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# THE VEGETATION OF THE BIGHORN MOUNTAINS OF WYOMING IN RELATION TO SUBSTRATE AND CLIMATE

by

© DON GARDNER DESPAIN

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled The Vegetation of the Bighorn Mountains of Wyoming in Relation to Substrate and Climate submitted by Don Gardner Despain in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

The Bighorn Mountains lie in the north-central portion of Wyoming at approximately $45^{\circ}$ N and $108^{\circ}$ E. The anticlinal form of the range provides comparable areas of equal altitude underlain by sedimentary and granitic rocks which facilitates study of the effect of substrate on the vegetation of the Range. Using geologic and timbertype maps of the Mountains it is shown that *Pinus contorta* forests are nearly restricted to granitic areas and may form a climax forest zone in these areas. In sedimentary areas *Pseudotsuga menziesii* performs a successional role similar to that of *Pinus contorta*.

The forest vegetation is described generally from 31 stands sampled. The typical Rocky Mountain zonal sequence is followed, with *Picea engelmannii*-*Abies lasiocarpa* forests occurring just below timberline followed by *Pinus contorta* forests, *Pseudotsuga menziesii* forests and *Pinus ponderosa* forests in that order.

The west side of the Mountains is drier than the east, the source of moisture to the west being blocked by the Rocky Mountains. This leaves only the grasslands to the north and east as sources of moisture, resulting in peak rainfall in the spring months and very little during summer.

Soil from each of the stands was analyzed. Those soils formed from shale and limestone are similar in many characteristics whereas those from granite are quite different.

Data on forest-meadow boundaries are presented that show different boundary characteristics for different forest types.

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## TABLE OF CONTENTS

Page

LIST OF TABLES

## LIST OF FIGURES

# INTRODUCTION

As one goes from the base of a mountain range to its summit a number of environmental conditions change e.g., air temperature, atmospheric pressure, air density, annual precipitation, time of snow melt, composition of the air, insolation, relative humidity, etc. Because of these changes in environment and the concomitant change in vegetation, mountains have been a popular subject for ecological studies (e.g. Shreve 1915, Daubenmire 1943, Whittaker 1960, Whittaker and Niering 1965, Fonda and Bliss 1969). Some of these variables, such as air density and temperature, change continuously from base to summit and others, as may happen with geologic substrate, change abruptly. Aspect occurs as an almost random pattern of mosaics whereas geologic substrates and tectonics may form a repeating series of mosaics. The resulting vegetational pattern is a complex one on any range, resulting from the various magnitudes, directions and relationships of the variables. Where one variable is strongly dominant the pattern is simple and easily correlated with that variable but where this is not the case correlation is not easily determined. Thus the vegetation of an area is a mosaic of species forming variable communities in response to a variable factor complex. The research reported here is an attempts to describe and explain some of the main mosaics.

Daubenmire (1943) reviewed the literature concerning the Rocky Mountains presenting a good overall picture of their general vegetational and environmental characteristics. Since then a number of papers have been published concerning various portions of the Rocky Mountains (Hayward 1945, Daubenmire 1946, 1952, Billings 1951, Oosting and Reed 1952, Marr 1961, Langenheim 1962, Patten 1963, Whittaker and Niering 1965). Those in the vicinity of the Bighorn Mountains include the description of spruce-fir forests of the Medicine Bow Mountains in south-central Wyoming (Oosting and Reed 1952), the description of a small portion of Jackson Hole along the northwestern border of Wyoming (Reed 1952), a classification of habitat types on the Wind River Mountains in west-central Wyoming (Reed 1969) and to the northwest of the Bighorns, Patten (1963) described vegetation and environmental patterns on a portion of the Madison Range.

The Bighorn Mountains lie to the east of the Rocky Mountain chain and are isolated from them. They are anticlinal in form with large areas of granite and sedimentary rocks at comparable elevations. Most areas below timberline are easily accessible and timbertype maps and geologic maps of the Range are available. All these factors provide an excellent opportunity to study the influence of many ecological factors in a relatively small area.

However, very little attention has been paid the Bighorn Mountains from a botanical point of view. Range surveys have been conducted (Beetle 1956, Fisser 1964). Hurd (1961) described the _Festuca idahoensis_ grasslands of the Bighorns. Aven Nelson made a few stops in the Bighorns on some of his collecting trips (Field notes at U. of Wyo.) and Rydberg (1915), Daubenmire (1943) and Cary (1917) mention the Bighorn Mountains but their comments indicate little time was spent there. Porter has made collections in many portions of the Bighorns (Personal communication). Theses concerning ecological aspects of some of the plant communities of the Bighorns have been written. Lofgren (1956) described the flora of an alpine region near Cloud Peak. Rolston (1961) worked on the subalpine forests, Miller (1964) described the _Cercocarpos ledifolius_ communities and King (1967) provides a description of _Pinus flexilus_ communities.

Those questions that were the object of this investigation were: 1) What influence does the rock type have on the vegetation; 2) how do soils influence the vegetational pattern and what soil factors are most influential; 3) what are the climatic patterns, what causes them and how are they influential; and 4) what are the general characteristics of the vegetational units on the Bighorns and how do they relate to other Rocky Mountain areas.

## DESCRIPTION OF AREA

### Location

The Bighorn Mountains lie near the center of Wyoming's northern border in rough NNE to SSE direction, concave slightly to the NE. They dip into the basal plain at about 45° N latitude at the north and about 43° 30' N latitude at the south end. They are bordered on the west by the Big Horn Basin and on the east by the Powder River Basin. The Pryor Mountains rise off the northwest corner and the southwest corner merges with the Owl Creek Range. This low Range forms the only connection with the main Rocky Mountain chain to the west. From the river basins on both sides, elevation 900 to 1220 m, the Mountains rise to a height of 4018 m at Cloud Peak. At 2400 to 2800 m, a subsummit surface occurs from which the high granite peaks arise.

### Geology

Though there is evidence of an ancestral range during Permian time (Demorest 1941), the present range was uplifted during the Laramide revolution, probably during Eocene times before the uplift of the Black Hills to the east but after the rise of the Beartooth, Absororka, and Wind River Mountains to the west (Sharp 1948). The uplift did not occur all at once but is the result of various stages or pulses (Sharp 1948).

The Bighorn Mountains were formed from the uplift of three large basement blocks resulting in a large, somewhat crescent shaped anticlinal massif near the edge of the cordilleran geosyncline (Bucher et al. 1933, Wilson 1938, Thom and Bucher 1953). The central block was tilted higher on the east side producing sharply dipping strata on the east flank but more gently sloping strata on the west. The two end blocks were tilted higher on the west producing the opposite effect (Wilson 1938, Thom and Bucher 1953). The northern and southern blocks are still overarched by sedimentary layers and reach present heights of 2700-3000 m in the north and 2400-2700 m in the south. The central block was lifted higher and it is here that the large granite peaks, such as Cloud Peak reaching 4018 m, are found.

The sedimentary layers remaining on the Range and comprising the flanks consist of Paleozoic shale, limestone, and dolomites. Resting on the granite is a thin discontinuous layer, the coarse Flathead sandstone 82-112 m thick. Overlying this is the Gros Ventre shale, a green shale 122-137 m thick, the upper portion of which is largely interbedded with limestone. These beds were deposited during mid to late Cambrian time in an eastward advancing sea. Upon this rests the Bighorn dolomite and limestone (92 m) deposited in seas during Ordovician time followed by 76-336 m of Madison limestone deposited during the Mississippian. The Amsden formation follows with 61-

112 m of red shale and white sandstone deposited during Mississippian and Pennsylvanian. The Tensleep sandstones deposited by wind and water during the Pennsylvanian are found around the flank of the Range forming many of the flatirons. They can also be found in some areas on top of the southern block (Darton 1906, Wilson 1938, Demorest 1941).

The beds deposited during the Mesozoic have been eroded away from the Mountains and are present only as hogbacks and in pediments around the Mountains. There remain in some areas, on the subsummit surface, some Tertiary gravels probably of Oligocene age (Sharp 1948).

The present relief is a combination of uplift and downgrading of the basins on both sides since the Tertiary (Macking 1937). This combination of sediments and uplifting has produced a massif with an exposed granite core surrounded by sedimentary rocks which sometimes dip almost vertically and sometimes slope more gently into the plains below. The shales produce rounded bald ridges, slumps, and landslides. The dolomite and limestones allow the formation o f steepwalled canyons around the edge of the Bighorns and bluffs or cliffs on the summit.

During the Pleistocene, glaciation occurred only in the higher valleys of the central portion and none of the glaciers reached the base of the Range. The lowest one reached 1980 m on the west side of the Mountains (Mathes 1900, Salisbury 1906). Glaciers covered twice as much area on the west side as on the east but the glaciers present on the Range in 1906 were on the east side (Salisbury 1906). Although there was no cap glacier, most of the surfaces between glaciers were covered with névé during much of the Pleistocene (Mathes 1900). It is in this area that Mathes (1900) discovered that ice and snow had to accumulate to a depth of 30-45 m before movement of a glacial nature would occur.

## Climate

The only Weather Bureau station in the Bighorns is located at Burgess Junction at 2500 m elevation on the northern third of the Mountains. It was established in 1960. Some storage gages have been in operation for a few years and the Soil Conservation Service has several snow courses in the Mountains. These, together with long established stations in the valleys on both sides, make it possible to generally characterize the climate.

In the Bighorn River Basin near the west side of the Mountains, average yearly rainfall ranges from 125 to 250 mm. Temperature ranges from -40 to 40 C with a mean annual temperature of 5 C. Precipitation minus potential evapotranspiration reaches a minimum of -125 mm in July and -330 to -410 mm for the year (U.S. Weather Bureau 1962).

In the Powder River Basin near the east side, precipitation ranges from 330 to 410 mm per year. Temperature ranges from -40 C to +40 C. The mean annual temperature is about 7 C. Precipitation minus potential evapotranspiration reaches -110 mm in July and for the year is around -200 to -250 mm. Frost free periods for both sides of the Mountains are 110 to 130 days (U.S. Weather Bureau 1962).

Between these basins the Bighorn Range has a climate typical of increases in elevation. At Burgess Junction rainfall increases to 510 to 760 mm per year, mean maximum temperature decreases to 7.8 C and mean minimum to -5.5 C. Frost can occur and snow fall during any month (U.S. Weather Bureau unpublished data). Compared with other Rocky Mountain areas, the Bighorns are relatively dry and have a unique monthly distribution of precipitation with a prominent peak in May (Baker 1944).

## Soils

The soils have not been intensively studied. However, Dunnewald *et al*. (1939) and Thorp *et al*. (1939) described in a general way the soils of Johnson and Sheridan Counties which included portions of the east side of the Bighorns. Dunnewald (1929) indicated that the west-face of the Bighorns had a zonation of soils similar to that of the soil regions of the U.S. and described an increase of available phosphorus with increase in elevation and the concurrent change in climate. Thorp (1931) noted the corresponding variation in the soils and climate from the Big Horn Basin across the Bighorns and into the Powder River Basin. He compared them with the existing U. S and Russian classification of world soils and found most of the larger categories represented. Development of the B horizon increases and the accumulation of lime decreases with increasing moisture availability.

## History

The presence on the Mountains of such ancient artifacts as medicine wheels, tepee rings and numerous arrow points indicates that man has long made use of the resources of this area. Findings of a survey team from the Smithsonian Institute in caves of the Bighorn Canyon, prior to its flooding by the reservoir of the Yellowtail Dam, show the presence of man in the area as long as 9000 years ago (Husted 1969). Archeological evidence indicates that there was probably a separate culture adapted to life in the mountains of the area and that these cultures made use of the resources of the mountains in both hunting and food gathering (Wedel, Husted and Moss 1968).

In the early 1800's, European man came to the Bighorns in search of valuable beaver pelts that were responsible for most of the early exploration of western North America. Such men as John Colter, Manuel Lisa, Wilson Price Hunt with the Astorians and other outstanding men from this period visited the slopes of the Bighorns (Coutant 1899), the first being F. A. Larocque in 1805 (Larocque 1910) or possibly LaVerendrye in 1743 (Smurr 1952). The Big Horn River was one of the routes used to carry pelts to the Yellowstone River and then to St. Louis.

In the 1860's and 70's, Indians defending what they termed their best hunting grounds along the east flank of the Bighorns waged war against the white intruders causing several military forts to be built (Coutant 1899). This culminated in Custer's Last Stand on the Little Bighorn River, a stream that heads in the northern section of the Bighorn Mountains.

During this same period, buffalo hunters were busy eliminating the large herds that roamed both flanks of the Bighorns. One account states that one of the last buffalo hunter's camps was on the Bighorn River in Big Horn Basin (Conner 1940). Shortly after this period, the government's promise to provide meat for the Indians created a large cattle market and during the 1880's large cattle companies were established on both flanks. As the major source of summer feed, the Mountains were especially important to those on the western flank (Briggs 1940).

Today these same slopes provide summer range for sheep and cattle of the local ranchers, numerous small streams and lakes with fish for fishermen, abundant mule and white tailed deer, herds of elk and a few moose for hunters, even a large wilderness area for those who like to get away from the mechanical world of man.

This history of use has had its effects. Very few lower stands do not have stumps left by ax and saw. Large areas support Pinus contorta 95-100 yrs old which indicate early fires set by Indians for defence or by white man from negligence. Today along the highways more recent fire scars are visible. Cattle can be seen grazing in the parks and grasslands throughout most of the summer and the remains of hunter camps can be seen along all the roads and jeep trails.

Most of the Bighorn Mountains have been under the supervision of the U. S. government since 1897. The lower slopes, especially on the west side, have been in the care of local ranchers and the Bureau of Land Management. The U. S. Forest Service reports 10 million board feet of timber harvested and 108 thousand head of livestock pastured in 1956. Many campsites are being maintained and more are being built each year. The number of recreationists is on the increase (U.S.D.A.-F.S. 1957). It is evident that if proper use is to be made of the resource potential of this area much knowledge of environmental conditions on this range must be gained and used.

## METHODS

### Vegetation

For the purposes of this study vegetation was viewed as a group of plant species occupying a certain area and distributed in this area according to their individual limits of tolerance to the set of environmental conditions associated with that area. Different species occur in the same unit area for one of two reasons assuming that disseminules are available to the area. First the species occupy different segments of the environmental complex of the site and secondly individuals of a species occupy different segments of the environmental complex. Thus individuals of a species have environmental requirements similar to those of individuals of other species.

If one environmental factor is dominant and it varies continuously on the ground, a continuum of species will be evident on the ground and separation of communities is arbitrary. But if dominance changes from factor to factor and these factors do not change continuously then a mosaic of recognizable communities or stands will result.

Each community or piece of mosaic will exhibit relative internal homogeneity. These communities may then be grouped into classes exhibiting internal homogeneity or common differences with other classes and referred to as a group (Whittaker 1967, Langenheim 1962). These groups have been termed communities, community types or associations causing some confusion. Because the grouping may take place at various levels, more confusion arises if it is not made clear to what level of resolution the class names have reference. In this study the term stand or community is used to designate, at a very low order of resolution, groups of areas covered by dominant species of overstory plants such as *Pinus contorta* stands.

Forest and shrub community types were sampled from the base of the Range to near timberline. Stands chosen for sampling were relatively uniform in aspect, slope and geologic substrate and without large ravines, rock outcrops or seepages. Where possible, stands of each major community type were sampled throughout their range of occurrence in the Mountains with the major emphasis on those types that covered the greatest area and in those areas of greatest coverage of the particular type.

Within each stand five points were chosen by taking a random number of steps, the final step becoming the center of a 500 $m^2$ circular plot. In the plot all trees over 10 cm DBH were measured and identified. Two 100 $m^2$ plots were located on the circumference of the larger plot alternating between up slope and across slope to the right and down slope and across slope to the left. In these plots tree seedlings and saplings over 30 cm high and less than 10 cm DBH were counted. Cover of herbaceous plants and dwarf shrubs was estimated inside rectangular plots 1 m x 0.5 m placed 3 m from the center of the two sapling plots, two parallel and two perpendicular to the slope (Fig. 1). Tree seedlings less than 30 cm tall were counted in these plots. This layer will be referred to as the herb layer. In each stand five 500 $m^2$ tree plots, ten 100 $m^2$ sapling plots and forty 0.5 $m^2$ herb plots were sampled. Cores from 5-10 large trees in each plot were taken to determine the age of the stand. Location of the stands is shown in Fig. 2.

In dense Pinus contorta stands five 100 $m^2$ plots were sampled and all trees greater than 2.5 cm were recorded by DBH and those less than 2.5 cm DBH by number only. Four 0.5 $m^2$ plots were placed in each plot in the manner described above.

Forest-meadow boundaries were sampled by line transects (Fig. 3) placed randomly along a segment of the boundary beginning at the tree nearest the random point determined by a random number of steps and extending 30 m into the forest and 30 m into the meadow along a line perpendicular to the boundary. At each 5 m interval two 0.5 $m^2$ rectangular plots were placed perpendicular to the line and on opposite sides wherein herb and dwarf shrub cover was estimated. The trees in each contiguous 5 x 5 m plot were also recorded by DBH and species and cores for age determination were taken from 5 random trees within each plot. The soil was sampled each 5 m by taking the top 8-10 cm from each of three 2.5 cm cores. Three such transects were taken along the forest boundary of a Picea engelmannii-

Figure 1. Diagram of sampling plot used in forest communities in the Bighorn Mountains, Wyoming.

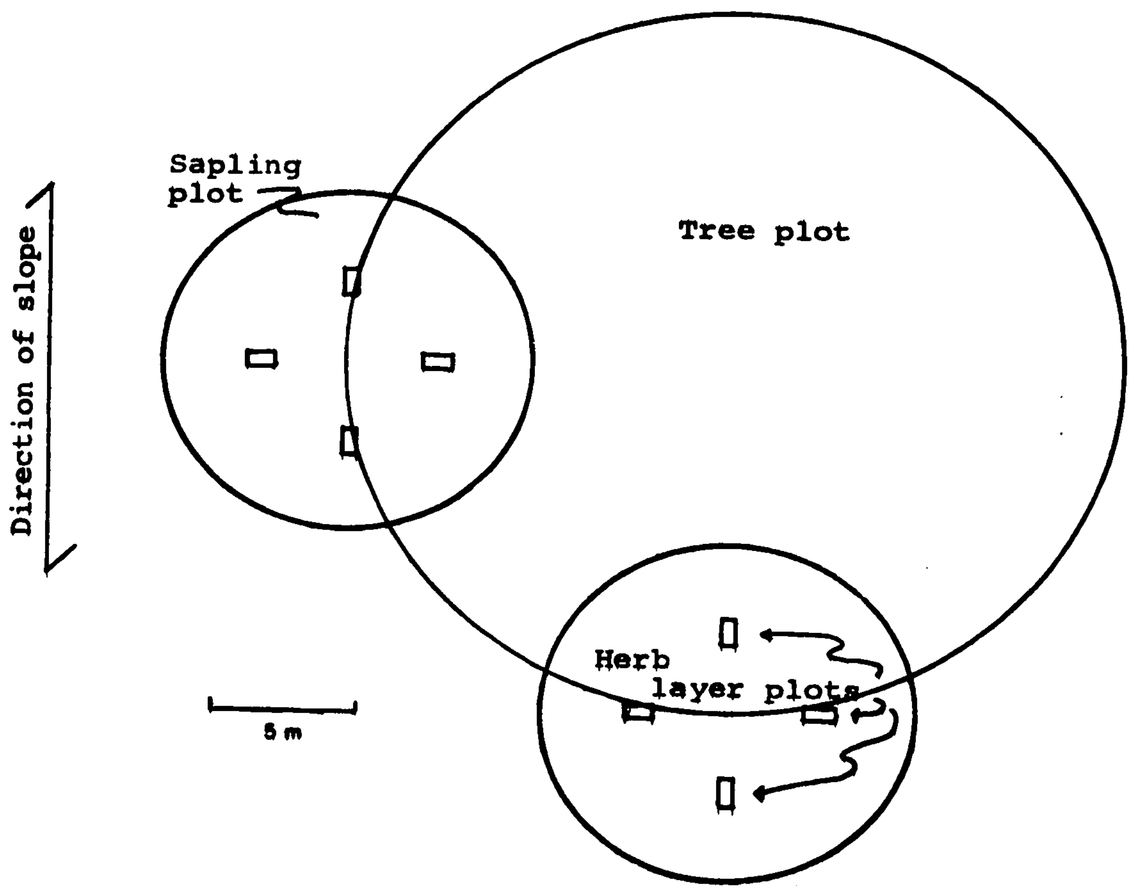


Figure 2. Location of stands sampled on the Bighorn Mountains, Wyoming.

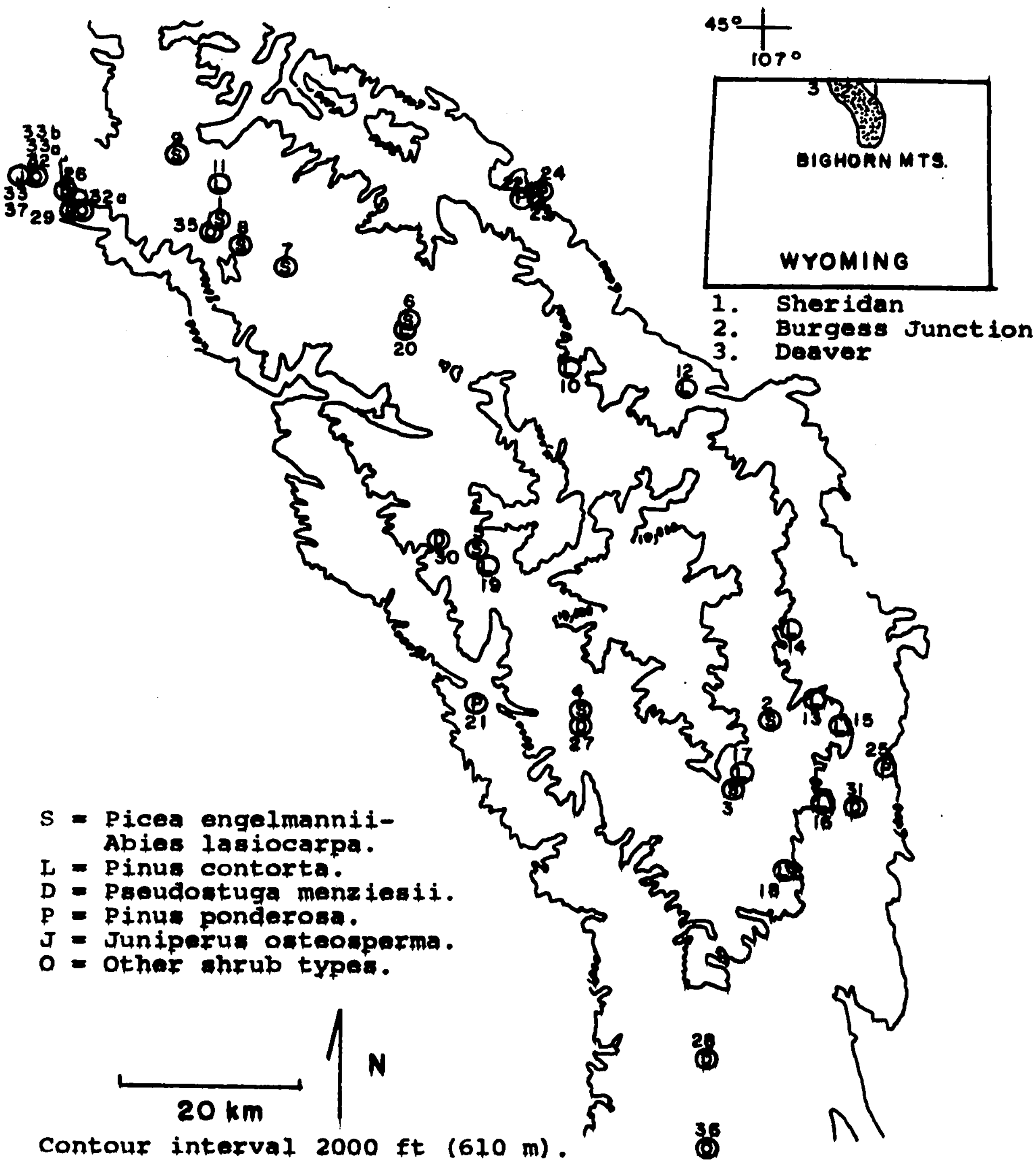
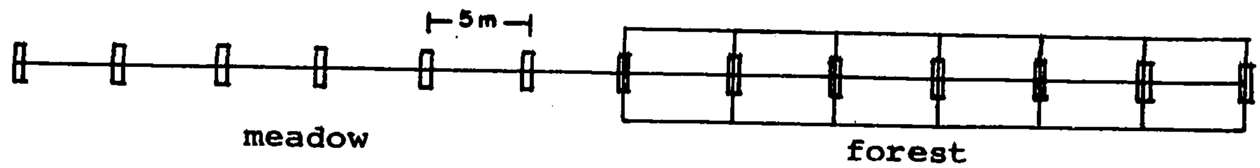


Figure 3. Diagram of transect used on forest-meadow boundary.




*Abies lasiocarpa* stand (Stand 1) and along a *Pinus contorta* stand boundary (Stand 16).

In shrub communities five random points were chosen in the same manner as in forest communities. Four 0.5 $m^2$ plots were established each 3 m from the center and shrub cover was estimated to the nearest dm by the line intercept method along a 30 m tape. Line direction from the center point was chosen by random compass readings. This line intercept method was also used in forest communities containing shrubs which appeared to cover at least 1% of the forest floor.

Seedling density along road cuts was sampled by transects using 1 $m^2$ contiguous plots perpendicular to the cut. These transects were 8 to 10 plots in length.

From the stand samples, tree and sapling data were averaged and standard error determined. For shrub data the average cover per line transect was obtained. For the herb layer the average cover per 0.5 $m^2$ plot in which a species occurred was obtained with its standard error.

This average was then multiplied by the square root of the frequency to give a prominence index (Beals 1960, La Roi 1964, Stringer 1966). This then became the value of the species' importance in the stand. These herb data were analyzed by a principal component factor analysis with orthogonal rotation on a matrix of Pearson correlations. This was accomplished with the aid of an IBM 360/67 computer at the University of Alberta, Edmonton, using a program from the Division of Educational Research Services called FACTØ 1. The data were fed in so as to produce a Q type factor analysis. Species recorded as present were given the value of 0.01 and the value of 1.0 was added to the prominence index to make those species with a very low prominence index more important in recognition of their presence.

Species names follow Porter (1963, 1964, and 1965) for gymnosperms and monocots, and Harrington (1964) or Booth and Wright (1959) for dicots. Specimens of most species reported are deposited at the herbarium of the University of Alberta and the Rocky Mountain Herbarium, Laramie, Wyoming. A list of these appears in Appendix 6.

## Soils

A soil pit was dug in each stand to a depth of at least 60 cm. Following profile descriptions (U. S. D. A. Soil Survey Manual 1951, 1962) a composite sample of each horizon was taken for analyses. Air dried samples were passed through a 2 mm screen and the less than 2 mm fraction was analyzed. Duplicate samples were analyzed in all tests except for exchangeable cations.

