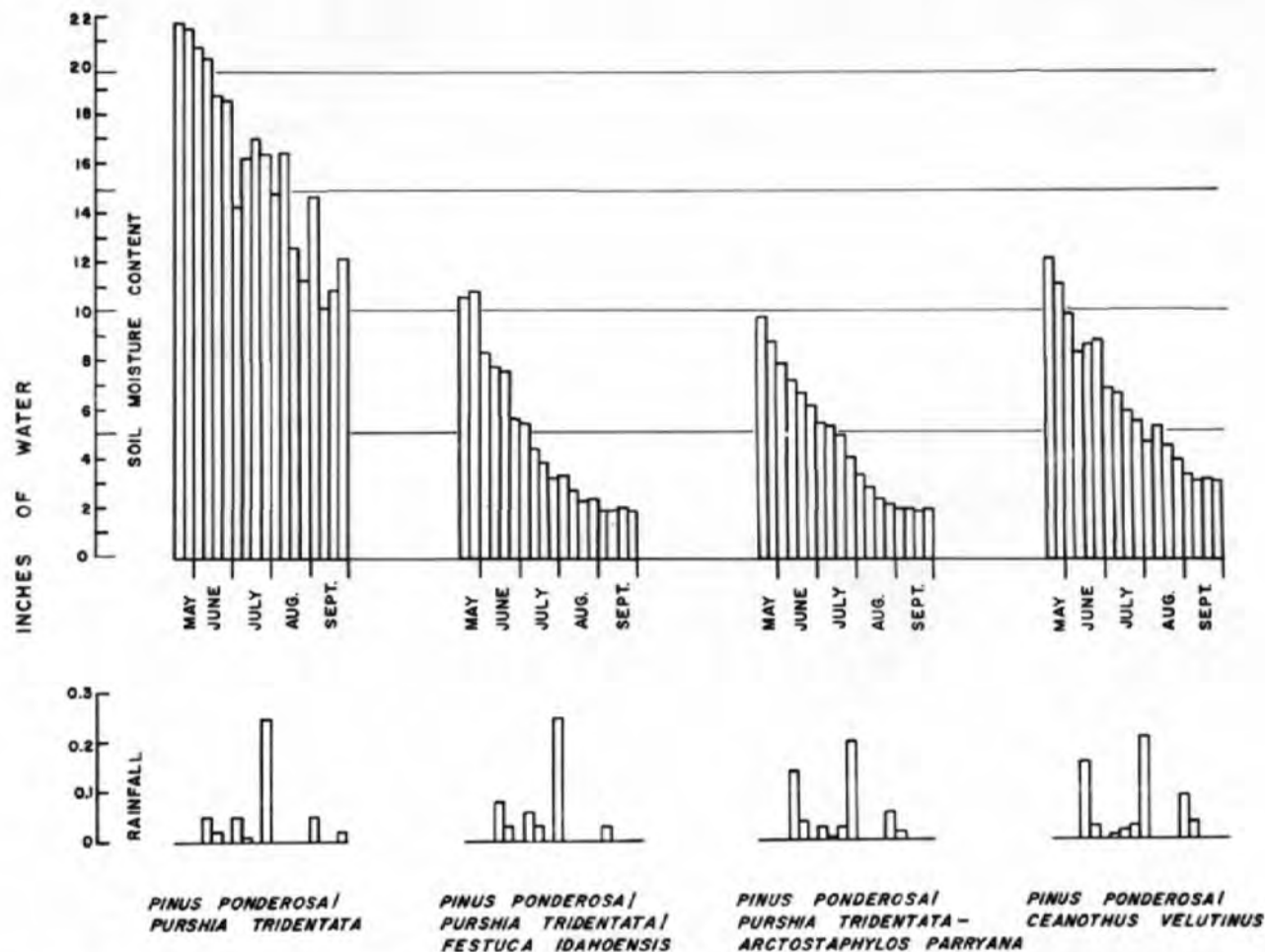


Figure 23. The trend of soil moisture depletion and accretion by rain in four plant communities (B plots) during the 1957 growing season. Moisture values are for the entire profile and represent the average for conditions under shrubs and in the open.

even within a small area. The sampling procedure consisted of the collection of a composite sample comprised of 4 or 5 cores obtained from a circular plot with a radius of approximately 25 feet. Apparently the local variations in soil moisture content are such that a greater number of subsamples would be required before a completely representative average value could be obtained.

Despite weekly fluctuations, the main trends in the pattern of soil moisture depletion within the four plant communities are readily apparent. Because amounts of rainfall were extremely small, soil moisture was depleted at a more or less constant rate until the permanent wilting percentage was approached. Comparison of Figure 22 with Figure 23 shows that the two plots located within the same plant community exhibit closely similar patterns of moisture use. The trend of moisture depletion at the two Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum plots very closely resembles that found for the Pinus ponderosa/Purshia tridentata/Festuca idahoensis habitat type. In both plant associations depletion proceeded at a fairly constant rate until almost no moisture available for plant use remained after the second or third week in August. In the Pinus ponderosa/Ceanothus velutinus community supplies of available moisture were depleted less rapidly, thus indicating more mesic conditions.

The dates soil moisture in each horizon reached permanent wilting percentage are illustrated in Figures 24 and 25. It will be noted that although the moisture content of the A₁ and AC horizons under

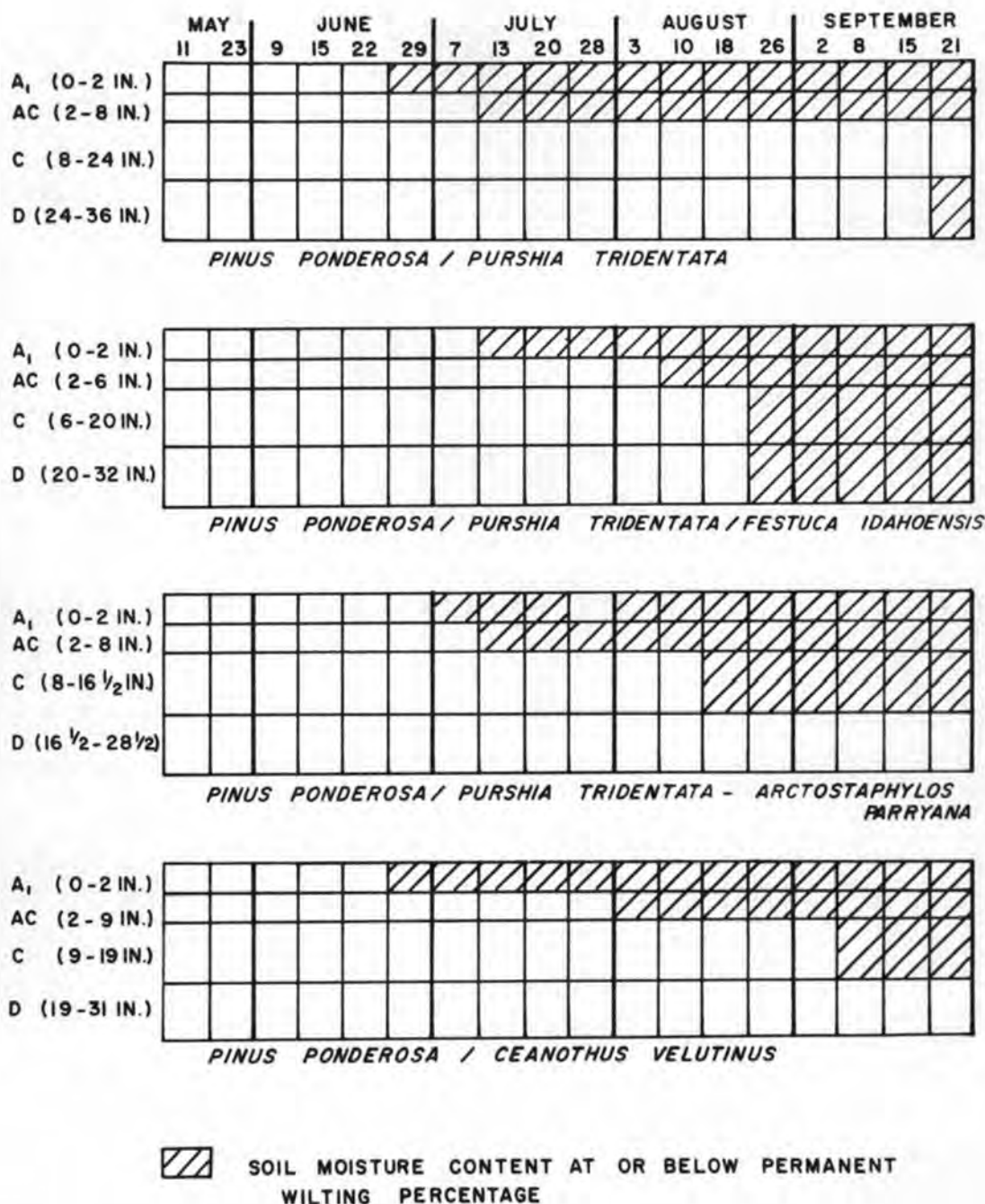
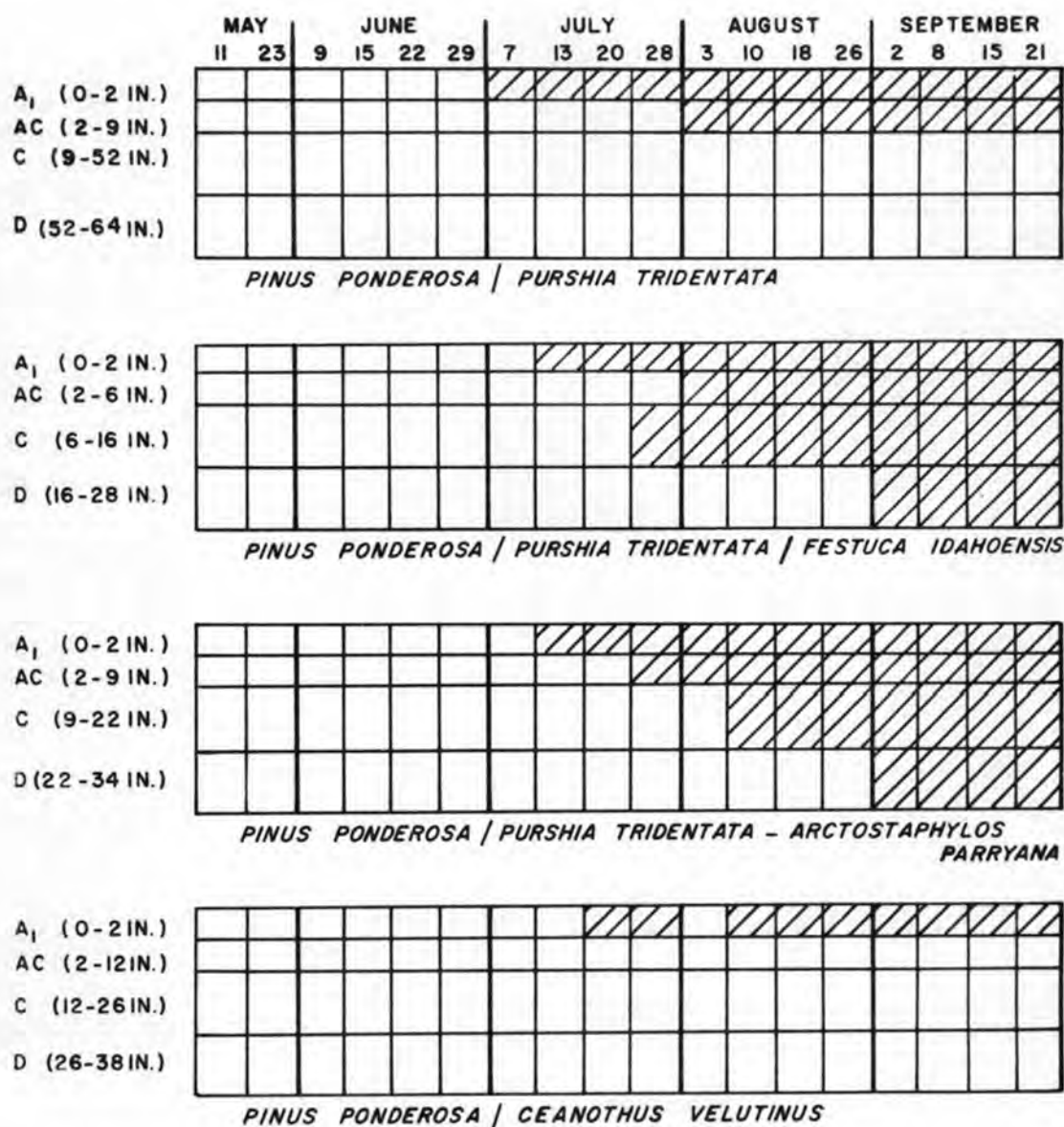


Figure 24. Dates soil moisture content of the various horizons under four plant communities (A plots) was at or below permanent wilting percentage (1957).



