A synecological study of the forested moraines of the valley floor of Grand Teton National Park, Wyoming

by Edward Theodore Oswald

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Botany
Montana State University

Abstract:
A study was conducted of physiognomic and dynamic relations of morainal forest communities of the Grand Teton National Park Valley floor. Forest community units considered were; Pinus contorta/Calamagrostis rubescens, P. contorta/Vaccinium scoparium, P. contorta/V. membranaceum, P, contorta/ Shephefdia canadensis, Pseudotsuga menziessii/V, membranaceum and Populus tremuloides/Geranium viscosissimum. Random pairs, line-intercept and 2X5 dm quadrat methods were employed in obtaining quantitative data. Some permanent plots were established to observe successional changes. An analysis of increment core samples was used to determine ages of stands, derive growth ratios of arboreal taxa under different environmental conditions and to determine dates of fires. A dial gauge dendrometer was employed to obtain some phenological data from Pinus contorta. The substrate of each community was characterized through field and laboratory analyses, Pinus contorta was the dominant taxon in the upper arboreal stratum but Abies lasiocarpa was the most abundant taxon in the reproductive layers. Stands of Pseudotsuga menziessii occupy the drier forested areas and appear to be regenerating themselves in these areas and advancing into the P. contorta dominated areas in some places. Populus tremuloides occurred on both dry and wet sites in the forested areas and appeared to be relatively stable on the wetter areas but is giving way to conifers in the drier areas. The substrates appear to be the primary limiting factor to arboreal taxa.

The outwash material is very coarse textured and generally does not support trees, although, under favorable conditions, conifers, especially P. contorta, become established and may grow relatively fast. The morainal materials exhibit less gravel and rock, have higher water holding capacities, and are forested. Community floristic maturity indices, community coefficients of floristic relationships and correlation coefficients among some taxa were calculated. A discussion of community classification and successional features is presented. Consideration is given to forest pathology in relation to succession. Representative soil profile descriptions and a systematic list of the plant taxa encountered (lichens, bryophytes and tracheophytes) along with the communities in which they were present are given in the appendix.

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Approved:

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES--Continued

LIST OF FIGURES

ABSTRACT

A study was conducted of physiognomic and dynamic relations of morainal forest communities of the Grand Teton National Park Valley floor. Forest community units considered were: Pinus contorta/Calamagrostis rubescens, P. contorta/Vaccinium scoparium, P. contorta/V. membranaceum, P. contorta/Shepherdia canadensis, Pseudotsuga menziessii/V. membranaceum and Populus tremuloides/Geranium viscosissimum. Random pairs, line-intercept and 2X5 dm quadrat methods were employed in obtaining quantitative data. Some permanent plots were established to observe successional changes. An analysis of increment core samples was used to determine ages of stands, derive growth ratios of arboreal taxa under different environmental conditions and to determine dates of fires. A dial gauge dendrometer was employed to obtain some phenological data from Pinus contorta. The substrate of each community was characterized through field and laboratory analyses.

Pinus contorta was the dominant taxon in the upper arboreal stratum but Abies lasiocarpa was the most abundant taxon in the reproductive layers. Stands of Pseudotsuga menziessii occupy the drier forested areas and appear to be regenerating themselves in these areas and advancing into the P. contorta dominated areas in some places. Populus tremuloides occurred on both dry and wet sites in the forested areas and appeared to be relatively stable on the wetter areas but is giving way to conifers in the drier areas. The substrates appear to be the primary limiting factor to arboreal taxa. The outwash material is very coarse textured and generally does not support trees, although, under favorable conditions, conifers, especially P. contorta, become established and may grow relatively fast. The morainal materials exhibit less gravel and rock, have higher water holding capacities, and are forested. Community floristic maturity indices, community coefficients of floristic relationships and correlation coefficients among some taxa were calculated. A discussion of community classification and successional features is presented. Consideration is given to forest pathology in relation to succession. Representative soil profile descriptions and a systematic list of the plant taxa encountered (lichens, bryophytes and tracheophytes) along with the communities in which they were present are given in the appendix.

INTRODUCTION

The vegetation of the Grand Teton National Park valley floor provides a sharp contrast in most areas by the presence of forest communities on moraines and sagebrush-grassland communities on outwash substrates. A preliminary reconnaissance revealed a coarse-textured, stony-surfaced soil on both the outwash and most of the moraines, which opened the question of why the vegetational units were so sharply delineated. Therefore, the primary objectives of this study were to describe the physiognomic and dynamic relations encountered in the morainal forest communities and to attempt to explain their distributional patterns.

Previous vegetation studies were conducted in the vicinity of the study area by Reed (1952) in the Jackson Hole Wildlife Park and by Shaw (1958) in Grand Teton National Park, both of whom presented qualitative data concerning plant communities and systematic plant lists along with relative frequencies. Craighead and Craighead (1952) described the plant communities of Jackson Hole Wildlife Park in more detail than did Reed and formulated a vegetation map of the area. Harry (1954) constructed a vegetation map of Grand Teton National Park from aerial photographs. Beetle (1961, 1962) described various aspects of vegetation in Teton County.

The preliminary reconnaissance was made from 12 to 15 September 1963. Full time field work was conducted during the periods 15 June through 15 September 1964 and 14 June through 1 September 1965. Two- or three-day visits made to the study area were initiated on 15 May 1964, 6 February and 28 May 1965.