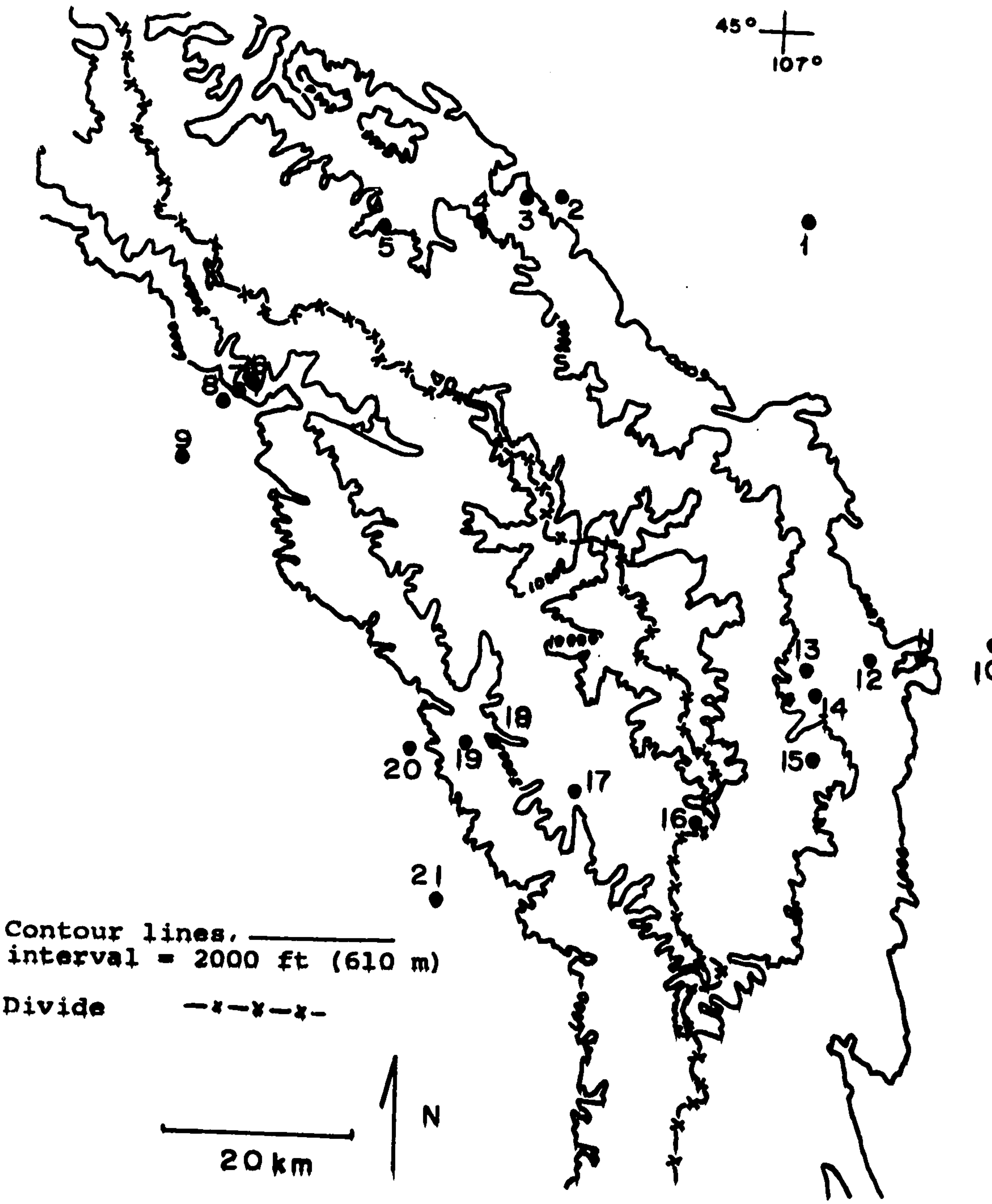
Soils were analyzed for texture by the hydrometer method (Bouyoucos 1951); for organic matter by the Walkley-Black method (1934); for Ca, Mg. K, Na by leaching with 1 N ammonium acetate and analyzing by atomic absorption; and for pH by the glass electrode method. Moisture desorption curves were obtained using a ceramic pressure plate apparatus (Soilmoisture Equipment Co., Cat. 60) and color was determined on moist samples with the Munsel color chips using natural light.

The Bouyoucos hydrometer method was modified by slaking the soils in 10% Calgon for 20-24 hrs followed by 1 hr shaking in a reciprocal shaker. For the desorption curve the same subsample was used for each of the four points; 0.33, 3, 10, and 15 bars. Between each point the samples were dried at 50 C. At the end of the last run the samples were dried at 50 and then 105 C with corrections made for all final calculations.

## Precipitation

From April to September 1969, observations on total precipitation were taken from rain gages placed along two transects across the Range, one across the northern and one across the southern end (Fig. 4). Sites were chosen to fall near the base, middle of each side, and near the top on each side of the Range. Two rain gages were placed at

Figure 4. Location of raingages used in transects in the Bighorn Mountains, Wyoming.



each site. The gages were # 10 cans over which a piece of # 8 hardware cloth was wired to keep out large insects and animals. About 5 mm transformer oil was placed in each can to prevent evaporation. To determine the effect of the screen on the measurements, 10 gages were placed in a small circle, 5 with and 5 without screens, and left for a two week period. This period included a major storm that measured 51 mm. There was no statistically significant difference at the 1% level in the amount of rain received.

The gages were read each month by measuring the volume of water with a graduate cylinder. Readings obtained from these gages were correlated with permanent U. S. Weather Bureau gages in the area. Snow course data published by the U.S.D.A. Soil Conservation Service (1968) were used to draw the lines of equal water content of snow in May (Fig. 9, p. 72).

## Map Study

A study utilizing the maps available of the Bighorn Mountains was undertaken. Much information of ecological interest is contained on maps of various types of the Bighorn Mountains. Darton (1906 a, b, c) produced geological maps of the Mountains using 30' quadrangle topographic maps produced in 1897-99 by the U. S. Geological Survey as base maps. The U. S. Forest Service has produced timber-type maps of the National Forest lands and the Bureau of Land Management has timbertype maps of the west side and a portion of the east side of the Mountains. These were prepared from air photos taken in 1956. These maps were used to draw the vegetation map, Fig. 10, p. 76.

These maps were also used to determine the relation between vegetation, aspect, geologic substrate and elevation. A restricted random sampling system of sampling one random point in each section of the townships occurring on the Mountains was used. For each of the 1811 resultant points the timber type, aspect, elevation and substrate were recorded. All points above 1500 m and below 3000 m for which all the information is available were included in the analysis.

Cole's index of association (Cole 1949) was used to determine the degree of association between vegetation type and each of the other variables. Only those classes representing 5% or more of the points were used.

For relationships between elevation, timbertype, and substrate, the percent of the total points occurring at each 100 ft (30 m) interval occupied by each specific timber type was determined. Before plotting, the curve was smoothed using a moving average with N = 3. Only those points were plotted where at least 1% of the total points occurred at that elevation. These calculations were accomplished with the aid of a cross tabulation program at the University of Alberta computing center.

# RESULTS

## Vegetation

For the purpose of this study the sampling method was adequate regarding number and basal area of the trees. For most stands a confidence interval at the 10% level of less than ±20% of the mean was obtained. The less frequently occurring trees and herbs were much less adequately sampled but the number of plots necessary to sample these adequately became prohibitive. The number of saplings in a stand were also less adequately sampled especially in the case of *Abies lasiocarpa* saplings. Because of the layering tendency of this species large numbers could be obtained in a plot and small numbers in other plots thus a large variance resulted and a 10% confidence interval of ±50% of the mean was more common. For the other species a narrower confidence interval was obtained.

## Forest Communities

The map study shows that forest covers about 60% of the Bighorns between 1500 and 3050 m, the lower and upper timberlines. Approximately 53% of this consists of *Pinus contorta* forests, 24% *Picea engelmannii-Abies lasiocarpa* forests, 17% *Pseudotsuga menziesii* forests and 6% *Pinus ponderosa* forests. Of the 31 forest stands sampled 9 were

Picea engelmannii-Abies lasiocarpa, 11 Pinus contorta, 6 Pseudotsuga menziesii and 5 Pinus ponderosa (Table 1).

Elevational zonation follows that generally described for the Rocky Mountains (Daubenmire 1943) with the addition of a Pinus contorta zone. Pinus ponderosa is the lowest forest zone followed by Pseudotsuga menziesii, Pinus contorta, and Picea engelmannii-Abies lasiocarpa in that order.

Picea engelmannii-Abies lasiocarpa Forests.

Forests dominated by Picea engelmannii and Abies lasiocarpa occur from about 2300 m to timberline at 3050 m but occur most commonly between 2600 and 2900 m. They are best developed on north-facing slopes especially on Gros Ventre shale on the northern third of the Range (Fig. 10).

These forests consist of large (38-64 cm DBH) well-spaced trees with much deadfall making movement through them quite laborious. Although the two dominant species are somewhat similar in density, 380 stems/ha for Picea engelmannii and 287 stems/ha for Abies lasiocarpa, Picea engelmannii has an average basal area 6 times greater than Abies lasiocarpa, 37.6 $m^2$/ha and 6.6 $m^2$/ ha respectively. An occasional Pinus contorta may be encountered in these forests but with no consistent pattern in the occurrence. In areas where limestone rocks occur at or above 2900 m, the Picea engelmanii-Abies lasiocarpa forests may also contain some Pseudotsuga menziesii (Table 2).

Table 1. General site characteristics of stands sampled on the Bighorn Mountains.

| Stand no | Pos | Elev m | Sl % | Asp deg | Substrate | Vegetation |
|---|---|---|---|---|---|---|
| 1 | W | 3255 | 22 | 342 | Shale | P. engelmannii-A. lasiocarpa |
| 2 | E | 3290 | 31 | 30 | Granite | P. engelmannii-A. lasiocarpa |
| 3 | E | 3185 | 10 | 30 | Granite | P. engelmannii-A. lasiocarpa |
| 4 | W | 3010 | 39 | 305 | Shale | P. engelmannii-A. lasiocarpa |
| 5 | W | 3325 | 18 | 305 | Granite | P. engelmannii-A. lasiocarpa |
| 6 | $T_w$ | 3115 | 14 | 5 | Shale | P. engelmannii-A. lasiocarpa |
| 7 | T | 3010 | 19 | 346 | Shale | P. engelmannii-A. lasiocarpa |
| 8 | T | 3185 | 43 | 299 | Shale | P. engelmannii-A. lasiocarpa |
| 9 | $T_w$ | 3185 | 35 | 39 | Shale | P. engelmannii-A. lasiocarpa |
| 10 | W | 3010 | 42 | 344 | Granite | P. contorta |
| 11 | $T_w$ | 2975 | 12 | 109 | Sandstone | P. contorta |
| 12 | E | 2660 | 22 | 351 | Granite | P. contorta |
| 13 | E | 2835 | 28 | 329 | Granite | P. contorta |
| 14 | E | 2905 | 12 | 108 | Granite | P. contorta |
| 15 | E | 2835 | 15 | 305 | Granite | P. contorta |
| 16 | E | 2870 | 10 | 110 | Granite | P. contorta |
| 17 | E | 3115 | 20 | 350 | Granite | P. contorta |
| 18 | E | 2765 | 15 | 160 | Granite | P. contorta |
| 19 | W | 3290 | 24 | 64 | Granite | P. contorta |
| 20 | W | 3045 | 21 | 40 | Shale | P. contorta |
| 21 | W | 2520 | 19 | 230 | Sandstone | P. ponderosa |
| 22 | E | 2275 | 68 | 117 | Limestone | P. ponderosa |
| 23 | E | 2240 | 64 | 320 | Limestone | P. ponderosa |
| 24 | E | 2065 | 38 | 340 | Limestone | P. ponderosa |
| 25 | E | 2275 | 37 | 70 | Sandstone | P. ponderosa |
| 26 | W | 2800 | 49 | 114 | Shale | P. menziesii |
| 27 | W | 2975 | 44 | 331 | Limestone | P. menziesii |
| 28 | T | 2800 | 36 | 320 | Limestone | P. menziesii |
| 29 | W | 2345 | 60 | 345 | Limestone | P. menziesii |
| 30 | $T_w$ | 3185 | 60 | 188 | Limestone | P. menziesii |
| 31 | E | 2765 | 24 | 89 | Limestone | P. flexilis |
| 32 | W | 1820 | 51 | 200 | Limestone | C. ledifolius |
| 33 | W | 2030 | 10 | 220 | Alluvium | C. ledifolius-J. osteosperma |
| 34 | W | 1995 | 3 | 260 | Alluvium | A. tridentata |
| 35 | W | 3255 | 22 | 215 | Shale | A. tridentata |
| 36 | T | 3010 | 7 | 35 | Limestone | A. tridentata |
| 37 | W | 2030 | 27 | 233 | Alluvium | J. osteosperma |
| 38 | E | 1925 | 12 | 242 | Alluvium | P. tremuloides |

Pos=Position on Mountain.
Sl=Slope.
Asp deg=Aspect degrees.
W=West flank.
E=East flank.
T=Subsummit surface.
$T_w$=Subsummit surface west side.

Table 2. Size class distribution of important tree species in *Picea engelmannii*-*Abies lasiocarpa* stands together with density, basal area and frequency. Distribution and frequency are based on 5 plots of 500 $m^2$.

| Stand no | Species | 5.1 cm size class Stems/ha 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | D T/ha | BA $m^2$/ha | F |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *P. engelmannii* | 340 | 0 | 16 | 0 | 8 | 28 | 44 | 28 | 32 | 16 | 8 | 4 | 0 | 192 | 29.84 | 5 |
| | *A. lasiocarpa* | 8728 | 180 | 92 | 56 | 20 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 364 | 9.15 | 5 |
| 2 | *P. engelmannii* | 440 | 80 | 76 | 56 | 84 | 96 | 40 | 68 | 32 | 0 | 4 | 0 | 0 | 536 | 40.35 | 5 |
| | *A. lasiocarpa* | 5512 | 76 | 32 | 8 | 8 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 140 | 5.58 | 5 |
| | *P. contorta* | | | | | | | | | | | | | | 52 | 2.53 | 4 |
| 3 | *P. engelmannii* | 490 | 56 | 48 | 36 | 48 | 44 | 24 | 24 | 20 | 40 | 4 | 8 | 0 | 352 | 32.48 | 5 |
| | *A. lasiocarpa* | 1180 | 16 | 12 | 4 | 0 | 4 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 1.59 | 3 |
| 4 | *P. engelmannii* | 38 | 24 | 44 | 72 | 84 | 60 | 60 | 40 | 28 | 0 | 8 | 0 | 0 | 440 | 46.95 | 5 |
| | *A. lasiocarpa* | 1870 | 16 | 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 32 | 0.60 | 3 |
| | *P. menziesii* | | | | | | | | | | | | | | 12 | 0.91 | 2 |
| 5 | *P. engelmannii* | 280 | 24 | 48 | 40 | 44 | 36 | 48 | 44 | 32 | 32 | 16 | 8 | 4 | 376 | 41.88 | 5 |
| | *A. lasiocarpa* | 2266 | 132 | 120 | 28 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 316 | 6.94 | 5 |
| | *P. contorta* | | | | | | | | | | | | | | 12 | 1.12 | 2 |
| 6 | *P. engelmannii* | 370 | 52 | 36 | 24 | 36 | 56 | 24 | 32 | 16 | 24 | 4 | 0 | 0 | 392 | 43.68 | 5 |
| | *A. lasiocarpa* | 2100 | 196 | 104 | 76 | 16 | 8 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 424 | 10.75 | 5 |
| | *P. contorta* | | | | | | | | | | | | | | 12 | 1.48 | 3 |
| 7 | *P. engelmannii* | 8 | 40 | 68 | 88 | 72 | 60 | 32 | 36 | 24 | 4 | 8 | 0 | 0 | 444 | 32.24 | 5 |
| | *A. lasiocarpa* | 3344 | 128 | 56 | 48 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 244 | 5.66 | 5 |
| | *P. contorta* | | | | | | | | | | | | | | 8 | 0.41 | 2 |
| 8 | *P. engelmannii* | 4 | 12 | 32 | 52 | 52 | 48 | 80 | 36 | 44 | 32 | 12 | 4 | 0 | 412 | 45.24 | 5 |
| | *A. lasiocarpa* | 2550 | 100 | 60 | 32 | 24 | 12 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 232 | 5.46 | 5 |
| 9 | *P. engelmannii* | 290 | 0 | 12 | 20 | 8 | 40 | 20 | 36 | 28 | 8 | 8 | 4 | 8 | 192 | 25.38 | 5 |
| | *A. lasiocarpa* | 12110 | 48 | 40 | 60 | 20 | 24 | 8 | 8 | 0 | 0 | 0 | 0 | 0 | 208 | 14.05 | 5 |

The understory is sparse consisting entirely of seedlings of the overstory trees, mostly *Abies lasiocarpa*. The ability of this species to layer accounts for very high numbers of seedlings and saplings but also results in very aggregated distribution.

In many stands *Ribes lacustre* or *R. montigenum* accounted for a sparse shrub layer but the cover from these species was always less than 1%. In the herb layer *Pyrola secunda*, *Vaccinium scoparium*, *Arnica cordifolia* and *Epilobium angustifolium* are usually present and may account for as much as 5% of the total ground cover (Table 3). Distribution of these species is relatively even though sparse.

By far the greatest amount of ground cover is accounted for by lichens and mosses, 20-30%. These occur on and among the litter and on the very rotten logs. No attempt was made to identify any of the species but most of the lichens were species of *Cladonia* and *Peltigera*. Bare soil and rock are rarely encountered in these stands because of the almost continuous litter layer which can be as much as 9-10 cm deep.

Size class distribution for *Picea engelmannii* shows the highest occurrence in a class near the center of the range of diameters with a mean DBH between 30-40 cm (Table 2). On the other hand, more individuals of *Abies lasiocarpa* fall into the smaller size classes and trees greater than 38 cm DBH are very rare. Saplings of *Abies lasiocarpa*

Table 3. Frequency and mean cover values of shrub and herb layer of Picea engelmannii-Abies lasiocarpa stands Only those herb-dwarf shrub species occurring in 10% or more of the 0.5 $m^2$ plots sampled are included. Frequency is to the left and mean cover (%) per occupied plot to the right of the colon; + = present.

| Species | Stands | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| **Shrub layer** | | | | | | | | | |
| Juniperus communis | - | + | + | + | - | - | - | - | - |
| Ribes lacustre | - | - | + | - | - | + | - | - | - |
| Ribes montigenum | + | - | - | + | - | - | - | - | + |
| **Herb layer** | | | | | | | | | |
| Wood | 40:13.3 | 36:18.6 | 36:8.2 | 40:16.3 | 18:19.1 | 15:27.3 | 17:9.2 | 19:14.7 | 40:15.0 |
| Rock | - | 18:6.8 | 3:1.0 | 5:1.0 | 10:7.9 | - | - | - | 2:0.6 |
| Soil | 3:1.4 | 1:3.0 | 5:30.4 | 12:38.0 | 3:23.3 | 1:3.0 | - | - | 6:4.2 |
| Herbs | 40:9.0 | 30:18.5 | 40:43.3 | 38:18.0 | 20:8.0 | 18:17.2 | 20:25.4 | 19:15 3 | 38:17.3 |
| Litter | 40:77.6 | 36:62 9 | 37:46.1 | 40:66.4 | 20:66.7 | 1:68.2 | 20:63.4 | 20:71.3 | 40:67.6 |
| Moss | 33:4.8 | 25:17.4 | 34:30.1 | 16:22.9 | 6:6.3 | 12:5.7 | 13:17.6 | 13:16.6 | 32:12.7 |
| Cladonia spp. | 14:0.2 | 18:0.4 | 10:0.2 | 7:0.2 | 13:2.5 | 2:1.0 | 2:4.0 | - | 12:0.1 |
| Peltigera spp. | 9:0.8 | 15:4.8 | - | 8:0.9 | 3:1.7 | - | 9:2.2 | 3:8.0 | - |
| Pyrola secunda | 17:1.2 | 11:1.9 | 25:1.1 | 14:0.8 | - | 3:1.7 | - | 3:2.0 | 11:1.9 |
| Arnica cordifolia A. latifolia | 30:2.8 | 7:1.2 | 10:1.0 | 24:5.5 | 2:0.6 | 14:5.1 | 17:4.8 | 3:4.0 | 31:3.3 |
| Vaccinium scoparium | 10:0.6 | 12:0.2 | 31:6.7 | - | 12:5.0 | 12:9.5 | - | 7:1 5 | 32:2.9 |
| Epilobium angustifolium | 6:0.2 | - | 9:0.3 | 10:0.5 | - | 5:0.8 | - | - | 4:0.3 |
| Calamagrostis canadensis | - | - | 9:0.1 | - | - | - | - | - | - |
| Trisetum spicatum | - | - | - | 5:0.1 | - | - | - | - | - |
| Poa spp. | 7:0.1 | - | - | - | - | - | - | - | 4:0.1 |
| Mitella pentandra | - | - | 9:3.0 | - | - | - | - | - | - |
| Mitella stauropetala | 10:0.5 | - | - | - | - | - | - | - | 4:0.1 |
| Luzula parviflora | 6:0.6 | - | 11:0.1 | 4:0.3 | - | - | - | - | - |
| Ranunculus eschschholtzii | 4:0.1 | - | - | - | - | - | - | - | - |
| Potentilla diversifolia | 5:0.3 | - | - | - | - | - | - | - | - |
| Epilobium halleanum | 6:0.2 | - | - | - | - | - | - | - | - |
| Mertensia ciliata | 6:3.7 | - | - | - | - | - | - | - | - |
| Cerastium arvense | 5:0.1 | - | - | - | - | - | - | - | - |
| Carex spp. | - | 4:0.1 | 39:3.6 | - | 6:2.2 | - | - | - | - |
| Ribes lacustre | - | - | 8:8.1 | - | - | - | - | - | - |
| Ribes montigenum | - | - | - | 13:3.8 | - | - | - | - | - |
| Fragaria virginiana | - | - | 9:0.1 | 15:1.4 | - | - | 6:1.7 | - | - |
| Equisetum arvense | - | - | 9:0.1 | - | - | - | - | - | - |
| Streptopus amplexifolius | - | - | 7:0.8 | - | - | - | - | - | - |
| Parnassia fimbriata | - | - | 11:0.3 | - | - | - | - | - | - |
| Trollius laxus | - | - | 7:0.6 | - | - | - | - | - | - |
| Saxifraga odontoloma | - | - | 9:3.0 | - | - | - | - | - | - |
| Polygonum viviparum | - | - | 20:0.6 | - | - | - | - | - | - |
| Senecio pauciflorus | - | - | 9:0.7 | - | - | - | - | - | - |
| Caltha leptosepala | - | - | 14:1.3 | - | - | - | - | - | - |
| Kalmia polifolia | - | - | 4:0.1 | - | - | - | - | - | - |
| Ranunculus cardiophyllus | - | - | 5:1.3 | - | - | - | - | - | - |
| Antennaria racemosa | - | - | - | 4:3.8 | - | - | 6:3.2 | 2:0.5 | - |
| Senecio streptanthifolius | - | - | - | 16:1.2 | - | - | - | - | - |
| Galium boreale | - | - | - | 10:0.3 | - | 2:1.0 | 6:0.7 | - | - |
| Lupinus sp. | - | - | - | 7:2.3 | - | - | - | 3:0.4 | - |
| Taraxacum sp. | - | - | - | 7:0.1 | - | - | - | - | - |
| Rosa acicularis | - | - | - | 4:1.1 | - | - | - | - | - |
| Valeriana dioica | - | - | - | 6:3.0 | - | - | - | - | - |
| Anemone multifida | - | - | - | 5:0.1 | - | - | - | - | - |
| Solidago multiradiata | - | - | - | 6:3.5 | - | - | - | - | - |
| Allium brevistylum | - | - | - | - | - | 2:1.5 | - | - | - |
| Senecio lugens | - | - | - | - | - | - | 2:3.5 | - | - |
| Linnaea borealis | - | - | - | - | - | - | 12:3.5 | - | - |
| Pedicularis racemosa | - | - | - | - | - | - | 3:0.7 | - | - |
| Total species | 21 | 13 | 37 | 25 | 6 | 10 | 16 | 9 | 17 |
| Plots sampled | 40 | 36 | 40 | 40 | 20 | 20 | 20 | 20 | 40 |

outnumber those of *Picea engelmannii* about 10 times. Seedlings of either species less than 25 cm high were not common in any of the stands and completely lacking in most of the stands sampled.

Due to their elevation and inaccessibility to early logging methods, these stands escaped much of the original lumbering activity. However harvest methods have changed, the price of lumber has risen and many of the *Picea engelmannii*-*Abies lasiocarpa* stands are now being cut. They will not be a very big contributor to the lumber industry however because they occur on sites of slow growth and long reestablishment periods. It will take hundreds of years for a new stand to reach harvestable size.

*Pinus contorta* Forests.

More than 50% of the forested area on the Bighorns is at present occupied by *Pinus contorta* forests. They are best developed on the central third of the Range where granite is exposed over a large area. Here they form almost continuous forest with only small parks scattered throughout. On the northern third, small stands occur as islands in *Picea engelmannii*-*Abies lasiocarpa* forests or alone and often associated with outcrops of granite or Flathead sandstone (Fig 10). Isolated stands occur on the southern third of the Range on Tensleep sandstone, granite, or occasionally on limestone rubble. They occur from 1980 m to timberline but are most prevalent between 2130 and 2900 m forming a wide band between *Picea engelmannii-Abies lasiocarpa* forests above and *Pseudotsuga menziesii* forests below.

These stands are highly variable in their characteristics. In some the trees are small and close together with more than 12,000 stems/ha and a mean diameter of about 6 cm. In others the trees are larger, nearer 20 cm mean DBH, and have a density of less than 600 stems/ha. The mean density for all stands sampled was 3005 stems/ha with a standard error of 1172. The basal area was not as variable as density ranging from 20.0 to 59.0 $m^2$/ha with a mean of 34.5 and standard error of 3.5 $m^2$/ha. The higher basal area values are generally associated with more dense stands. Because these stands are fairly even aged, nearly all of the trees fall into two or three size classes near the mean with only a few trees in the extremes (Table 4).

More open stands are generally older, 125-225 yrs, but stand 16 with 12,900 stems/ha is the same age, 50 yrs, as stand 12 with 920 stems/ha. Stand 12 is in a more moist position and the seedlings may have had more competition with grasses and herbs during their establishment reducing the number of seedlings that survived. The overstory of the dense stands is all *Pinus contorta* but in the others *Picea engelmannii*, *Abies lasiocarpa* and occasionally *Pseudotsuga menziesii* may be found. Where an understory

Table 4. Size class distribution of important tree species in *Pinus contorta* stands together with density, basal area and frequency. Frequency is based on 5 plots of 500 $m^2$, 100 $m^2$, or 250 $m^2$.

| Stand No. | Species | Stems/ha 5.1 cm size class 1[a] | 2 | 3 | 4 | 5 | 6 | 7 | 8 | D T/ha | BA $m^2$/ha | F |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10[b] | *P. contorta* | 1810 | 1920 | 430 | 20 | 0 | 0 | 0 | 0 | 7400 | 31.0 | 5 |
| | *A. lasiocarpa* | 222 | | | | | | | | 180 | 2.4 | 3 |
| | *P. engelmannii* | 20 | | | | | | | | 40 | 0.2 | 2 |
| 11 | *P. contorta* | -- 502 -- | | 79 | 103 | 37 | 24 | 8 | 0 | 920 | 22.6 | 5 |
| | *P. engelmannii* | 80 | | | | | | | | | | |
| | *A. lasiocarpa* | 40 | | | | | | | | | | |
| 12 | *P. contorta* | - 4458 -- | | 92 | 168 | 220 | 64 | 12 | 0 | 560 | 20.0 | 5 |
| 13 | *P. contorta* | - 5310 -- | | 376 | 176 | 200 | 128 | 32 | 4 | 568 | 24.0 | 5 |
| | *P. engelmannii* | 133 | | | | | | | | 16 | 0.3 | 3 |
| 14 | *P. contorta* | - 1492 -- | | 644 | 460 | 88 | 20 | 4 | 0 | 1280 | 25.0 | 5 |
| 15[b] | *P. contorta* | 9360 | 2710 | 240 | 0 | 0 | 0 | 0 | 0 | 645 | 37.2 | |
| 16[b] | *P. contorta* | 3470 | 2990 | 670 | 40 | 10 | 0 | 0 | 0 | 12380 | 59.0 | 5 |
| 17 | *P. contorta* | --- 90 -- | | 116 | 136 | 172 | 120 | 20 | 0 | 564 | 21.2 | 5 |
| | *P. engelmannii* | -- 689 -- | | 84 | 60 | 48 | 20 | 4 | 4 | 228 | 6.9 | 5 |
| | *A. lasiocarpa* | - 4998 -- | | 52 | 48 | 16 | 4 | 8 | 4 | 132 | 3.4 | 4 |
| 18[b] | *P. contorta* | - | 1520 | 820 | 190 | 20 | 0 | 0 | 0 | 5600 | 46.0 | 5 |
| 19[c] | *P. contorta* | -- 154 -- | | 860 | 1460 | 960 | 240 | 0 | 0 | 1424 | 41.0 | 5 |
| 20 | *P. contorta* | -- 252 -- | | 196 | 340 | 292 | 156 | 44 | 12 | 1048 | 38.3 | 5 |
| | *P. engelmannii* | 138 | | | | | | | | 48 | 0.8 | 4 |
| | *A. lasiocarpa* | 90 | | | | | | | | 16 | 0.5 | 2 |
| | *P. menziesii* | - | | | | | | | | 4 | 0.04 | 1 |

[a]Class 1 = Transgressives greater than 30 cm high and less than 5.1 cm DBH.
[b]100 $m^2$ plots sampled.
[c]250 $m^2$ plots sampled.

occurs it is composed of saplings of *Picea engelmannii*, *Abies lasiocarpa* and *Pinus contorta*. These species occur in the understory either alone or in combination with either or both of the other species. *Picea engelmannii* and *Abies lasiocarpa* are more important both in the overstory and the understory of those stands that are surrounded by *Picea engelmannii*-*Abies lasiocarpa* forest.