SOIL MOISTURE CONTENT AT OR BELOW PERMANENT
WILTING PERCENTAGE

Figure 25. Dates soil moisture content of the various horizons under four plant communities (B plots) was at or below permanent wilting percentage (1957).

Pinus ponderosa/Purshia tridentata vegetation was reduced to the 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 season. This is somewhat surprising in view of the fact that species composition and nature of the timber stand both indicate that the Pinus/Purshia association denotes the driest sites capable of supporting ponderosa pine in the study area. Some possible reasons for this anomaly are discussed in a later section. The Pinus ponderosa/Purshia tridentata/Festuca idahoensis association, on Shanahan soil, utilized all available soil moisture by the last week in August and the first week in September respectively. Although some tree roots undoubtedly extend deeper than the maximum depth of sampling, the amount of water in the buried soil at depths greater than 12 inches is probably small due to its generally stony nature. The progressively deepening zone of soil moisture depletion at Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum plot B presents an interesting pattern. As shown in Figure 25, the 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 two weeks later. After an interval of three more weeks the upper 12 inches of the D horizon was also at the permanent wilting percentage. The pattern encountered at Pinus/Purshia-Arctostaphylos plot A is almost identical except for the fact that the soil moisture content of the D horizon remained above the permanent wilting percentage. The soil at

plot A within the Pinus ponderosa/Ceanothus velutinus community was the only one in which all horizons with the exception of the A₁ still contained available moisture at the end of the sampling period.

Total consumptive water use for the period beginning June 9 and ending September 21, 1957 is listed for each of the 8 sampling plots in Table 10. It will be noted that consumptive use was appreciably higher at the Pinus ponderosa/Purshia tridentata plots than in the other 3 plant communities. There are several possible reasons for this. First, as a result of its location at lower elevations, the Pinus/Purshia association begins growth earlier in the spring and therefore the period of water uptake and transpirational loss is somewhat extended. Second, water loss by evaporation is almost certainly greatest in the Pinus/Purshia habitat type due to more sparse vegetative cover, an incomplete cover of litter on the soil surface, and higher daytime temperatures. There are indications that evaporation in conjunction with upward vapor movement in the soil profile may result in a considerable amount of water loss in the central Oregon pumice region. This hypothesis, as yet untested, is based on the observed high proportion of macropore spaces in pumice soils coupled with the very great diurnal temperature fluctuations which are characteristic of the area.

On the basis of these results it may be concluded that soil moisture is of considerable importance in controlling the distribution of the plant communities in the Antelope Unit. If the 1957 growing season was typical for the area with respect to moisture conditions,

Table 10. Total consumptive use of soil moisture during the summer of 1957 under four plant communities

Sampling Plot	Depth Sampled (in.)	Inches of Water Used (June 9 - Sept. 21)
<u>Pinus ponderosa/Purshia tridentata</u> - A	36	8.08
B	64	9.05
<u>Pinus ponderosa/Purshia tridentata/</u>	A 32	6.56
<u>Festuca idahoensis</u>	B 28	7.04
<u>Pinus ponderosa/Purshia tridentata-</u>	A 28 1/2	5.87
<u>Arctostaphylos parryana</u>	B 34	6.41
<u>Pinus ponderosa/Ceanothus velutinus</u>	A 31	5.66
B	38	7.36

the data indicate that soil drought becomes less severe with increasing elevation. This is especially noticeable in the case of the Pinus ponderosa/Ceanothus velutinus community where at plot A soil moisture depletion was delayed until late in the growing season, and at plot B soil moisture was apparently never limiting. The conclusions reached here are in accord with those of McMinn (50). From the results of a study conducted in the northern Rocky Mountains he concluded that the distribution of plant associations was definitely influenced by differing amounts of soil drought.

The unusual pattern of soil moisture depletion at the Pinus ponderosa/Purshia tridentata sampling plots is best explained by a consideration of soil morphology and root distribution in these areas. As was pointed out in the section covering the morphology of the Lapine soil, the C horizon in areas supporting the Pinus/Purshia association was found to consist of pumice sands and gravels which had undergone very little mixing with finer material from the D horizon. It was stated that this condition is accompanied by an almost complete lack of plant roots in the C horizon. Since this description also applies to the soils at both Pinus/Purshia moisture sampling plots, the great majority of plant roots were located in the A₁, AC, and D horizons. On the other hand, roots were well distributed throughout the soil profile at the sampling plots situated within the Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana var. pinetorum and Pinus ponderosa/Ceanothus velutinus 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 the A₁, AC, and D horizons, while only small amounts are removed from the C horizon. The consumptive use data for the two Pinus ponderosa/Purshia tridentata plots (Table 10) bear out this conclusion. It should be noted that despite the fact the C horizon at plot B was 28 inches thicker than that at plot A, only one additional inch of water was utilized. Figure 26 compares soil moisture trends in the A₁, AC, and C horizons at Pinus/Purshia plot B with those for the same horizons at Pinus/Purshia-Arctostaphylos plot B. The difference in moisture levels between the two C horizons clearly reflects the very great influence root distribution exerts on the rate and magnitude of soil moisture depletion.

The Effect of Shrubs on Soil Moisture Depletion

A comparison of soil moisture values for samples collected under shrubs with those for samples obtained in the open indicated early in the study that perhaps soil moisture levels in the surface horizons were slightly higher under shrubs than in the open. To further explore this phenomenon, sampling procedures were modified during the 1957 growing season. Instead of including the A₁ and AC horizons in the same sample, as was the practice in 1956, the two layers were sampled separately. In this manner it was possible to determine whether the apparent difference was caused solely by variations in the

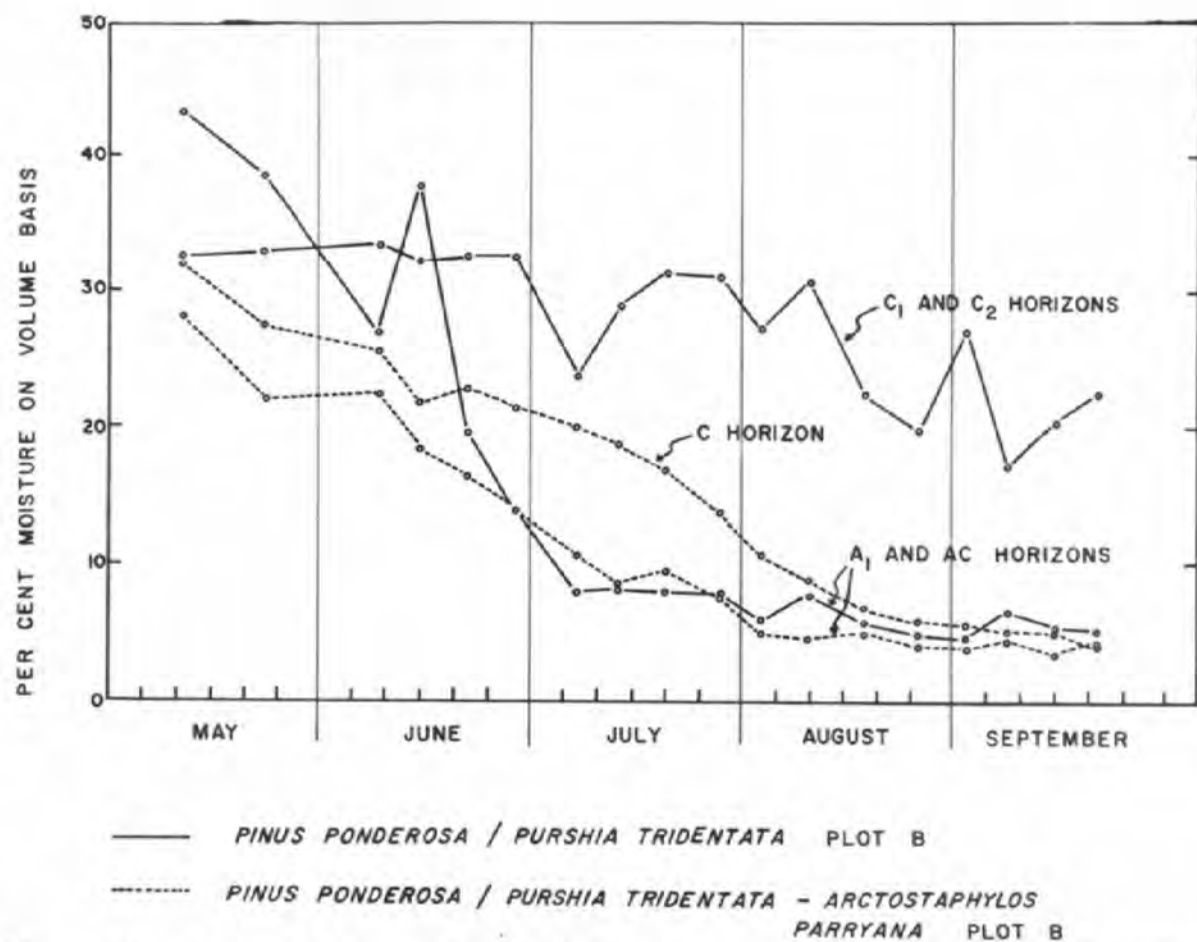


Figure 26. Soil moisture depletion in the A₁, AC, and C horizons at Pinus ponderosa/Purshia tridentata plot B and Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana plot B during the 1957 growing season.

moisture content of the A_1 or in both the A_1 and AC. Results obtained indicated that although differences in moisture levels in the open and under shrubs were generally somewhat greater in the A_1 horizon, the AC also tended to have a slightly higher moisture content under shrub cover. No consistent differences in moisture content in connection with sample location could be detected in the C and D horizons.

Although soil moisture data obtained during the summers of 1956 and 1957 showed a generally consistent correlation between shrub cover and higher soil moisture values in the A_1 and AC horizons, differences were usually quite small. Figure 27, showing soil moisture depletion curves for the surface horizons under shrubs and in the open, is representative in that it shows maximum differences of approximately 0.3 to 0.4 inches of water and, more commonly, differences of only 0.1 inch or less. However, these margins are often sufficient to cause the surface soil in the open to reach the permanent wilting percentage 1 to 3 weeks before this same level is reached under shrub cover. This fact is illustrated by Table 11; out of a total of 12 separate observations, 10 show that the surface soil under shrubs maintained available moisture at least one week longer than it did in the open.