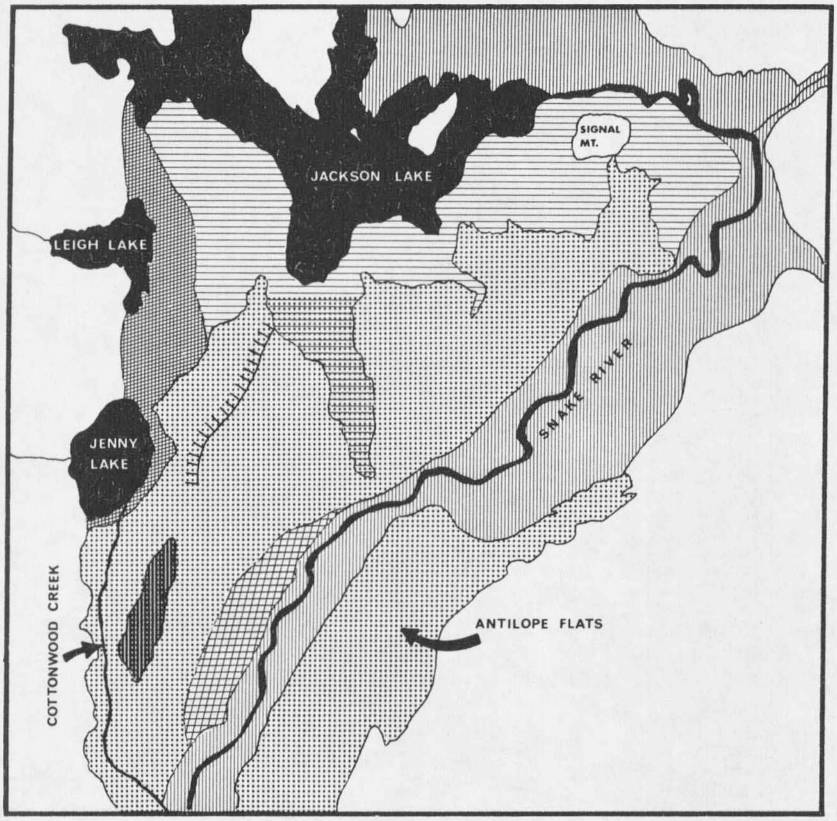
DESCRIPTION OF THE AREA

Geologic Features

The orogeny leading to the initial development of the Teton Mountain Range apparently occurred during the late Cretaceous period forming folded and thrust-faulted mountains. Prior to this time the area was covered by water (Dunbar 1956). Following the orogeny several disturbances occurred that led to the present topography of the area. To the south, the mountains in the Teton National Forest are considered by Love (1956b) to be the result of the St. John, Absaroka, and Darby thrust faults of pre-Paleocene to early Paleocene age. Contemporaneous with the faults, and occurring throughout most of the Tertiary period, was active vulcanism to the northeast which partially buried the Teton Mountain Range and probably deposited a considerable amount of volcanic material in Jackson Hole (Carey 1956).

A simultaneous downdropping of the Jackson Hole valley floor and an uplifting along the Teton normal fault occurred in the Pliocene period exposing the prominent peaks of the Teton Mountain Range as we know them today (Love and Montagne 1956). Two major erosion cycles, the Union Pass cycle and the Blackrock cycle, are believed by Blackwelder (1915) and Horberg, Edmund and Fryxell (1955) to have occurred during the early Pleistocene period resulting in depositions which developed a mature topography approximately 1,000 feet above the present valley floor. More recent work has indicated that the topography beneath the pre-Wisconsin ice that invaded Jackson Hole from the north and east was anything but subdued, and in fact, this great piedmont ice sheet covered both the buttes on the floor of Jackson Hole, and the topography beneath the present floor of this valley simultaneously (Montagne, personal communications 1966).

Three known glaciations occurred during Pleistocene time which are largely responsible for the present topograph of Jackson Hole (Figure 1). The earliest, the Buffalo glacial stage, moved across the Jackson Hole valley from the north removing as much as 200 feet of substrate in some areas (Blackwelder 1951, Edmund 1956, Fryxell 1930 and Love 1956b). The material deposited by the Buffalo glaciation has mostly decomposed except for some quartzitic types and essentially no morainal topography remains (Montagne 1956). The only evidence of this material in Grand Teton National Park is quartzitic boulders on Blacktail Butte at 7,685 feet elevation (Fryxell 1930). The Bull Lake glacial stage is considered by Flint (1957) to be contemporaneous with the early Wisconsin continental glacial features. Glaciers moved across the valley floor from the Teton Range and again removed an undetermined amount of substrate. Terraces remain at present that were considered by Blackwelder (1915) and Fryxell (1930) to have been formed by the Bull Lake glacial outwash. Apparently a dry, windy period occurred during the next interglacial period resulting in a deposition of 5 to 6 feet of aeolian material on Timbered Island, a Bull Lake glacial moraine, which is not detectable on moraines of more recent glaciations. Blackwelder (1915) and Fryxell (1930) have considered Timbered Island and Burnt Ridge to be of the same age but the occurrence of the aeolian deposition sheds doubt on this and Love and Montagne (personal communications, 1965) suggest that Burnt Ridge is early Pinedale in age. The last major glaciation was the Pinedale glacial stage which was contemporaneous with the late Wisconsin formation. It also moved down from the Teton Range but, for the most part, stopped a short distance from the base of the mountains leaving moraines in



Alluvial bottoms, Recent.

Moraines of Jackson Lake piedmont glaciers, Pinedale.

Moraines of Teton valley glaciers, Pinedale.

Burnt Ridge moraine, early Pinedale

Outwash plain, Bull Lake and Pinedale

Pinedale terraces

Timbered Island moraine, Bull Lake

Conspicuous bluff

Figure 1. Geological features of the study area modified from Fryxell (1930) by suggestions of Montagne and Love (personal communications, 1965, 1966).

various parts of the valley. It is responsible for most of the present glacial lakes occurring on the valley floor (Blackwelder 1915, Fryxell 1930). The outwash material left by the melting glaciers forms the surface of most of the present outwash plains. During the late Pinedale glacial stage, several volcanoes erupted to the northeast of the valley depositing ash southeast of Jackson Lake (Love 1956b). Recurring faults and earthquakes during the glacial and interglacial intervals in the Teton and Hoback Mountain Ranges served to give Jackson Hole a westerly tilt (Love 1956b). Geological activity is still in progress as exemplified by landslides and earth tremors during the last century (Hayden 1956b, Keefer and Love 1956).

The result of the geological activity is an essentially flat outwash plain interrupted by protruding moraines along the western part of the valley (Figure 1). The elevation, 6,900 feet at the northern end of the valley floor, drops to about 6,700 feet at the southern end over a distance of about 15 miles. Knob and kettle ("pothole") topography is conspicuous in the north-central section and terraces are sharply delineated along the Snake River drainage. The outwash soil contains a high proportion of rounded Precambrian quartzite cobbles and is coarse textured. The morainal soil contains variously broken rock fragments and cobbles and is finer textured than the outwash soils. Timbered Island is capped with an aeolian deposit, as mentioned above. Some potholes to the south of Burnt Ridge have depositions of fine-textured material on the north-facing banks and in the bottoms that conceivably could have resulted from secondary deposition of previously deposited aeolian material on Timbered Island. Depositions of fine-textured material, which possibly could have originated from the volcanic ash deposited during the late Pinedale stage, also occur in indentations on the north face of Signal Mountain.

The valley is drained by the Snake River which meanders in a southwesterly direction across the valley. Cottonwood and Taggart Creeks drain some of the glacial lakes near the base of the Teton Mountain Range and enter the Snake River at the southern end of the valley.

Climatic Patterns

Probably the most significant climatic features limiting the vegetation of Jackson Hole are the abundant snowfalls and the long cold winters. Records of weather conditions have been kept at Moran, Wyoming, elevation 6,770 feet, located near Jackson Lake Dam, since 1911. The average annual precipitation is 21.3 inches; as depicted in Figure 2, July is the driest month and May the wettest. Approximately 120 inches of snow falls annually making up about two-thirds of the precipitation and it may fall during any month. Jackson Hole is included in the subhumid climatic category according to Thornthwaite (1941).

The average annual temperature at Moran is 34.7 F; as depicted in Figure 2, July is the warmest month and January the coldest. The maximum temperature recorded is 93 F and the minimum is minus 52 F. The temperature has reached below minus 50 F in December, January and February. Frost may occur during any month.