In some open stands a shrub layer is found consisting of *Ribes lacustre* where conditions are more moist and *Juniperus communis* in drier stands. *Ribes lacustre* never accounts for as much as 1% cover but *Juniperus communis* may cover as much as 1-2%.

The herb layer usually contains *Arnica cordifolia*, *Vaccinium scoparium*, species of *Carex*, grasses, *Antennaria rosea*, *Senecio spp*. and *Lupinus spp*. Mosses and lichens are less abundant in these forests than in the *Picea engelmannii*-*Abies lasiocarpa* forests having a much lower cover, less than 10%. In the dense stands these species are represented by few widely scattered individuals and most of the forest floor is covered by litter. In the more open stands *Vaccinium scoparium* may be almost continuous but the growth form of this species does not produce high cover values. *Antennaria rosea* occurs in scattered patches but the other species are more evenly distributed (Table 5).

*Pinus contorta* is the most important timber species on the Bighorns. It comprises by far the largest forests and when the trees reach 20-25 cm DBH, a process of 150 to

Table 5. Frequency and mean cover values of shrub and herb layers of *Pinus contorta* stands. Only those herb-dwarf shrub species occurring in 10% or more of the 0.5 $m^2$ plots sampled are included. Frequency is to the left and mean cover (%) per occupied plot to the right of the colon; + = present.

| Species | Stands | | | | |
|---|---|---|---|---|---|
| | 10 | 11 | 12 | 13 | 14 |
| Shrub layer | | | | | |
| *Juniperus communis* | - | - | - | 9 | + |
| *Ribes montigenum* | - | - | - | - | - |
| Herb layer | | | | | |
| Wood | 40:17.8 | 40:17.8 | 39:5.9 | 40:10.4 | 40:5.2 |
| Rock | 27:10.3 | - | 20:2.2 | 24:4.1 | 23:2.9 |
| Soil | 6:1.5 | 3:6.7 | 9:3.9 | 3:4.3 | 1:0.1 |
| Herbs | 39:3.3 | 40:20.2 | 40:23.7 | 34:9.8 | 34:9.8 |
| Litter | 40:72.0 | 40:61.5 | 40:86.2 | 40:62.9 | 40:85.2 |
| *Pyrola secunda* | 15:0.4 | - | + | 11:0.7 | - |
| *Vaccinium scoparium* | 36:0.5 | 40:13.6 | 38:3.3 | 33:5.7 | + |
| Mosses | 33:1.3 | 8:0.1 | 24:1.5 | 25:6.1 | 11:3.1 |
| *Cladonia spp.* | 27:0.2 | - | 20:0.7 | 26:0.1 | 5:0.3 |
| *Peltigera spp.* | 16:1.9 | - | 10:2.1 | 9:0.6 | 5:0.1 |
| *Lupinus spp.* | 7:2.6 | 20:3.7 | 9:1.9 | 36:7.1 | 23:4.2 |
| *Linnaea borealis* | 10:1.1 | - | - | 32:4.8 | - |
| *Thalictrum occidentale* | - | 31:3.4 | - | + | - |
| *Arnica cordifolia* | - | 38:3.1 | - | - | - |
| *Poa spp.* | + | 14:0.1 | - | - | 11:0.3 |
| *Koeleria cristata* | - | - | - | 14:0.1 | - |
| *Epilobium angustifolium* | - | 8:0.3 | - | 6:0.1 | - |
| *Carex spp.* | + | 5:0.1 | + | 9:1.7 | 9:0.5 |
| *Fragaria virginiana* | - | 7:0.8 | - | 4:0.1 | - |
| *Antennaria rosea* | 5:0.1 | - | 27:1.8 | 19:1.6 | + |
| *Hieracium albiflorum* | - | - | 16:0.1 | - | - |
| *Spiraea betulifolia* | - | - | 23:0.3 | 20:0.3 | - |
| *Senecio streptanthifolius* | - | - | 4:0.3 | 7:0.2 | 10:0.7 |
| *Arctostaphylos uva-ursi* | - | - | - | 12:7.7 | 23:7.7 |
| *Gentiana amerella* | - | - | - | 6:0.1 | - |
| *Penstemon sp.* | - | - | - | - | 5:0.2 |
| *Rosa acicularis* | - | - | - | + | - |
| *Campanula rotundifolia* | - | - | - | - | 4:0.1 |
| *Antennaria racemosa* | - | + | - | + | - |
| *Aster conspicuus* | - | - | - | - | - |
| Total species | 10 | 14 | 13 | 22 | 14 |
| Plots sampled | 40 | 40 | 40 | 40 | 40 |

Table 5--Continued.

| Species | 15 | 16 | 17 | 18 | 19 | 20 |
|---|---|---|---|---|---|---|
| | Stands | | | | | |
| Shrub layer | | | | | | |
| Juniperus communis | + | | + | | - | + |
| Ribes montigenum | - | | - | | - | + |
| | | | | | | |
| Herb layer | | | | | | |
| Wood | 40:11.6 | | 40:9.8 | | 12:15.5 | 9:15.6 |
| Rock | 3:0.7 | | 15:2.6 | | 9:10.7 | 1:3.0 |
| Soil | - | | 9:2.6 | | 1:6.0 | 1:10.0 |
| Herbs | 39:3.2 | | 38:7.7 | | 20:47.3 | 20:39.0 |
| Litter | 40:85.2 | | 40:81.4 | | 17:37.3 | 20:53.2 |
| Pyrola secunda | 4:0.1 | | 17:0.8 | | - | + |
| Vaccinium scoparium | 18:1.4 | | 30:0.3 | | 20:40.0 | 20:33.2 |
| Mosses | 14:0.4 | + | 29:7.3 | + | 4:2.3 | 5:3.0 |
| Cladonia spp. | 23:0.3 | | 26:0.2 | + | 5:1.0 | - |
| Peltigera spp. | 17:1.9 | | 9:3.5 | | - | + |
| Lupinus spp. | 8:2.3 | | + | | 6:3.8 | 2:7.5 |
| Linnaea borealis | - | | - | | - | + |
| Thalictrum occidentale | - | | - | | - | - |
| Arnica cordifolia | 5:0.1 | + | 6:0.6 | | 5:2.0 | 11:1.6 |
| Poa spp. | - | | 5:0.1 | + | - | - |
| Koeleria cristata | - | | - | | - | - |
| Epilobium angustifolium | 7:0.1 | | - | | - | 7:1.0 |
| Carex spp. | + | + | 5:0.5 | + | - | - |
| Fragaria virginiana | + | | - | + | - | - |
| Antennaria rosea | - | | + | | - | 9:3.0 |
| Hieracium albiflorum | - | | - | | - | - |
| Spiraea betulifolia | 7:0.4 | | - | | - | - |
| Senecio streptanthifolius | 23:0.3 | | 6:0.1 | | 4:1.8 | 2:0.6 |
| Arctostaphylos uva-ursi | 7:1.7 | | - | | - | - |
| Gentiana amerella | + | | - | | - | - |
| Penstemon sp. | + | | - | | - | - |
| Rosa acicularis | 20:0.3 | | - | | - | - |
| Campanula rotundifolia | 4:0.1 | | - | | - | - |
| Antennaria racemosa | - | | 7:0.5 | | - | - |
| Aster conspicuus | - | | - | | 4:4.0 | - |
| Total species | 17 | 3 | 13 | 5 | 9 | 12 |
| Plots sampled | 40 | 0 | 40 | 0 | 20 | 20 |

200 yrs, the stands are clearcut. Large barren areas can be seen today where previous forests have been harvested. In some areas reproduction is good but in others it is not; much remains yet to be learned about the management of *Pinus contorta* forests on the Bighorns.

*Pseudotsuga menziesii* Forests.

Forests dominated by *Pseudotsuga menziesii* occur between 1830 and 2740 m but occur most commonly between 1980 and 2290 m. On the east flank of the Range, they form a band between the *Pinus contorta* forests above and *Pinus ponderosa* forests below. On much of the west flank they are the lowest forest type due to the lack of *Pinus ponderosa*. Here they occur along the north-facing slopes of the many canyons cut through the sedimentary rocks and are almost restricted to these sites especially at lower elevations. They are best developed on limestone or dolomite derived soils and only occasionally do forests of *Pseudotsuga menziesii* occur on granitic substrates. They extend the full length of the Range on both sides and can be found on the summit of the southern third. Near the upper limits of their range *Picea engelmannii* is often present in the overstory.

At lower elevations *Pinus flexilis* ranges from a minor species to dominance of the overstory.

In some places in this zone Pinus flexilis can also form pure stands (Stand 31).

In mature well-developed Pseudotsuga menziesii stands the trees are medium sized, 25-51 cm DBH and well-spaced. There is some deadfall but not as much as in Picea engelmannii-Abies lasiocarpa forests. Density averaged 639 stems/ha with a standard error of 86. Basal area ranged from 8.5 to 64.4 $m^2$/ha (Table 6).

The understory consists mostly of reproduction of the tree species of the stands. At higher elevations Picea engelmannii is the most common species in the understory but lower Pseudotsuga menziesii remains as the most abundant species. In the shrub layer Juniperus communis is present in some stands and in others Ribes lacustre can be found. In one Pinus flexilis stand sampled (Stand 31) Juniperus communis covered almost 50% of the ground. In other stands shrubs accounted for less than 1% cover.

The forest floor is comparatively well covered with about 30% herbs and dwarf shrubs. The species in this layer are quite variable from stand to stand and of the five stands included in the comparison only grasses, lichens, and mosses occurred in more than two of the stands. Hesperachloa kingii and Poa sp. were the common grass species and the lichens were species of Cladonia and Peltigera (Table 7). This layer does not seem characteristic of Pseudotsuga menziesii stands but rather is derived from neighboring communities. For example in the higher

Table 6. Size class distribution of important tree species in Pseudotsuga menziesii stands together with density, basal area and frequency. Distribution and frequency are based on 5 plots of 500 $m^2$.

| Stand No. | Species | Stems/ha 5.1 cm size class 1[a] | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | D T/ha | BA $m^2$/ha | F |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 26 | P. menziesii | 568 | 140 | 88 | 44 | 36 | 12 | 8 | 16 | 4 | 4 | 0 | 4 | 360 | 15.4 | 5 |
| | P. flexilis | 69 | 28 | 40 | 68 | 48 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 264 | 10.3 | 5 |
| | J. scopulorum | 10 | | | | | | | | | | | | 8 | 0.1 | 2 |
| | A. lasiocarpa | 40 | | | | | | | | | | | | | | |
| | A. glabrum | 30 | | | | | | | | | | | | | | |
| 27 | P. menziesii | 210 | 16 | 0 | 28 | 28 | 48 | 92 | 64 | 48 | 8 | 0 | 0 | 396 | 49.1 | 5 |
| | P. engelmannii | 180 | 28 | 40 | 60 | 64 | 24 | 20 | 8 | 8 | 0 | 0 | 0 | 252 | 15.3 | 5 |
| 28 | P. menziesii | 50 | 24 | 124 | 204 | 196 | 112 | 16 | 4 | 4 | 0 | 0 | 0 | 644 | 31.6 | 5 |
| | P. engelmannii | 4 | 84 | 80 | 88 | 44 | 20 | 4 | 8 | 0 | 0 | 0 | 0 | 384 | 17.7 | 5 |
| 29[b] | P. menziesii | 176 | 430 | 310 | 90 | 10 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 496 | 8.5 | 5 |
| 30 | P. menziesii | 121 | 84 | 80 | 32 | 24 | 12 | 8 | 16 | 0 | 0 | 0 | 0 | 288 | 18.4 | 5 |
| | P. flexilis | 10 | | | | | | | | | | | | 104 | 4.2 | 5 |
| | P. engelmannii | 20 | | | | | | | | | | | | 28 | 2.5 | 3 |
| 31 | P. flexilis | 397 | 176 | 164 | 112 | 36 | 52 | 24 | 4 | 4 | 0 | 0 | 0 | 596 | 22.0 | 5 |
| | P. pondorosa | 10 | | | | | | | | | | | | 16 | 1.3 | 1 |
| | P. menziesii | 80 | | | | | | | | | | | | | | |

[a]Class 1 = Transgressives greater than 30 cm high and less than 10.2 cm DBH.
[b]100 $m^2$ plots sampled.

Table 7. Frequency and mean cover values of shrub and herb layers of *Pseudotsuga menziesii* stands. Only those herb-dwarf shrub species occurring in 10% or more of the 0.5 $m^2$ plots sampled are included. Frequencies are to the left and mean cover (%) per occupied plot to the right of the colon; + = present.

| Species | Stands 26 | 27 | 28 | 30 | 31 |
|---|---|---|---|---|---|
| Shrub layer | | | | | |
| *Juniperus communis* | + | + | - | 5 | 49 |
| *Ribes lacustre* | - | + | - | - | - |
| *Ribes cereum* | + | - | - | + | - |
| *Juniperus scopulorum* | - | - | - | + | - |
| *Symphoricarpos sp.* | + | - | - | - | - |
| | | | | | |
| Herb layer | | | | | |
| Wood | 40:7.4 | 40:16.7 | 40:21.0 | 18:8.4 | 28:3.7 |
| Rock | 31:8.5 | 27:3.3 | 12:2.4 | 11:4.4 | 36:4.4 |
| Soil | 10:9.6 | 6:2.7 | 3:3.0 | 5:9.0 | 17:4.1 |
| Herbs | 29:3.6 | 38:8.9 | 35:3.6 | 17:10.8 | 33:1.6 |
| Litter | 40:81.1 | 40:22.2 | 39:72.9 | 20:78.7 | 40:90.4 |
| *Aster foliaceus* | 4:0.1 | - | - | 12:4.7 | - |
| *Balsamorhiza sagittata* | 8:5.4 | - | - | - | - |
| *Berberis repens* | 5:5.6 | - | 6:0.4 | 13:3.1 | - |
| Mosses | 6:1.4 | 36:6.3 | 31:2.8 | - | 10:0.4 |
| *Symphoricarpos oreophilus* | 6:1.7 | - | - | - | - |
| *Lithospermum ruderale* | 4:0.1 | - | - | - | - |
| *Arnica cordifolia* | - | 17:4.6 | 5:0.5 | 11:3.3 | 14:0.1 |
| *A. gracilis* | | | | | |
| *Antennaria racemosa* | - | - | 5:0.5 | - | - |
| *Senecio streptanthifolius* | - | 5:0.5 | - | - | - |
| *Pyrola secunda* | - | 15:0.5 | 13:0.1 | - | - |
| *Valeriana dioica* | - | 4:0.1 | - | - | - |
| *Cladonia spp.* | - | 14:0.1 | 31:0.2 | - | 7:0.4 |

Table 7--Continued.

| Species | Stands 26 | 27 | 28 | 30 | 31 |
|---|---|---|---|---|---|
| Peltigera spp. | - | 10:0.6 | 17:0.8 | - | 11:0.2 |
| Fragaria virginiana | - | - | - | 6:1.4 | - |
| Poa spp. | 8:0.1 | - | - | - | 31:0.1 |
| Hesperochloa kingii | 6:0.1 | - | - | 7:2.6 | 20:0.1 |
| Swertia radiata | - | - | - | 2:2.0 | 20:0.1 |
| Astragalus miser | - | - | - | - | 16:0.2 |
| Galium boreale | - | - | - | - | 24:0.1 |
| Potentilla concinna | - | - | - | - | 11:0.1 |
| Phlox multiflora | - | - | - | - | 16:0.1 |
| Cerastium arvense | - | - | - | - | 7:0.1 |
| Arenaria congesta | - | - | - | - | 19:0.1 |
| Campanula rotundifolia | - | - | - | - | 16:0.1 |
| Achilla millefolium | - | - | - | - | 15:0.1 |
| Allium schoenoprasum | - | - | - | - | 10:0.1 |
| Antennaria pulchesrima | - | - | - | - | 8:0.1 |
| Symphoricarpos oreophilus | - | - | - | - | 11:0.1 |
| Delphinium bicolor | - | - | - | - | 15:0.1 |
| Taraxicum sp. | - | - | - | - | 19:0.2 |
| Potentilla ovina | - | - | - | - | 5:0.1 |
| Potentilla fissa | - | - | - | - | 8:0.1 |
| Total species | 15 | 12 | 12 | 11 | 40 |
| Plots sampled | 40 | 40 | 40 | 20 | 40 |

cooler stands near Picea engelmannii-Abies lasiocarpa forests the herb layer is composed of species from the Picea engelmannii-Abies lasiocarpa forest and in the lower warmer stands the species are derived from the neighboring Pinus ponderosa forest or grassland.

Some of the stands appear to be stable with Pseudotsuga menziesii being most abundant in the smaller size classes (Stand 28, Table 6). Some are very young and small resulting from reproduction after a fire (Stand 32, Table 6) and some are successional to Picea engelmannii-Abies lasiocarpa forests (Stands 29 and 30, Table 6) with most trees in the larger size classes and many Picea engelmannii in the smaller classes. The older stands are approximately 250-300 yrs old.

Thus a general picture for the behavior of Pseudotsuga menziesii emerges. In the warm dry environments of the lower slopes, Pseudotsuga menziesii is restricted to steep north-facing slopes with conditions too extreme for Picea engelmannii and Abies lasiocarpa and Pseudotsuga menziesii becomes the sole forest forming species providing both the seral and climax forests. In the cooler, moister environments of higher elevations the species grows not only on the north-facing slopes of canyons but also on the gentler slopes of any aspect. Here Picea engelmannii and Abies lasiocarpa can grow and Pseudotsuga menziesii is relegated to a seral forest only. All of this occurs on sedimentary rocks, principally limestone and dolomite.

*Pinus contorta* does not form the seral stage in these areas as it is restricted to granitic rocks (Figs. 10, 11, and Table 15).

Because these forests are near the base of the Bighorns they are easily accessible and remain so throughout the year. Thus they have been extensively harvested during the settlement period of the river basins of both sides. Very few stands of merchantable timber remain and these are being harvested rapidly. Because of their limited extent *Pseudotsuga menziesii* forests will not play an important role in future lumbering.

*Pinus ponderosa* Forests.

The lowest forests on the Bighorns are dominated by *Pinus ponderosa*. These occur on the east slope down to the alluvial fans at the base of the Mountains at 1520 to 1830 m. They are quite common on the flatirons on the entire east flank of the Range but do not extend into the shale strata between the flatirons or onto the alluvium. They may reach an elevation of 2340 m but are most common between 1520 and 2140 m. There are no juniper communities below the *Pinus ponderosa* on the east side, rather the forest ends abruptly in grassland at the base of the Mountains. On the west flank of the Range these forests are nearly absent except in the southern quarter where they occur on broad areas of exposed Tensleep sandstone. In this area a well developed *Juniperus osteosperma* community is found between the valley floor and the Pinus ponderosa forests and in the more favorable sites Pseudotsuga menziesii forests may occur.

The trees are often loosely clumped in their distribution with 350 to 700 stems/ha but young stands in favorable sites may be more closed with as many as 1400 stems/ha. Average basal area ranges from 8.8 to 24.8 $m^2$/ha with the higher values associated with denser forests. Pseudotsuga menziesii and Pinus flexilis are usually represented in these forests but are sparse (Table 8).

The understory consists of saplings of the overstory with Pinus ponderosa being most abundant. Some forests are successional to Pseudotsuga menziesii and these have a higher proportion of Pseudotsuga menziesii saplings (Stand 23). The shrub layer is highly variable. In dense stands a layer of Physocarpus monogynus and Symphoricarpos alba occurs with about 5 to 10% cover. In other stands Physocarpus monogynus, Juniperus communis and Shepherdia canadensis are present but scattered and of very low cover. In stands that are more open and have very little shrub cover the herb layer may have the characteristics of an Agropyron spicatum grassland with only litter under the dense clumps of trees. Clematis sp., Symphoricarpos sp., and Galium boreale are usually present. Mosses and lichens are present but usually have low cover values (Table 9).

These forests are characteristically young (60-100 yrs) and evidence of fire and logging is abundant. The position

Table 8. Size class distribution of important tree species in *Pinus ponderosa* stands together with density, basal area and frequency. Distribution and frequency are based on 5 plots of 500 $m^2$.

| Stand No. | Species | Stems/ha 5.1 cm size class 1[a] | 2 | 3 | 4 | 5 | 6 | 7 | 8 | D T/ha | BA $m^2$/ha | F |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 21 | *P. ponderosa* | 200 | 56 | 108 | 72 | 72 | 52 | 8 | 0 | 368 | 16.2 | 5 |
| | *P. menziesii* | 0 | | | | | | | | 4 | 0.1 | 1 |
| | *P. flexilis* | 0 | | | | | | | | 16 | 0.2 | 1 |
| 22 | *P. ponderosa* | 300 | 184 | 116 | 96 | 12 | 16 | 8 | 4 | 456 | 13.3 | 5 |
| | *P. flexilis* | 586 | 156 | 52 | 8 | 8 | 0 | 0 | 0 | 236 | 5.0 | 5 |
| | *P. menziesii* | 20 | | | | | | | | 20 | 0.3 | 2 |
| 23 | *P. ponderosa* | 166 | 360 | 276 | 76 | 12 | 0 | 0 | 0 | 752 | 16.3 | 5 |
| | *P. menziesii* | 440 | 72 | 108 | 16 | 0 | 0 | 0 | 0 | 196 | 4.4 | 5 |
| | *P. flexilis* | 44 | 60 | 56 | 8 | 0 | 0 | 0 | 0 | 128 | 2.6 | 5 |
| | *P. engelmannii* | 10 | | | | | | | | 36 | 1.5 | 4 |
| 24[b] | *P. ponderosa* | 170 | 300 | 400 | 320 | 80 | 20 | 0 | 0 | 1420 | 36.4 | 5 |
| | *P. flexilis* | 0 | | | | | | | | 60 | 0.8 | 1 |
| | *P. menziesii* | 10 | | | | | | | | | | |
| 25 | *P. ponderosa* | 2212 | 424 | 84 | 12 | 0 | 8 | 0 | 0 | 584 | 8.8 | 5 |

[a]Class 1 = Transgressives greater than 30 cm high and less than 10.2 cm DBH.
[b]100 $m^2$ plots sampled.

Table 9. Frequency and mean cover values of shrub and herb layers of *Pinus ponderosa* stands[a]. Only those herb-dwarf shrub species occurring in 10% or more of the 0.5 $m^2$ plots sampled are included. Frequencies are to the left and mean cover (%) per occupied plot to the right of the colon; + = present.

| Species | Stands 21 | 22 | 23 | 24 | 25 |
|---|---|---|---|---|---|
| Shrub layer[b] | | | | | |
| *Juniperus communis* | 1:+ | 8:1 | 6:+ | 4:+ | 2:+ |
| *Juniperus scopulorum* | 4:+ | 9:+ | 3:+ | 2:+ | - |
| *Shepherdia canadensis* | - | 2:+ | - | 1:+ | - |
| *Rhus triloba* | - | 1:+ | - | - | - |
| *Physocarpus monogynus* | - | 2:+ | 8:+ | 10:20 | - |
| *Acer glabrum* | - | - | 4:+ | - | - |
| | | | | | |
| Herb layer | | | | | |
| Wood | 23:10.7 | 10:3.0 | 17:5.8 | 8:5.0 | 32:3.7 |
| Rock | 8:4.5 | 18:37.4 | 16:4.6 | 14:3.6 | 38:9.2 |
| Soil | 17:60.5 | 15:18.1 | - | - | 26:14.3 |
| Herbs | 20:6.8 | 20:11.7 | 20:27.5 | 20:23.0 | 40:3.6 |
| Litter | 32:52.6 | 20:35.4 | 20:61.0 | 20:73.3 | 40:75.5 |
| *Berberis repens* | 16:2.3 | - | - | 7:3.6 | - |
| *Hesperochloa kingii* | 8:0.4 | - | - | - | 15:0.1 |
| *Agropyron spicatum* | - | 7:2.6 | - | - | 6:0.3 |
| *Mertensia oreophila* | 12:2.9 | - | - | - | - |
| *Cerastium arvense* | 4:0.1 | - | - | - | 10:0.1 |
| *Peltigera sp.* | 5:1.8 | - | 5:1.6 | 3:6.7 | 7:0.1 |
| *Polygonum sawatchense* | 4:1.0 | - | - | - | - |
| *Achillea millefolium* | 5:0.1 | 2:1.1 | - | - | 9:0.1 |
| *Spiraea betulafolia* | 4:2.0 | - | 20:7.8 | 20:6.6 | - |
| *Arctostaphylos uva-ursi* | - | 11:7.0 | - | - | - |
| *Rosa acicularis* | - | 2:1.6 | 4:1.8 | 4:1.5 | - |
| *Apocynum androsaemifolium* | - | 11:2.0 | - | - | - |
| *Balsamorhiza sagitata* | - | 4:9.0 | - | 3:6.7 | - |

Table 9--Continued.

| Species | Stands 21 | 22 | 23 | 24 | 25 |
|---|---|---|---|---|---|
| *Clematis pseudoalpina* | - | 5:1.2 | 14:2.9 | 13:3.6 | - |
| *Geum triflorum* | - | 2:0.1 | - | - | - |
| *Galium boreale* | - | 13:0.6 | 14:1.0 | 6:0.4 | 26:0.1 |
| *Hedysarum sulphurescens* | - | 2:1.5 | - | - | - |
| *Symphoricarpos alba* | - | 7:0.8 | 7:1.4 | 16:3.4 | - |
| *Symphoricarpos oreophilus* | - | - | - | - | 10:0.1 |
| *Rhus radicans* | - | 3:3.0 | - | - | - |
| *Aster conspicuus* | - | 6:2.0 | 13:5.1 | 9:7.8 | - |
| *Carex sp.* | - | 10:1.6 | - | - | 30:0.2 |
| *Cladonia spp.* | - | - | 7:1.8 | 2:0.1 | - |
| *Smilacina stellata* | - | - | 6:3.2 | 4:1.8 | - |
| Mosses | - | - | 14:10.6 | 4:6.5 | 7:0.4 |
| *Antenaria racemosa* | - | - | 9:4 3 | - | - |
| *Anemone cylinderica* | - | - | 5:0.8 | - | - |
| *Zygadenus elegans* | - | - | 4:1.0 | - | - |
| *Disporum trachycarpum* | - | - | 4:3.5 | - | - |
| *Anemone multifida* | - | - | - | 8:1.4 | - |
| *Senecio streptanthifolius* | - | - | - | - | 16:0.1 |
| *Arabis nuttallii* | - | - | - | - | 5:0.1 |
| *Phlox multiflora* | - | - | - | - | 25:0.6 |
| *Campanula rotundifolia* | - | - | - | - | 15:0.1 |
| *Astragalus striatus* | - | - | - | - | 7:0.1 |
| *Silene menziesii* | - | - | - | - | 5:0.1 |
| *Phlox hoodii* | - | - | - | - | 5:0.5 |
| *Penstemon laricifolia* | - | - | - | - | 6:0.1 |
| *Taraxicum sp.* | - | - | - | - | 9:0.1 |
| *Liatrus punctata* | - | - | - | - | 5:0.1 |
| *Bupleurium americanum* | - | - | - | - | 8:0.1 |
| *Crepis acuminata* | - | - | - | - | 5:0.1 |

Table 9--Continued.

| Species | Stands 21 | 22 | 23 | 24 | 25 |
|---|---|---|---|---|---|
| *Potentilla fissa* | - | - | - | - | 9:0.1 |
| *Gilia spicata* | - | - | - | - | 4:0.1 |
| *Linum lewisii* | - | - | - | - | 4:0.1 |
| Total species | 15 | 21 | 21 | 18 | 39 |
| Plots sampled | 32 | 20 | 20 | 20 | 40 |

[b]Frequencies based on 10 plots of 100 $m^2$.

of the forest next to the grassland suggests that fire was more common throughout its history. Also during the settlement of the area these forests were the nearest source of logs and lumber for the early houses and forts. Stumps of trees that were probably 25-50 cm DBH are common in some of the stands. Today there is not much lumbering activity in these except in those stands that were not accessible to earlier logging methods. The main use of such stands today is grazing.