Youngberg (103, 104), working in areas north of the Antelope Unit, also found that surface soil moisture levels were significantly higher under shrubs than in the open. His work was centered on the Lapine and a Lapine-like soil formed on pumice deposits originating

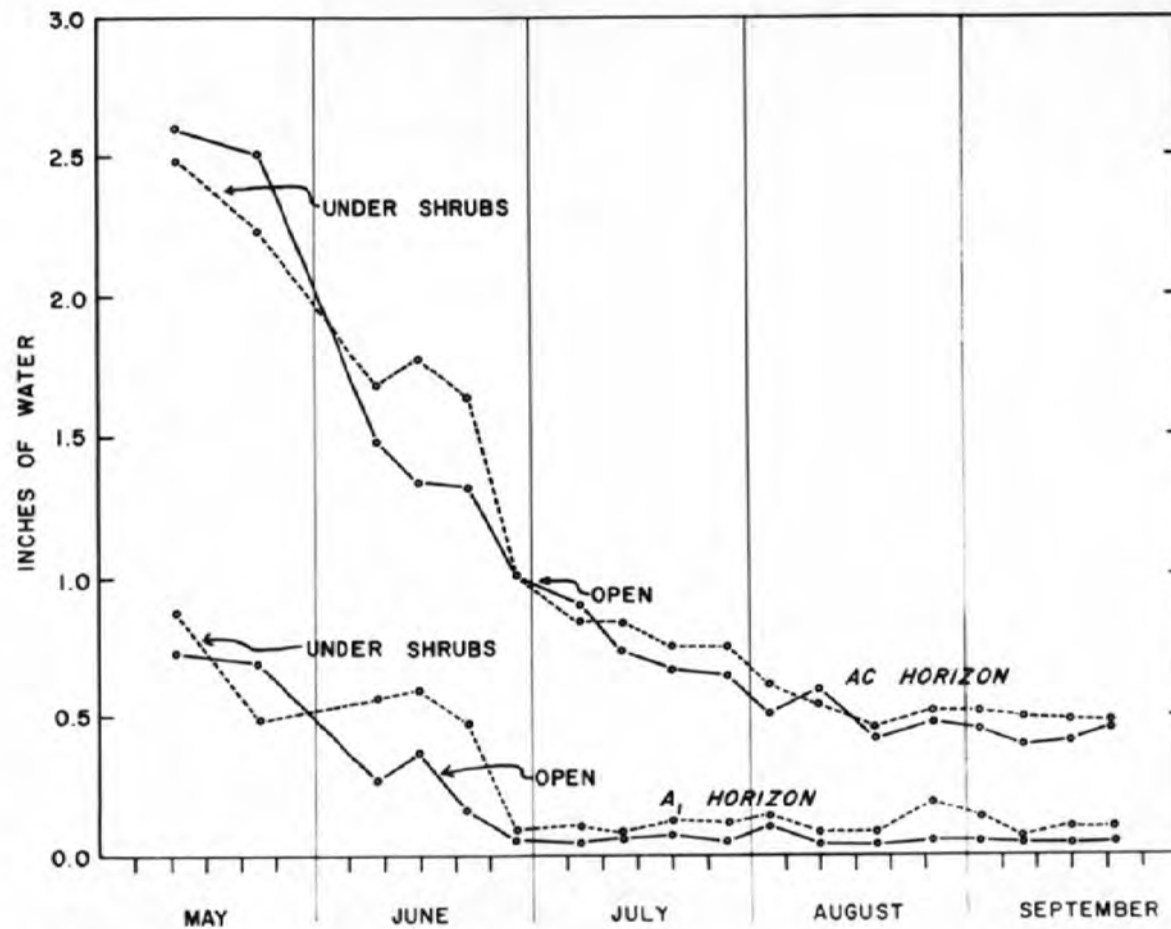


Figure 27. Soil moisture depletion of the A₁ and AC horizons in the open and under shrubs during the 1957 growing season. Pinus ponderosa/Ceanothus velutinus plot A.

Table 11. Date the combined A₁ and AC horizons first reached the permanent wilting percentage under shrubs and in the open in 4 plant communities

Soil Moisture Sampling Plot	1956		1957	
	Open	Under Shrubs	Open	Under Shrubs
<u>Pinus/Purshia</u>	- A Aug. 13	Sept. 9	July 13	July 13
	- B		July 7	July 20
<u>Pinus/Purshia/Festuca</u>	- A Aug. 13	Aug. 13	July 13	July 20
	- B		July 13	July 20
<u>Pinus/Purshia-</u>	- A Aug. 5	Aug. 13	June 29	July 13
<u>Arctostaphylos</u>	- B		July 20	Aug. 3
<u>Pinus/Ceanthus</u>	- A Aug. 19	Aug. 26	July 20	Aug. 3
	- B		Aug. 3	Sept. 15

from Newberry Crater. Soil moisture trends were followed under Purshia tridentata, Chrysothamnus viscidiflorus, Ribes sp., and Artemisia tridentata. Youngberg also reported that a mulch of ponderosa pine needles on the soil surface delayed exhaustion of available moisture in the surface 2 inches by as much as 2 weeks.

The larger quantities of soil moisture under shrubs may be largely attributed to decreased evaporation as a result of the shade and mulch provided by these plants. In addition, the data indicate that the roots of shrub species in these particular soils are widely distributed and are not concentrated to any great extent immediately under the plant. Consequently, the quantities of moisture conserved by means of decreased rates of evaporation more than offsets moisture use by the shrub itself.

Undoubtedly the extended period of soil moisture availability is a factor of considerable importance in encouraging the survival of coniferous seedlings under shrubs in the study area. Wahlenberg (96), working in western Montana, found that the survival rate of ponderosa pine seedlings planted under Ceanothus velutinus was much higher than for seedlings planted in open positions. His investigations indicated that greater quantities of available moisture coupled with the lower temperatures under shrub cover accounted for the wide difference in survival.

General Moisture Relations in the Lapine Soil

Pumice soils, due to their unusually low bulk density and the nature of their porosity, might be expected to exhibit physical characteristics which are considerably different from those of conventional mineral soils. Certainly this was the case with regard to the moisture relationships of the soils with which this study was concerned. The inescapable conclusion is that pumice soils are somewhat unique in their moisture relations and it is therefore necessary to revise certain concepts and procedures if these soils are to be fully understood. Among the very few investigations of the physical properties of pumice soils, Packard's (57) recent work in New Zealand is probably the most valuable. After studying soil moisture properties of several pumice soils he concluded that they more closely resembled peat than any other class of soils in such characteristics as moisture holding capacity and range of available moisture.

One of the most striking properties of the Lapine soil is its ability to hold large quantities of water, despite its generally coarse sandy texture. This was especially noticeable in data obtained from the spring samplings conducted in 1957. For example, on May 11th the 52 inch thick pumice mantle at Pinus ponderosa/Purshia tridentata sampling plot B contained approximately 23 inches of water. Although the soils at other Lapine sampling plots contained smaller total volumes of water, the quantities in all cases amounted to more than 30% on a volume basis. It is interesting to note that the gravelly C₁ horizon is apparently capable of holding larger amounts of water than

is the finer-textured C_2 . This relationship can be seen in Table 12, both for the 0.1 atmosphere data and approximate field capacity values as well. The higher moisture holding capacity of pumice gravels suggests that perhaps their interior pore space arrangement differs from that of sand-sized pumice particles.

Soil moisture constants for each horizon at the two Pinus ponderosa/Purshia tridentata sampling plots were determined in the laboratory by the pressure membrane extraction procedure (66, pp. 103-106). These data were then compared with values for approximate field capacity and permanent wilting percentage as determined by early spring sampling and the sunflower method respectively. Results of the 0.1 atmosphere determinations were found to agree most closely with approximate field capacity values. However, as may be seen in Table 13, the majority of "field capacity" moisture levels are somewhat higher than the figures for 0.1 atmosphere. There are two possible reasons for these discrepancies: (1) It is possible that moisture in Lapine soils may reach the unstable equilibrium of field capacity at tensions considerably lower than the generally accepted $1/3$ atmosphere. Since pore spaces within individual pumice particles are undoubtedly discontinuous, the retarded movement of soil moisture held at low tensions may account for this. (2) Soil moisture content at the time of sampling may have been above representative values for field capacity due to incomplete drainage of gravitational water. If Lapine soils possess properties similar to those of Taupo pumice soils

Table 12. Two soil moisture constants for the Lapine soil, each obtained by two different methods. (1) "Field capacity" by soil moisture sampling in the field on May 11th, and by determining moisture held at 0.1 atmospheres (pressure membrane extraction method). (2) Permanent wilting percentage by the sunflower method, and by the determination of moisture held at 15 atmospheres (pressure membrane).

	Horizon	Approx. Field Cap. (May 11) (% by Vol.)	0.1 Atmos. (% by Vol.)	Permanent Wilting Pct. (Sunflower Method) (% by Vol.)	15 Atmos. (% by Vol.)
<u>Pinus/Purshia</u> Plot A	A ₁	37.00	32.02	13.30	12.02
	AC	34.17	40.62	7.77	5.79
	C ₁	43.33	36.27	4.82	2.75
	C ₂	40.10	29.75	5.23	2.67
	D	43.00	27.19	9.97	8.35
<u>Pinus/Purshia</u> Plot B	A ₁	47.00	43.27	9.00	6.68
	AC	42.00	46.26	8.10	6.32
	C ₁	38.80	35.20	3.50	2.19
	C ₂	29.16	26.56	3.11	2.72
	D	32.50	28.25	11.08	8.26

in New Zealand, perhaps both of these possibilities are equally true. Packard (57, p. 278), after correlating field sampling data with results of laboratory determinations, found good agreement between moisture content at 0.19 atmospheres and field capacity.

Values for permanent wilting percentage and those obtained at tensions of 15 atmospheres are generally in fairly close agreement (Table 12). However, it will be noted that the moisture percentages at 15 atmospheres are uniformly 1 to 3% lower than the permanent wilting values determined phytometrically. Perhaps moisture contained in the central portions of large pumice particles is inaccessible to plant roots in spite of the fact it is held at tensions lower than 15 atmospheres. Packard (57, p. 278) reports that 15 atmosphere values were substantially the same as sunflower permanent wilting percentages for Taupo pumice soils.

In addition to a large moisture holding capacity, the Lapine soil exhibits an extremely wide range of available moisture. On the basis of comparisons with conventional soils it appears that the Lapine most closely resembles a loam in moisture retention properties, but is more like a sandy-textured soil in its release of stored moisture. The ranges of available moisture for the 5 horizons comprising a Lapine profile are presented in Figure 28. It can be seen that the total range of available moisture in pumiceous horizons is in every case much greater than the corresponding quantity in the surface layer of Chehalis loam.

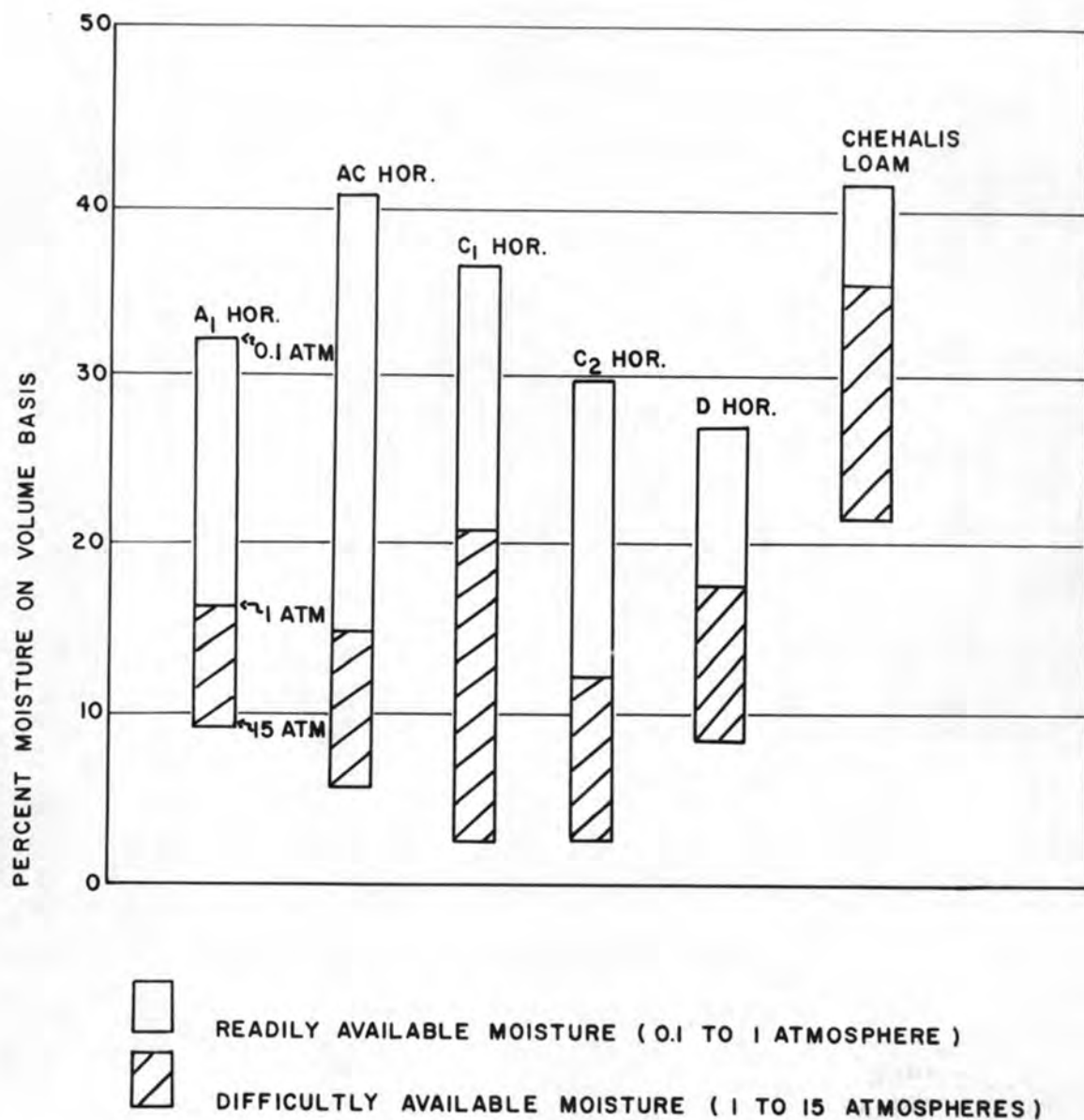


Figure 28. Ranges of available moisture in the 5 horizons of the Lapine soil and in the surface 6-inch layer of Chehalis loam. (Based on moisture values obtained by the pressure membrane extraction procedure.)