Domestic History

Trappers and hunters began entering Jackson Hole during the early 19th century although Indian artifacts date back 1,000 years. Searches for gold

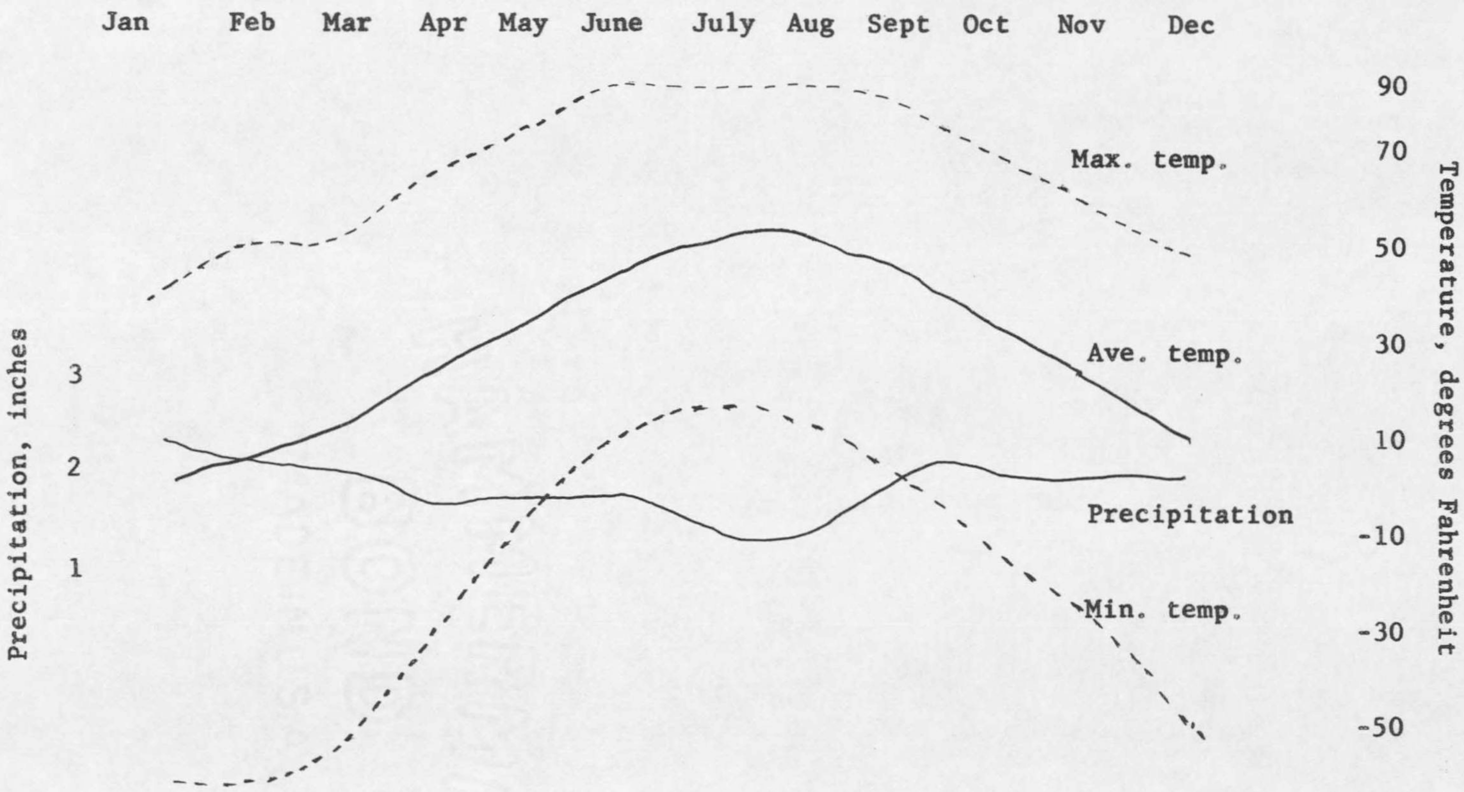


Figure 2. Average monthly temperatures and precipitation and maximum and minimum temperatures (from U. S. Weather Bureau 1930, and substantiated with data collected from the weather station located at Moran, Wyoming).

and silver brought in miners about 1850 but by 1890 the hunter and miner populations began decreasing. Buffalo and wapiti (elk) were abundant during much of this period but the buffalo were slaughtered almost to extinction (Collins 1952, Hayden 1956a).

Settlers began entering Jackson Hole in 1883, bringing cattle with them and cutting many trees for building purposes. Some valley land was plowed but farming was not successful. The increase of settlers and their livestock affected elk populations and the ranchers began feeding them prior to the turn of the century. A government feeding program began in 1909 and an elk refuge was established in 1913 (Hayden 1956a). The present elk status has been documented by Martinka (1965).

The Teton Forest Reserve was organized in 1897 to protect the forests from undue misuse and as a fire control measure. It was later placed under the control of the United States Forest Service when the Forest Service was organized in 1905. The Grand Teton National Park was established in 1929 but included only the eastern portion of the Teton Mountain Range and a few lakes. It was enlarged in 1950 by adding the Jackson Hole National Monument area which had been established in 1943 (Hayden 1956a).

Vegetational Patterns

Fossil records of plant life from late Cretaceous to Recent time have been documented by Dorr (1956) and Love (1956a,b). The present vegetation consists of sagebrush-grassland on the outwash plains and of coniferous forest on the moraines. Some lowland areas are dominated by a willow-sedge community and conifers and deciduous trees occur along the streams.

Artemisia tridentata (big-sagebrush) dominates most of the outwash plain but in localized areas Artemisia arbuscula (low-sagebrush)-dominated communities occur. The most abundant conifer on the moraines is Pinus contorta var. latifolia (lodgepole pine), but Pseudotsuga menziessii (Douglas fir) and Abies lasiocarpa (alpine fir) are variously intermingled in the forest stands. Picea engelmanni (Engelmann's spruce) is rare on the moraines in Grand Teton National Park but is frequently encountered on the slopes of the Teton Mountain Range.

SOIL ANALYSIS

Methods

Soil profiles were examined in pits and field determinations of horizon depth and thickness, texture, structure, consistency and boundaries, dry and moist color and pH were made. The vegetation and physiography of each site were described. Depths and thicknesses of horizons were measured with a six-foot steel tape measure, using the top of the mineral soil as a reference level. Texture, structure, consistency and boundaries were recorded according to the outline presented by the Soil Survey Staff (1951). The Munsell color notation was used for recording soil colors (Soil Survey Staff 1951). The pH was determined by using indicator dyes compared to appropriate color charts.

Horizons of representative profiles were sampled for laboratory analysis. Preliminary investigations indicated insignificant differences between the chemical analyses of outwash and morainal soils but a significant difference in the mechanical analysis. The mechanical analysis was conducted by the Plant and Soil Science Department, Montana State University, Bozeman. Soil texture was determined by the Bouyoucos method (Bouyoucos 1936) on all samples and also by the pipette method (Anderson 1963) on some samples. A 15-atmosphere moisture retention percentage (U. S. Salinity Laboratory Staff, 1954) was determined on all samples. The pH of the collected samples was measured with a Beckman Zeromatic pH meter.

Results

The range of data obtained from the mechanical analyses is presented in Table I for the outwash and morainal soils. A marked difference occurs in

TABLE I. HORIZON SEQUENCE, THICKNESS, MECHANICAL ANALYSIS[1], 15-ATMOSPHERE PERCENT[2], COLOR[3], AND pH[4] OF OUTWASH AND MORAINAL SOILS. EACH SET OF DATA IS BASED ON TWO PEDONS.