At the lower elevations and on dry ridges these forests are probably the climax vegetation (Stands 22, 23, 26). Here it is too dry for Pseudotsuga menziesii to compete successfully with Pinus ponderosa for permanent occupation of the site. However at the higher limits of these forests it is evident that they will be replaced by Pseudotsuga menziesii and thus are a seral stage (Stand 23). The stands are all so young that the size class distribution is not meaningful especially since early loggers were selective in the trees that they removed.

## Shrub Communities

There are several community types dominated by shrubby species on the Bighorns. On the west flank are Juniperus osteosperma and Cercocarpus ledifolius communities and throughout the Range can be found Artemisia tridentata communities. Because of their importance in natural range, they have been studied in conjunction with range surveys and range analyses. Rangelands, being economically the most important plant communities on the Bighorns, have received the most extensive research of an ecological and management nature (Beetle 1956, Hurd 1961, Fisser 1964, Alley 1965, etc.). For this reason these community types were not examined closely in the present study. However a brief description of these important types is given from data taken in the field and from published reports.

Juniperus osteosperma Stands

Juniperus osteosperma communities occur along the lower western flank of the Range in a broken band from north to south. They appear best developed in areas where bedrock, yielding a coarse soil, is not covered by alluvial fan material. In areas where the bedrock dips steeply under this alluvial material, Juniperus osteosperma is usually lacking or poorly represented and a grassland dominated by Agropyron spicatum and Artemisia tridentata occurs. No Juniperus osteosperma stands were found on the east flank.

The dominant species in these areas is Juniperus osteosperma. Juniperus scopulorum is found in moist areas along drainage ways but is a minor component. No pinyon pines reach this far north but in some places, near the upper limits, Pinus flexilis may perform the same ecological function. These stands extend from about 1520 to 2140 m. Crown cover of Juniperus osteosperma is approximately 30%.

Associated with these stands are: Agropyron spicatum, Opuntia polyacantha, Chrysothamus sp., and various other species all with very low cover values (Table 10).

The Juniperus osteosperma stands are so low and scrubby that they have very little economic value aside from a few odd fence posts for the local rancher. The grass layer is usually so sparse that grazing is not profitable. Some studies have been undertaken to determine the possibility of eradicating the Juniperus osteosperma to provide more rangeland (Fisser personal communication). Wight and Fisser (1968) give a good description of this community type.

Cercocarpus ledifolius Stands.

Cercocarpus ledifolius forms stands on the steep slopes of the western face of the Range from about 1830 to 2140 m. They are mostly associated with calcareous substrates or substrates with a definite calcareous influence. A few scattered stands occur on the east side of the Range at about 1520 m on outcrops of limestone.

Soils are usually poorly developed and often only incidental to the occurrence of this species as individuals can be seen growing on nearly vertical walls of the canyons. On the north-facing talus slopes and outwash fans they may reach a crown cover value of 60% or more while on south-facing slopes crowns cover only 30% of the surface. In areas where these contact Juniperus osteo-

Table 10. Frequency and mean cover values of shrub and herb layers of shrub communities. Frequencies are to the left and mean cover (%) per occupied plot to the right of the colon; + = present.

| Species | 32 | 32a | Stands<br>33 | 33a | 33b |
|---|---|---|---|---|---|
| Shrub layer | | | | | |
| *Artemisia tridentata* | - | 32.7 | - | - | - |
| *Cercocarpus ledifolius* | 60.9 | - | - | 64.2 | 30.0 |
| *Juniperus osteosperma* | - | - | 34.0 | - | - |
| *Symphoricarpos oreophilus* | 7.3 | - | - | - | - |
| *Rhus trilobata* | + | - | - | - | - |
| | | | | | |
| Herb layer | | | | | |
| Wood | 10:13.6 | - | 2:37.5 | | |
| Rock | 18:13.3 | - | 20:26.4 | | |
| Soil | 2:7.5 | - | 17:38.0 | | |
| Herbs | 15:9.0 | 11:11.9 | 17:20.2 | + | 12:12.2 |
| Litter | 20:74.8 | - | 7:49.7 | | |
| Plots sampled | 20 | 11 | 20 | 0 | 12 |

Table 10--Continued.

| Species | Stands 34 | 35 | 36 | 37 |
|---|---|---|---|---|
| Shrub layer | | | | |
| *Artemisia tridentata* | 20.6 | 42.1 | 25.1 | - |
| *Cercocarpus ledifolius* | - | - | - | 14.8 |
| *Juniperus osteosperma* | - | - | - | 17.6 |
| *Symphoricarpos oreophilus* | - | - | - | - |
| *Rhus trilobata* | - | - | - | - |
| | | | | |
| Herb layer | | | | |
| Wood | | 6:5.2 | 2:1.5 | 11:10.9 |
| Rock | | - | - | 18:25.9 |
| Soil | | 5:21.6 | 15:7.8 | 16:41.4 |
| Herbs | | 20:39.1 | 16:28.8 | 14:10.8 |
| Litter | | 18:55.5 | 16:64.3 | 15:41.2 |
| Plots sampled | | 20 | 16 | 20 |

sperma stands, the cover seems to be split between the two species. In one stand sampled Cercocarpus ledifolius covered 15% of the ground surface and Juniperus osteosperma 18% (Table 10).

All of the individuals are strongly hedged as a result of heavy browsing by domestic and wild animals. Some of these stands are important calving areas for elk and all are important wintering areas of both deer and elk. For a more complete description and discussion see Miller (1964).

Artemisia tridentata Stands.

Stands of Artemisia tridentata can be found from the base of the Mountain Range to near timberline indicating a broad range of ecological variation. They are usually associated with deep soils or areas of deep accumulations of fine soil particles although they do extend onto the limestone rubble at higher elevations. The associated species are those of the grassland of the particular area in which Artemisia tridentata happens to be. At higher elevations this is Festuca idahoensis grassland and at the base of the Range, Agropyron spicatum grasslands.

Rhus trilobata, Physocarpus monogynus, Symphoricarpos sp., and Lupinus greenii may be associated with it in some areas on the western flank mainly in warm dry areas of lower middle elevations.

Cover estimates of Artemisia tridentata run from 20% at lower elevations where they are 15-30 cm high to 42%

at higher elevations where they may reach 100 cm in height (Table 10).

These stands are important to deer as both cover and browse during certain periods of the year and also to sage chickens that inhabit these areas. Many of these stands have been sprayed with herbicides as range improvement for livestock (Alley 1965).

## Factor Analysis of Herb Layer Data

The factor analysis indicated 9 factors affecting the composition of the herb layer. With such a wide spectrum of stands this is not surprising.

If all stands with high loadings on a particular factor axis are considered as a related group it is found that the unrotated, quartimax and varimax rotations all give similar though not identical groupings. These are shown in Table 11. Stands were placed where they scored highest. If a stand scored about equally high in more than one factor it was placed in each of the factors. Because quartimax rotation appears to give a more definite grouping, i.e. fewer stands in more than one factor, it will be the basis of the following discussion.

Factor 1 contains all but two of the *Picea engelmannii-Abies lasiocarpa* stands. The two left out are on the west side and are probably drier. Also included in this group are four *Pinus contorta* stands, two *Pseudotsuga menziesii* stands and one *Pinus ponderosa* stand. Factor 2 contains

Table 11. Groups of stands as determined by Q type factor analysis. Stands are placed with the factor where they have the highest loading. Where this is similar in more than one factor, the stand is placed in each factor.

| | | Stands | | | | |
|---|---|---|---|---|---|---|
| Rotation | Factor | P. eng-A. las. | P. contorta | P. pon. | P. men. | Shrubs |
| Unrotated | 1 | 1 2 3 4 5 6 7 8 9 | 10 13 16 17 18 | 23 | 27 28 | |
| | 2 | 5 6 | 11 12 13 19 20 | | | |
| | 3 | | 18 | 21 25 | | 29 32 34 35 36 37 |
| | 4 | | 13 14 15 | 22 | | |
| | 5 | | | 21 | 26 30 | |
| | 6 | | | 24 | | |
| | 7 | | | 25 | 31 | |
| | 8 | | | | | 33 35 |
| | 9 | | | 21 | | 33 38 |
| Quartimax | 1 | 1 2 3 4 7 8 9 | 10 16 17 18 | 23 | 27 28 | |
| | 2 | 5 6 | 11 12 13 19 20 | | | |
| | 3 | | | | | 29 32 33 34 36 37 |
| | 4 | | 14 15 | 22 | | |
| | 5 | | | | 30 | |
| | 6 | | | 25 | 31 | |
| | 7 | | | | | 35 |
| | 8 | | | 24 | 26 | |
| | 9 | | | 21 | 26 | 38 |

the two *Picea engelmannii*-*Abies lasiocarpa* stands not included in factor 1 and all but two of the remaining *Pinus contorta* stands. Factor 3 contains all but one of the shrub communities. These three factors account for 71% of the stands.

Another way to look at this is to observe that the *Picea engelmannii*-*Abies lasiocarpa* stands occur in factors 1 and 2. *Pinus contorta* in factors 1, 2, and 4; *Pseudotsuga menziesii* stands in 1, 5, and 8 or 9; *Pinus ponderosa* stands in 1, 4, 6, 8, and 9; shrub stands in 3 and 7.

## Reproduction

Reproduction data of two types were taken. Two road cuts were chosen, one in a *Picea engelmannii*-*Abies lasiocarpa* forest and the other in a *Pinus contorta* forest. Here 1 m wide transects were sampled. Two other sites were chosen. These were in burned areas which were sampled by circular plots of 100 $m^2$ and 500 $m^2$. The data are summarized in Table 12.

Although the sampling was not extensive enough to be conclusive, the data do indicate some possible trends. Mixed stands of *Pinus contorta* and *Picea engelmannii* can begin at the seedling stage as in the Powder River Pass and Sawmill Lakes sites. Reproduction on sedimentary substrates is much more difficult as shown by the Mann Creek site where densities are 1 to 2 orders of magnitude different. General observations of old burns also bear this out; on the

Table 12. Forest reproduction data from four locations on the Bighorn Mountains, Wyoming.

| | Site Characteristics | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Loc. | Elev. m | Disturbance | Substrate | Pico[a] T/ha | Pien T/ha | Abla T/ha | Psme T/ha | Pifl T/ha |
| 1 | 2770 | Road cut | Granite | 17000 | 42000 | - | - | - |
| 2 | 2680 | Road cut | Granite | 57000 | - | - | - | - |
| 3 | 2560 | Fire[b] | Granite | 2200 | - | 1600 | - | - |
| 4 | 2440 | Fire[c] | Sediment | 122 | 18 | - | 204 | 484 |

[a]Pico = *Pinus contorta*, Pien = *Pinus engelmannii*, Abla = *Abies lasiocarpa*, Psme = *Pseudotsuga menziesii*, Pifle = *Pinus flexilis*.

[b]*Pinus contorta* forest that burned in 1957.

[c]Could have been part of fire described by Town (1899) which burned in 1898.

Location 1, Powder River Pass; 2, Porcupine Creek; 3, Sawmill Lakes; 4, Mann Creek.

west side of the Bighorns in areas of sedimentary rock, forests that burned 40 to 60 yrs ago are still unforested. Whether this is the result of climatic change or the reflection of the difficulty encountered in the establishment of tree species under these conditions is an area worthy of further study. In granitic areas on the east side of the Range, repopulation begins within 1-2 yrs after disturbance. The seedlings on the Sawmill Lakes burn which occurred in 1957, were estimated to be 10-12 yrs old and observations in the area of other fires support this view.

## Forest-meadow Boundaries

Two forest-meadow boundaries were sampled, one between a *Picea engelmannii*-*Abies lasiocarpa* community and meadow on shale derived soils and one between a *Pinus contorta* community and meadow on granitic derived soils. Both were on the north-facing side of the forest community. Each of these communities was sampled and appear as stand 1 and stand 16 in the discussion of forest communities.

The *Pinus contorta* boundary was characterized by an area about 20-30 m wide where large well-spaced trees occurred. Behind the first row of trees, the second or third 5 m segment usually was free of trees then beyond this the trees became smaller and closer together toward the forest. The forest is quite dense beyond this border. The age of the trees in the boundary is quite variable in contrast to that of the forest with some as old as 250 yrs and a general decrease occurs from the border into the forest. The forest is fairly even aged at 60-70 yrs.

Total herb cover decreased almost linearly from an average at 30 m of 26% down to present at 15 to 20 m into the forest (Fig. 5). Linear regression analysis of the herb data gave the following relationship between mean total herb cover and distance along the transect beginning 30 m into the meadow and ending 15 m into the forest beyond which herb cover was less than 1%: $Y = 26.1-0.5x$, $r = 0.97$. The characteristics of the grassland were described by Hurd (1961) and Beetle (1956) with *Festuca idahoensis* the most important species with about 10% cover in favorable areas. Most of the decrease in herb cover was due to the decrease of this one species.

Figure 5. Average herb cover along forest-meadow boundary transects.

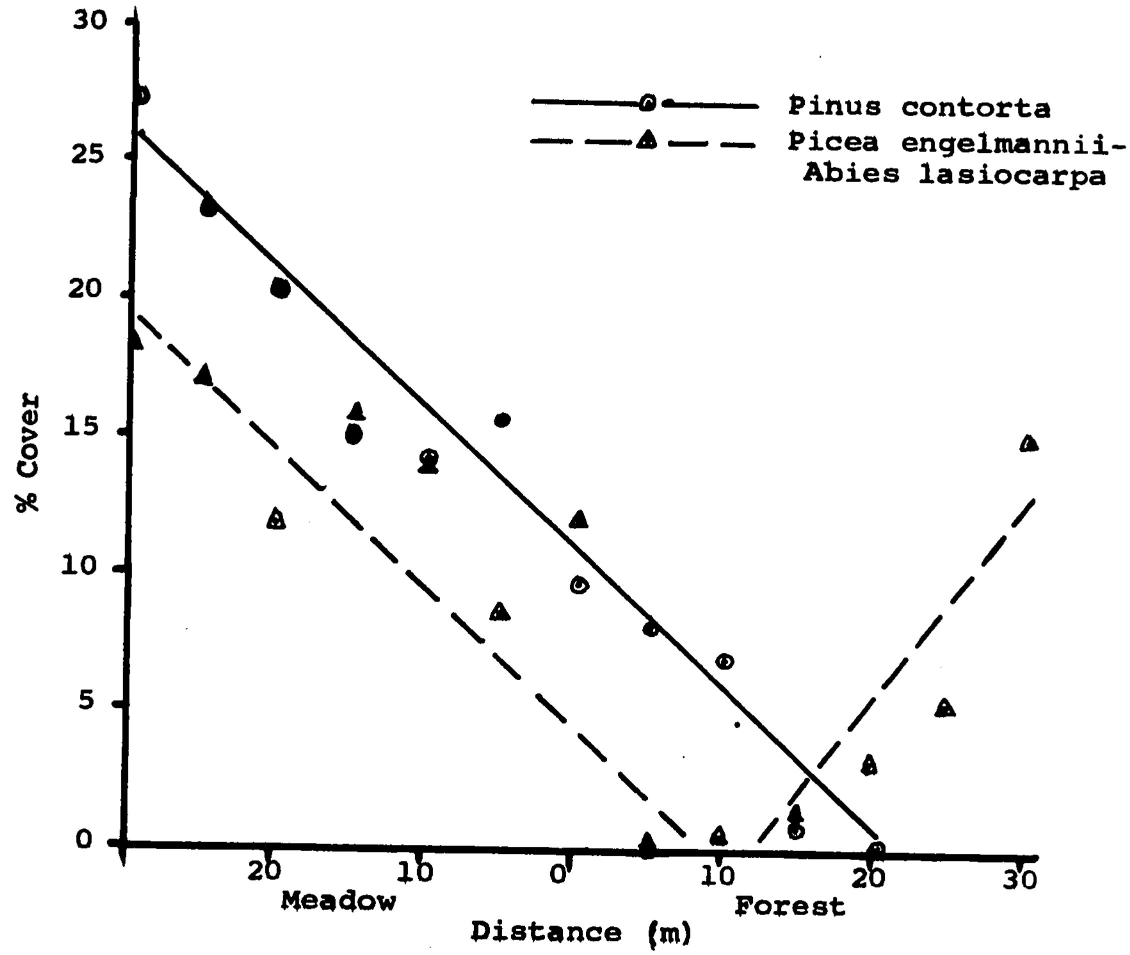
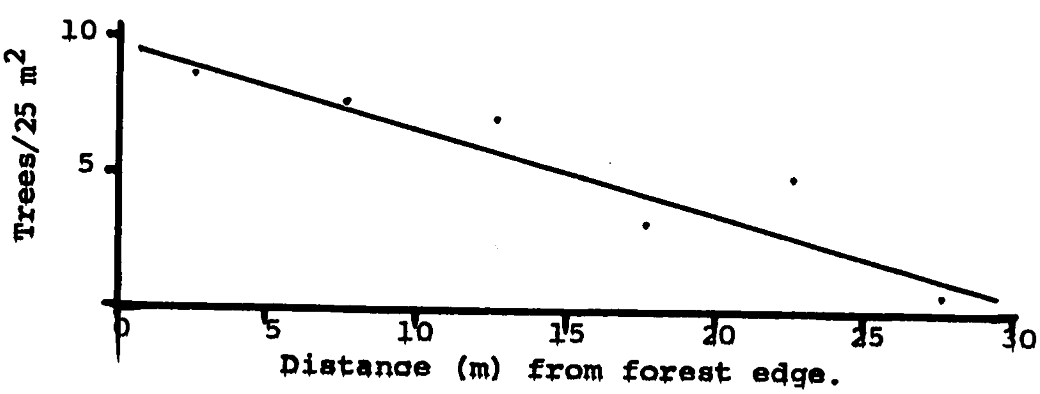



Figure 6. Average tree density along Picea engelmannii-Abies lasiocarpa forest-meadow boundary transects.



A species of *Senecio* was the only addition to the species list on entering the forest boundary area.

The *Picea engelmannii*-*Abies lasiocarpa* boundary was quite different, almost opposite to that of *Pinus contorta*. The trees next to the meadow were small and very close together with 7-11 trees in the first 5 m segment The average number of trees per 25 $m^2$ plots then decreases at the rate of about 0.3 trees/m, r = 0.92, until the typical conditions of the *Picea engelmannii*-*Abies lasiocarpa* community were obtained (Fig. 6). The youngest trees were in the first 5 m segment of the forest but average age was about the same for the second and third segments, about 65-75 yrs, after this trees of 75 to 130 yrs occur as well as some very young ones. Mean DBH increases with distance from the boundary.

Average total herb cover decreased from the meadow at a rate almost equal to that of the *Pinus contorta* boundary but started lower and ended abruptly at the boundary of the forest. After the first 5 to 10 m it again increased (Fig. 5). The species of the forest were almost completely different than those of the meadow and much fewer in number.

Both boundaries had animal trails just at the tree-meadow boundary, both were grazed by sheep and the *Picea engelmannii*-*Abies lasiocarpa* area was also grazed by a herd of elk. The effects of these animals on the forest boundary merits further study.

The depth of the $A_1$ horizon remained fairly constant with a sudden decrease in thickness upon entering the forest. There an $A_2$ horizon occurred and was most prominant. The acidity of the soil increased abruptly from a pH of 5.8 in the meadow to 5.2 in the forest. Charcoal was present in the soils on both sides of the boundary.

## Soils

Summaries of the results of laboratory analyses of the soils are shown in Table 13. The values shown or used for comparison are weighted profile averages which were arrived at by multiplying a particular value by the horizon thickness for each horizon of the profile and dividing by total thickness. Texture was reduced to a sand:clay ratio for comparison purposes. Because many of the soil pits did not go beyond 50-70 cm, only the first 50 cm of the profile were used. It is assumed that the characteristics of this portion of the solum are most influential on the vegetation. The terminology used here is that of the Soil Classification 7th Approximation (U.S.D.A. 1960).

Soils derived from granitic substrates were divided into those sites occupied by *Pinus contorta* and those occupied by other vegetation, i.e. *Picea engelmannii-Abies lasiocarpa* and grassland.

The *Pinus contorta* sites were used in the substrate comparisons as the sites on the other substrates were

Table 13a. Soil profile characteristics for the different substrates occurring on the Bighorns. The values used to obtain the means were derived from profile averages obtained as explained in the text.

| | Mean | | | | | | |
|---|---|---|---|---|---|---|---|
| Substrate | % avail. water | % OM | K mg/100g | Ca mg/100g | Mg mg/100g | Sand: clay ratio | % less than 2mm |
| Granite (LP) | 8.30 | 1.09 | 0.04 | 35.1 | 7.10 | 7.16 | 67.6 |
| Limestone | 14.92 | 3.85 | 0.57 | 56.8 | 11.10 | 2.86 | 56.2 |
| Gros Ventre Shale | 13.54 | 2.26 | 0.49 | 46.8 | 9.22 | 1.51 | 89.0 |
| Granite (non-LP) | 11.34 | 2.65 | | | | 6.23 | 84.4 |

Table 13b. Values of $t$ associated with differences in the means of the soil profile characteristics given in Table 13a.

| | $t$ values | | | | | | |
|---|---|---|---|---|---|---|---|
| Substrate means compared | % avail. water | % OM | K mg/100g | Ca mg/100g | Mg mg/100g | Sand: clay ratio | % less than 2mm |
| Gr-Ls | 7.43 | 7.66 | 2.12 | 7.42 | 3.40 | 6.41 | 1.28* |
| Gr-Sh | 4.33 | 4.68 | 1.50* | 3.56 | 1.64* | 7.24 | 3.68 |
| Ls-Sh | 1.31* | 3.38 | 0.88* | 2.85 | 1.29* | 2.50 | 3.23 |
| LP-non LP | 0.96* | 3.00 | | | | 0.97* | 2.85 |
| non LP-Sh | 0.53* | 0.57* | | | | 4.21 | 0.86 |

*not significant at 5% level.
Gr = derived from granite.
Ls = derived from limestone.
Sh = derived from shale.
LP = covered by *Pinus contorta*.
non LP = covered by grassland or *Picea engelmannii*-*Abies Lasiocarpa* forest.

covered by forest except one limestone site in a shrub community that was left out of the calculations. Only granite, limestone and shale are compared because these cover 95% of the Range and insufficient soil pits were dug in the other substrates to make meaningful comparisons. Limestones include the Madison formation, part of the Amsden formation and the Bighorn dolomite. Shale includes the shale portion of the Gros Ventre formation. The complete results of the analyses may be found in Appendix 1 to 5.

The results show that the substrate from which the soils are derived plays a major role in the characteristics of the soil.

The only comparisons of physical properties among substrates that the t test did not show to be significantly different were between limestone and shale in water holding capacity and between granite and limestone in % field sample less than 2 mm, Table 13. Of the chemical properties however, only the amount of calcium was shown to be different among all combinations.

Vegetationally it is interesting to note that *Pinus contorta* sites differ from non-*Pinus contorta* sites in organic matter and in % less than 2 mm and that granitic non-*Pinus contorta* sites differ from shale sites only in the sand to clay ratio.

Comparison of pH values shows granite and shale to be acid, ranging from 4.8 to 6.8, and limestone soils to be basic, ranging from 7.1 to 8.0. The upper horizons of two of the limestone soils were acid (5.5 and 6.4) and most profiles were more acid in the upper horizons. The acid limestone soils were occupied by *Pseudotsuga menziesii*-*Picea engelmannii*-*Abies lasiocarpa* stands and the others by *Pseudotsuga menziesii*, *Pinus ponderosa* or shrub communities.

Soils above 2340 m have generally well-developed horizons in non-glaciated areas while those on glacial features and at lower elevations often have only A-C profiles. Typical profile descriptions of each of the three substrates are presented here for comparison purposes.

The soils, for the most part, are developed on erosional surfaces and are thus strongly influenced by the rock type from which they were derived. Granitic derived soils are shallower and less well-developed than shale derived soils and are much coarser in texture.

Location: Billy Creek Access Road T. 48N. R. 84W. Sec. 2. Parent material: Granitic alluvium. Slope: 0-5%. Vegetative cover: *Pinus contorta* forest.

| Horizon | Description |
|---|---|
| O | 0-2 cm; pine needles, whole on top, matted with fungal mycelium and fine roots in the lower portion. |
| $A_{11}$ | 2-5 cm; moist color 10 YR 2/1, dry color 10 YR 3/2; silty; medium, fine crumb; friable; reaction 6.0; less than 2 mm, 96.2%; charcoal present; smooth boundary to horizon below. |

$A_{12}$ 5-10 cm; moist color 7.5 YR 3/2, dry color 7.5 YR 6/2; sandy silt; medium, fine crumb; friable; reaction 5.7; less than 2 mm 82.6%; some roots most at boundary; smooth boundary to horizon below.

$A_2$ 10-25 cm; moist color 10 YR 4/3, dry color 10 YR 7/2; sandy; moderate to weak, medium sub-angular blocky; friable; reaction 5.2; less than 2 mm 67.6%; some roots; smooth boundary to horizon below.

B 25-35 cm; moist color 10 YR 4/4, dry color 10 YR 6/4; sandy; moderate to weak, medium subangular blocky; friable; reaction 5.2; less than 2 mm 67.4%; few roots, iron accumulation; wavy boundary to horizon below.

C 35+ cm; moist color 10 YR 4/3, dry color 10 YR 6/3; sandy; single grain; reaction 5.2; less than 2 mm 67.4%; fine roots, rocks.

Vegetation also exerts a strong influence on profile development. The following profile description was taken from granitic derived soils but under the influence of grassland vegetation. It is much deeper with thicker horizons, has no $A_2$ horizon and a very thick $A_1$.

Location: Roadcut north of Spanish Point T. 52N. R. 88W. Sec. 28. Parent material: Decomposed granite. Slope: 7%. Vegetative cover: *Artemisia tridentata*.

| Horizon | Description |
| --- | --- |
| $A_1$ | 0-20 cm; moist color 5 YR 2/2, dry color 7.5 YR 4/2; silt loam; moderate, fine to medium crumb; reaction 5.4; less than 2 mm 93.3%; many fine roots; clear and wavy boundary to horizon below. |

$B_1$ 20-55 cm; moist color 10 YR 3/4, dry color 10 YR 4/3; sandy clay loam, moderate, medium to large prismatic; reaction 5.2; less than 2 mm 77.5%; plentiful fine roots, root and gopher channels; clear and wavy boundary to horizon below.