It has been fairly well established that soil moisture is most available to plants when held at tensions lower than 1 atmosphere (67, p. 104). In most medium and fine-textured mineral soils this range of "readily available" moisture constitutes much less than half of the total available moisture supply. However, as can be seen in Figure 28, a large proportion of the total soil moisture in the Lapine is under tensions ranging from 0.1 to 1 atmospheres.

Unsaturated water movement in the Lapine soil is apparently quite slow. This is demonstrated by the fact that Lapine samples require 1 to 2 weeks in the pressure membrane apparatus before moisture equilibrium is reached. As Packard (57, p. 287) points out, this low permeability may have some influence on plant-soil moisture relationships. He states, "Plant growth in pumice soils may possibly be retarded earlier than in normal mineral soils because of plants using moisture faster than it can be replaced in the thin layers of soil adjacent to root hairs."

SOIL CHEMICAL PROPERTIES

Relationships Between Chemical Properties of the Lapine Soil and Associated Plant Communities

The pumice mantle on which the Lapine soil has developed was, at the time of its deposition, undoubtedly fairly uniform in its chemical composition. Since that time differences in amounts and degree of availability of soil nutrients have developed. These changes have been caused largely by two factors which have a dominating influence

on soil fertility relationships. The first factor, which possibly is of more importance in pumiceous soil than in any other type, is the rate of weathering of the pumice particles. Although Mt. 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 (102, p. 152). These essential elements are released in available forms at more or less constant rates by means of weathering processes. The importance of weathering in the release of nutrient elements from pumiceous material has been stressed by van Woud't (93, p. 168). The second factor which is undoubtedly of importance in affecting 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 the 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 A_1 and AC horizons. Two samples of these horizons from each of the 5 vegetation types were analyzed in order to determine whether the plant communities are accompanied by changes in soil fertility. Samples were collected in the open, away from direct shrub and tree influence, to preclude the possibility of obscuring general trends by local variations caused by differences in litter source.

The results, presented in Table 13, show that differences in soil fertility among plant associations are generally minor. As is expected, the greatest range in nutrient levels occurs in the A_1 horizon. The

A₁ samples collected under the Pinus ponderosa/Ceanothus velutinus and the Abies concolor/Ceanothus velutinus communities contained somewhat greater amounts of available P, exchangeable Ca, and total N than did the A₁ in the remaining three habitat types. These differences can be largely attributed to more abundant organic matter deposition and the fact that snowbrush litter contains relatively large amounts of these elements.

The fertility of the AC horizon apparently remains fairly uniform, regardless of the associated plant community. The greatest difference involves the higher level of available P within the Abies concolor/Ceanothus velutinus habitat type.

The Effects of Vegetative Cover on the Fertility of Lapine Soil

In the summer of 1957 a secondary study was initiated to determine the local variability of chemical properties of the Lapine soil. Since litter source might be expected to exert the dominant influence on microsite differences in soil fertility, the analysis of samples collected under various types of vegetative cover appeared to offer the most promising approach. Accordingly, a representative area within the Pinus ponderosa/Ceanothus velutinus community was selected and litter and soil samples were collected in the open and directly under ponderosa pine, snowbrush, and manzanita. Separate samples were taken of the A₁, AC and C horizons, as well as of litter. Two sets of samples were collected under each cover condition. The 32 litter and soil samples were analyzed for the following properties: soil

Table 13. Fertility of the Lapine A₁ and AC horizons under 5 plant communities
(Averages of 2 values)

	pH	Avail. P ppm	Exchang. K me/100 g	Exchang. Ca me/100 g	Exchang. Mg me/100 g	Cation Exchange Capacity me/100 g	Organic Matter %	Total Nitrogen %
<u>A₁ Horizon</u>								
<u>Pinus ponderosa/Purshia</u> <u>tridentata</u>	6.2	11.75	0.48	2.35	0.40	13.97	6.41	0.135
<u>Pinus ponderosa/Purshia</u> <u>tridentata-Arctostaphylos</u> <u>parryana</u>	6.4	8.75	0.46	3.60	0.67	13.58	5.36	0.105
<u>Pinus ponderosa/Ceanothus</u> <u>velutinus-Purshia tridentata</u>	6.0	15.00	0.44	3.50	0.58	15.61	6.87	0.160
<u>Pinus ponderosa/Ceanothus</u> <u>velutinus</u>	5.8	18.70	0.53	4.25	0.60	19.54	9.54	0.165
<u>Abies concolor/Ceanothus</u> <u>velutinus</u>	6.2	19.50	0.46	6.10	0.65	19.28	8.84	0.230
<u>AC Horizon</u>								
<u>Pinus ponderosa/Purshia</u> <u>tridentata</u>	6.3	6.25	0.30	1.20	0.45	7.22	1.57	0.030
<u>Pinus ponderosa/Purshia</u> <u>tridentata-Arctostaphylos</u> <u>parryana</u>	6.5	6.25	0.46	2.00	0.62	7.15	1.44	0.035
<u>Pinus ponderosa/Ceanothus</u> <u>velutinus-Purshia tridentata</u>	6.5	6.25	0.28	1.60	0.42	6.31	1.23	0.040
<u>Pinus ponderosa/Ceanothus</u> <u>velutinus</u>	6.3	6.75	0.36	1.40	0.45	6.56	1.23	0.040
<u>Abies concolor/Ceanothus</u> <u>velutinus</u>	6.2	9.00	0.39	2.00	0.55	7.48	1.17	0.030

reaction, amounts of available phosphorus, amounts of exchangeable potassium, calcium, and magnesium, cation exchange capacity, and percentages of total nitrogen and organic matter.

The results (Table 14) indicate significant differences in amounts of several of the nutrient elements among the different litter types. Both snowbrush and manzanita litter contained larger amounts of all nutrients except phosphorus than did litter collected in the open or under ponderosa pine. Snowbrush litter contained the largest quantities of nitrogen and calcium, while manzanita litter was slightly higher in potassium and magnesium. The amounts of Ca, K, and Mg in shrub litter were at least twice as high as the corresponding figures for ponderosa pine litter. The chemical composition of litter collected in the open is similar to that for the litter under ponderosa pine cover inasmuch as it consists largely of ponderosa pine needles.

Youngberg¹⁰ also found that snowbrush litter has unusually high amounts of nitrogen and calcium. There are indications that the greater supply of nitrogen may be due to the presence of symbiotic nitrogen-fixing bacteria contained in root nodules. Recent tests in California (95, 37) have demonstrated that root nodules on deerbrush (Ceanothus integerrimus) and chaparral whitethorn (Ceanothus leucodermis) apparently supply these species with additional nitrogen.

¹⁰ Unpublished data, Dept. of Soils, Oregon State College.

Table 14. The fertility of the Lapine soil in the open and under ponderosa pine, snowbrush, and manzanita (averages of two values)

	pH	Avail. P ppm	Exch. K me/100 g	Exch. Ca me/100 g	Exch. Mg me/100 g	Cation exchange capacity me/100 g	Organic Matter %	Total N %
<u>LITTER</u>								
Open	4.6	29.85	0.96	11.12	2.55	60.46	59.85	0.714
Under Ponderosa	4.4	47.98	0.73	12.28	2.71	45.10	60.38	0.710
Under Snowbrush	5.4	29.20	1.16	39.72	6.74	51.88	51.05	1.144
Under Manzanita	5.2	44.30	1.54	27.15	7.07	52.40	50.36	0.802
<u>A₁ HORIZON</u>								
Open	5.9	15.15	0.32	2.26	0.28	13.31	5.16	0.098
Under Ponderosa	6.0	33.75	0.49	2.32	0.53	15.68	4.66	0.077
Under Snowbrush	6.6	21.40	0.84	11.38	1.52	19.41	6.86	0.173
Under Manzanita	6.1	41.35	0.74	5.58	1.19	21.96	10.78	0.176
<u>AC HORIZON</u>								
Open	6.2	11.12	0.28	1.86	0.27	6.28	1.51	0.017
Under Ponderosa	6.5	9.45	0.33	3.39	0.53	9.99	2.00	0.037
Under Snowbrush	6.8	13.00	0.61	4.34	0.78	9.24	1.94	0.026
Under Manzanita	6.2	14.42	0.52	2.05	0.63	8.58	1.96	0.047
<u>C HORIZON</u>								
Open	6.4	2.12	0.20	1.29	0.31	6.62	0.36	Tr
Under Ponderosa	6.0	4.02	0.41	1.36	0.62	8.20	1.60	0.010
Under Snowbrush	6.1	3.70	0.74	3.05	0.94	6.58	0.50	0.018
Under Manzanita	6.0	2.66	0.38	1.44	0.44	5.58	0.36	0.012

Bottomley (11), in 1915, isolated bacteria from root nodules on snowbrush (Ceanothus velutinus) which appeared to be identical with Bacillus radicumicola, commonly found in legume nodules. Bacterial cultures, tested for their nitrogen fixing ability, showed gains in nitrogen content which were similar to those obtained with cultures of bacteria from Alnus root nodules.

The influence of litter source on soil fertility is quite marked in the A₁ and AC horizons, but becomes less noticeable in the C. Amounts of exchangeable Ca and Mg in the A₁ horizon under snowbrush and manzanita are more than twice as large as quantities in the open and under ponderosa pine. In addition, the levels of K and N in the A₁ are also somewhat higher under shrubs. The AC horizon apparently contains larger amounts of available P and K when situated under shrub cover. However, levels of the other nutrient elements show very little difference among cover types, with the possible exception of Ca which is still appreciably higher under snowbrush.

These results demonstrate that the fertility of the Lapine surface soil may vary appreciably within a small area and is influenced a great deal by litter source. Such a variability could be expected to cause considerable difficulty in any attempt to establish broad relationships between soil chemical properties and associated plant communities.

The generally higher fertility level under shrubs may have some effect in encouraging the survival and growth of coniferous tree seedlings in these locations. Although temperature and soil moisture

supply are undoubtedly of primary importance, it has been shown that an improved nutrient balance enables plants to utilize soil moisture more efficiently.

Carbon-Nitrogen Ratios in the Surface Horizons of the Lapine and Shanahan Soils

The amount of organic matter incorporated into pumice soils, or in any regosolic soil, is of utmost importance. It is important not only for its nutrient-supplying role, but also for its activity in hastening weathering and soil development. In addition, organic matter generally increases both the moisture holding and cation exchange capacities of the soil. As can be seen in Table 15, the surface soil throughout the study area contains fairly large quantities of organic matter. The amounts in the A₁ appear to be unusually high, especially in view of the relatively dry climate of the area.