Soil type	Horizon sequence	Thickness (inches)	Mechanical Analysis % sand	% silt	% clay	15-atmos. pct.	Color	pH
Outwash	A_1	4-9	77-85	11-17	3-6	2.8-4.2	D. 5-7 YR 4/3-4 M. 10 YR 3-4/4	5.5-5.9
	B_2	5-6	67-78	15-23	5-11	3.2-5.3	D. 5-7 YR 4-5/3-4 M. 7.5-10 YR 4/4	5.7-5.9
	B_3	4-8	80-82	12-15	4-7	3.0-3.4	D. 5 YR 4/4 M. 7.5-10 YR 4/4	5.7-6.0
	C		89-94	2-7	3-4	1.3-2.8		5.8-6.2
Moraine	A	2-4	26-68	23-64	9-10	5.1-6.1	D. 10 YR 3-6/2-3 M. 10 YR 2-7/2-3	5.5-5.6
	B_1	5-10	34-69	22-56	8-10	5.1-5.8	D. 10 YR 4-6/3 M. 10 YR 3-5/2-3	5.4-5.5
	B_2	9-24	9-73	17-77	10-13	4.3-6.3	D. 10 YR 5-7/2-3 M. 10 YR 4-6/2	5.1-5.4
	C		56-77	15-32	8-12	4.5-4.8	D. 10 YR 5-6/3 M. 10 YR 4/2	5.6

1/ Determined by the Bouyoucos (1936) method.

2/ Method proposed by the U. S. Salinity Laboratory Staff (1954).

3/ Munsel color notation (Soil Survey Staff 1951) on the dry and moist soil.

4/ Determined with a Beckman Zeromatic pH meter after samples had been stored in plastic bags for about two months.

the percent of sand, silt and clay between the two soil types. The difference in texture is furthur substantiated by the 15-atmosphere moisture retention which was higher in the moraines. The outwash soils are generally shallower than those of the moraines.

The individual profile characteristics are presented in the Appendix. In general, the outwash soils are coarser textured and contain more cobbles than the morainal soils (Figures 3 and 4), although some scattered boulders and rock outcroppings occur on the moraines. The structure of the outwash soil was very fine granular to structureless throughout the profile. The moraines had a fine granular to platy structure in the A horizon which graded into a blocky to prismatic B horizon. In consistency, the outwash soil profile was uniformly friable, slightly sticky to nonsticky and slightly plastic to nonplastic throughout. The morainal soil was friable, slightly sticky and slightly plastic in the A horizon and the stickiness and plasticity increased in the B horizon. The pH ranged from 5.5 to 6.2 in the outwash soil and from 5.0 to 6.3 in the morainal soil.

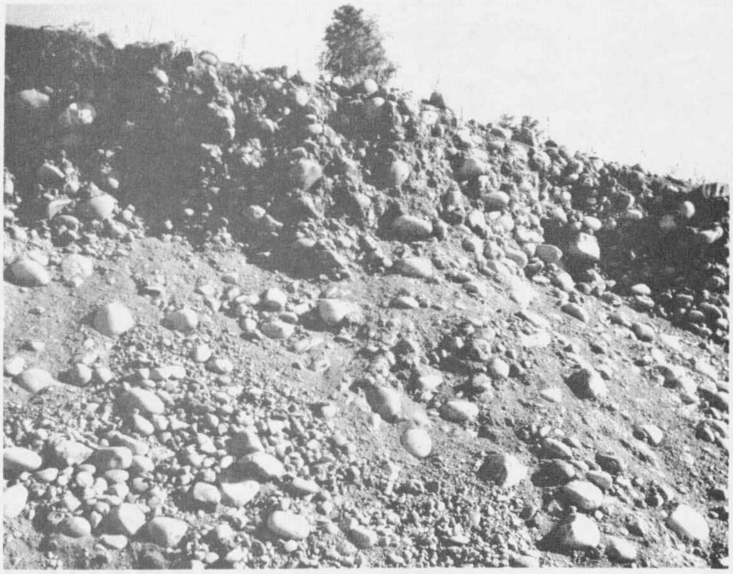


Figure 3. Outwash soil profile

Figure 4. Morainal soil profile.

VEGETATIONAL ANALYSIS

Methods

Preliminary reconnaissance indicated the occurrence of distinct unions within the forest vegetation. The following communities, based on dominating floristic unions, were recognized for sampling purposes:

Pinus contorta/Calamagrostis rubescens Community

Pinus contorta/Vaccinium scoparium Community

Pinus contorta/Vaccinium membranaceum Community

Pinus contorta/Shepherdia canadensis Community

Pseudotsuga menziessii/Vaccinium membranaceum Community

Populus tremuloides/Geranium viscosissimum Community

Each community was sampled quantitatively in various places where it occurred throughout the forest unit by the random pairs method (Cottam and Curtis 1949) for the trees, 2 X 5 dm quadrats using six coverage classes (Daubenmire 1959) and list-count (Oosting 1948) techniques for the field layer, and the line-intercept method (Canfield 1941) for the tall shrubs. The *Flora of Idaho*, by Davis (1952), was used to identify most plants with the aid of Booth (1950), Booth and Wright (1959), Harrington (1954), and Hitchcock, Conquist, Ownbey and Thompson (1955, 1959, 1961, 1964).

The mean distance between trees, relative density, relative dominance, relative frequency, mean area occupied by an individual, density or number of individuals per acre, total basal area, importance value and frequency were calculated according to the formulae presented by Phillips (1959) for use with data obtained from the random pairs method of analyses of trees. Trees over 2.5 m tall were considered in the calculations of the upper stratum and trees less than 2.5 m tall, except for first year seedlings, in the lower stratum. The number, cover class and frequency were calculated for each taxon in the field layer occurring in the 2 X 5 dm plots.

Some plots were established for studying the successional trends of the forest unit both inside and outside of the present forested areas over an extended period of time. Those plots within the forest unit were placed close to or at the boundary between two forest communities and those outside were located near the ecotone between forest and sagebrush-grassland where a change appeared to be taking place. The sizes of the plots vary, ranging from 10 X 20 m to 20 X 40 m, depending upon location and/or present vegetation. Only the trees and tall shrubs were considered in most of these plots.

The outwash plains possess a sagebrush-grassland type of vegetation in general and were sampled only near the ecotones adjoining forest communities of the moraines. The plots used for sampling this vegetation were 0.5 X 1 m and were laid in lines at 100 m intervals, thus 0, 5, 10, 20, and 30 m intervals from the forest margin were sampled.

Increment samples were taken from trees in various areas for determination of ages of stands and of dates of fires, and to establish growth rate factors for each arboreal taxon occurring in a stand. The growth rate factors were calculated by dividing the number of growth rings (considered to be the age of the tree) into the diameter of the tree at the point where the increment samples were extracted; compression wood and other evident deformities were avoided.

Dendrometer readings were taken throughout the summer of 1965 on four P. contorta located at the Biological Research Station, using a dial gauge dendrometer modified after Daubenmire (1945).

Results

A list of all plant species encountered is contained in Table XVII of the Appendix. The vegetation units or communities in which each taxon occurs are indicated by (x) for presence and (X) for abundant. Three-hundred-eighty-two species of vascular plants representing 58 families, 13 species of lichens and 46 species of bryophytes are listed.