$B_2$ 55-70 cm; moist color 10 YR 5/6, dry color 10 YR 5/8; sandy loam; moderate, medium to large prismatic; reaction 5.2; less than 2 mm 82.3%; few fine roots.

Soils derived from shale have well-developed structure and are quite fine in texture. Some sand-sized particles occur either from impurities in the original shale or from mixing from an adjacent geologic formation. The following description is typical of such soils under forest vegetation:

Location: Dry Owen Creek T. 54N. R. 88W. Sec. 7. Parent material: Gros Ventre shale. Slope: 15%. Vegetative cover: <u>Picea engelmannii-Abies lasiocarpa</u> forest.

| Horizon | Description |
|---|---|
| O | 0-1.5 cm; whole needles above; mat of needles, roots and fungal mycelium below. |
| $A_1$ | 1.5-18 cm; moist color 7.5 YR 3/2, dry color 5 YR 5/3; silty; weak, medium crumb; reaction 5.4; less than 2 mm 99.5%; roots; abrupt, smooth boundary to horizon below. |
| $A_2$ | 18-23 cm; moist color 7.5 YR 3/2, dry color 10 YR 6/2; silty; weak, medium crumb; reaction 5.2; less than 2 mm 97.4%; roots; abrupt, smooth boundary to horizon below. |
| $B_{21}$ | 23-45 cm; moist color 10 YR 5/4, dry color 10 YR 6/3; silty loam; strong, fine subangular blocky; reaction 5.4; less than 2 mm 97.1%; clear, smooth boundary to horizon below. |

$B_{22}$ 45-70 cm; moist color 5 Y 6/3, dry color 5 Y 6/3; silty clay loam; strong, medium subangular blocky; reaction 5.6; less than 2 mm 90.8%; abrupt, smooth boundary to horizon below.

C 70-80 cm; moist color 2.5 Y 5/4, dry color 2.5 Y 7/4; silty loam, moderate, medium subangular blocky; reaction 5.8; less than 2 mm 82.6%.

The tendency of limestone and dolomite to fragment results in rocky soils with many pebbles greater than 2 mm. However, the chemical weathering products of limestone produce very fine soil particles; thus these soils can have characteristics of both coarse and fine soils. They are usually not as well-developed as shale derived soils but can be quite deep. The profile description given here has a thick O horizon but otherwise is characteristic of limestone and dolomite derived soils in the Bighorns.

Location: Pass Creek T. 46N. R. 85W. Sec. 27.
Parent material: Dolomite. Slope: 35%.
Vegetative cover: *Picea engelmannii-Abies lasiocarpa* with *Pseudotsuga menziesii*.

| Horizon | Description |
|---|---|
| O | 0-15 cm; whole needles above, mat of needles, roots and fungal mycelium below. |
| $A_2$ | 15-30 cm; moist color 7.5 YR 3/2, dry color 7.5 YR 5/4; silty; moderate, fine crumb, friable, reaction 5.5; less than 2 mm 98.5%; few roots; wavy boundary to horizon below. |
| $B_2$ | 30-56 cm; moist color 7.5 YR 3/2, dry color 7.5 YR 5/4; silty clay loam; weak to moderate, fine to medium subangular blocky, friable; reaction 6.8; less than 2 mm 99.9%; some large roots; wavy boundary to horizon below. |

$B_3$ 56+ cm; moist color 10YR 3/3, dry color 10 YR 5/3; silty loam; weak, fine to medium subangular blocky, friable; 7.6; less than 2 mm 86.8%; some roots and rocks.

The timbered soils would be classed as Inceptisols or Alfisols and the grassland soils belong to the Molisols. In the higher elevations these would fall into the Boralf and Boroll suborders.

Precipitation

The rain gages gave readings that were intermediate between established Weather Bureau gages at lower elevations and Forest Service gages at higher elevations. The two gages at each site also agreed with each other within ± 5 mm at most. Usually they were within ± 1.0 mm. During the month of June two general storms occurred and were of sufficient magnitude to over-run some of the gages. The data from the rain gage transects are presented in Table 14. Fig. 7 shows these data plotted against elevation.

For the period April-Sept, about 80% fell during the first half. The northern transect received more than the southern transect and the north-east section received about twice as much as the other portions. An increase in precipitation with elevation was more apparent during the first half of the period than the last. These observations are in agreement with the trends indicated by stations with longer records. The absolute amounts have little meaning with only one year's precipitation data. Weather Bureau

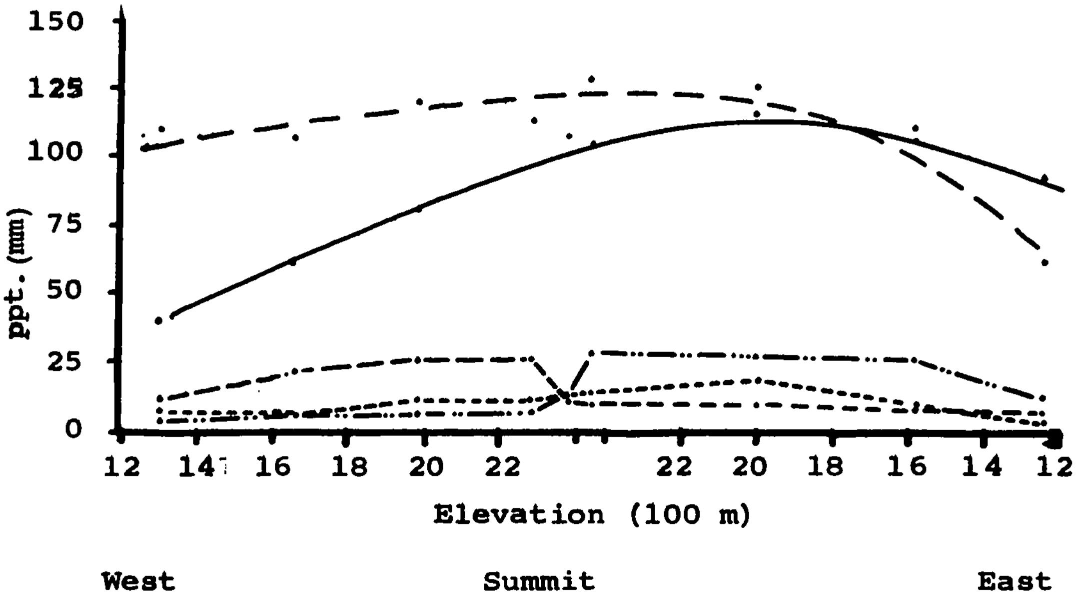
Table 14. Rain gage data from transects, April-Sept., 1969.

| Location | Elev. m | Apr-May mm | June mm | July mm | Aug. mm | Sept. mm |
|---|---|---|---|---|---|---|
| 1 | 1208 | 92 | 62 | 12 | 6 | 2 |
| 2 | 1585 | 105 | 110 | 25 | 8 | - |
| 3 | 2012 | 115 | 125 | 26 | 9 | 13 |
| 4 | 2438 | 104 | 128 | 27 | 9 | 14 |
| 5 | 2377 | - | 108 | 13 | 11 | 13 |
| 6 | 2286 | - | 114 | 6 | 25 | 10 |
| 7 | 1981 | 78 | 119 | 6 | 25 | 10 |
| 8 | 1615 | 61 | 107 | 5 | 20 | 10 |
| 9 | 1303 | 40 | 111 | 2 | 10 | 6 |
| 10 | 1416 | 40 | 100 | 21 | 4 | 24 |
| 11 | 1585 | 30 | 132 | 14 | - | 11 |
| 12 | 2073 | 44 | 106 | 36 | 2 | 17 |
| 13 | 2256 | - | 119 | 51 | 2 | 17 |
| 14 | 2377 | 53 | 110 | 28 | 2 | 10 |
| 15 | 2531 | 67 | 97 | 22 | 2 | 7 |
| 16 | 2896 | 66 | 65 | 14 | 6 | 7 |
| 17 | 2560 | - | 99 | 15 | 5 | 11 |
| 18 | 2377 | - | 127 | 13 | 5 | 15 |
| 19 | 2134 | 73 | -* | 8 | 6 | 10 |
| 20 | 1707 | 56 | 131 | 3 | 7 | 15 |
| 21 | 1463 | 73 | 170 | 12 | - | 1 |

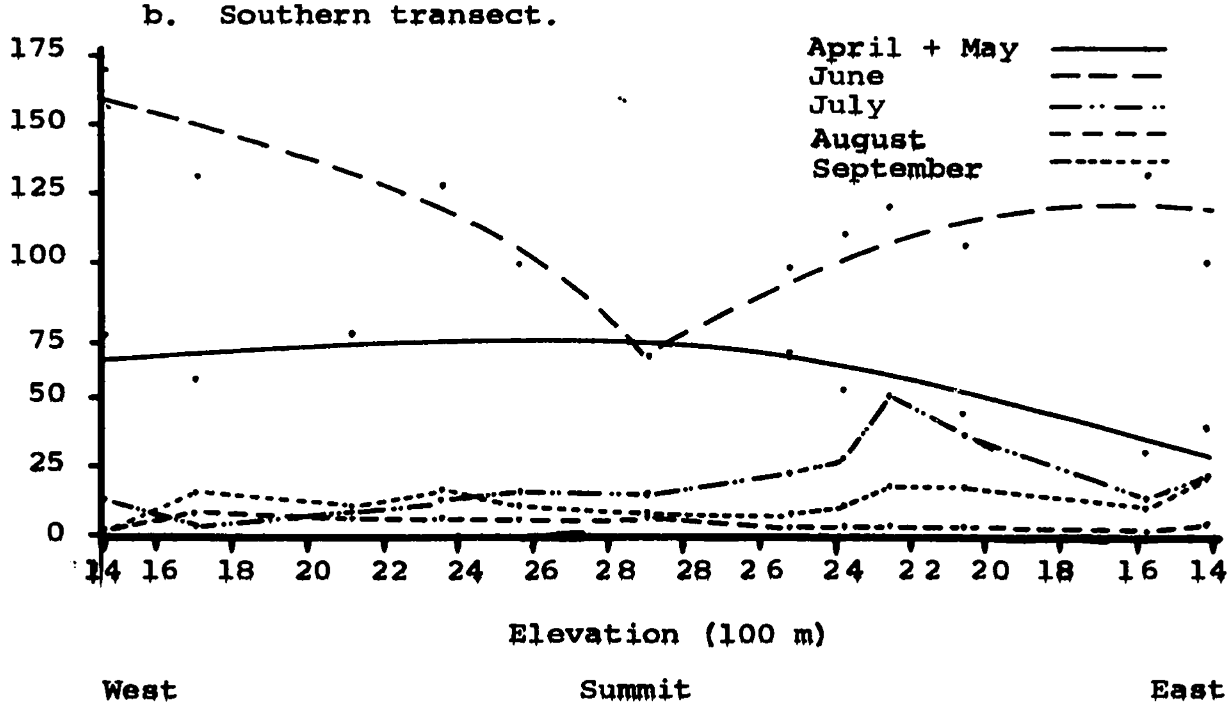
*More precipitation was received than gage could hold ca. 150 mm.

Figure 7. Relationship of precipitation to elevation across the Bighorn Mountains, Wyoming, from April through September 1969.

a. Northern transect.




b. Southern transect.



stations around the flanks of the Bighorns with records going back to 1931 show the following departures from the 30 year normal: April +8 to +18 mm, May +5 to +20 mm, June +25 to +64 mm; July, August and September were all about 13 to 25 mm below normal. From this it may be surmised that the spring months are a little higher than normal and the summer months a little lower than normal and that June was somewhat atypical.

Mean monthly rainfall for three Weather Bureau stations in the area are plotted in Fig. 8. Sheridan is on the east, Deaver on the west, and Burgess Junction on top of the Range. The shape of the curves for all three stations is the same, only the amounts are different. Two facts can be drawn from Fig. 8. First, most of the rain falls between April and June. Second, the amount of rainfall during the summer months, July to September, is almost negligible.

Because snow melt doesn't occur until May or early June (U. S. Soil Conservation Service 1968), most of the year's moisture supply is present on the Mountains in the form of snow about the first of May. The distribution of this moisture is shown in Fig. 9. This map was derived from snow survey data published by the U. S. Soil Conservation Service (1968). The most striking feature of this distribution is the north-south gradient with highest water content on the north third of the Mountains. This may help in explaining

Figure 8. Mean monthly precipitation for selected weather stations on and near the Bighorn Mountains, Wyoming.

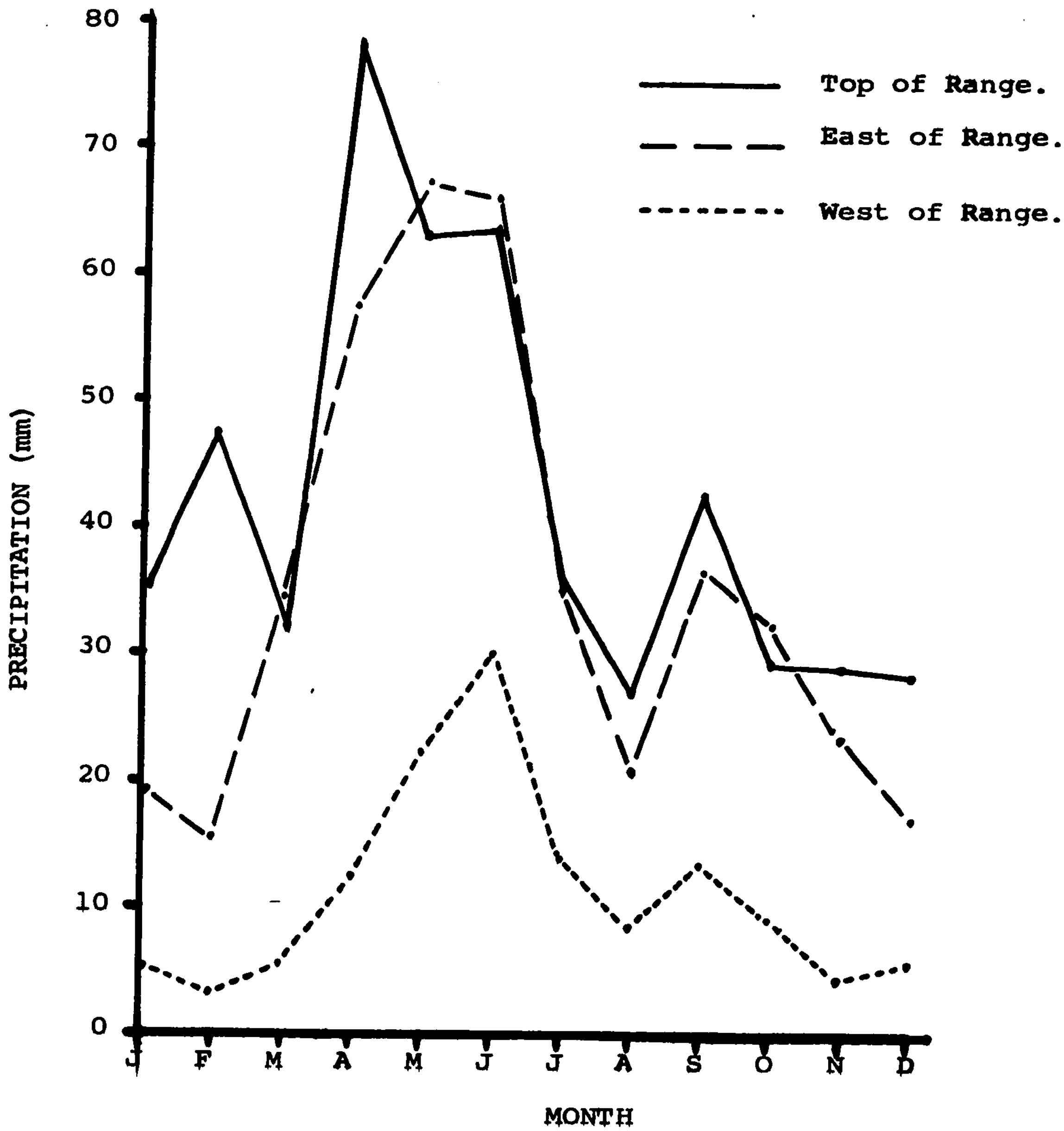
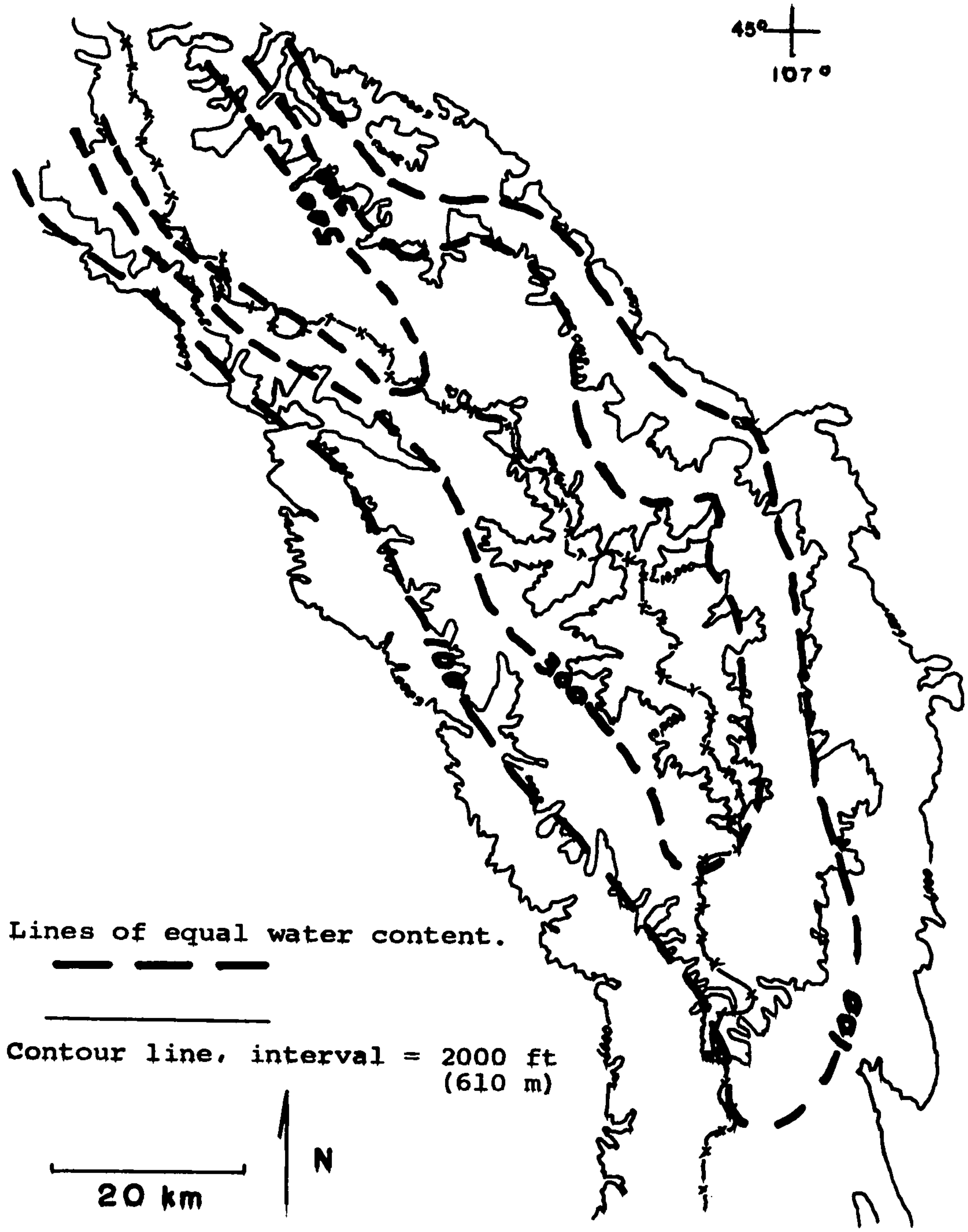


Figure 9. Mean water content of snow on the Bighorn Mountains, Wyoming, about May 1.



the relative abundance of *Picea-engelmannii-Abies lasiocarpa* forests in this portion of the Range.

## Map Study

To determine the relationship of aspect and substrate to forest type 2 x 2 tables were obtained and chi square values calculated. Those relationships significant at the 10% level are listed in Table 15. Cole's Index (Cole 1949) was calculated to give a measure of the magnitude of the association between a timbertype and aspect. The points were first separated as to granitic and sedimentary substrate. Only *Picea engelmannii-Abies lasiocarpa*, *Pinus contorta* and *Pseudotsuga menziesii* types were tested because occurances of other types were too few to be meaningful. Only data from the optimal elevational range of each type were used. No aspect was represented by fewer than 18 points.

*Picea engelmannii-Abies lasiocarpa* stands show no association with any aspect on granitic sites but are negatively associated with south-facing slopes of sedimentary substrates. *Pinus contorta* stands on granitic sites are negatively associated with south and west-facing slopes but are positively associated with east and northeast-facing slopes. On sedimentary sites *Pinus contorta* is associated negatively with south-facing slopes and positively with north-facing slopes. *Pseudotsuga menziesii* stands show a positive association with north-facing slopes

Table 15. Timbertype-aspect relationships in optimal elevational ranges having significant chi squared values.

| Timbertype | Elevational Range (m) | Substrate | Aspect | Cole's Index |
|---|---|---|---|---|
| *Picea engelmannii-Abies lasiocarpa* | 2600-2900 | Sedimentary | S | -42 +0.18 |
| | | Sedimentary | NW | +0.27 ±0.11 |
| *Pinus contorta* | 2300-2750 | Sedimentary | N | +0.16 ±0.05 |
| | | Granitic | NE* | +0.33 ±0.16 |
| | | Granitic | E | +0.46 ±0.18 |
| | | Sedimentary | S | -0.58 ±0.28 |
| | | Granitic | S | -0.21 ±0.08 |
| | | Granitic | W* | -0.17 ±0.09 |
| *Pseudotsuga menziesii* | 2000-2450 | Granitic | SW | +0.55 ±0.16 |
| | | Sedimentary | SW | -0.43 ±0.19 |
| | | Sedimentary | N | +0.30 ±0.08 |

*Significant at 10% level all others significant at 5% level.

on sedimentary sites. They associate positively with southwest-facing slopes on granitic sites but negatively on sedimentary slopes.

The vegetation map (Fig. 10) shows a fringe of *Picea engelmannii*-*Abies lasiocarpa* forests just below timberline on granite and it is possible that here the unfavorable conditions produced by granite are ameliorated sufficiently to allow *Picea engelmannii* and *Abies lasiocarpa* to compete successfully with *Pinus contorta*. It is shown in Table 15 and Fig. 11 that response of *Pinus contorta* and *Picea engelmannii*-*Abies lasiocarpa* forests to the environment is quite different.

When percent occurrence for each timbertype is plotted against elevation (Fig. 11a), the curves have the appearance of a group of species along a gradient (Whittaker 1967) with approximately bell-shaped curves such as *Pinus contorta* and some approximately S-shaped as in the case of *Picea engelmannii*-*Abies lasiocarpa* stands. Non-forest, in this case a highly variable species, is S-shaped on both ends.

This graph also shows the zonation of *Pinus ponderosa*, the lowest and *Picea engelmannii*-*Abies lasiocarpa*, the highest forest community types. *Pinus ponderosa* has an approximate peak at 1830 m, *Pseudotsuga menziesii* at about 2140 m, *Pinus contorta* at about 2440-2680 m and *Picea engelmannii*-*Abies lasiocarpa* at about 2750 m. It appears that timberline comes rather abruptly at or before *Picea engelmannii*-*Abies lasiocarpa* reaches its full development and

Figure 10. Vegetation map of the Bighorn Mountains, Wyoming. This was compiled from timbertype maps prepared by the U. S. Forest Service and Bureau of Land Management from aerial photographs. The Sheridan quadrangle 1:250,000 series was used as base map for the compilation.

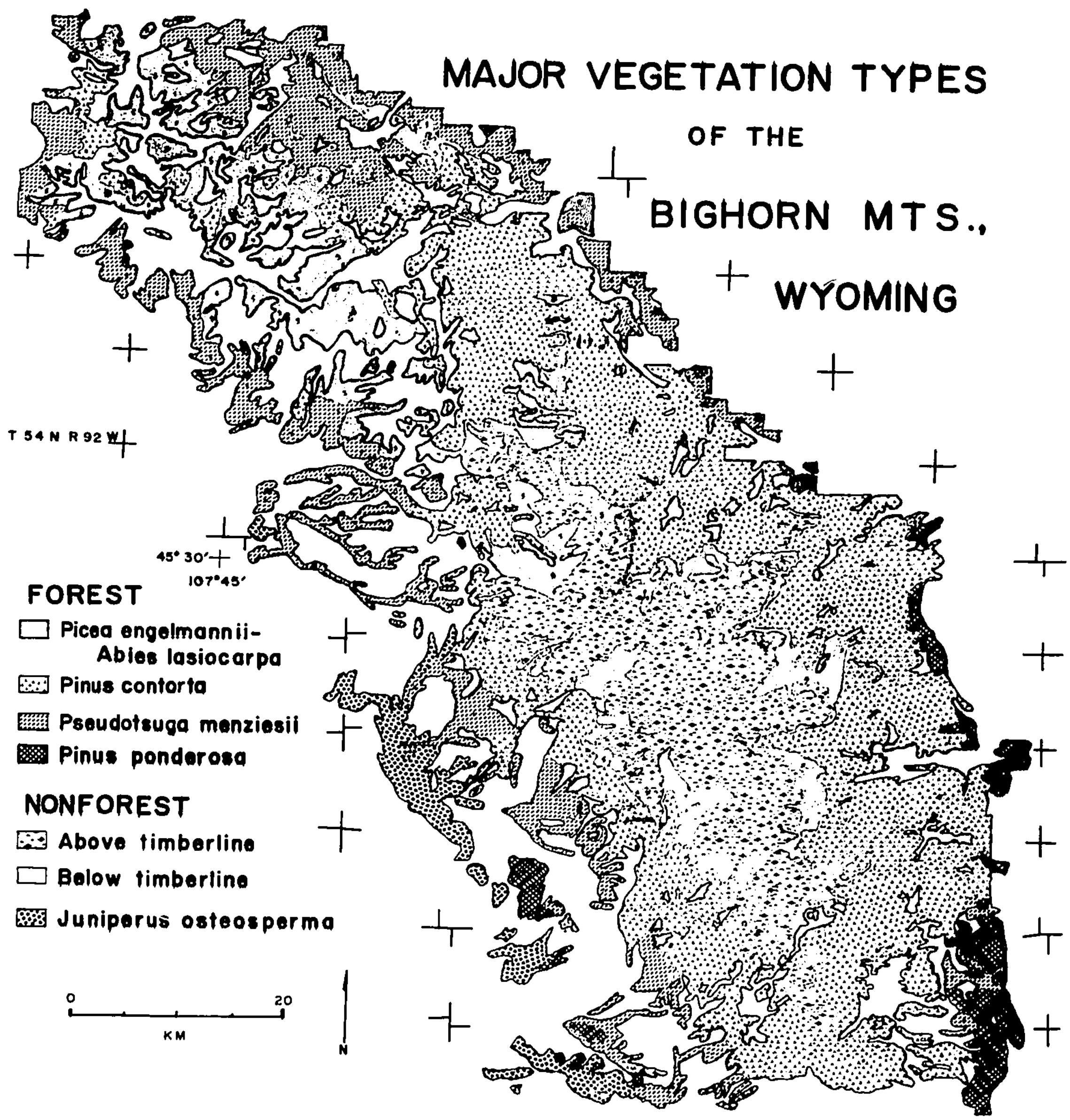

MAJOR VEGETATION TYPES
OF THE
BIGHORN MTS.,
WYOMING
T 54 N R 92 W
45° 30'
107°45'
FOREST
Picea engelmannii-Abies lasiocarpa
Pinus contorta
Pseudotsuga menziesii
Pinus ponderosa
NONFOREST
Above timberline
Below timberline
Juniperus osteosperma
0
20
KM
N

Figure 11. Relationship of timbertype to elevation and geologic substrate on the Bighorn Mountains, Wyoming.

a. Total points.