The carbon-nitrogen ratio serves as a useful index of the general state of organic matter with respect to humification. The originally wide carbon-nitrogen ratio of fresh plant residues becomes progressively narrower as a result of microbial breakdown until a constant value, characteristic of the soil, is reached. The data presented in Table 15 indicate that the carbon-nitrogen ratios of the A₁ horizon do not differ greatly among the six plant communities. However, amounts of incorporated organic matter are apparently greater in the more mesic communities. The mean organic matter content of the A₁ horizon under the Abies concolor/Ceanothus velutinus association was 8.97%. This is

Table 15. Amounts of organic matter and total nitrogen and carbon-nitrogen ratios under 6 plant communities

Plant Community	% Organic Matter	% Total Nitrogen	C/N Ratio
<u>A₁ HORIZON</u>			
<u>Pinus ponderosa/Purshia tridentata</u>	3.78-6.93 ² 5.85 ¹	.083-.140 .120	17.5-37.9 28.8
<u>/Purshia tridentata/Festuca idahoensis</u>	3.00-7.69 4.89	.085-.130 .107	19.8-34.3 25.7
<u>/Purshia tridentata-Arctostaphylos parryana</u>	5.21-9.23 6.54	.097-.146 .118	27.5-36.7 31.9
<u>/Ceanothus velutinus-Purshia tridentata</u>	4.77-8.51 6.79	.117-.205 .151	23.0-34.3 26.3
<u>/Ceanothus velutinus</u>	4.00-12.45 7.57	.120-.210 .158	19.1-34.4 27.5
<u>Abies concolor/Ceanothus velutinus</u>	6.84-11.76 8.97	.117-.280 .200	22.0-35.4 26.9
<u>AC HORIZON</u>			
<u>Pinus ponderosa/Purshia tridentata</u>	0.80-1.75 1.31	.030-.035 .031	15.0-33.8 24.5
<u>/Purshia tridentata/Festuca idahoensis</u>	0.65-2.22 1.30	.026-.055 .039	14.5-23.4 18.8
<u>/Purshia tridentata-Arctostaphylos parryana</u>	0.98-1.60 1.28	.022-.043 .032	16.3-34.5 24.6
<u>/Ceanothus velutinus-Purshia tridentata</u>	0.96-1.74 1.25	.030-.063 .043	11.2-22.4 17.2
<u>/Ceanothus velutinus</u>	1.15-1.66 1.31	.030-.050 .041	13.3-25.6 19.3
<u>Abies concolor/Ceanothus velutinus</u>	1.00-1.49 1.35	.030-.037 .032	19.3-28.8 24.4

¹ Mean values are based on the results of 6 determinations with the exception of the Pinus ponderosa/Purshia tridentata/Festuca idahoensis habitat type where each mean represents 5 values.

² Range of values

almost twice the amount found in the Pinus ponderosa/Purshia tridentata/Festuca idahoensis habitat type. In conjunction with higher levels of organic matter, there is 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 under the various vegetation types show some minor differences: however, they are of insufficient magnitude to be considered significant.

Carbon-nitrogen ratios of the Lapine and Shanahan soils appear to be unusually high when they are compared to values for conventional mineral soils. A survey of unpublished data has indicated that the surface horizons of forested soils in Oregon possess carbon-nitrogen ratios ranging from approximately 10 to 25. The mean value, based on 48 determinations involving 10 soil series, was found to be 17. It will be noted that in no case was the carbon-nitrogen ratio of the Shanahan or Lapine A₁ horizon lower than 17.5. In addition, values higher than 30 were very common. Although the carbon-nitrogen ratios of the AC horizon are somewhat lower, they too are generally higher than those encountered in residual soils.

The surprisingly wide carbon-nitrogen ratios in these two pumice soils indicate that organic matter decomposition is proceeding at a rather slow rate. The reason for this situation is very difficult to explain, inasmuch as 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 (3, p. 420) 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.

General Fertility of the Lapine and Shanahan Soils

It may be stated as a broad generalization that both the Shanahan and Lapine soils possess medium to low fertility levels. Although it is difficult, if not impossible, to arrive at average figures for the nutrient contents of the two soils, analysis results have indicated that the Shanahan generally contains slightly larger quantities of several nutrient elements.

Both soils exhibit surprisingly high cation exchange capacities, especially in the surface horizons. Although part of this exchange capacity undoubtedly stems from the contribution of colloidal organic matter, the pumiceous material itself has considerable activity in this respect. Despite their very low clay content, the Lapine C horizons possess capacities on the order of 5 to 15 milliequivalents per 100 grams. As can be seen in Table 16, gravel-sized pumice particles possess cation exchange capacities which are more than twice as great as capacities found for the less than 2 mm fractions. The reason for this is, as yet, not completely understood. However, it appears that an extremely large specific surface due to the porous nature of the gravel-sized pumice may at least partially account for

Table 16. Lapine C horizon fertility

	pH	P ppm	K me/100 g	Ca me/100 g	Mg me/100 g	TN %	OM %	CEC me/100 g
C ₂ Pure	6.6	1.5	0.14	0.70	0.30	0.01	0.21	5.25
C ₂ Sl. Mixed	6.4	2.5	0.22	0.70	0.55	0.01	0.24	7.93
D	5.8	3.5	0.83	4.60	3.40	0.02	0.28	17.32
C ₁ (0-2 mm)	6.5	1.5	0.07	0.30	0.32	-	-	7.02
C ₁ (2-6 mm)	-	2.7	0.14	0.60	0.54	-	-	16.87
C ₂ (0-2 mm)	6.4	1.5	0.13	0.78	0.42	-	-	3.17
C ₂ (2-6 mm)	-	4.5	0.15	0.82	0.54	-	-	11.66

it. These results also suggest that the major portion of the cation exchange capacity in the C horizons is contributed by sand-sized particles or larger and that the small amounts of clay contribute very little to the total exchange capacity.

Complete fertility data for modal profiles of the Lapine and Shanahan soils are presented in Table 17. The data for the Lapine soil indicate that levels of P and N are considerably higher in the A₁ and AC horizons than in the C₁ and C₂. It will also be noted that the D horizon contains an amount of exchangeable K equal to that in the A₁, as well as greater quantities of exchangeable Ca and Mg. Although the nutrient requirements of ponderosa pine have not been definitely established, it would appear that the A₁ and AC horizons of the Lapine soil contain adequate amounts of the major nutrient elements. On the other hand, levels of available P and total N in the C and D horizons are quite low. The Shanahan soil contains larger amounts of exchangeable K and Mg than does the Lapine. In addition, since a raw, unweathered C horizon is generally absent, the Shanahan exhibits a less abrupt decrease with soil depth in amounts of P and N.

The very low amounts of P and N in the C₂ horizon of the Lapine suggests that perhaps an unfavorable fertility level restricts root growth in this portion of the profile. However, results of analyses of mixed zones in the C₂ apparently do not bear out this hypothesis. As can be seen in Table 16, mixed C₂ material exhibited only slight increases in amounts of P, K, and Mg, while quantities of N and Ca were equal to those in unmixed portions. These small differences

Table 17. Results of chemical analysis of Modal profiles of the Lapine and Shanahan soils
(samples comprised of particles less than 2 mm in diameter)

		pH	Avail. P ppm	Exchang. K me/100 g	Exchang. Ca me/100 g	Exchang. Mg me/100 g	Total N %	Organic Matter %	Cation Exchange Capacity me/100 g
LAPINE (under <u>Pinus ponderosa</u> / <u>Purshia tridentata</u>)									
(co. sandy loam)	A ₁	6.2	14.5	0.53	2.4	0.45	0.13	6.65	15.22
(gravelly loamy co. sand)	AC	6.1	7.5	0.23	1.0	0.35	0.03	1.40	7.61
(very gravelly co. sand)	C ₁	6.2	3.0	0.16	0.9	0.35	0.01	0.21	4.85
(gravelly co. sand)	C ₂	6.9	2.5	0.44	1.1	0.55	0.01	0.18	4.20
(fine sandy loam)	D	7.0	4.0	0.53	4.9	4.20	0.01	0.17	13.12
SHANAHAN (under <u>Pinus ponderosa</u> / <u>Purshia tridentata</u> / <u>Festuca idahoensis</u>)									
(loamy co. sand)	A ₁	5.6	11.7	0.64	5.2	1.11	0.12	5.77	18.20
(gravelly loamy co. sand)	AC	5.7	12.0	0.47	2.7	1.11	0.03	1.14	11.31
(fine sandy loam)	D ₁	5.9	4.9	0.56	4.7	3.47	0.02	0.32	12.93
(clay loam)	D ₂	5.8	1.7	0.94	7.5	12.40	0.02	0.46	37.47

between the pure and slightly mixed zones of the C₂ horizon with respect to amounts of P, K, and Mg do not appear to offer an adequate explanation for the more abundant root growth observed in mixed material. This does not, however, preclude the possibility that nutrient deficiencies limit root growth in the C₂ horizon, inasmuch as levels of secondary and trace nutrient elements in this layer are as yet unknown. Greenhouse experiments with alfalfa as the test plant have indicated that soil material from unmixed zones in the Lapine C₂ horizon is very markedly deficient in B and perhaps also in Mo.¹¹ It is possible that a lack of these trace elements may, to some extent, inhibit root growth in the C₂ horizon. Another factor which should not be overlooked, however, is the effect of the physical characteristics of this layer on root growth. Since the mixed zones are finer-textured, they may offer less resistance to root penetration.

Greenhouse Experiments with the Lapine C Horizon

Greenhouse experiments were initiated in the fall of 1958 in order to obtain more definite information on the fertility status of the Lapine subsoil. The general procedure consisted of determining the response of ponderosa pine seedlings to several nutrient elements applied at varying rates to unmixed Lapine C₁ and C₂ soil material. These trials were undertaken for two main reasons. First, the interpretation of laboratory data concerning amounts of available nutrients

¹¹ Data obtained by Dr. T. L. Jackson, Dept. of Soils, Oregon State College.

was uncertain, largely due to a lack of experience in dealing with pumice soils. These experiments were designed to measure the response of pine seedlings to additions of those elements shown to be deficient by laboratory analysis. Second, the observed limited root growth in unmixed C₁ and C₂ material prompted the desire to learn whether or not these horizons could support satisfactory tree growth with the addition of nutrients. Additional necessary information included the identification of those elements limiting tree growth, and rates of application for optimum growth of pine seedlings.

The experimental setup used is a modified composite design and all treatments were replicated three times. The design is similar to that described by Hader et al. (29) except that 8 additional treatments were applied, thus making a total of 23 rather than 15. By the use of this design it is possible to calculate response surfaces from a much smaller number of treatments than is necessary with complete factorials. The same basic experiment was carried out on both C₁ and C₂ horizon soil. For the C₁ horizon the 23 treatments consisted of various combinations of 5 levels each of nitrogen, phosphorus, and potassium, and in the case of the C₂ the variables were nitrogen, phosphorus, and calcium. The levels applied of the various nutrient elements are presented in Table 18. In addition to the 23 treatments involving N, P, and Ca, 6 treatments using 3 levels of N and S were also applied to C₂ horizon material (Table 18). This secondary experiment followed a 3 x 3 factorial experimental design in which 3 of the treatments (those not involving the addition of S) had already been

Table 18. Amounts and source of nutrients added to Lapine C₁ and C₂ horizon material for ponderosa pine greenhouse experiment

<u>C₁ HORIZON</u>	<u>Level No.</u>	<u>N ppm</u>	<u>P ppm</u>	<u>K ppm</u>
	1	0	0	0
	2	50	50	25
	3	100	100	50
	4	150	150	75
	5	200	200	100
<u>C₂ HORIZON</u>	<u>Level No.</u>	<u>N ppm</u>	<u>P ppm</u>	<u>Ca ppm</u>
	1	0	0	0
	2	50	50	150
	3	100	100	300
	4	150	150	450
	5	200	200	600
	3 x 3 Factorial	<u>Level No.</u>	<u>N ppm</u>	<u>S ppm</u>
		1	0	0
		2	100	50
		3	200	100

NUTRIENT SOURCES

N - NH_4NO_3

P - H_3PO_4

Ca - CaCl_2

K - KCl

S - $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$

applied in the main experiment. Levels of P and Ca were 100 and 300 ppm respectively for all 9 treatments.