Pinus contorta/Calamagrostis rubescens Community

Pinus contorta var. *latifolia* is the dominant taxon in the upper arboreal stratum of the community with dominance values (Table II) ranging from 89 to 97. *Abies lasiocarpa* makes up the remainder of the upper stratum in all areas where the community occurred except in the northeast ecotone between forest and sagebrush-grassland of Timbered Island and the southwest corner of Burnt Ridge. In both of these areas, *Pseudotsuga menziessii* was associated with *Pinus contorta*. The density of the upper stratum is variable, ranging from approximately 590 to over 2,700 trees per acre, the height increasing with decreasing density. There is also a tendency toward increasing dominance of *A. lasiocarpa* with decreasing density.

Abies lasiocarpa is the most abundant taxon in the reproductive layer (up to 2.5 m tall), ranging from 34% to 80% of the seedlings and saplings, in almost all the areas where the community occurred. *Pinus contorta*, *P. flexilis* and *Pseudotsuga menziessii* seedlings and saplings made up the remainder of the reproductive layer. Where the upper stratum was more dense than about 2,000 trees per acre there were few or no seedlings or saplings.

TABLE II. QUANTITATIVE CHARACTERS OF THE UPPER AND LOWER STRATA OF THE PINUS CONTORTA/CALAMAGROSTIS RUBESCENS COMMUNITY GROUPED ACCORDING TO THE DENSITY OF THE UPPER STRATUM.

Quantitative character	Tree density/Acre						
	550-650 1/		650-750 2/		750-950 3/		1500-3000 4/
	upper stratum	lower stratum	upper stratum	lower stratum	upper stratum	lower stratum	upper stratum
Mean dist.*	10.7	7.0	10.0	7.4	9.0	9.3	5.0
Rel. den.							
P.c.*	74	28	92	34	91	18	94
A.l.*	26	70	8	36	9	78	6
other	--	2	--	30	--	3	--
Rel. dom.							
P.c.	89	--	96	--	95	--	97
A.l.	11	--	4	--	5	--	3
other	--	--	--	--	--	--	--
Rel. freq.							
P.c.	68	34	86	34	87	28	89
A.l.	32	63	14	34	13	73	11
other	--	3	--	31	--	4	--
Mean area	73	31	64	35	52	55	16
No./Acre	594	1390	682	1246	840	790	2720
T.B.A.*	4410	--	4810	--	5230	--	10880
Importance							
P.c.	231	--	274	--	273	--	280
A.l.	69	--	26	--	27	--	20
other	--	--	--	--	--	--	--
Frequency							
P.c.	92	48	100	52	100	26	100
A.l.	44	87	16	52	17	82	12
other	--	4	--	48	--	6	--

1/ Data obtained from six sets of 25 random pair points.

2/ Data obtained from eight sets of 25 random pair points.

3/ Data obtained from four sets of 25 random pair points.

4/ Data obtained from three sets of 25 random pair points; the lower stratum was too sparse to measure.

* Mean dist. -- mean distance between trees, in feet.
P.c. -- *Pinus contorta*.
A.l. -- *Abies lasiocarpa*.
T.B.A. -- total basal area (ft^2/acre).

The field layer is composed of Calamagrostis rubescens, Carex geyeri and several forbs (Table III and Figure 5). The forbs attaining a frequency of 50% or more include Arnica cordifolia, Arctostaphylos ura-ursi, Lupinus parviflorus and Spiraea betulifolia. Spiraea, although common in the community, does not attain full size and therefore does not provide much cover compared to communities where it is more vigorous.

Pinus contorta/Vaccinium scoparium Community

Pinus contorta is the most abundant taxon in the upper stratum of the community but in some places Abies lasiocarpa makes up to 45% of the arboreal layer. The density of the trees never reaches the high values obtained in the previous community but varies from about 500 to 1,000 trees per acre (Table IV). The reproductive layer is variable in composition, the most abundant taxon usually being A. lasiocarpa, although there are some areas associated with a canopy opening resulting from windfall, snow breakage, insect damage, or other cause, where P. contorta is more abundant.

The taxon providing the most coverage in the field layer is Vaccinium scoparium (Figure 6) and the taxa with frequency values of 50% or more in one or more areas are Arnica cordifolia, Arctostaphylos uva-ursi, Calamagrostis rubescens, Carex geyeri, Spiraea betulifolia and Vaccinium membranaceum (Table V). In any one area, usually not more than one of the subordinate taxa provides a high percentage of cover in relation to that provided by V. scoparium. There are some areas where the Calamagrostis rubescens union grades into the Vaccinium scoparium union making a boundary difficult to establish.

TABLE III. NUMBER/COVER CLASS/FREQUENCY 1/ DETERMINATIONS CALCULATED FROM 2 X 5 dm QUADRATS IN THE FIELD LAYER OF THE PINUS CONTORTA/ CALAMAGROSTIS RUBESCENS COMMUNITY, ARRANGED ACCORDING TO THE DENSITY OF THE UPPER TREE STRATUM.

Taxon	Tree Density/Acre			
	2/ 550-650	3/ 650-750	4/ 750-950	5/ 1500-3000
Arctostaphylos uva-ursi	1/1/50	1/1/40	1/1/20	--
Arnica cordifolia	4/2/90	1/1/20	1/1/10	--
Berberis repens	1/2/10	--	--	--
Calamagrostis rubescens	-/5/80	-/2/60	-/2/50	-/2/30
Campanula rotundifolia	1/1/15	*/1/2	*/1/5	--
Carex geyeri	-/5/60	-/3/40	-/3/30	-/2/30
Chimaphila umbellata	*/1/10	2/1/10	1/1/4	--
Corallorrhiza spp.	--	1/1/5	*/1/5	--
Epilobium angustifolium	*/1/10	--	--	--
Lonicera utahensis	--	--	*/2/5	*/2/3
Lupinus parviflorus	2/2/50	1/2/20	1/2/10	--
Pterospora andromedea	--	*/1/2	1/1/10	*/1/3
Pyrola spp.	--	*/1/10	1/1/10	1/1/15
Rubus parviflora	--	--	--	*/1/3
Senecio spp.	--	*/1/2	--	--
Spiraea betulifolia	1/1/50	2/2/60	1/2/30	1/1/20
Vaccinium membranaceum	--	1/1/10	1/1/15	--
Vaccinium scoparium	1/2/20	1/2/20	2/2/30	--
Viola spp.	*/1/15	*/1/5	1/1/10	--
Mosses & lichens	-/2/60	-/2/40	-/2/40	-/1/40
Litter	-/5/100	-/6/100	-/6/100	-/6/100

1/ The number indicates individuals per square meter, the cover is calculated from six cover classes and the frequency is in terms of frequency per square meter, all values being means.

2/ Data obtained from six sets of ten 2 X 5 dm plots.

3/ Data obtained from eight sets of ten 2 X 5 dm plots.

4/ Data obtained from four sets of ten 2 X 5 dm plots.

5/ Data obtained from three sets of ten 2 X 5 dm plots.

* Values less than one.

\- Too numerous or impractical to count.

-- Absent.

Figure 5. Pinus contorta/Calamagrostis rubescens Community.

Figure 6. Pinus contorta/Vaccinium scoparium Community.