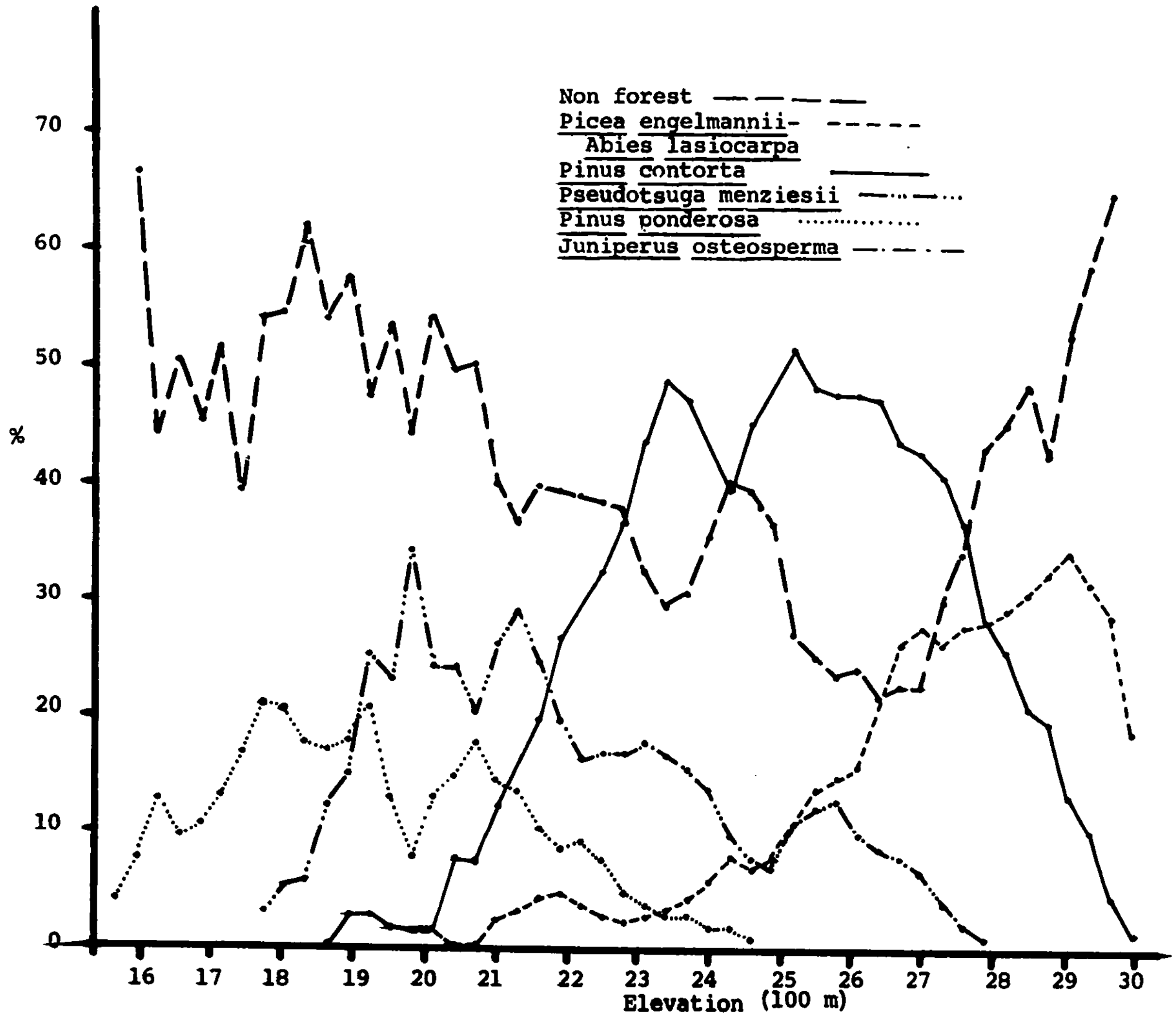


Figure 11--Continued.

b. Points occurring on granitic substrates.

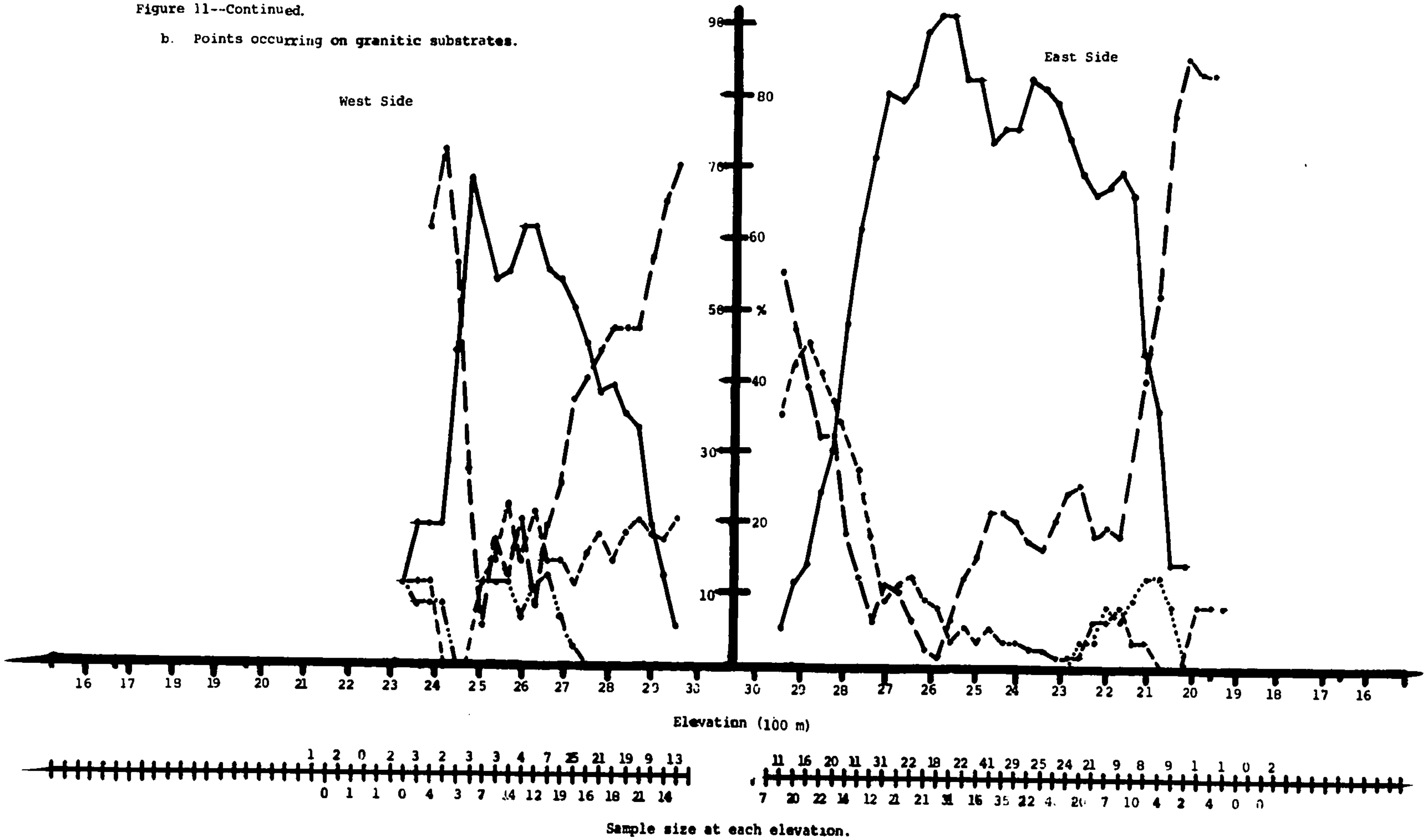
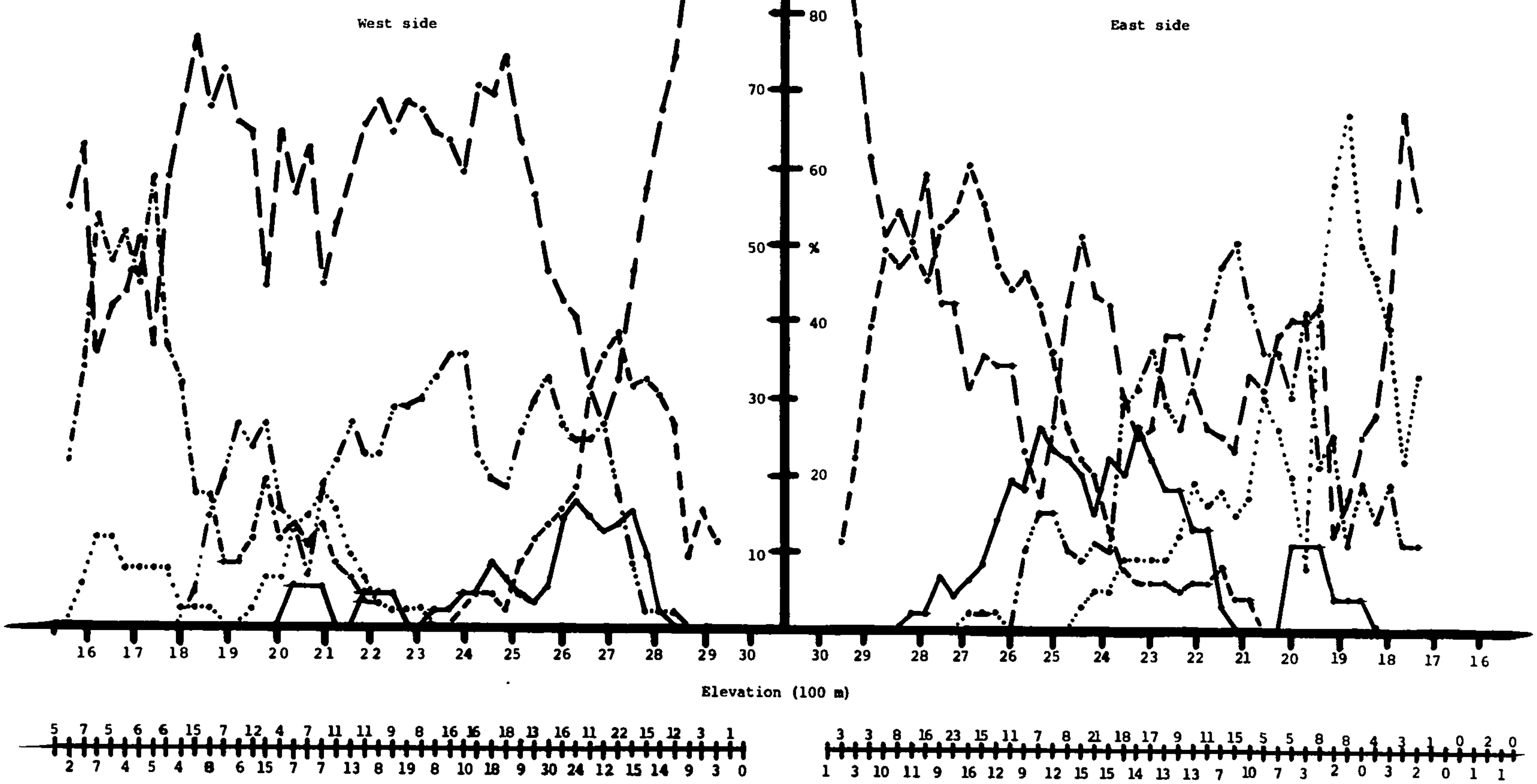


Figure 11--Continued.

c. Points occurring on sedimentary substrates.




Sample size at each elevation.

the other half of the bell-shape is not present. Non-forest communities are most important from the base of the Range to 2290 m and above 2750 m. Between 2290 and 2750 m, Pinus contorta is most important.

When the data are plotted according to east or west flank and according to granite or sedimentary substrates, some striking relationships are evident (Fig. 11b and 11c). The relationship between granite and Pinus contorta is again demonstrated and is apparent on both flanks where those communities cover most of the granitic sites. Near timberline Picea engelmannii-Abies lasiocarpa stands increase in cover until they become more important than Pinus contorta. On granitic substrates Pseudotsuga menziesii and Pinus ponderosa make only an insignificant contribution to forest cover.

On sedimentary substrates Pinus contorta is of much less importance. On the west side, forest communities cover less area than nonforest communities; Picea engelmannii-Abies lasiocarpa stands are not very important; Pseudotsuga menziesii covers a very broad altitudinal band and Juniperus osteosperma can be seen on the lower slopes becoming more important than nonforest.

The sedimentary rocks on the east side show a pattern different from that on the west. Most striking is the preponderance of forest communities. Picea engelmannii-Abies lasiocarpa stands are best developed; Pseudotsuga menziesii, though not covering as broad a band is still a major component; juniper stands are missing and *Pinus ponderosa* provides significant cover at the lower elevations. The peak of non-forest cover at about 2400 m is interesting in light of the *Pinus contorta* zone on the granite substrates. This could perhaps indicate a set of environmental factors at this particular elevational zone that is responsible for producing climax *Pinus contorta* stands on granitic substrates but is expressed here as grassland. It lies in a position after *Pseudotsuga menziesii* begins to lose importance but before *Picea engelmannii*-*Abies lasiocarpa* stands become important.

Some error is introduced into the data as a result of using different maps with different scales and different accuracies for vegetation and other variables. A particular slope covers a small area and a small difference in the maps could put a point on one aspect in one map and on the other aspect in the other map. Thus the probability that the aspect recorded is the true aspect is less than one. The same holds true for substrate but because the area covered by a particular substrate is larger, the probability of the recorded substrate being the true substrate is greater. These errors would have the effect of reducing the magnitude of Cole's index.

# DISCUSSION

## Physical and Climatic Patterns

### Geology

The anticlinal form of the Bighorns has resulted in a pattern of granite at the surface over much of the central third of the Range down to an elevation of about 2200 m. The northern and southern thirds as well as the flanks of the central third are covered by sedimentary rocks. The influence of the rock types through soil characteristics on the vegetation accounts for most of the pattern of community types shown in Fig. 10. *Pinus contorta* covers nearly all of the granitic areas and occcurs only in small isolated areas on sedimentary derived soils. These areas are probably burned areas with successional stands of *Pinus contorta* on them.

Sedimentary rocks occur from timberline to the river basins on the northern third and are very influential in the remaining vegetation types. Limestone and shales produce soils with many similar characteristics (Table 12). Having higher moisture holding capacity and more exchangeable cations than granitic derived soils, they support grassland and forests of *Picea engelmannii*-*Abies lasiocarpa* at higher elevations and *Pseudotsuga menziesii* and *Pinus ponderosa* at lower elevations. Forests are restricted to north-facing slopes on shales and at lower elevations on limestone as well.

It is evident that precipitation is marginal enough to allow the influence of geologic substrate to become dominant through its effect on the water storage capacity of the soil through organic matter and particle size.

## Topography

The anticlinal form also is responsible for topographical influences of the Mountains. The elevational pattern is one of roughly concentric elipses and the vegetation responds in the expected manner, with communities adapted to cool moist environments at higher elevations, and those adapted to warm dry environments at lower elevations. Elevation exerts an influence on the vegetation by causing the air to rise. As it rises it cools adiabatically producing lower air temperatures and causing moisture to be precipitated if conditions are suitable. Elevation of a mountain range and the area above a particular elevation is a prominant factor in the moisture regime of the range (Shreve 1919, see also Shreve 1922).

Another influence of the rock type is exerted in the land forms produced as they weather and erode. The thick layers of limestone have resulted in canyons in the lower slopes. The upper ends of these canyons are forested on both sides, as are the uplands between the canyons, but towards the lower end the forest is confined to the north-facing sides. Between the canyons the slopes are controlled by the dip and strike of the beds. The pattern as shown in Fig. 10 along the west flank is largely explained by these factors. On top of the Bighorns shales weather to rounded hills with gently sloping flanks. Where these flanks face north, they are covered by forest but on south-facing slopes the combination of little precipitation and fine soil dictates the occurrence of grassland vegetation.

## Soil

Soil patterns on the Bighorns exhibit well the fact that soil is a function of parent material, climate, organisms, topography and time (Jenny 1941).

Vegetation plays an important role in soil formation. Forest-covered soils have an $A_2$ and a very thin $A_1$ horizon and soil developed under grassland vegetation has no $A_2$ horizon but a thick $A_1$. This is quite evident in the soils of the Bighorns (Thorp 1931).

The influence of time is seen in the poor development of soils on glacial till. In adjacent areas not covered by till the soils are quite well-developed and there appears to be little difference in climate. Parent material might account for part of the difference but it is granitic in both areas (compare stand 5 with 19 which are geographically close and share a common climate, in appendix 1 and 2).

Substrate is also quite important in determining the pattern exhibited by soils. Granite yields coarse soils poor in nutrients and mostly forest vegetation while shale, at the other extreme, produces fine soils high in nutrients and much grass vegetation. Between these extremes limestone and dolomite, because of their weathering characteristics, produce a hybrid soil high in nurtients with both very coarse and very fine particles. On steep, north-facing slopes forest vegetation is favored and in other topographic positions grassland vegetation is favored.

Because vegetation is a function of the same variables as soils there is a close correlation between vegetation patterns and soil patterns.

## Precipitation

The geographical location of the Bighorn Mountains has a definite effect on precipitation patterns. Being on the east side of the Rocky Mountains, any winds from a westerly direction are downslope winds, and thus very dry. The Pryor Mountains on the northwest and the Owl Creek Mountains on the southwest keep moisture laden winds from reaching the west flank of the Mountains. If it were not for the large gap between the Pryor Mountains and the Beartooth Mountains, to the west, the meager rainfall on the west slope of the Bighorn Mountains would be even more meager.

Rainfall on the west slope, other than local thunder showers, comes from regional weather patterns that produce an air flow from the north or northwest. This allows moisture laden air to enter the Big Horn Basin through the gap between the Pryor and Beartooth Ranges. The air then releases its moisture as it rises orographically over the Bighorn Mountains. Thus the driest part of the Range is along the northwest flank and a rain shadow occurs southeast of Cloud Peak. The source area for this moisture is the grasslands in Montana to the north and northwest along the Rocky Mountains. The east slope receives moisture from easterly winds coming from the prairies. The major storm tracks, being to the north, produce winds mostly from the northeast yielding higher precipitation on the northeast section of the Range and intensifying the rainshadow southeast of Cloud Peak.

Air flow patterns of this type can arise from both low and high pressure systems. If the center of a low pressure cell passes over the northern portion of the area, the counterclockwise flow will bring air into the Big Horn Basin and with it rain. If the pressure cell is shallow, weak and fast-moving, very little rain falls. However if it goes deep into the atmosphere, is strong and slow-moving, more rain falls. This case results from the inland movement of Pacific storms and though the source of the disturbance is the Pacific Ocean, the source of precipitation is the prairies to the north and east.

Histograms of daily precipitation for stations in and around the Mountains for 1969 indicate that spring rains come from general weather systems and all stations are affected similarly. Summer precipitation comes more in the form of local thunder showers with their attendant variability.

Because of seasonal distribution, effective precipitation at higher elevations comes in the form of snow. Thus the vegetation is subject to the peculiarities of moisture received in this fashion. Date of release from snow thus becomes important and would be later at higher elevations than at lower ones and earlier in parks than in forests. Redistribution of the snow by wind, after it has fallen, brings into play topography and wind patterns i.e., more moisture being deposited on the lee side of hills and rocks. Billings (1969) has demonstrated the importance of this phenomenon in explaining ribbon forests of high altitudes. Snow melt in the spring brings soil characteristics into the picture in the form of porosity and because the soil is frozen, the type of frozen ground under the snow is important (Haupt 1967).

The moisture available to plants for a season's growth is present in the soil by the end of June as the amount of summer precipitation does not contribute significant additions. Therefore the amount of moisture a soil can store and the depth to which it is stored become important factors influencing vegetation.

The zonation from base to summit is the result of the increase in precipitation as well as a decrease in temperature and thus a decrease in the evaporative power of the air and a prolongation of snow cover and decrease in the length of growing season (Larsen 1930).

The distribution of Pinus ponderosa on the Bighorns is probably a result of the precipitation pattern. It is best developed along the east flank which is the region of highest rainfall within the altitudinal limits of Pinus ponderosa. On the west side it occurs on the southern portion. Along the drier northern portion no Pinus ponderosa occur. The dry nature of the west side also accounts in part for the presence of the Juniperus osteosperma zone and the abundance of grasslands along the entire west slope. The higher precipitation on the east slope has resulted in more area covered by forest communities even on sedimentary substrates (Fig. 11).

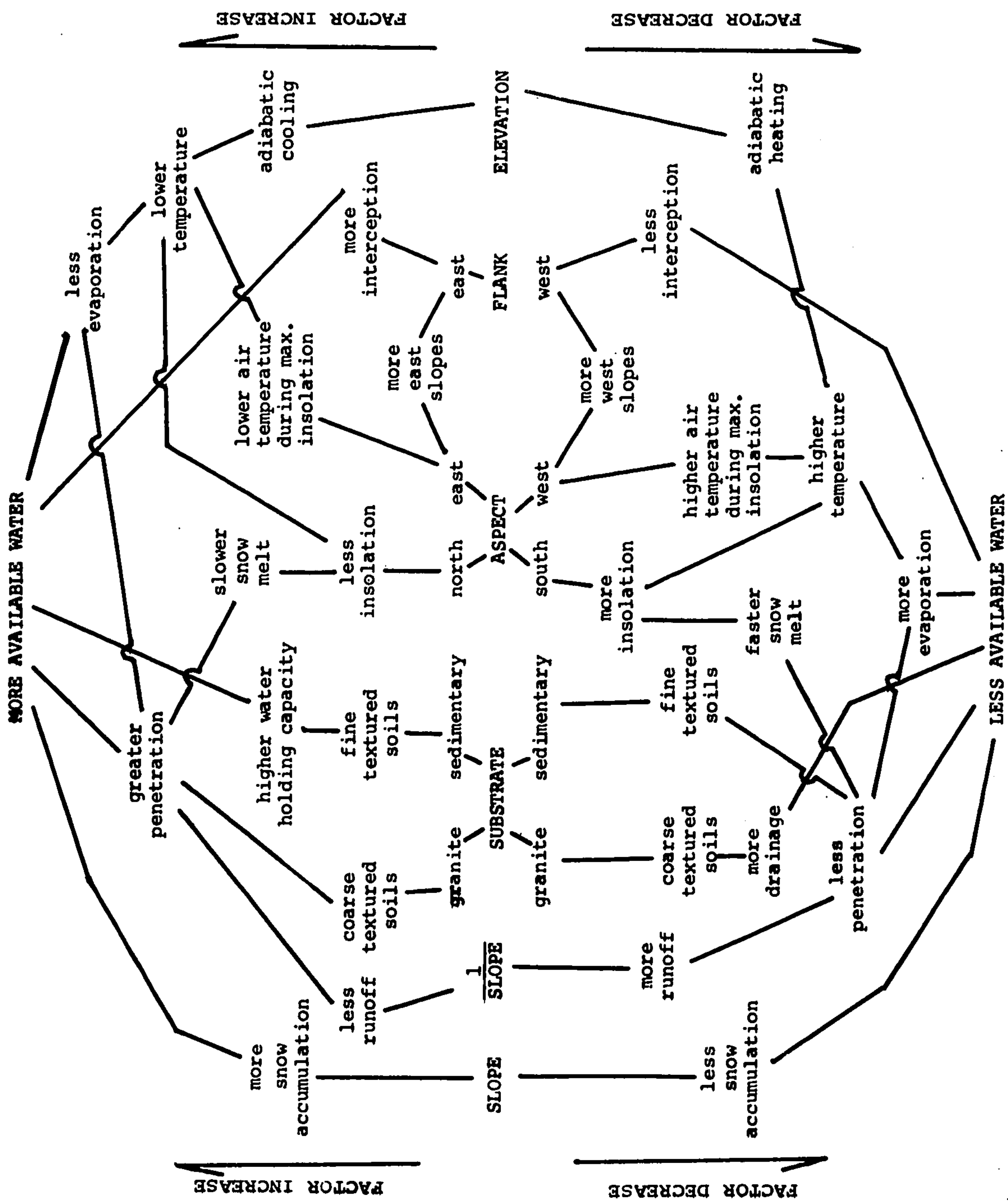
The rain shadow southeast of the granitic peaks is expressed in the form of large areas of grassland in the Pinus contorta zone on the granitic substrates. Where moisture is more abundant the granite is usually covered with Pinus contorta trees or Picea engelmannii-Abies lasiocarpa stands.

## Vegetation Patterns

The distribution of community types as shown by the map study is probably a result of a combination of marginal rainfall and the influence of the sedimentary rocks on the soil. Because rainfall is in the lower region of the tolerance curve for forest communities, available moisture is easily influenced by other environmental factors. Any feature of the environment that results in a departure from the average of available moisture results in a different community type, often of different physiognomy. Some of these factors and relationships are shown in Fig. 12. Like any ecological factor the relationships of the various components to each other are complex and the moisture available at a given site is a function of many factors including soil, topography and the amount of water delivered to the site by meterological processes.

The volume of water in a soil which is available to plants is dependent on a number of variables including the ability of the plant to extract water. A plant which can extract water at lower water potentials has available to it more water. Fine soils hold more water in an available form than coarse soils but require more water to bring the water potential from a point below availability to within the range of avilability. Thus coarse granite soils may have more available water following a rainshower during a dry period. Bulk density of a soil must also be taken into account when comparing the amount of water available from two different soils. Moisture content is expressed on a percent of dry weight basis. Thus a soil that has a greater percentage of water available may have less actual water available if the weight of soil in a unit volume is significantly less.

Figure 12. Diagramatic representation of some of the factors and relationships producing the moisture regime of a habitat.


FACTOR INCREASE
FACTOR DECREASE
ELEVATION
adiabatic cooling
adiabatic heating
lower temperature
less evaporation
FLANK
east
west
more interception
less interception
more east slopes
more west slopes
ASPECT
east
west
north
south
lower air temperature during max. insolation
higher air temperature during max. insolation
higher temperature
less insolation
more insolation
slower snow melt
faster snow melt
more evaporation
MORE AVAILABLE WATER
LESS AVAILABLE WATER
SUBSTRATE
sedimentary
granite
fine textured soils
coarse textured soils
higher water holding capacity
more drainage
greater penetration
less penetration
1/SLOPE
less runoff
more runoff
SLOPE
more snow accumulation
less snow accumulation
FACTOR INCREASE
FACTOR DECREASE

Soils from both the shales and limestones have similar sand:clay ratios whereas granitic derived soils have considerably higher sand:clay ratios (Table 13); thus more water would be held in the sedimentary derived soils. Summer thunder showers, because of their short duration and small amounts of precipitation, would probably be held in the upper few inches of sedimentary soils, being more advantageous to grass than trees.

Topography becomes more important, especially at lower elevations, where forests are restricted to the north-facing slopes. Soil aeration may also be a factor. Granite derived soils being coarse allow more aeration.

All of these factors acting together have resulted in a vegetation pattern unique to the Bighorns but similar in many ways to other Rocky Mountain areas. Elevational zonation begins at the lowest level with _Juniperus osteosperma_ stands followed by _Pinus ponderosa_ forests. These grade into _Pseudotsuga menziesii_ forests which form a narrow and limited zone in the central third but a broader zone in the northern and southern third. _Pinus ponderosa_ stands are best developed on the eastern flank, where _Juniperus osteosperma_ is lacking, and are completely missing from the north half of the west flank, where _Juniperus osteosperma_ is best developed.