The experimental soil was obtained from soil moisture sampling plot B where total depth of the pumice mantle is 48 inches and both the C₁ and C₂ horizons show very little mixing. In the latter part of October, 1958 approximately 1200 grams on an air-dry basis of either C₁ or C₂ material were placed in plastic pots. Twenty-five ponderosa pine seeds were then sown in each pot. During the second week in December, after the seedlings had germinated and become well-established, the nutrient treatments were applied in solution. The seedlings were irrigated at regular intervals with distilled water and all excess water drained into individual waxed cups so that leachate could be returned to the pots. During the last week of January, 1959 the seedlings were thinned to 12 per pot. In May of 1959 the majority of the seedlings ceased growing and set terminal buds. Very few of the seedlings broke dormancy during the following summer and fall. Since the photoperiod was uniformly kept at 16 hours, it appears that possibly the lack of a chilling treatment may have been responsible for the extended dormancy. The tops of all the seedlings were harvested during the final week of November, 1959 and their air-dry weights determined. At the time of harvesting the seedlings were approximately 13 months old.

The data presented in Table 19 clearly indicate that ponderosa pine seedlings growing in unmixed C₁ and C₂ material respond to additions of N and P. Despite the early onset of dormancy, the seedlings

Table 19. Observed weights of ponderosa pine seedling tops after 13 months growth in Lapine C₁ and C₂ horizon soil to which varying amounts of N, P, K, and Ca had been added

Treatment Level		Average Seedling Top Weight (gm.)	
C ₁	C ₂	C ₁	C ₂
N ₅ P ₁ K ₁	N ₅ P ₁ Ca ₁	.35	.37
N ₅ P ₅ K ₁	N ₅ P ₅ Ca ₁	.60	.58
N ₁ P ₅ K ₁	N ₁ P ₅ Ca ₁	.15	.15
N ₁ P ₁ K ₁	N ₁ P ₁ Ca ₁	.20	.17
N ₁ P ₁ K ₅	N ₁ P ₁ Ca ₅	.14	.15
N ₁ P ₅ K ₅	N ₁ P ₅ Ca ₅	.15	.16
N ₅ P ₅ K ₅	N ₅ P ₅ Ca ₅	.61	.50
N ₅ P ₁ K ₅	N ₅ P ₁ Ca ₅	.33	.33
N ₂ P ₂ K ₂	N ₂ P ₂ Ca ₂	.36	.37
N ₄ P ₂ K ₂	N ₄ P ₂ Ca ₂	.40	.43
N ₄ P ₄ K ₂	N ₄ P ₄ Ca ₂	.53	.55
N ₂ P ₄ K ₂	N ₂ P ₄ Ca ₂	.30	.39
N ₄ P ₂ K ₄	N ₄ P ₂ Ca ₄	.45	.44
N ₄ P ₄ K ₄	N ₄ P ₄ Ca ₄	.49	.70
N ₂ P ₄ K ₄	N ₂ P ₄ Ca ₄	.30	.37
N ₂ P ₂ K ₄	N ₂ P ₂ Ca ₄	.31	.35
N ₃ P ₃ K ₃	N ₃ P ₃ Ca ₃	.40	.45
N ₃ P ₃ K ₁	N ₃ P ₃ Ca ₁	.41	.51
N ₃ P ₃ K ₅	N ₃ P ₃ Ca ₅	.40	.43
N ₃ P ₁ K ₃	N ₃ P ₁ Ca ₃	.34	.34
N ₃ P ₅ K ₃	N ₃ P ₅ Ca ₃	.38	.43
N ₁ P ₃ K ₃	N ₁ P ₃ Ca ₃	.18	.19
N ₅ P ₃ K ₃	N ₅ P ₃ Ca ₃	.47	.52

grew rapidly for several months following the application of the nutrient treatments. Seedling response, as indicated by differences in height growth, became evident early in the course of the experiment. As Figure 29 shows, nutrient responses were quite marked 3 months after the treatment applications. In addition to an evident response to additions of N and P, it soon became apparent that there existed a very noticeable interaction with regard to these two nutrient elements. This is borne out by a consideration of observed seedling top weights (Table 19). It will be noted that weights for the controls ($N_1P_1K_1$ and $N_1P_1Ca_1$) were .20 and .17 grams respectively, and that additions of 200 ppm of P with no increase in N ($N_1P_5K_1$ and $N_1P_5Ca_1$) actually resulted in reduced yields in each case as evidenced by the weight figures of .15 grams. However, when N was added in conjunction with P there was a very noticeable seedling response to the latter element. For example, the average seedling top weights for the treatments $N_5P_1K_1$ and $N_5P_1Ca_1$ were .35 and .37 respectively. These figures were almost doubled to .60 and .58 grams with the application of 200 ppm of P along with an equal amount of N ($N_5P_5K_1$ and $N_5P_5Ca_1$). As may be seen in Table 19, the pine seedlings did not respond noticeably to additions of Ca and K.

Seedling top weights for the various treatments did not vary appreciably between plants growing on C_1 and C_2 horizon soil (Table 19). Therefore the results of this experiment suggest that these two layers possess nearly equivalent productive capacities, at least in so

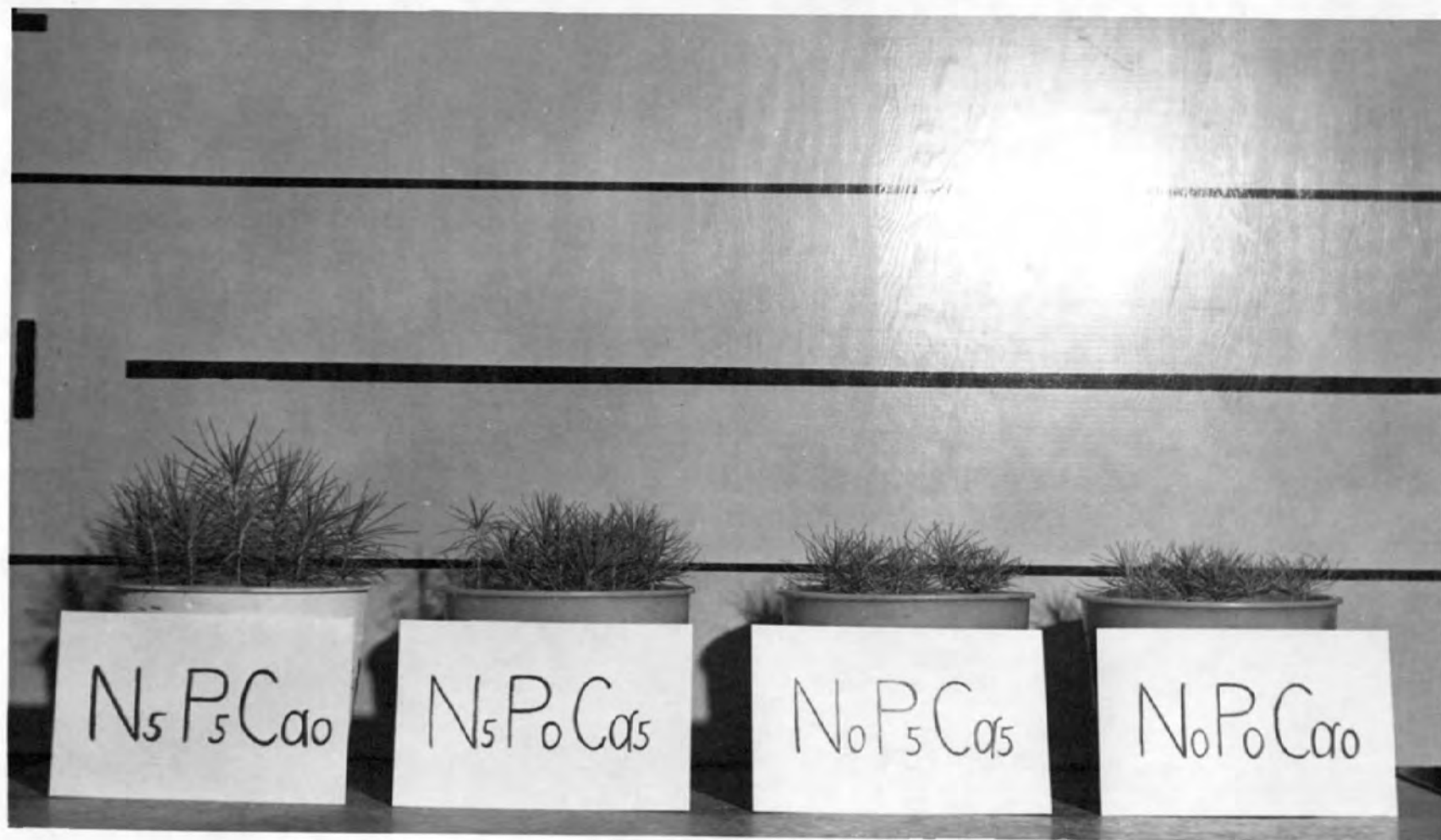


Figure 29. Four month-old ponderosa pine seedlings growing in Lapine C_2 horizon soil 3 months after the application of nutrient treatments. (Treatment levels are as follows: 0 = no addition, 5 = 200 ppm in the case of N and P, and for Ca, 600 ppm.)

far as the growth of ponderosa pine seedlings is concerned. This is, of course, not surprising when only soil chemical properties are considered, for both horizons are comprised of relatively unaltered pumice of uniform mineralogical composition. However, the two layers differ markedly with respect to at least one physical property, namely soil texture. As pointed out in the discussion of Lapine morphology, the C_1 horizon not only contains larger quantities of gravel-sized pumice than the C_2 , it also includes many angular particles, commonly 2 inches or more in diameter. It has been suggested that the coarse nature of the C_1 horizon may have an adverse effect on root development as a result of mechanical impedance. The results of this experiment do not tend to bear out this hypothesis, since the pine roots were apparently able to occupy the entire soil mass in the case of both horizons. It should be borne in mind, however, that the conditions under which this experiment was conducted bear little resemblance to conditions as they exist in the field.

Statistical analysis of the data in Table 19 is presented in Table 20. Both the linear and quadratic effects of N and P are statistically significant, as is the $N \times P$ interaction. The observed lack of seedling response to K and Ca is corroborated by the low, nonsignificant F values for the two elements. Regression coefficients were also calculated according to the procedure outlined by Hader et al. (29). These regression coefficients were then used to derive prediction equations. Equations for the yield of seedling tops (dry weight in grams) as a function of treatment levels of N, P, and K in

Table 20. Analysis of variance and prediction equations for Lapine C₁ and C₂ horizon greenhouse experiments

ANALYSIS OF VARIANCE

Source	Degrees of Freedom	C ₁ Horizon		C ₂ Horizon	
		Mean Squares	F Values	Mean Squares	F Values
Replications	2	.0006	.29	.0086	2.32
N	1	.8402	400.11**	.8372	226.27**
P	1	.0841	40.05**	.1248	33.74**
K(C ₁) Ca(C ₂)	1	.0029	1.37	.0052	1.40
N X P	1	.4763	226.80**	.2746	74.21**
N X K(C ₁)	1	.0026	1.26	.0038	1.04
N X Ca(C ₂)	1	.0077	3.66	.0003	.09
P X K(C ₁)	1	.0077	3.66	.0003	.09
P X Ca(C ₂)	1	.0368	17.53**	.1028	27.77**
N ²	1	.0094	4.49*	.0489	13.21**
P ²	1	.0012	.60	.0006	.17
K ² (C ₁) Ca ² (C ₂)	1	.0021		.0037	
Error	44				

** Significant at the 1% level

* Significant at the 5% level

PREDICTION EQUATIONS

To solve equations the following coded levels are substituted for the treatment levels:

Treatment Level:	1	2	3	4	5
Coded Level:	-2	-1	0	1	2

C₁ Horizon:

$$\text{Yield} = .406 + .076 N + .024 P - .004 K + .063 NP + .005 NK + .008 PK - .017 N^2 - .009 P^2 + .003 K^2$$

C₂ Horizon:

$$\text{Yield} = .483 + .076 N + .029 P - .006 Ca + .048 NP - .006 NCa + .002 PCa - .028 N^2 - .019 P^2 + .002 Ca^2$$

the case of the C_1 horizon, and N, P, and Ca for the C_2 are presented in Table 20. These equations also describe the response surfaces for yield.