TABLE IV. QUANTITATIVE CHARACTERS OF THE UPPER AND LOWER STRATA OF THE PINUS CONTORTA/VACCINIUM SCOPARIUM COMMUNITY ACCORDING TO DENSITY IN THE UPPER STRATUM.

Quantitative character	Tree density/Acre 500-750 1/		750-1000 2/	
	upper stratum	lower stratum	upper stratum	lower stratum
Mean distance	10	6.4	9	7.8
Rel. density				
P. contorta	60	16	78	12
A. lasiocarpa	40	84	22	88
Rel. dominance				
P. contorta	55	--	84	--
A. lasiocarpa	45	--	16	--
Rel. frequency				
P. contorta	57	21	68	22
A. lasiocarpa	43	79	32	78
Mean area	64	26	51	39
No./Acre	681	1670	853	1120
Total Basal Area	4490	--	5285	--
Importance				
P. contorta	172	--	226	--
A. lasiocarpa	127	--	70	--
Frequency				
P. contorta	80	24	88	21
A. lasiocarpa	60	92	34	90

1/ Data obtained from means of four sets of 25 random pair points.

2/ Data obtained from means of three sets of 25 random pair points.

Pinus contorta/Vaccinium membranaceum Community

Pinus contorta is the dominant taxon of this community and makes up to 98% dominance values, although some areas have a greater proportion of Abies lasiocarpa which attains dominance values of up to 60% (Table VI). The density of trees in the upper stratum is from 500 to 850 per acre, and is inversely proportional to size of trees. Generally, the areas with the highest proportion of A. lasiocarpa have the lowest densities, and this is

TABLE V. NUMBER/COVER CLASS/FREQUENCY 1/ DETERMINATIONS CALCULATED FROM 2 X 5 dm QUADRATS IN THE FIELD LAYER OF THE PINUS CONTORTA/VACCINIUM SCOPARIUM COMMUNITY AND THE PINUS CONTORTA/VACCINIUM MEMBRANACEUM COMMUNITY ARRANGED ACCORDING TO DENSITY AND RELATIVE PROPORTIONS OF P. CONTORTA TO ABIES LASIOCARPA IN THE UPPER STRATUM.

	Community			
	P. contorta/ V. Scoparium		P. contorta/ V. Membranaceum	
	Tree Density/Acre			
	500-750 2/	750-1000 3/	600-850 2/	500-700 2/
Taxon	Proportions of P. contorta to A. lasiocarpa			
	high	low	high	low
Arctostaphylos uva-ursi	1/1/40	1/1/20	1/1/20	--
Arnica cordifolia	1/1/20	1/1/10	*/1/10	*/1/5
Calamagrostis rubescens	-/3/98	-/2/40	-/1/10	-/1/5
Carex geyeri	--	*/1/10	*/1/10	--
Chimaphila umbellata	1/2/20	1/1/10	--	1/1/10
Lonicera utahensis	--	--	*/1/10	*/1/10
Lupinus parviflorus	1/2/30	*/1/5	--	--
Shepherdia canadensis	*/1/10	--	*/1/10	1/2/10
Spiraea betulifolia	1/2/80	*/1/10	1/1/20	1/2/20
Vaccinium membranaceum	1/2/50	2/2/20	3/4/100	3/4/100
Vaccinium scoparium	4/4/100	3/4/100	1/2/10	1/2/10
Mosses & lichens	-/3/80	-/2/80	-/2/70	-/2/70
Litter	-/6/100	-/6/100	-/6/100	-/6/100

1/ The number indicates individuals per square meter, the cover is calculated from six cover classes and the frequency is in terms of frequency per square meter, all values being means.

2/ Data obtained from four sets of ten 2 X 5 dm quadrats.

3/ Data obtained from three sets of ten 2 X 5 dm quadrats.

* Values less than one.

\- Too numerous or impractical to count.

-- Absent.

TABLE VI. QUANTITATIVE CHARACTERS OF THE UPPER AND LOWER STRATA OF THE PINUS CONTORTA/VACCINIUM MEMBRANACEUM COMMUNITY ARRANGED ACCORDING TO RELATIVE ABUNDANCE OF ABIES LASIOCARPA AND DENSITY OF THE UPPER STRATUM.

Quantitative character	Proportions of P. contorta to A. lasiocarpa: 96-100/0-4 1/		55-75/25-45 1/	
	Tree Density/Acre			
	upper stratum	lower stratum	upper stratum	lower stratum
Density	680-850	--	500-700	--
Mean distance	9.3	8.9	9.4	5.7
Rel. density				
P. contorta	98	12	65	7
A. lasiocarpa	2	84	35	92
other	--	4	--	1
Rel. dominance				
P. contorta	93	--	57	--
A. lasiocarpa	7	--	43	--
other	--	--	--	--
Rel. frequency				
P. contorta	98	17	59	88
A. lasiocarpa	2	77	41	10
other	--	6	--	2
Mean area	55	51	57	21
No./Acre	790	862	765	2100
Total basal area	5174	--	4996	--
Importance				
P. contorta	289	--	181	--
A. lasiocarpa	11	--	119	--
other	--	--	--	--
Frequency				
P. contorta	100	21	74	18
A. lasiocarpa	2	96	62	100
other	--	8	--	4

1/ Data obtained from four sets of 25 random pair points.

probably due to the growth form of A. lasiocarpa. The lower tree stratum contains up to 90% A. lasiocarpa except occasionally in areas where the canopy has been disturbed. The density of the reproductive layer is from 600 to 1,000 trees per acre.

Vaccinium membranaceum, the only taxon having a frequency of over 50%, provides a high proportion of cover in the field layer (Table V), although there are a few small areas included in this union where V. scoparium and/or Spiraea betulifolia form significant amounts of cover. Figure 7 shows some of the associates of this union.

Pinus contorta/Shepherdia canadensis Community

The upper stratum of the community is dominated by Pinus contorta in most areas but in some areas, especially on north slopes, Abies lasiocarpa is more abundant and in other areas the two taxa are in nearly equal proportions. The density of the upper stratum is from 400 to 900 trees per acre (Table VII). The lower tree stratum is dominated by A. lasiocarpa in most areas and the density is from 300 to 3,800 trees per acre. One area with 30% Picea engelmanni in the reproductive layer occurs on the steep northern exposure of Signal Mountain.

Shepherdia canadensis provides the most coverage in the shrub layer, due more to its robust growth form than to numbers of individuals (Figure 8). Spiraea betulifolia, Vaccinium membranaceum and occasionally V. scoparium make up significant proportions of the cover and often occur in greater numbers than Shepherdia canadensis (Table VIII). The height of the S. canadensis is usually between 4 and 5 feet, and individual plants may

Figure 7. Pinus contorta/Vaccinium membranaceum Community.

Figure 8. Pinus contorta/Shepherdia canadensis Community.

TABLE VII. QUANTITATIVE CHARACTERS OF THE UPPER AND LOWER STRATA OF THE PINUS CONTORTA/SHEPHERDIA CANADENSIS COMMUMITY ARRANGED ACCORDING TO THE COMPOSITION OF THE UPPER STRATUM.