Immediately above these zones _Picea engelmannii-Abies lasiocarpa_ forests occur in areas of sedimentary rock, but in areas of granite a broad zone of _Pinus contorta_ occurs between the *Pseudotsuga menziesii* and *Pinus engelmannii*-*Abies lasiocarpa* forests. The occurrence of this *Pinus contorta* zone is clearly connected with granitic substrates. The strong positive association between *Pinus contorta* and granitic substrates and the strong negative association between *Pseudotsuga menziesii* and granite (Fig. 10) suggest that these species respond differently to the soil conditions produced by granitic and sedimentary rocks. Gail and Long (1935) showed that *Pinus contorta* growth increased with increasing aeration of the soil. The coarse nature of granitic derived soils allows for more aeration than the heavier sedimentary derived soils. The response of *Pseudotsuga menziesii* to root aeration is unknown but it may be that *Pseudotsuga* can tolerate lower soil aeration than *Pinus* which would help explain the patterning. Mineral nutrition enters the picture also. Daubenmire (1953) demonstrated a higher Ca, K, and P content in the needles of *Pseudotsuga menziesii* than *Pinus contorta*. *Picea engelmannii* and *Abies lasiocarpa* also contained more Ca and P but K was in the same range with *Pinus contorta*. If the content of the needles is a reflection of the mineral requirements and not a reflection of the soil in which the plant is growing, at least part of the behavior of *Pinus contorta* and *Pseudotsuga menziesii* may have an explanation in these findings. Indeed *Pseudotsuga menziesii* showed stronger symptoms of calcium deficiency, when grown in a low Ca medium, than *Picea engelmannii* and *Pinus ponderosa*

(Murison 1959) but more work needs to be done on the mineral nutrition of Pinus contorta and Pseudotsuga menziesii.

## Herb Layer Relationships

The factor analysis indicates that the herb layer may be indicative of site potentialities. The inclusion of Pinus contorta stand 17 and Pseudotsuga menziesii stands 27 and 28 with Picea engelmannii-Abies lasiocarpa type indicates that although they are presently dominated by other tree species they may be successional and may eventually become Picea engelmannii-Abies lasiocarpa stands. This is also indicated by the sapling seedling data (Table 4). The inclusion of Picea engelmannii-Abies lasiocarpa stands 5 and 6 in factor 2 and their low loading in factor 1 is probably a function of the very low herb cover values (Table 3) making them more similar to Pinus contorta stands. Stand 23 is a Pinus ponderosa forest but it occurs on a north-facing slope near the upper limit of this community in that area.

The overstory influences the environment of the herb layer but if forests with different dominant species do not affect the factors critical to the species of the herb layer the communities will have similar herb layers. Other criteria must be considered in inferences regarding the stability of a certain forest community and the potential vegetation of a particular site.

The grouping of most of the Pinus contorta and Picea engelmannii-Abies lasiocarpa stands in the first two factors and the inclusion of few other stands indicates that these two types are closely related. In many regions of the Rocky Mountains, Pinus contorta is successional (Clements 1910, 1920, Daubenmire 1943). However to say that all Pinus contorta stands are successional seems a bit of an overstatement. Their relatedness in ordinations, factor analyses, and other phytosociological analyses may be more a function of the fact that few species can tolerate the conditions produced by a Pinus contorta canopy and that these same species can tolerate a Picea engelmannii-Abies lasiocarpa canopy.

The shrub dominated communities are all in one group except for stand 35. This stand is much higher in elevation than the rest and is more likely a shrubby phase of an Idaho fescue association described by Beetle (1956) and Hurd (1961). It is interesting to note that the shrub communities at lower elevations have similar understories though they may have Juniperus osteosperma, Cercocarpus ledifolius or Artemisia tridentata as an overstory.

The Pseudotsuga menziesii stands are somewhat dispersed among the factors. This means that the overstory is not important in determining the limits of the herb layer in these forests.

The Pinus ponderosa stands are each in a different factor group indicating a high variability of the understory and perhaps even independence of the understory from the canopy. Considering the open nature of many of the stands this is not surprising.

The applicability of factor analysis for such a set of data may certainly be questioned, especially in light of recent findings that the breadth of the environmental spectrum included in the analyses does affect the outcome (Swan 1970) and the result of the analysis of a broad spectrum is not reliable. It is interesting, however, to note that the position of many of the stands in this analysis can be explained by environmental factors. It must be kept in mind, however, the limitations imposed by the very wide range of the environment.

## Forest-meadow Boundaries

Although not enough boundaries were studied intensively, some indications and trends are evident. Soil properties indicate that the boundaries have been fairly stable for some time. This was also noted by Dunnewald (1930) and Jackson (1957). Town (1899) blames fires for the grasslands but his brief description of the soils indicates that even at that time a good grassland soil had developed in the meadows. This means that the vegetational characteristics are not indicative of advance or retreat of the forest but rather indicate stable ecotones of environment and each has a characteristic boundary unique to the variables most influential at that point. This boundary would be reestablished after each disturbance.

At the edge of burned Pinus contorta forests can be seen a fringe of trees that were not affected by the fire and the boundary peculiar to this community is still largely intact. Some minor changes will probably occur as the young forest grows inside this boundary but not many.

The treeless band just behind the first trees may the the result of drifted snow (Patten 1963, Billings 1969). Indeed this may be the main force shaping this type of boundary. This is an area where snow blown from the adjacent meadow would be deposited. The effect of snow depth on Pinus contorta has not been studied but some casual observations indicate that there is probably an optimum snow depth above which the seedlings are not released early enough in the spring to grow and below which they are killed by low temperature during the winter. The absence of this tree-free zone and the heavy establishment of trees right at the edge of Picea engelmannii-Abies lasiocarpa communities would indicate that they respond differently to snow drifts. This may be a factor in the establishment of Pinus contorta and Picea engelmannii-Abies lasiocarpa communities at higher elevations. Certainly this relationship should be the subject of future research.

The steady and parallel decrease in herbaceous cover at bouth boundaries indicates that the same environmental complex is in operation. Many of these factors were described by Patten (1963) in a mountain range about 350 km west of the Bighorns. Yet many questions remain to be answered before the problem of meadows in a forested region can be solved. Among these are: What role does snow accumulation play in the establishment of tree seedlings; does aeration have a differential effect on the species involved; just what property of fine soils affects tree seedlings; etc.

## Sources of Disturbance

### Fire

When European man came to the Mountains he brought with him his carelessness with fire and since he went into the forested areas for lumber, great areas near lumber camps were burned. Because these camps were low in the valleys, fires could burn great distances before reaching a natural barrier. Accounts of fires burning for several weeks and consuming hundreds of acres come from this period (Conner 1940, Town 1899). There is also one account of the Indians setting a large fire. In 1876, the Sioux Indians, retreating from General Crook, set fire to the forest to slow the pursuit of the enemy, burning an estimated 200,000 ha (Conner 1940). Town (1899) reported large areas of timber burned 25-30 yrs earlier and tells of other recent large fires reportedly set by Indians. His main impression of the Bighorns was how much damage fires had done and he attributed the many parks in the Range to fire.

However, since this brief but colorful period, European man has declared fire a public enemy and now fires are put out as quickly as possible. Though about 56% of the fires in the last 60 yrs (1909-1968) were man-caused, only 7 fires greater than 0.2 ha have occurred on the Bighorns in the past 10 yrs (Simmons 1970, personal communication). The remaining 44% (an average of 6 fires per year) caused by lightning probably indicate the frequency of natural fires. Fires have been in the past and will continue to be a major factor in what vegetation is present at any one time in any particular place. Fire effects on site conditions have been well documented in other areas and need not be repeated here (Clements 1910, Ives 1941, Stahelin 1943, Ahlgren and Ahlgren 1960).

Most people who have written about the Bighorns have mentioned the importance of fire in shaping the present vegetational patterns. Perhaps the earliest and most emphatic mention of this was Town (1899) who described the forests shortly after it was given the protection of the U. S. government. His description leaves the impression that the Bighorns are so subject to fire as to be worthless. He considered charcoal in the soil, large areas covered by *Pinus contorta* and the many parks and large areas of grassland as evidence of past fire. Certainly his assessment was also influenced by the unusually large area burned 23 years earlier by the Indians.

What one takes as an indication of past fires greatly influences the extent to which he believes fires have played a role in shaping the landscape. Charcoal in the soil is certainly an indication of past fire but it is also a very stable form of carbon and remains in the soil for hundreds of years. Therefore it is an indication only of a fire and tells us nothing about frequency of fires at that site. Because *Pinus contorta* is a known seral species, its extent can be taken as an indication of the extent of fires withing the last one hundred or so years, however long one estimates it takes for the climax stand to become re-established. However if a *Pinus contorta* exists as a climax species then this would result in an over assessment of the role of fire. As far as the existence of grassland or parks in otherwise heavily timbered forest as an indication of fire much caution should be excerised. *Pinus contorta* produces seed at the very early age of 6-10 yrs (U.S.D.A.-F.S. 1965) and fires would have to be very frequent in a particular area in order to keep *Pinus contorta* from germinating and growing to a small tree. In the Bighorns it is my observation that frequent fires produce denser populations of pine not parks. When fire does burn a *Pinus contorta* stand adjacent to a grassland area the boundary of the stand usually remains unburned and forest reoccupies the area that was previously forested. This is reflected in the soils as well.

## Wind

Tornadoes occasionally occur on the Mountains and leave in their wake a path of wind-thrown and broken trees. This usually covers small areas of less than 16-20 ha. Unlike fire, wind does not destroy the understory and the organic matter is not removed from the community. This has its effect on the characteristics of the site. Usually the forest grows again from the seedlings and saplings that survived. One such stand that was destroyed in 1962 had an average of 496 *Pseudotsuga menziesii* and 52 *Pinus flexilis* per ha, all less than 10 cm DBH. These densities are similar to the density of trees in mature stands.

## Landslides

The presence of steeply dipping, thick beds of shale has resulted in much movement. Landslides in forested areas usually result in downed trees. New parent material which is less suitable for plant growth is brought to the surface and mixed with the developed soil mantle so the long slow process of recolonization and soil formation begins once more. Although wind and landslides are not major factors and occur only sporadically, they do play a role.

## Man

Although the forest communities are not very suitable for lumbering, these activities have contributed and are

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now contributing to the destruction of many forests. Large tracts of mature *Pinus contorta* have been cleared away and many of the earlier unavailable *Picea engelmannii*-*Abies lasiocarpa* are now being cut. Man undoubtedly will continue to be a disturbing force in the communities of the Bighorns not only by fire but also by lumbering and recreational activities.

## Succession

The most common type of succession is autogenic succession which is dependent on the ability of one group of organisms to modify the environment sufficiently to allow for the establishment of another group (Tansley 1929). As the extremes of the environment are approached the amount of environmental change necessary increases, the length of time needed to effect the change increases, and the ability of the seral community to modify the environment decreases. The tolerance range of the seral community may also extend beyond that of the climax. Eventually a point is reached where the seral community is unable to cause the requisite changes and thus becomes the permanent occupier of the area especially if no other species are better adapted or are available to the site.

This is evident and recognized in the case of the Rocky Mountain *Pseudotsuga menziesii* (Oosting 1956) where the species that succeed it in the Pacific Northwest are not present in the Rocky Mountains. *Populus tremuloides* in certain areas of Wyoming and Colorado is also considered to be a climax species (Daubenmire 1968). In the Bighorns this same relationship is observed. At higher elevations on sedimentary substrates *Pseudotsuga menziesii* is seral to *Picea engelmannii* and *Abies lasiocarpa*, and at lower elevations *Pseudotsuga menziesii* forms the climax forest.

At higher elevations on granitic substrates *Pinus contorta* is seral to *Picea engelmannii*-*Abies lasiocarpa* as it is in other areas of the Rocky Mountains (Daubenmire 1943, Oosting and Reed 1952, Reed 1969). It does not appear to be seral to *Pseudotsuga menziesii* at middle elevations as it is is the Colorado Front Range (Marr 1961, Moir 1969), but forms a climax in a zone between *Pseudotsuga menziesii* and *Picea engelmannii*-*Abies lasiocarpa* as it does in the Front Range (Moir 1969).

That *Pinus contorta* stands are not necessarily *Picea engelmannii*-*Abies lasiocarpa* or *Pseudotsuga menziesii* sites temporarily occupied by *Pinus contorta* is suggested by the factor analysis that separated these types by herb layer characteristics (Table 11).

Some *Pinus contorta* stands at higher elevations have an understory of *Picea engelmannii* and *Abies lasiocarpa* and the trees of the overstory are large and relatively widely spaced. These stands are clearly in a simple successional train leading to a climax *Picea engelmannii*-*Abies lasiocarpa* forest. They are, howver, not very widespread. Older stands of a mixture of *Picea engelmannii*, *Abies lasiocarpa*, *Pinus contorta* occur but all the trees are of comparable ages.

Reproduction data from the Powder River Pass area, Table 12, indicate that at least in cool moist areas a mixed forest may start right from the seedling stage. Size class distribution of all the *Picea engelmannii*-*Abies lasiocarpa* stands sampled showed the highest number of *Picea engelmannii* is not reproducing under its own shade; seedlings in the first few years of growth were very rarely encountered in any of the stands sampled. The data indicate that the stand which establishes after a disturbance merely grows to maturity with adjustments in the density of the individuals of the species involved whereupon it stagnates until the next disturbance and it can start over. Why this is so is not clear. The activities of man could account for large areas of successionally young stands or seral stages produced by logging and fire but most of the stands predate European man's arrival, and the use of fire before that time by the Indians in the area is purely speculation. These activities also fail to explain the meager reproduction in established stands. The same argument holds for fire from natural causes.

Some workers have suggested that a lack of seed source accounts for such large areas of *Pinus contorta* (Daubenmire 1943, Reed 1969) but on the Bighorns both *Picea engelmannii* and *Abies lasiocarpa* can be found along all the small streams and in moist areas within the *Pinus contorta* forests. Thus it appears that establishment rather than seed source is the cause and we must look elsewhere to solve the problem.

Clements (1910) found that the response of *Pinus contorta* to soil moisture conditions was such that, other conditions being equal, *Pinus contorta* forests would crowd out other forests in areas of low soil moisture. It appears from his writing, however, that he was measuring the effect of soil texture on waterholding capacity rather than water availability. Still it was evident to him that moisture conditions played an important role in the behvior of *Pinus contorta* forests in relation to their neighboring plant communities. Total annual precipitation for the Bighorns is not very different from that of other Rocky Mountain areas (Daubenmire 1943, Oosting and Reed 1952, Patten 1963); however, in some mountains it is distributed more evenly throughout the year rather than most precipitation falling in the early spring. Thus the effective amount of moisture available in the critical summer months is less on the Bighorns.

It is possible that on the Bighorns, rainfall is low enough that on granitic soils moisture conditions prevent the establishment of *Picea engelmannii* and *Abies lasiocarpa* even though *Pinus contorta* shades the soil surface and snow accumulates in the forests. On non-granitic soils and at higher elevations, *Pinus contorta* stands provide an environment suitable for the establishment of *Picea engelmannii* and *Abies lasiocarpa*. That *Pinus contorta* forests are initiated and extended by fire (Whitford 1905, Clements 1910) may be true but they are not necessarily maintained by fire. A *Pinus contorta* zone similar to one described by Moir (1969) in Colorado covers a large area on the Bighorns (50% of forests).

In the understory of *Picea engelmannii*-*Abies lasiocarpa* forests, *Abies lasiocarpa* saplings greatly outnumber the *Picea engelmannii* saplings. This is commonly interpreted to mean that *Abies lasiocarpa* will ultimately dominate the overstory because of its superior reproduction (Daubenmire 1968, Reed 1969). *Abies lasiocarpa* reproduce largely by layering resulting in a very aggregated distribution. Thus each seedling must compete quite strongly with other individuals of the same species. It is evident that all or even a large number of these seedlings will not survive to become members of the overstory. *Picea engelmannii* on the other hand reproduce only by seed producing widely scattered seedlings and saplings which do not need to compete with other individuals of the same species. The chances of a seedling becoming part of the overstory are greater.

Average lifespan is also important when considering how the next forest will look. *Picea engelmannii* on the Bighorns commonly live to be 300-350 yrs old whereas *Abies lasiocarpa* are usually 150 to 200 yrs old. Thus twice as many *Abies lasiocarpa* must survive and become part of the overstory to maintain the present composition. This together with the intraspecific competition brought about by the reproductive method of *Abies lasiocarpa* would indicate that in the future, the present forest probably will not be much different from the present even though *Abies lasiocarpa* seedlings are so much more abundant than *Picea engelmannii* seedlings (Oosting and Reed 1952, Beil 1966).

## Relationship to Other Rocky Mountain Areas

The Bighorns belong floristically to the Central Rockies. Although they lie north of the division Daubenmire (1943) suggested between Central and Northern Rockies none of the species he lists as peculiar to Northern or Southern Rockies occur in the Bighorns.

The Bighorns have all the vegetation zones described for the Central Rocky Mountains (Fig. 10). The Pinyon-Juniper zone dominated by *Juniperus osteosperma* and *Cercocarpus ledifolius* is characteristic of Nevada (Reveal 1944), Utah and Arizona (Woodbury 1947). The presence of *Juniperus osteosperma* and the minor role of *Juniperus scopulorum* separates this zone from others east of the Continental Divide (Woodin and Lindsey 1954) and from those to the west and north (Oosting 1956). The absence of any of the Pinyon pines indicates its affinities to the more northern expressions of this zone (Woodin and Lindsey 1954, Oosting 1956). This zone is apparently lacking or poorly developed in the neighboring ranges studied by other workers (Madison Range, Patten 1963; Wind River Range, Reed 1969; Colorado Front Range, Marr 1967).

*Pinus ponderosa* has the widest range of any North American pine (Mirov 1967) ranging from southern British Columbia to central Mexico and from the Pacific coast to central Nebraska (USDA-FS 1965). However in the mountains adjacent to the Bighorns it is lacking or poorly represented (Larsen 1930). Wells (1965) considered the *Pinus ponderosa* stands of the Bighorns to be scarp woodlands.

The herb layer of *Pinus ponderosa* stands in the Bighorns shares very few species with other areas. Many of the stands are quite open and *Pinus ponderosa* occurs as a last outpost of tree habitation. It is possible that the influence of the trees on the forest floor is not enough to create a habitat sufficiently different to provide for a special set of herbaceous species. The flora is thus derived from neighboring plant communities. This is borne out in Washington and Oregon where the *Pinus ponderosa* zone was discussed on a geographical basis by Franklin and Dyrness (1969) rather than as a floristic unit. The Bighorns then are like most other areas in that the *Pinus ponderosa* stands do not have their own peculiar herb layer.

In the *Pseudotsuga menziesii* zone the lower stands also show affinities to more southern ranges with the occurrence of *Ribes cereum* and *Acer glabrum* and the absence of shrubs such as *Ribes lacustre*, *Vaccinium spp*. and *Pachistima myrsinites*, species common to northern

Pseudotsuga menziesii forests (USDA-FS 1965). Pseudotsuga menziesii stands at higher elevations (Stands 27 and 28) are more moist and contain Ribes montigenum and Pyrola secunda but their floristic similarity to stands further north is marginal. The Pseudotsuga menziesii forests of the Wind River (Reed 1969), the Madison Range (Patten 1963), and Banff and Jasper National Parks in Canada (Stringer 1966) also have much higher cover in the shrub and herb layers.

Populus tremuloides occurs on the Bighorns but is very minor. Small patches occur scattered throughout the Range but are seldom larger than 0.5 to 1 ha in extent. In the east central portion many of the Pinus contorta forests have a fringe of Populus tremuloides. These stands have an extention of the neighboring grasslands as an understory. A Populus tremuloides forest, similar to those described by Reed (1969) in the Wind Rivers and Hayward (1945) in the Uintas, was found on the north-facing side of an east tending escarpment on the east flank. The trees were very small, 6-15 cm DBH and about 6 to 8 m tall. An understory of Prunus, Crataegus, and Amelanchier occurred and a well developed herb layer was present. Aside from this one area, Populus tremuloides is quite unimportant as a community dominant in both climax and seral stands. This is quite different from the situation in Colorado (Robbins 1910, Baker 1925), Utah (Sampson 1916) and the Flathead Valley in Montana (Whitford 1905).

The *Pinus contorta* stands form a zone similar to that described by Moir (1969) in the Colorado Front Range. The only places that *Picea engelmannii* or *Abies lasiocarpa* seedlings can be found in *Pinus contorta* stands is in the higher elevations where the climate is more moist or along streams or in seeps, areas of snow accumulation or other moist areas. Stands thinned many years ago have considerable *Pinus contorta* reproduction in the understory. The herb layer of this zone is quite sparse and cover values are low. This seems to be in agreement with what was found by Moir (1969).

It is difficult to determine the relationship of this zone to other areas because it has not been recognized but considered a successional phase of either *Picea engelmannii-Abies lasiocarpa* or *Pseudotsuga menziesii* forests (Clements 1910, Moir 1969, Reed 1969). Reed (1969) included a number of *Pinus contorta* stands in his study of the Wind River Mountains because they covered so much of the area but he assigned them to a habitat type of one of the other climaxes. On the Bighorns the shrub layers of *Arctostaphylos uva-ursi*, *Mahonia repens*, and *Pachistima myrsinites* do not occur. Although *Arctostaphylos uva-ursi* may be present, *Juniperus communis* is more common. Even these stands are dominated by *Vaccinium scoparium* as they are in Reed's *Picea engelmannii/Vaccinium scoparium* habitat type.

Because *Pseudotsuga menziesii* and *Pinus contorta* stands are so nearly restricted in their substrate preferences on the Bighorns there is little or no chance for _Pinus contorta_ to be successional to _Pseudotsuga menziesii_ as it is in the Front Range (Marr 1967, Moir 1969). _Pinus contorta_ stands in Alberta appear clearly assignable to a seral role and no climax _Pinus contorta_ zone exists, only some isolated climax stands (Cormack 1953, Hnatiuk 1969). It is possible that a _Pinus contorta_ zone exists only in the southeastern portion of the range of the species and only on granitic substrates. This would group the Bighorns more with the southern forests than the northern ones.

The Bighorns differ from the Wind River Mountains to the southwest as described by Reed (1969) by the absence of a _Populus tremuloides_ zone and the presence of a _Pinus ponderosa_ zone. The Bighorns have a lower base level (1200 m vs. 2100 m) thus the lower zones extend further down the slopes. The _Pseudotsuga menziesii_ forests begin about 2300 m in the Wind Rivers whereas they end at that elevation in the Bighorns. Reed does not recognize a _Pinus contorta_ zone but many of the stands he assigns to the _Abies lasiocarpa-Pyrola secunda_ habitat type appear similar to stands in this zone in the Bighorns. The elevational limits of forest types are also quite similar as are the elevational limits of _Picea engelmannii-Abies lasiocarpa_ forests. Timberline is slightly higher (200 m) in the Wind Rivers.

The _Picea engelmannii-Abies lasiocarpa_ stands in the Bighorns are quite similar to those of the Medicine Bow

Range in southern Wyoming as are most subalpine forests in the Rocky Mountains (Oosting and Reed 1952). The dry nature of the Bighorns is manifest here in a smaller basal area per hectar; 46.9 to 29.8 $m^2$/ha as compared to 65.9 to 23.0 $m^2$/ha for *Picea engelmannii* and 10.7 to 0.6 as 16.6 to 4.1 for *Abies lasiocarpa*.

Timberline in the Medicine Bow Mountains is about 300 m higher allowing for better development of the *Picea engelmannii*-*Abies lasiocarpa* forests although the lower limits are similar.

Timberline in the Madison Range, southwestern Montana (Patten 1963), is near 2900 m but the forests there are quite different with essentially only two zones; a *Pseudotsuga menziesii* zone up to about 2300 m and a *Picea engelmannii*-*Abies lasiocarpa* zone from there to timberline. *Pinus contorta* stands are most common below 2750 m in the Madison Range whereas they extend commonly to 2900 m in the Bighorns. Those of the Madison Range are probably successional to other communities.

*Pinus albicaulis*, common at timberline in the Madison Range, is present in the Bighorns and Wind Rivers but totally lacking in Colorado (Harrington 1964) and the Medicine Bow Range thus the Bighorns are at the southern limits of this species. The Bighorns also represent an eastward extention of *Cercocarpus ledifolius* (Miller 1964).

The Black Hills lie 400 km to the east but there is little in common between the main vegetation associations described by McIntosh (1931) and those present in the Bighorns. They are probably not high enough to have a climate suitable for Picea engelmannii-Abies lasiocarpa stands and perhaps this could also explain the poor representation of Pinus contorta there. Pinus ponderosa forms a major portion of the forest communities in the Black Hills and shows some affinities with those of the east side of the Bighorns. Pseudotsuga menziesii is lacking in the Black Hills, and the Bighorns lack eastern and boreal species found in the Black Hills such as Quercus macrocarpa, Ostrya virginiana, Ulmus americana, Betula papyrifera, and Picea glauca.

The lower relief of the Black Hills and the climatic differences are probably responsible for the vegetational differences. History may have played a role in this but it seems probable that communities that could reach the Black Hills from either the west or north would have migrated past the Bighorns and thus have left remnants and any communities reaching the Black Hills from the east would not find any insurmountable obstacle between there and the Bighorns.

## SUMMARY

The vegetation of the Bighorns follows the elevational changes commonly described for the Rocky Mountain region with *Pinus ponderosa* forests and *Juniperus scopulorum* stands lowest followed by *Pseudotsuga menziesii* forests, *Pinus contorta* forests and *Picea engelmannii*-*Abies lasiocarpa* forests in that order. The zones are higher on the west; *Pinus ponderosa* forests are limited in extent and juniper communities are much more extensive than on the east side. *Cercocarpus ledifolius* communities are more common on the west flank. Communities dominated by *Artemisia tridentata* occur from the River Basins to near timberline and are probably not members of the same community type but rather are shrubby phases of grassland community types which were not studied in the course of this investigation.

Two types of forest boundaries were studied. *Pinus contorta* forests are bounded by a belt of few large trees with a gradually decreasing herb layer but increasing tree density. This belt remains after fires, often little affected by them. *Picea engelmannii*-*Abies lasiocarpa* forests are bounded by a dense belt of many small young trees with no herb layer and tree density decreases toward the forest. Soil data indicate the boundaries have been stable for quite some time.

Soils varied according to substrate differences. Those derived from shales and limestone were similar in texture, exchangeable cations, and moisture holding capacity but differed from soils derived from granite. Granitic soils were coarse and less fertile than sedimentary derived soils.

The Bighorns lie in a geographic position that results in the west side receiving less precipitation than the east side and the source of moisture in the area is from the prairies north and east. Summer rainfall is scant, less than 50 mm during July, August, and September. Peak rainfall is in April or May in the Mountains and June in the River Basins. Thus summer drought is quite common in most of the Range.

The Bighorn Mountains, being anticlinal in form with the center raised higher than either end, has provided sufficient granitic and sedimentary substrates at comparable elevations to provide an excellent opportunity to study the relationship of geological substrate and vegetation. Vegetation types respond strikingly to geologic substrate with *Pinus contorta* forests most common and nearly restricted to granitic areas. On sedimentary areas *Pseudotsuga menziesii* and *Picea engelmannii*-*Abies lasiocarpa* forests are the important forest communities but non-forest communities are more important even at higher elevations. The communities appear distributed along the elevational gradient like individual species. Forest regeneration and succession are also strongly influenced by geologic substrate. In moist granitic areas, such as at high elevations, Pinus contorta establishes rapidly then gives way successionally to Picea engelmannii-Abies lasiocarpa forests. In lower drier regions of granite, Pinus contorta is a climax forest. In these same regions underlain by sedimentary rocks, forest regeneration is very slow possibly accounting for a lot of the grassland or non-forested areas and often Pseudotsuga menziesii forms the seral forest.

Although the gradient is very broad and exceeds the tolerance limits of many species, factor analysis of the herb layer grouped those stands with overstories of Pinus contorta and Picea engelmannii-Abies lasiocarpa stands but Pseudotsuga menziesii and Pinus ponderosa stands were put in several groups indicating a more diverse and less distinctive herb layer.

The Bighorn Mountains appear to border on the climatic conditions that are sufficient to produce forest. If some part of the local environment causes a shift in the balance to one side grasslands predominate. The geologic substrate is very influential in tipping the balance one way or the other but just what factors and forces are involved is not yet known. The Bighorns may prove to be a suitable area for the illumination of these factors.