A response surface obtained by solving the C_2 horizon prediction equation is shown in Figure 30. As might be expected, a similar response surface plotted for the C_1 horizon has an almost identical appearance. This graph vividly portrays the interaction which exists between N and P. It may easily be seen that at the lower rates of N the application of P, especially in fairly large quantities, resulted in a marked decrease in seedling growth. Conversely, at high rates of N application the pronounced stimulatory effect of P is readily apparent. The response surface also indicates that seedling growth would most probably be increased by the application of still larger quantities of N and P. It will be noted that even at the highest levels (200 ppm), the yield surface has not yet leveled off and is continuing in an upward direction.

The results of the 3×3 factorial experiment consisting of all possible combinations of 3 levels each of N and S are presented in Table 21. Once again the data clearly indicate the existence of an interaction between N and another nutrient element. In those cases where no N was applied the addition of S apparently had very little effect on seedling growth. However, the application of S in conjunction with 100 ppm of N noticeably increased yield; and the effect of S was even greater when the N level was at 200 ppm. At both the 100 and 200 ppm N levels seedling top weights reached a maximum for the

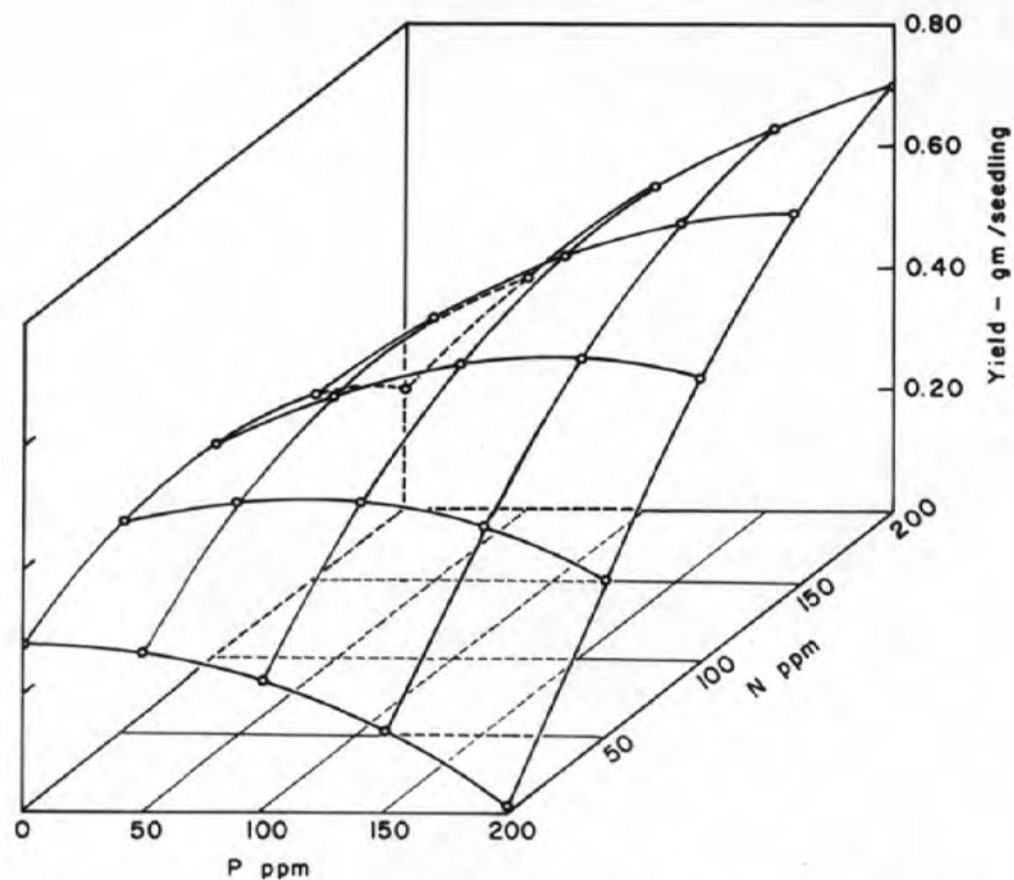


Figure 30. Response surface showing yield (air-dry weight of ponderosa pine seedling tops) as a function of various combinations of 5 levels each of N and P added to Lapine C₂ horizon material. For purposes of calculation Ca level was held at 300 ppm.

Table 21. Observed weights of ponderosa pine seedling tops after 13 months growth in Lapine C₂ horizon soil to which varying amounts of N and S had been added. (All pots received a blanket application of 100 ppm P and 300 ppm Ca.)

<u>Treatment Level</u>	<u>Average Seedling Top Weight (gm.)</u>
N ₁ S ₁	.19
N ₁ S ₂	.15
N ₁ S ₃	.17
N ₂ S ₁	.45
N ₂ S ₂	.53
N ₂ S ₃	.52
N ₃ S ₁	.52
N ₃ S ₂	.78
N ₃ S ₃	.75

ANALYSIS OF VARIANCE

<u>Source</u>	<u>Degrees of Freedom</u>	<u>Mean Squares</u>	<u>F Values</u>
N	2	.6077	164.24**
S	2	.0294	7.95**
N X S	4	.0196	5.30**
Error	44	.0037	

** Significant at the 1% level

L.S.D. at 1% level = .077

L.S.D. at 5% level = .058

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treatments involving the medium level of S (50 ppm). If a quadratic response curve is assumed, it may be concluded that the optimum rate of S application lies somewhere between 50 and 100 ppm.

Differences among treatments with respect to criteria other than seedling top weight were very apparent throughout the course of the experiment. For example, seedlings growing in soil to which no N had been added exhibited extremely sparse foliage having a pronounced chlorotic appearance. The most vigorous seedlings, as denoted by their very dark green foliage, were those growing in soils receiving additions of S, as well as P and N. Other readily discernable differences were, as previously mentioned, variations in height growth. Nevertheless, the determination of top weights appears to offer a most rapid and sensitive measurement of the response of ponderosa pine seedlings to variations in soil fertility and in this study was satisfactory in every respect.

SUMMARY AND CONCLUSIONS

A total of six plant communities occurring within the Pinus ponderosa and Abies concolor zones were identified in the study area. These plant groupings were characterized by means of measurements conducted in 35 representative stands. At each plot location the soil profile was investigated and samples collected for laboratory analysis. Soil moisture trends were followed in four plant communities during the summers of 1956 and 1957 through weekly collection of soil samples.

The interpretive vegetation units, listed in order of increasing effective moisture, 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
- (6) Abies concolor/Ceanothus velutinus

Since annual precipitation is dependent largely on elevation, the plant groupings as listed are also arranged in the approximate order of their occurrence with respect to elevation (from 5,000 to 6,200 feet). With the exception of the Pinus ponderosa/Ceanothus velutinus community these units were considered to be comprised of climax vegetation. The Pinus/Ceanothus community was interpreted as

constituting a seral stage within the Abies concolor/Ceanothus velutinus habitat type. All climax associations were classified as edaphic climaxes. The Pinus ponderosa/Purshia tridentata/Festuca idahoensis association is restricted to areas of Shanahan loamy coarse sand, while the remaining five units all occur on soils belonging to the Lapine series. Both soils are Regosols developed on aeolian pumice deposits.

In all Lapine soil areas the amounts of grass and forb cover were extremely low and the number of species was correspondingly small. Although in some respects this simplifies vegetation classification, in another sense it causes considerable difficulty as a result of the relative obscurity, and in some cases near absence, of species which can be considered characteristic of an association. 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. Fortunately the distribution of shrub species in the study area is such that their relative abundance generally offers a fairly reliable means of identifying the various communities. The Pinus ponderosa/Purshia tridentata/Festuca idahoensis association and areas of Shanahan soil are rather easily recognized as a result of the comparatively dense stands of Festuca idahoensis, a species seldom encountered on Lapine soil.

Each plant community was found to be accompanied by changes in timber stand characteristics, as well as shifts in species composition of the understory vegetation. The Pinus ponderosa/Purshia tridentata

association is, in the area studied, characterized by widely spaced mature and nearly mature ponderosa pines with very little advance regeneration. Ponderosa pines growing in areas of Pinus ponderosa/Purshia tridentata/Festuca idahoensis are generally of low vigor and stagnated stands of saplings are common. With increasing effective moisture, plant communities on the Lapine soil include greater amounts of tree reproduction and are accompanied by a progressively more dense arborescent cover. White fir (Abies concolor) is present in limited quantities in the Pinus ponderosa/Ceanothus velutinus association and gains dominance in the Abies concolor/Ceanothus velutinus type.

The Lapine soil, generally exhibiting A₁, AC, C₁, C₂, and D (buried soil) horizons, was found to vary considerably in morphological characteristics. A portion of these variations, such as differences in depth to underlying material, occurred independently of plant cover and were due largely to location with respect to distance from the pumice source. Other profile characteristics influencing plant root distribution, namely thickness of the gravelly C₁ horizon and the amount of mixing of C₂ material with the buried soil, although subject to considerable local variation, showed some apparent correlations with plant communities. Mean values for the various vegetation units indicated that the Lapine soil under the Pinus ponderosa/Purshia tridentata and Pinus ponderosa/Ceanothus velutinus-Purshia tridentata associations had comparatively thick C₁ horizons (7.0 and 10.5 inches respectively) and the smallest amounts of mixing in the C₂ (both 18%). The soil associated with the Pinus ponderosa/Ceanothus velutinus

community was at the opposite end of the scale, exhibiting a mean C₁ horizon thickness of 3.3 inches and a C₂ horizon containing an average of 75% mixed material. Plant roots were generally well distributed throughout the C₂ horizon in the case of the latter community, whereas in soils possessing a thick C₁ and little mixing in the C₂ plant roots are restricted largely to the A₁, AC, and D horizons. Other than changes in the texture of the C₂ horizon brought about by mixing, the particle size distribution of the Lapine soil was found to be fairly uniform among the 5 plant communities.

Soil moisture studies indicated that depth and time of onset of soil drought are important factors in controlling the distribution of plant communities within the study area. An apparent exception was found in the case of the Pinus ponderosa/Purshia tridentata habitat type where the Lapine C horizons retained appreciable quantities of available soil moisture throughout the growing season. This was attributed to the scarcity of plant roots in these layers. It was also found that amounts of soil moisture in the A₁ and AC horizons were often depleted to the permanent wilting percentage 1 to 3 weeks earlier in the open than under shrub cover.

Investigations conducted in the Pinus ponderosa/Ceanothus velutinus community demonstrated that the fertility of the Lapine surface soil is strongly influenced by litter source. Amounts of K, Ca, Mg, and N contained in A₁ horizon were shown to be very much greater when located under Ceanothus velutinus and Arctostaphylos

parryana litter than in areas where the covering of litter consisted primarily of Pinus ponderosa needles. Despite this local variability, there were indications that the more mesic plant communities are accompanied by higher levels of several nutrient elements in the A₁ horizon. For example, the A₁ horizon under Pinus ponderosa/Ceanothus velutinus and Abies concolor/Ceanothus velutinus vegetation contained appreciably greater quantities of available P, exchangeable Ca, and total N. These differences appeared to be confined to the A₁ horizon, however, as levels of most nutrient elements remained fairly constant in the AC horizon, regardless of associated vegetation. Carbon-nitrogen ratios of Lapine and Shanahan A₁ and AC horizons failed to demonstrate any consistent correlation with plant groupings. However, values were found to be very much higher than those encountered in the surface horizons of zonal forested soils, probably due to unusually slow rates of organic matter decomposition. Organic matter content of the Lapine A₁ horizon was considerably higher under the more mesic plant communities. For example, the A₁ horizon contained an average of 5.85% organic matter in the Pinus ponderosa/Purshia tridentata association, as compared to an average of 8.97% under Abies concolor/Ceanothus velutinus vegetation.

Ponderosa pine seedlings growing in the greenhouse on Lapine C₁ and C₂ horizon material showed a significant response to applications of nitrogen, phosphorus, and sulfur. In all cases nitrogen appeared to be the most important limiting nutrient, inasmuch as the seedlings did not respond to additions of phosphorus or sulfur unless they were

accompanied by an application of nitrogen. Earlier tests had indicated that the C₂ horizon may be markedly deficient in boron and also to some extent, in molybdenum. It was suggested that perhaps a lack of essential nutrient elements may be an important factor in causing the low root concentration observed in the Lapine subsoil.