Quantitative character	Proportions of P. contorta/A. lasiocarpa			
	45-60/40-55 1/		60-100/0-40 1/	
	upper stratum	lower stratum	upper stratum	lower stratum
Density	400-700	--	500-900	--
Mean distance	9.8	4.2	9.6	8.1
Rel. density				
P. contorta	50	4	95	23
A. lasiocarpa	50	94	5	77
other	--	2	--	--
Rel. dominance				
P. contorta	42	--	94	--
A. lasiocarpa	58	--	6	--
other	--	--	--	--
Rel. frequency				
P. contorta	50	7	92	26
A. lasiocarpa	50	89	8	74
other	--	4	--	--
Mean area	62	11	59	42
No./Acre	710	3860	740	1040
Total basal area	4560	--	4797	--
Importance				
P. contorta	142	--	281	--
A. lasiocarpa	158	--	19	--
other	--	--	--	--
Frequency				
P. contorta	64	8	100	31
A. lasiocarpa	64	100	9	89
other	--	4	--	--

1/ Data obtained from three sets of 25 random paid points.

TABLE VIII. NUMBER/COVER CLASS/FREQUENCY 1/ DETERMINATIONS CALCULATED FROM 2 X 5 dm QUADRATS IN THE FIELD LAYER OF THE PINUS CONTORTA/ SHEPHERDIA CANADENSIS AND THE PSEUDOTSUGA MENZIESSII/VACCINIUM MEMBRANACEUM COMMUNITIES ARRANGED ACCORDING TO THE COMPOSITION OF THE UPPER STRATUM.

Taxon	Community: P. contorta/ S. canadensis — Proportions of P. contorta/A. lasiocarpa 45-60/40-55 2/	Community: P. contorta/ S. canadensis — Proportions of P. contorta/A. lasiocarpa 60-100/0-40 2/	Community: P. menziessii/ V. membranaceum 3/
Arctostaphylos uva-ursi	1/1/40	1/1/20	1/1/30
Arnica cordifolia	--	*/1/20	2/2/40
Calamagrostis rubescens	-/1/20	-/1/30	-/2/80
Calypso bulbosa	*/1/5	--	*/1/5
Carex geyeri	-/1/20	-/2/30	*/1/20
Ceanothus velutinus	--	1/3/2 #	--
Eriogonum subalpinum	--	--	2/2/30
Fragaria sp.	*/1/5	--	*/1/5
Lonicera utahensis	--	--	1/2/20
Shepherdia canadensis	12/49/23 #	8/35/21 #	--
Sorbus scopulina	*/1/* #	--	--
Spiraea betulifolia	14/12/29 #	14/10/34 #	2/3/90
Vaccinium membranaceum	22/17/45 #	18/12/41 #	1/2/90
Vaccinium scoparium	1/1/2 #	1/*/2 #	2/2/30
Mosses and lichens	-/2/70	-/2/80	-/2/90
Litter	-/4/100	-/5/100	-/5/100

1/ The number indicates individuals per square meter, the cover is calculated from six cover classes and the frequency is in terms of frequency per square meter, all values being means.

2/ Data obtained from three sets of ten 2 X 5 dm quadrats.

3/ Data obtained from two sets of ten 2 X 5 dm quadrats.

* Values less than one.

\- Too numerous or impractical to count.

-- Absent.

\# Average number per 100 feet/average cover/relative frequency obtained by 100 feet line-intercepts, three where A. lasiocarpa is most abundant and four in the other.

have a crown diameter of 6 feet or more, therefore this species often overshadows many other types of shrubs.

Pseudotsuga menziessii/Vaccinium membranaceum Community

Pesudotsuga menziessii dominates the upper stratum of the community but Pinus contorta, Abies lasiocarpa and occasionally Pinus flexilis occur in varying proportions (Table IX). The community usually occurs on relatively dry areas and this probably accounts for the retardation of Abies lasiocarpa regeneration. In addition, the closed canopy provided by Pseudotsuga menziessii probably hinders the regeneration of Pinus contorta, thus Pseudotsuga menziessii is the most abundant taxon in the arboreal reproductive layer.

Vaccinium membranaceum and Spiraea betulifolia dominate the field layer of this community (Table VIII). Calamagrostis rubescens is abundant in the community but the preponderance of shrubs is the most characteristic visual aspect. Acer glabrum, Alnus tenuifolia, Amelanchier alnifolia, Eleagnus argentea, Rubus parviflorus, Sorbus scopulina and Symphoricarpos tetonensis also occur in the community but were not encountered in any plots or line intercepts. They are commonly associated with rock outcroppings or openings in the canopy and do not represent the community as a whole.

Populus tremuloides/Geranium viscosissimum Community

Populus tremuloides dominates the upper stratum of the community and most areas have few conifers. The density of the upper stratum is approximately 500 trees per acre (Table IX) and this number is about doubled in the reproductive layer. The reproductive layer is composed chiefly of P. tremuloides suckers and/or seedlings with few conifers (Figure 9).

TABLE IX. QUANTITATIVE CHARACTERS OF THE UPPER AND LOWER STRATA OF THE PSEUDOTSUGA MENZIESSII/VACCINIUM MEMBRANACEUM COMMUNITY AND THE POPULUS TREMULOIDES/GERANIUM VISCOSISSIMUM COMMUNITY.

Quantitative character	Community			
	P. menziessii/ V. membranaceum 1/		P. tremuloides/ G. viscosissimum 1/	
	upper stratum	lower stratum	upper stratum	lower stratum
Density	600-900	--	500-1000	--
Mean distance	7.4	9.3	11.8	8.2
Rel. density				
P. contorta	10	20	8	2
P. menziessii	86	70	11	3
P. tremuloides	--	--	78	93
other	4	10	3	2
Rel. dominance				
P. contorta	9	--	4	--
P. menziessii	89	--	9	--
P. tremuloides	--	--	85	--
other	2	--	2	--
Rel. frequency				
P. contorta	16	23	9	1
P. menziessii	78	68	13	2
P. tremuloides	--	--	74	96
other	6	9	4	1
Mean area	35	55	89	43
No./Acre	1246	790	490	1014
Total basal area	9950	--	3975	--
Importance				
P. contorta	35	--	21	--
P. menziessii	252	--	33	--
P. tremuloides	--	--	237	--
other	13	--	9	--
Frequency				
P. contorta	21	28	11	5
P. menziessii	100	89	16	7
P. tremuloides	--	--	98	100
other	8	14	5	5

1/ Data obtained from two sets of 25 random pair points.

Figure 9. Populus tremuloides/Geranium viscosissimum Community.

Figure 10. Ecotone between morainal forest and outwash vegetation, Timbered Island.

Geranium viscosissimum was arbitrarily selected as an identifying taxon of the field union from a variable grass-forb matrix associated with the P. tremuloides union. The composition of the matrix varies from one area to another but G. viscosissimum is the taxon most consistently present. Many segments of the Populus tremuloides union occur as narrow bands bordering conifer communities and were not sampled, which underestimates the representation of G. viscosissimum. Agropyron spp., Eriogeron speciosus, Lupinus parviflorus, Melica spectabilis and Spiraea betulifolia have frequency values of 50% or more in the community (Table X).