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Appendix 1. Soil data for *Picea engelmannii*-*Abies lasiocarpa* forests.

| Stand No. | Horizon | Depth cm | Exchangeable Cations (me/100g) K | Ca | Mg | Sand % | Silt % | Clay % | pH | Moist Color | % less than 2 mm | O.M. % | Substrate |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | $A_{11}$ | 0-3 | 0.26 | 22.4 | 3.8 | 36 | 46 | 18 | 5.4 | 7.5YR3/2 | 99.6 | 5.03 | Shale |
| | $A_{12}$ | 3-30 | 0.48 | 19.9 | 2.5 | 40 | 41 | 19 | 5.5 | 10YR3/3 | 95.3 | 3.13 | |
| | $A_{13}$ | 30-56 | 0.28 | 21.9 | 1.1 | 49 | 36 | 16 | 6.4 | 7.5YR3/2 | 78.1 | 1.60 | |
| | B | 56+ | 0.35 | 22.4 | 0.7 | 44 | 26 | 30 | 7.4 | 5Y4/3 | 58.6 | 0.83 | |
| 2 | $A_1$ | 0-5 | 0.82 | 9.4 | 2.7 | 57* | 31* | 11* | 5.4 | 10YR3/1 | 95.9 | 7.23 | |
| | $A_2$ | 5-20 | 0.19 | 10.6 | 1.0 | 75* | 17* | 8* | 5.0 | 10YR3/3 | 81.8 | 1.15 | Granite |
| | $B_{21}$ | 20-36 | 0.19 | 7.4 | 1.8 | 73* | 17* | 19* | 5.2 | 10YR3/4 | 70.8 | 0.54 | |
| | $B_{22}$ | 36-59 | 0.15 | 4.1 | 1.2 | 79* | 11* | 9* | 5.0 | -- | 69.3 | 0.41 | |
| | $C_1$ | 59+ | 0.15 | 5.3 | 1.2 | 78* | 15* | 7* | 5.4 | 7.5YR3/2 | 68.5 | 0.26 | |
| 4 | $A_{11}$ | 0-5 | 0.93 | 32.4 | 3.7 | 39* | 38* | 23* | 6.4 | 7.5YR6/3 | 98.5 | 8.27 | |
| | $A_{12}$ | 5-13 | 1.06 | 30.6 | 1.6 | 20* | 36* | 44* | 6.8 | 7.5YR3/2 | 95.3 | 3.00 | Shale |
| | $B_{21}$ | 13-46 | 0.67 | 29.9 | 1.2 | 25* | 33* | 42* | 7.4 | 5Y5/4 | 84.4 | 1.52 | |
| | $B_{22}$ | 46-64 | 0.58 | 28.4 | 1.0 | 27* | 39* | 34* | 7.7 | 10YR3/3 | 46.4 | 1.33 | |
| | $A_1b$ | 64-81 | 0.86 | 34.1 | 1.2 | 30* | 43* | 27* | 7.8 | 10YR3/2 | 75.2 | 1.50 | |
| | $B_{21}b$ | 81+ | 0.46 | 16.8 | 1.4 | 28* | 32* | 40* | 8.0 | 2.5YR6/4 | 57.2 | 2.20 | |
| 5 | $A_2$ | 0-5 | 0.80 | 8.1 | 4.1 | 75 | 19 | 7 | 4.0 | 5YR2/2 | 95.9 | 17.0 | |
| | $B_2$ | 5-56+ | 0.51 | 3.8 | 3.1 | 56 | 39 | 10 | 4.6 | 5YR2/2 | 98.9 | 3.77 | Granite |
| 6 | $A_1$ | 0-18 | 0.58 | 35.6 | 1.3 | 27 | 47 | 25 | 5.4 | 7.5YR3/2 | 99.5 | 0.64 | |
| | $A_2$ | 18-23 | 0.43 | 12.4 | 1.3 | 26 | 51 | 23 | 5.2 | 7.5YR3/2 | 97.4 | 1.16 | Shale |
| | $B_{21}$ | 23-45 | 0.45 | 14.3 | 1.3 | 28 | 34 | 38 | 5.4 | 10YR5/4 | 97.1 | 1.50 | |
| | $B_{22}$ | 45-70 | 0.51 | 21.8 | 1.3 | 31 | 36 | 33 | 5.6 | 5Y6/3 | 90.8 | 0.42 | |
| | C | 70-80 | 0.42 | 20.0 | 2.5 | 37 | 38 | 25 | 5.8 | 2.5Y5/4 | 82.6 | 0.44 | |

Appendix 1. Continued.

| Stand No. | Horizon | Depth cm | Exchangeable Cations (me/100g) K | Ca | Mg | Sand % | Silt % | Clay % | pH | Moist Color | % less than 2 mm | O.M. % | Substrate |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 9 | $A_2$ | 2-7 | 1.01 | 11.2 | 3.7 | 44 | 32 | 24 | - | 10YR5/3 | 99.3 | 5.82 | Shale |
| | $A_1b_1$ | 7-15 | 1.24 | 11.2 | 2.5 | 54* | 35* | 11* | 5.0 | 10YR4/3 | 99.1 | 6.08 | |
| | $A_1A_2$# | 15-43 | 0.54 | 9.1 | 2.0 | 36 | 42 | 22 | 5.1 | 10YR3/3 | 95.4 | 2.00 | |
| | $A_1A_2$+ | 15-43 | 0.48 | 8.8 | 2.0 | 35* | 41* | 24* | 4.8 | 10YR3/3 | 81.6 | 1.79 | |
| | $B_2$ | 43-84 | 0.36 | 11.2 | 3.9 | 42 | 30 | 28 | 4.8 | 7.5YR3/2 | 79.1 | 0.54 | |

*Values are from a single run not the average of two replicates.

#Sample taken from $A_1$ portion.

+Sample taken from $A_2$ portion.

Appendix 2. Soil data for *Pinus contorta* forests.

| Stand No. | Horizon | Depth cm | Exchangeable Cations (me/100g) K | Ca | Mg | Sand % | Silt % | Clay % | pH | Moist Color | % less than 2 mm | O.M. % | Substrate |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10 | $A_{21}$ | 0-10 | 0.51 | 3.1 | 1.2 | 47 | 40 | 14 | 4.8 | 7.5YR3/2 | 86.3 | 3.68 | Granite |
| | $A_{22}$ | 10-33 | 0.15 | 1.9 | 0.2 | 70 | 22 | 8 | 5.0 | 10YR3/4 | 79.9 | 0.78 | |
| | $A_3$ | 33-59+ | 0.12 | 1.9 | 1.8 | 80 | 14 | 7 | 5.3 | 10YR3/4 | 54.0 | 0.35 | |
| 11 | $A_1$ | 0-10 | 0.61 | 8.7 | 0.6 | 41 | 40 | 20 | 5.0 | 7.5YR3/2 | 97.4 | 3.17 | Shale |
| | $A_2$ | 10-15 | 0.48 | 9.9 | 3.1 | 43 | 36 | 22 | 4.9 | 7.5YR3/2 | 95.5 | 1.47 | |
| | $B_{21}$ | 15-56 | 0.42 | 7.4 | 1.9 | 42 | 32 | 26 | 5.0 | 10YR5/3 | 94.1 | 0.96 | |
| | $B_{22}$ | 56+ | 0.26 | 11.2 | 2.4 | 61 | 18 | 20 | 5.0 | 10YR3/3 | 61.9 | 0.64 | |
| 12 | $A_2$ | 0-18 | 0.99 | 36.9 | 4.3 | 68 | 21 | 11 | 5.2 | 7.5YR3/2 | 86.3 | 3.68 | Granite |
| | $B_2$ | 18-49+ | 0.13 | 6.9 | 2.5 | 86 | 4 | 10 | 5.2 | 10YR6/4 | 37.2 | 0.12 | |
| 13 | $A_1$ | 0-8 | 0.66 | 3.1 | 1.8 | 62* | 29* | 9* | 5.7 | 7.5YR3/2 | 70.1 | 2.20 | Granite |
| | $A_2$ | 8-16 | 1.16 | 7.5 | 1.4 | 75* | 18* | 7* | 5.8 | 2.5Y5/4 | 60.2 | 0.81 | |
| | $A_3$ | 16-28 | 0.52 | 8.7 | 1.9 | 72* | 19* | 8* | 5.3 | 10YR4/3 | 63.6 | 0.74 | |
| | $B_2$ | 28-49 | 0.46 | 7.2 | 2.0 | 76* | 16* | 8* | 5.4 | 10YR2/1 | 55.6 | 0.37 | |
| | $C_1$ | 49+ | 0.43 | 13.7 | 4.1 | 76* | 15* | 10* | 5.3 | 10YR4/3 | 32.5 | 0.51 | |
| 14 | $A_{21}$ | 0-8 | 0.31 | 7.5 | 0.6 | - | - | - | 5.9 | 7.5YR3/2 | 90.9 | 1.31 | Granite |
| | $A_{22}$ | 8-18 | 0.24 | 4.1 | 4.3 | 72* | 13* | 17* | 5.5 | 10YR5/4 | 74.4 | 0.78 | |
| | $B_{21}$ | 18-28 | 0.41 | 10.6 | 3.7 | 70* | 13* | 17* | 5.5 | 10YR2/1 | 80.4 | 0.90 | |
| | $B_{22}$ | 28-59+ | 0.51 | 13.1 | 4.7 | 68* | 18* | 14* | 5.6 | 10YR5/3 | 64.0 | 0.39 | |
| 15 | $A_1$ | 0-6 | 0.56 | 9.4 | 1.8 | 67* | 24* | 9* | 5.9 | 10YR4/3 | 89.6 | 3.43 | Granite |
| | $A_2$ | 6-41 | 0.18 | 4.3 | 1.3 | 67* | 23* | 19* | 5.4 | 10YR4/3 | 82.4 | 0.81 | |
| | $B_2$ | 41-79 | 0.25 | 7.5 | 3.7 | 65* | 21* | 14* | 5.8 | 10YR4/3 | 77.3 | 0.68 | |
| | $C_1$ | 79-125+ | 0.13 | 9.7 | 2.9 | 81* | 9* | 9* | 6.0 | 10YR6/4 | 50.5 | 0.56 | |
| 16 | $A_{11}$ | 0-3 | 1.09 | 14.1 | 2.7 | 56* | 35* | 9* | 6.0 | 10YR4/4 | 96.2 | 7.76 | Granite |
| | $A_{12}$ | 3-8 | 0.42 | 5.6 | 1.2 | 68* | 23* | 10* | 5.7 | 10YR3/3 | 82.6 | 1.60 | |
| | $A_2$ | 8-23 | 0.27 | 4.4 | 2.5 | 72* | 19* | 9* | 5.2 | 10YR3/3 | 67.6 | 0.68 | |
| | B | 23-34 | 0.30 | 6.6 | 2.0 | 75* | 12* | 13* | 5.2 | 10YR4/4 | 67.4 | 0.55 | |
| | C | 34+ | 0.22 | 13.1 | 4.7 | 80 | 8 | 12 | 5.2 | 10YR4/3 | 66.4 | 0.37 | |

Appendix 2. Continued.

| Stand No. | Horizon | Depth cm | Exchangeable Cations (me/100g) K | Ca | Mg | Sand % | Silt % | Clay % | pH | Moist Color | % less than 2 mm | O.M. % | Substrate |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 17 | $A_{11}$ | 0-6 | 0.68 | 5.6 | 1.6 | 51* | 38* | 11* | 4.9 | 7.5YR3/2 | 69.1 | 3.13 | Granite |
| | $A_{12}$ | 6-26 | 0.48 | 6.8 | 2.2 | 60* | 27* | 13* | 4.8 | 10YR3/2 | 61.6 | 1.32 | |
| | $B_2$ | 26-82 | 0.23 | 5.0 | 2.2 | 65* | 19* | 16* | 4.9 | 10YR3/2 | 61.6 | 1.32 | |
| 19 | A | 0-10 | 0.51 | 27.5 | 4.5 | 52 | 38 | 10 | 5.5 | 10YR2/1 | 83.3 | 5.64 | Granite |
| | C | 10-40+ | 0.13 | 26.2 | 2.2 | 70 | 22 | 8 | 5.2 | 7.5YR4/4 | 76.0 | 0.51 | |

*Values are from a single run not the average of two replicates.

Appendix 3. Soil data for <u>Pinus ponderosa</u> forests.

| Stand No. | Horizon | Depth cm | Exchangeable Cations (me/100g) K | Ca | Mg | Sand % | Silt % | Clay % | pH | Moist Color | % less than 2 mm | O.M. % | Substrate |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 21 | A | - | 0.13 | 4.3 | 0.5 | 90 | 6 | 4 | 6.4 | 10YR4/3 | 99.7 | 0.60 | Sandstone |
| | C | - | 0.04 | 1.9 | 0.4 | 92 | 3 | 4 | 6.6 | 10YR4/3 | 99.5 | 0.19 | |
| 22 | A | 0-12 | 0.77 | 40.6 | 4.7 | 42 | 40 | 18 | 7.6 | 7.5YR3/2 | 67.8 | 5.56 | Limestone |
| | $C_1$ | 12-40+ | 0.29 | 36.2 | 4.7 | 64 | 24 | 12 | 7.7 | 7.5YR5/4 | 69.3 | 2.99 | |
| 23 | $A_1$ | 0-5 | 1.31 | 33.1 | 4.9 | 48 | 37 | 15 | 7.1 | 10YR3/2 | 69.1 | 5.59 | Limestone |
| | $B_2$ | 5-20 | 0.89 | 31.2 | 4.7 | 32 | 44 | 23 | 7.4 | 5YR3/3 | - | 3.42 | |
| | $C_1$ | 20-66 | 0.35 | 38.8 | 4.7 | 42 | 38 | 18 | 7.6 | 5YR4/4 | - | 3.68 | |
| | $C_2$ | 66+ | 0.33 | 37.5 | 4.1 | 42 | 41 | 18 | 7.6 | 5YR4/3 | - | 2.82 | |
| 25 | A | 0-8 | 0.54 | 19.3 | 6.7 | 58 | 30 | 12 | 7.5 | 10YR3/1 | 71.3 | 5.00 | Limestone |
| | B | 8-38 | 0.23 | 40.6 | 9.4 | 58 | 30 | 12 | 7.8 | 10YR4/2 | 59.4 | 4.84 | |
| | C | 38-64+ | 0.19 | 54.4 | 7.7 | 43 | 38 | 18 | 7.6 | 7.5YR4/2 | 69.8 | 2.15 | |

Appendix 4. Soil data for <u>Pseudotsuga menziesii</u> forests.

| Stand No. | Horizon | Depth cm | Exchangeable Cations (me/100g) K | Ca | Mg | Sand % | Silt % | Clay % | pH | Moist Color | % less than 2 mm | O.M. % | Substrate |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 27 | $A_2$ | 0-15 | 1.02 | 19.9 | 6.5 | 33* | 49* | 18* | 6.4 | 5YR3/2 | 99.2 | 3.64 | Limestone |
| | $B_{21}$ | 15-71 | 0.37 | 27.5 | 9.2 | 51* | 39* | 10* | 7.7 | 7.5YR3/2 | 21.1 | 5.35 | |
| | $B_{22}$ | 71+ | 0.31 | 33.1 | 8.2 | 35 | 35 | 30 | 8.0 | 10YR3/2 | 23.0 | 1.35 | |
| 28 | $A_2$ | 0-15 | 1.16 | 8.8 | 7.2 | 29* | 53* | 18* | 5.5 | 10YR4/4 | 98.5 | 3.78 | Limestone |
| | $B_2$ | 15-41 | 1.21 | 16.8 | 11.7 | 22 | 48 | 30 | 6.8 | 7.5YR3/2 | 99.9 | 2.14 | |
| | $B_3$ | 41+ | 0.45 | 16.9 | 8.6 | 39* | 41* | 19* | 7.6 | 10YR3/3 | 86.8 | 1.87 | |
| 30 | A | 0-10 | 1.92 | 34.9 | 10.0 | 34 | 50 | 16 | 7.6 | 7.5YR3/2 | 67.4 | 6.51 | Limestone |
| | C | 10-40+ | 0.50 | 38.8 | 7.6 | 44 | 36 | 20 | 7.8 | 10YR3/3 | 18.3 | 3.85 | |
| 31 | $A_1$ | 0-18 | 0.89 | 25.6 | 10.4 | 37 | 39 | 24 | 7.1 | 7.5YR3/2 | 62.4 | 4.01 | Limestone |
| | $B_{21}$ | 18-36 | 0.29 | 38.8 | 10.0 | 44 | 36 | 20 | 7.8 | 5YR4/2 | 52.2 | 1.47 | |
| | $B_{22}$ | 36+ | 0.16 | 34.3 | 5.9 | 51 | 30 | 19 | 7.8 | 10YR5/3 | 28.5 | 1.59 | |
| G# | A | 0-28 | 0.70 | 46.9 | 9.2 | 48 | 36 | 16 | 7.5 | 7.5YR3/2 | 57.8 | 6.26 | Limestone |
| | $C_1$ | 28-36 | 0.17 | 32.4 | 11.9 | 47 | 37 | 16 | 8.2 | 10YR5/3 | 24.1 | 2.22 | |

*Values are from a single run not the average of two replicates.
#Soil pit dug but no stand data taken. Forest was blown down by a tornado in 1962.

Appendix 5. Soil data for shrub and grassland areas sampled.

| Stand No. | Horizon | Depth cm | Exchangeable Cations (me/100g) K | Ca | Mg | Sand % | Silt % | Clay % | pH | Moist Color | % less than 2 mm | O.M. % | Sub-strate | Veg. Type |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 32 | $A_1$ | - | 1.12 | 35.6 | 10.9 | 54 | 38 | 7 | 7.6 | 5YR3/2 | 35.5 | 6.48 | LS | 1 |
| | $B_2$ | - | 0.29 | 39.9 | 6.6 | 52 | 30 | 18 | 7.6 | 7.5YR5/4 | 46.0 | 3.53 | | |
| | $IIB_2$ | - | 0.29 | 35.0 | 6.6 | 45 | 36 | 19 | 8.0 | 7.5YR5/4 | 43.7 | 1.56 | | |
| 33 | A | 0-10 | 0.41 | 38.7 | 2.9 | 64 | 28 | 8 | 7.6 | 7.5YR3/2 | 79.7 | - | LS | 2 |
| | $B_{2a}$ | 10-38 | 0.43 | 33.8 | 11.1 | 46 | 34 | 20 | 8.0 | 5YR7/4 | 94.5 | 1.47 | | |
| | $IIB_2$ | 38-92 | 0.51 | 26.9 | 15.4 | 42 | 34 | 24 | 8.3 | 5YR5/6 | 91.4 | 0.68 | | |
| | C | 92+ | 0.58 | 21.2 | 17.0 | 68 | 24 | 8 | 8.8 | 5YR4/6 | 74.6 | 0.80 | | |
| C | $A_1$ | 0-15 | 0.66 | 8.8 | 2.0 | 63* | 27* | 10* | 6.0 | 7.5YR4/4 | 70.1 | 4.56 | Gr | 3 |
| | $B_{21}$ | 15-25 | 0.41 | 13.1 | 3.9 | 60 | 23 | 16 | 6.1 | 10YR4/3 | 72.2 | 0.81 | | |
| | $B_{22}$ | 25-36 | 0.40 | 14.9 | 5.1 | 65* | 19* | 16* | 6.2 | 10YR4/3 | 75.0 | 0.52 | | |
| | C | 36-100+ | 0.52 | 11.8 | 3.2 | 80 | 8 | 12 | 6.3 | 10YR6/3 | 83.1 | 0.06 | | |
| D | $A_1$ | 0-28 | - | 9.9 | 1.5 | 78 | 16 | 6 | 6.2 | 5YR2/2 | 80.9 | 2.23 | Gr | 3 |
| | $A_2$ | 28-51 | 0.30 | 10.6 | 3.3 | 76 | 13 | 11 | 6.4 | 5YR3/2 | 72.8 | 0.77 | | |
| | $B_2$ | 51=84 | 0.24 | 8.7 | 2.6 | 76 | 13 | 12 | 6.6 | 10YR3/1 | 30.4 | 0.36 | | |
| | $IIB_2$ | 84-112 | 0.19 | 12.4 | 3.3 | 80 | 12 | 8 | 6.8 | 10YR3/1 | 30.4 | 0.36 | | |
| | C | 112+ | 0.04 | 5.6 | 3.1 | 88 | 8 | 4 | 6.8 | 10YR3/4 | 81.3 | 0.01 | | |
| E | $A_1$ | 0-20 | 1.02 | 17.5 | 3.9 | 59 | 35 | 8 | 5.4 | 5YR2/2 | 93.3 | 6.11 | Gr | 3 |
| | $B_1$ | 20-56 | 0.42 | 16.8 | 3.3 | 48 | 26 | 26 | 5.4 | 5YR2/2 | 93.3 | 6.11 | | |
| | $B_2$ | 56-69 | 0.41 | 25.0 | 5.1 | 65 | 14 | 20 | 5.2 | 7.5YR5/6 | 82.3 | 0.39 | | |
| F | $A_2$ | 0-15 | 0.15 | 5.0 | 2.5 | 52 | 40 | 8 | 7.6 | 7.5YR4/4 | 37.1 | 0.68 | LS | 3 |
| | B | 15-36 | 0.18 | 38.7 | 3.3 | 64 | 28 | 8 | 7.6 | 10YR7/4 | 56.0 | 1.73 | | |
| | C | 36-53 | 0.04 | 33.7 | 2.0 | 54 | 38 | 8 | 7.8 | 10YR8/3 | 72.9 | 0.67 | | |

*Values are from a single run not the average of two replicates.
LS = Limestone, Gr = Granite.
1. _Cercocarpus ledifolius_ shrubs. 2. _C. ledifolius-Juniperus osteospermum_ shrubs. 3. Grasslands.

Appendix 6. Species list of plants collected during the course of this study.

PINACEAE
- Abies lasiocarpa
- Picea engelmannii
- Pinus albicaulis
- Pinus contorta
- Pinus flexilus
- Pinus ponderosa
- Pseudotsuga menziesii

CUPRESSACEAE
- Juniperus communis
- Juniperus horizontalis
- Juniperus osteosperma
- Juniperus scopulorum

GRAMINEAE
- Agropyron smithii
- Agropyron spicatum
- Andropogon scoparius
- Calamagrostis canadensis
- Hesperochloa kingii
- Koeleria cristata
- Phleum alpinum
- Poa compressa
- Poa cusickii
- Poa fendleriana
- Poa nervosa
- Poa sp.
- Poa tracyi
- Trisetum spicatum

CYPERACEAE
- Carex brevipes
- Carex petasata
- Carex raynoldsii
- Carex scopulorum
- Carex sp.

JUNCACEAE
- Juncus mertensianus
- Luzula parviflora

LILIACEAE
- Allium brevistylum
- Allium schoenoprasum
- Disporum trachycarpum

LILIACEAE (Cont.)
- Smilacina stellata
- Streptopus amplexifolius
- Zigadenus venenosus

ORCHIDACEAE
- Goodyeara oblongifolia

SANTALACEAE
- Comandra pallida (umbellata)

POLYGONACEAE
- Eriogonum subalpinum
- Polygonum bistortoides
- Polygonum viviparum

CHENOPODIACEAE
- Atriplex canescens

CARYOPHYLLACEAE
- Arenaria congesta
- Arenaria obtusiloba
- Cerastium arvense
- Sagina saginoides
- Silene menziesii

RANUNCULACEAE
- Aquilegia caerulea
- Anemone cylindrica
- Anemone multifida
- Caltha leptosepala
- Clematis pseudoalpina
- Delphinium bicolor
- Ranunculus eschscholtzii
- Thalictrum occidentale
- Trollius laxus

BERBERIDACEAE
- Mahonia (Berberis) repens

CRUCIFERAE
- Arabis nuttallii
- Erysimum asperum
- Lesquerella alpina

Appendix 6--Continued.

CRASSULACEAE
*Sedum lanceolatum*

SAXIFRAGACEAE
*Heuchera parvifolia*
*Mitella pentandra*
*Mitella stauropetala*
*Parnassia fimbriata*
*Saxifra arguta*
*Saxifraga odontoloma*
*Saxifraga rhomboidea*

GROSSULARIACEAE
*Ribes cereum*
*Ribes lacustre*
*Ribes montigenum*

ROSACEAE
*Cercocarpus ledifolius*
*Fragaria virginiana*
*Physocarpus monogynus*
*Potentilla arguta*
*Potentilla concinna*
*Potentilla diversifolia*
*Potentilla fissa*
*Potentilla pennsylvanica*
*Rosa acicularis*
*Sibbaldia procumbens*
*Spiraea betulifolia*

LEGUMINOSAE
*Astragalus alpinus*
*Astragalus miser*
*Astragalus striatus*
*Hedysarum sulphurescens*
*Oxytropis lagopus*
*Lupinus lepidus*
*Lupinus sp.*
*Vicia americana*

LINACEAE
*Linum lewisii*

ANACARDIACEAE
*Rhus radicans*
*Rhus trilobata*

ACERACEAE
*Acer glabrum*

RHAMNACEAE
*Ceanothus velutinus*

ELAEGNACEAE
*Shepherdia canadensis*

ONAGRACEAE
*Epilobium angustifolium*
*Epilobium halleanum*
*Epilobium saximontanum*

UMBELLIFERAE
*Bupleurum americanum*
*Lomatium eastwoodae*
*Osmorhiza depauperata*

ERICACEAE
*Arctostaphylos uva-ursi*
*Gaultheria humifusa*
*Kalmia polifolia*
*Moneses uniflora*
*Pyrola dentata*
*Pyrola secunda*
*Pyrola virens*
*Vaccinium scoparium*

GENTIANACEAE
*Gentiana amarella*
*Swertia radiata*

APOCYNACEAE
*Apocynum androsaemifolium*

POLEMONIACEAE
*Gilea sp.*
*Gilea spicata*
*Phlox hoodii*
*Phlox multiflora*

BORAGINACEAE
*Lithospermum ruderale*
*Mertensia oreophila*
*Mertensia ciliata*

LABIATAE
*Monarda fistulosa*

Appendix 6--Continued.

SCROPHULARIACEAE
- *Penstemon aridus*
- *Penstemon glaber*
- *Penstemon larcifolus*
- *Penstemon rydbergii*
- *Penstemon sp.*
- *Pedicularis racemosa*
- *Veronica wormskjoldii*

RUBIACEAE
- *Galium boreale*

CAPRIFOLIACEAE
- *Linnaea borealis*
- *Symphoricarpos albus*
- *Symphoricarpos oreophilus*

CAMPANULACEAE
- *Campanula rotundifolia*

VALERIANACEAE
- *Valeriana dioica*
- *Valeriana occidentalis*

COMPOSITAE
- *Achillea millefolium*
- *Antennaria corymbosa*
- *Antennaria parvifolia*
- *Antennaria racemosa*
- *Antennaria rosea*
- *Antennaria umbrinella*
- *Arnica cordifolia*
- *Arnica gracilis*
- *Artemisia arbuscula*
- *Artemisia frigida*
- *Artemisia tridentata*
- *Aster ciliolatus*
- *Aster conspicuus*
- *Aster foliaceus*
- *Aster glaucodes*
- *Aster integrifolius*
- *Aster sibiricus*
- *Balsamorhiza sagittata*
- *Cirsium canescens*
- *Cirsium hookerianum*
- *Cirsium undulatum*
- *Chrysopsis villosa*
- *Crepis acuminata*
- *Erigeron acris*
- *Erigeron compositus*

COMPOSITAE (Cont.)
- *Erigeron ochroleucus*
- *Erigeron peregrinus*
- *Gaillardia aristata*
- *Gutierrezia sarothrae*
- *Hymenoxys acaulis*
- *Liatris punctata*
- *Senecio integerrimus*
- *Senecio pauciflorus*
- *Senecio streptanthifolius*
- *Senecio sp.*
- *Senecio lugens*
- *Solidago multiradiata*
- *Taraxicum sp.*