Several factors have necessitated the consideration of soil-plant relationships reported in this thesis as somewhat tentative. Probably the most important of these is the substantial variation in soil characteristics within a small area, especially with regard to the Lapine. Therefore, it is extremely difficult, if not impossible, to precisely define correlations between soil properties and associated plant communities, in that local variations may be of greater magnitude than are differences over wide areas. Several examples of soil features which varied markedly within a small area are thickness of the 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 all the more surprising in view of the uniformity of its parent material.

Another factor causing difficulty in the interpretation of data is the fact that in many cases the number of observations was limited. In addition, the study was confined to a 60,000 acre area; and although it is believed to be representative of a large portion of the central Oregon pumice region, variations with respect to vegetative and soil characteristics are to be expected, especially in areas of

more abundant precipitation. Consequently, results of this study are probably not applicable over the entire range of the Lapine and Shanahan soil series, but rather only in those areas with approximately equivalent climatic conditions.

Some Practical Applications in Forest Management

The identification, characterization, and mapping of vegetation units in conjunction with standard soil surveys is especially important in areas of immature soils. Soils, such as pumice soils, which are comparatively young tend to exhibit little change over large areas in those soil characteristics which serve 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 environmental factors important in tree growth. In the present study five distinct plant communities were found to occur on the Lapine soil, each one indicative of a different effective environment. However, soils supporting stands of these communities were frequently assigned to the same soil mapping unit as well. For example, three macroplots in the Pinus ponderosa/Purshia tridentata community, three in the Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana, one plot in the Pinus ponderosa/Ceanothus velutinus-Purshia tridentata, two within the Pinus ponderosa/Ceanothus velutinus, and three macroplots in the Abies concolor/Ceanothus velutinus community were all located on soil mapped as Lapine loamy coarse sand moderately deep to

underlying material on a 3 to 25% slope. A situation such as this demonstrates quite conclusively that in these areas a soil map alone does not furnish an adequate basis for the stratification necessary in intensive forest management. Consequently, the understory vegetation assumes a most important role, inasmuch as it serves as a more sensitive indicator of changes in the many variables regulating tree growth.

A map showing the distribution of the various plant communities within the Antelope Unit has been prepared. This information is currently being utilized by Weyerhaeuser Company as an aid in formulating management plans. For example, one of the more important timber stand characteristics that was found to vary with the plant community was the amount of advance regeneration. Since the volume of timber which can be safely removed in logging depends to a large extent on amounts of young growing stock present, the plant communities provide a basis for the broad stratification of cutting intensities. In addition, information regarding the association of advance regeneration and shrub species indicates that brush control should be an operation to release existing regeneration rather than to facilitate regeneration following logging.

A knowledge of the relationships between the vegetation and soil properties may also be of practical value. It would be expected, for example, that survival of planted seedlings would be poorer within the Pinus ponderosa/Purshia tridentata habitat type than in areas of Pinus ponderosa/Ceanothus velutinus vegetation because of the differences in

the thickness of the C₁ horizon and rates of soil moisture depletion in the surface layer. The value of shrubs in improving soil fertility should also be considered before any widespread eradication program is undertaken. The absence of roots from Lapine C₁ and C₂ horizons in Pinus ponderosa/Purshia tridentata areas and the consequent surplus of available soil moisture suggests that seedling survival and growth rate might be increased by measures designed to encourage root growth in these layers. Possibilities are the addition of fertilizers to the C horizon or the manipulation of the soil, perhaps by deep plowing, in order to increase amounts of mixing.

Certain of the plant groupings appear to be accompanied by a high degree of susceptibility to several forest pests. Examples are the Pinus ponderosa/Purshia tridentata/Festuca idahoensis association which is accompanied by high bark beetle hazard and the relationship between large scale mistletoe infestation and the Pinus ponderosa/Ceanothus velutinus community. Cuttings in these areas will of necessity be aimed at eliminating high beetle risk trees and possible mistletoe seed sources.

The Pinus ponderosa/Ceanothus velutinus and Abies concolor/Ceanothus velutinus communities each present a separate problem to the forest manager. Despite the fact these two plant groupings occupy sites comprising a single habitat type (i.e. an area where potentially only one climax association will dominate), they differ appreciably in tree species composition. This difference, a result of a difference in successional status, is perhaps best explained by variations in the

time and severity of past disturbances. Although the climax tree species in the Pinus ponderosa/Ceanothus velutinus community is white fir, these sites are very productive for ponderosa pine and perhaps may be reserved for the production of this species for at least several rotations through judicious cutting practices including the removal of large white fir seed trees. On the other hand, in areas of Abies concolor/Ceanothus velutinus vegetation succession has advanced to the stage where the climax tree species, white fir, has gained dominance. In this vegetation unit it would perhaps be more advantageous to manage for the climax species, rather than to attempt conversion to stands of ponderosa pine. Such attempts would present more management problems than would the maintenance of ponderosa pine as the dominant tree species in the Pinus ponderosa/Ceanothus velutinus community, even though it is a seral species in both locations. Lodgepole pine is also more aggressive in this habitat type, as well as in the Pinus ponderosa/Purshia tridentata-Arctostaphylos parryana, and timber marking procedures will have to be designed accordingly in order to minimize its occurrence.

These are but a few of the practical uses which can be made of soil-vegetation information in intensive land management. Other aspects, here completely ignored, include range management, watershed management, and forest engineering. However, a more complete discussion would be beyond the scope of this study.

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APPENDIX

APPENDIX

Common and Scientific Names of Species Mentioned in the Text

<u>Scientific Name</u>	<u>Common Name</u>
<u>Trees</u>	
<u>Abies concolor</u> Lindl.	white fir
<u>Abies lasiocarpa</u> (Hook.) Nutt.	alpine fir
<u>Juniperus occidentalis</u> Nutt.	Sierra juniper
<u>Larix occidentalis</u> Nutt.	western larch
<u>Picea engelmanni</u> (Parry) Engelm.	Engelmann's spruce
<u>Pinus cembroides</u> Zucc.	pinyon pine
<u>Pinus contorta</u> Dougl.	lodgepole pine
<u>Pinus lambertiana</u> Dougl.	sugar pine
<u>Pinus ponderosa</u> Laws.	ponderosa pine
<u>Pinus radiata</u> D. Don	Monterey pine
<u>Populus tremuloides</u> Michx.	quaking aspen
<u>Pseudotsuga menziesii</u> (Mirb.) Franco	Douglas-fir
<u>Salix</u> sp. [Tourn.] L.	willow
<u>Thuja plicata</u> Don	western red cedar
<u>Tsuga heterophylla</u> (Raf.) Sarg.	western hemlock
<u>Shrubs</u>	
<u>Arctostaphylos nevadensis</u> Gray	pinemat manzanita
<u>Arctostaphylos parryana</u> var. <u>pinetorum</u> (Rollins) Wies. & Schr.	manzanita
<u>Arctostaphylos uva-ursi</u> (L.) Spreng.	bearberry

<u>Artemisia tridentata</u> Nutt.	big sagebrush
<u>Ceanothus integerrimus</u> H. & A.	deerbrush
<u>Ceanothus leucodermis</u> Greene	chaparral whitethorn
<u>Ceanothus velutinus</u> Dougl.	snowbrush
<u>Chrysothamnus viscidiflorus</u> (Hook.) Nutt.	Douglas rabbitbrush
<u>Haplopappus bloomeri</u> (Gray) H.M. Hall	rabbitbrush goldenweed
<u>Physocarpus malvaceus</u> (Greene) Kuntze	mallow ninebark
<u>Prunus emarginata</u> (Dougl.) Walp.	bitter cherry
<u>Purshia tridentata</u> (Pursh) D.C.	bitterbrush
<u>Ribes viscosissimum</u> Pursh	sticky currant
<u>Spiraea</u> sp. [Tourn.] L.	spiraea
<u>Symphoricarpos rivularis</u> Suks.	snowberry

Grasses and Sedges

<u>Agropyron spicatum</u> (Pursh) Scribn. & Sm.	bluebunch wheatgrass
<u>Agrostis scabra</u> Willd.	bentgrass
<u>Calamagrostis rubescens</u> Buckl.	pinegrass
<u>Carex geyeri</u> Boott.	elk sedge
<u>Carex nebraskensis</u> Dew.	Nebraska sedge
<u>Carex praeegracilis</u> Boott.	meadow sedge
<u>Carex rossii</u> Boott.	Ross sedge
<u>Danthonia intermedia</u> Vas.	timber danthonia
<u>Deschampsia caespitosa</u> (L.) Beauv.	tufted hairgrass
<u>Festuca idahoensis</u> Elm.	Idaho fescue
<u>Juncus</u> sp. [Tourn.] L.	rush

<u>Koeleria cristata</u> (L.) Pers.	prairie Junegrass
<u>Poa</u> sp. L.	bluegrass
<u>Sitanion hystrix</u> (Nutt.) J.G. Sm.	bottlebrush squirreltail
<u>Stipa occidentalis</u> Thurb.	western needlegrass

Forbs

<u>Achillea lanulosa</u> Nutt.	western yarrow
<u>Agoseris</u> sp. Raf.	agoseris
<u>Antennaria corymbosa</u> E. Nels.	corymbose pussytoes
<u>Antennaria geyeri</u> Gray	pinewoods pussytoes
<u>Apocynum androsaemilifolium</u> L.	spreading dogbane
<u>Arabis rectissima</u> Greene	rockcress
<u>Aster campestris</u> Nutt.	aster
<u>Balsamorhiza sagittata</u> (Pursh) Nutt.	arrowleaf balsamroot
<u>Chimaphila umbellata</u> (L.) Nutt.	princespine
<u>Collinsia parviflora</u> Dougl.	littleflower collinsia
<u>Cryptantha affinis</u> (Gray) Greene	cryptantha
<u>Delphinium menzeisii</u> Hook.	Menzies larkspur
<u>Epilobium angustifolium</u> L.	fireweed
<u>Equisetum</u> sp. L.	horsetail
<u>Eriophyllum lanatum</u> (Pursh) Forbes	wooly eriophyllum
<u>Fragaria cuneifolia</u> Nutt.	strawberry
<u>Fritillaria autropurpurea</u> Nutt.	purplespot fritillary
<u>Galium</u> sp. L.	bedstraw
<u>Gayophytum diffusum</u> T. & G.	bigflower groundsmoke

<u>Geranium</u> sp. [Tourn.] L.	geranium
<u>Hieracium</u> <u>cynoglossoides</u> Arv.-Touv.	houndstongue hawkweed
<u>Horkelia</u> <u>fusca</u> Lindl.	tawny horkelia
<u>Lactuca</u> sp. [Tourn.] L.	wild lettuce
<u>Linanthus</u> <u>ciliata</u> (Benth.) Greene	gilia
<u>Lomatium</u> <u>triternatum</u> (Pursh) C. & R.	nineleaf lomatium
<u>Lupinus</u> <u>caudatus</u> Kell.	tailcup lupine
<u>Lupinus</u> <u>minimus</u> Dougl.	least lupine
<u>Madia</u> <u>minima</u> (Gray) Keck	tarweed
<u>Mentzelia</u> <u>albicaulis</u> Dougl.	whitestem mentzelia
<u>Microseris</u> <u>nutans</u> Schultz	nodding microseris
<u>Paeonia</u> <u>brownii</u> Dougl.	Browns peony
<u>Penstemon</u> sp. [Mitch.] Ait.	penstemon
<u>Phacelia</u> <u>heterophylla</u> Pursh	varileaf phacelia
<u>Phlox</u> <u>gracilis</u> (Hook.) Greene	phlox
<u>Pyrola</u> <u>picta</u> Smith	whitevein pyrola
<u>Ranunculus</u> <u>occidentalis</u> Nutt.	western buttercup
<u>Senecio</u> <u>integerrimus</u> Nutt.	lambstongue groundsel
<u>Smilacina</u> <u>sessilifolia</u> (Baker) Nutt.	false Solomonseal
<u>Taraxacum</u> <u>officinale</u> L.	dandelion
<u>Trifolium</u> <u>longipes</u> Nutt.	longstalk clover
<u>Viola</u> <u>purpurea</u> Kell.	goosefoot violet