Forest-grassland Ecotone Vegetation

Table XI contains a list of taxa occurring in the ecotone grouped according to distance from the forest margin and gives the average cover class and frequency of each. Thirty-six percent of the taxa occurred in all strips and another 17% of the taxa occurred in the first strip and one or more other strips but not in all. The first strip had 11% unique to it and 36% did not occur in it. Artemisia tridentata provides the most coverage and Antennaria rosea, Collinsia parviflora, Collomia linearis, Galium bifolium, Linanthus septentrionalis, and Senecio integerrimus have high frequency values in all strips. Figure 10 shows the sharp ecotone existing between morainal forests and outwash vegetation.

Increment Core Analysis

An analysis of 438 increment core samples involving the computation of a diameter to age ratio of trees located in different parts of the study area indicates insignificant differences in growth of Pinus contorta in

TABLE X. NUMBER/COVER CLASS/FREQUENCY 1/ DETERMINATIONS CALCULATED FROM 2 X 5 dm QUADRATS IN THE FIELD LAYER OF THE POPULUS TREMULOIDES/ GERANIUM VISCOSISSIMUM COMMUNITY.

Taxon	Number/cover class/frequency
Agostache urticifolia	1/2/40
Agropyron spp.	-/2/50
Amelanchier alnifolia	1/2/20
Arctostaphylos uva-ursi	*/1/5
Arnica cordifolia	1/1/10
Astragalus spp.	1/2/30
Berberis repens	1/2/10
Calamagrostis rubescens	-/2/30
Carex geyeri	-/2/40
Epilobium angustifolium	2/2/30
Eriogeron speciosus	2/2/60
Geranium viscosissimum	2/2/80
Helianthella uniflora	1/2/20
Lonicera utahensis	1/2/40
Lupinus parviflorus	2/2/50
Melica spectabilis	2/1/80
Poa spp.	-/1/30
Rubus parviflorus	1/2/20
Spiraea betulifolia	2/1/60
Thalictrum spp.	1/1/40
Vaccinium membranaceum	1/1/20
Mosses & lichens	-/2/30
Litter	-/5/100

1/ The number indicates individuals per square meter, the cover is calculated from six cover classes and the frequency is in terms of frequency per square meter, all values being means of two sets of ten 2 X 5 dm quadrats.

* Values less than one.

\- Too numerous or impractical to count.

TABLE XI. COVER CLASS/FREQUENCY DETERMINATIONS CALCULATED FROM 0.5 X 1 m QUADRATS IN THE FOREST-GRASSLAND ECOTONE ARRANGED ACCORDING TO DISTANCE OUT FROM FOREST MARGIN.

Taxon	Meters from Forest Margin				
	1/ 0	1/ 5	1/ 10	1/ 20	1/ 30
Agropyron spp.	1/20	2/67	1/33	1/40	2/33
Agoseris glauca	1/13	1/13	1/40	1/53	1/53
Antennaria rosea	2/53	2/98	2/98	2/98	2/100
Arabis holboellii	1/7	1/13	1/47	1/13	1/60
Arenaria congesta	1/13	1/20	1/20	1/53	1/60
Artemisia cana	2/13	2/27	2/13	2/13	2/13
Artemisia tridentata	2/27	3/53	3/80	3/53	3/74
Aster spp.	1/13	1/13	1/7	1/13	1/7
Collinsia parviflora	1/80	2/100	1/98	1/80	1/87
Collomia linearis	2/60	1/80	1/98	1/98	1/87
Eriogonum subalpinum	2/33	2/33	2/60	2/53	2/67
Galium bifolium	2/67	1/80	1/74	1/60	1/46
Grass (various species)	2/20	2/40	2/53	2/20	2/33
Linanthus septentrionalis	1/48	1/73	1/67	1/73	1/53
Lupinus leucophyllus	2/20	2/20	2/20	2/20	2/33
Poa pratensis	2/33	3/27	2/27	2/20	1/27
Sedum stenopetalum	1/4	1/13	2/13	1/13	1/13
Senecio integerrimus	2/48	2/40	2/53	2/53	2/60
Viola nuttallii	1/48	1/13	1/33	2/33	1/53
Delphinium nelsoni	2/27	1/7	1/7	1/7	--
Perideridia gairdneri	1/40	1/47	1/46	--	1/13
Monotropa uniflora	1/27	--	2/67	1/47	1/27
Taraxacum officinale	1/7	--	2/13	2/27	2/20
Achillea millefolium	1/7	2/13	--	2/7	--
Balsamorrhiza sagittata	2/4	--	2/7	--	2/7
Lupinus parviflorus	2/20	--	--	1/7	--
Geranium viscosissimum	2/13	2/20	--	--	--
Lithophragma parviflora	1/20	1/7	--	--	--
Alnus tenuifolia	2/7	--	--	--	--
Arotostaphylos uva-ursi	1/7	--	--	--	--
Arnica cordifolia	1/20	--	--	--	--
Calamagrostis rubescens	2/20	--	--	--	--
Carex geyeri	2/33	--	--	--	--
Pterospora andromedea	1/4	--	--	--	--
Arabis drummondii	--	1/7	--	--	--
Fritillaria atropurpurea	--	1/4	--	--	--
Hackelia floribunda	--	1/4	--	--	--
Helianthella uniflora	--	2/20	--	--	--
Spergularia rubra	--	1/4	--	--	1/4
Lithophragma bulbifera	--	1/13	1/20	--	2/7

TABLE XI. Continued.

Taxon	Meters from Forest Margin 1/ 0	1/ 5	1/ 10	1/ 20	1/ 30
Carex sp.	--	2/7	2/7	2/7	1/7
Castilleja spp.	--	2/13	1/13	1/40	2/27
Dodecatheon pauciflorum	--	1/7	1/13	1/33	1/27
Hordeum jubatum	--	2/7	1/13	1/7	1/7
Melica spectabilis	--	2/27	1/46	2/53	1/33
Fritillaria pudica	--	--	1/13	1/7	2/13
Berberis repens	--	--	1/7	--	--
Lomatium simplex	--	--	1/7	--	--
Eriogonum spp.	--	--	--	1/7	--
Hydrophyllum capitatum	--	--	--	2/7	--
Melilotus officinalis	--	--	--	2/7	--
Festuca idahoensis	--	--	--	--	1/7
Pinus contorta	--	--	--	--	1/4
Mosses & lichens	2/80	1/53	1/48	1/53	1/20
Litter	3/100	2/100	2/100	2/100	2/100
Bare ground	3/100	4/100	4/100	4/100	4/100

1/ Data are averages of one-hundred-twenty 0.5 X 1 m quadrats.

different forest communities with the exception of those growing in dense areas and those growing in open ecotonal areas (Tables XII and XIII). Almost all stands are less than 100 years old. Timbered Island possesses the oldest _P. contorta_ with a few trees exceeding 200 years of age. The _P. contorta_ with the highest growth rate occurs in outwash plains in the ecotones between sagebrush-grassland and forest communities. Most of these trees are less than 50 years old, and the average yearly diameter increase may exceed 0.5 inch. In areas where the density of trees exceeds about 1500 per acre, the average diameter increase is less than 0.1 inch per year. These trees often had a much higher growth rate during the first 10 years or so and then it was supressed, indicating that they came in when the forest was open, probably after a fire. This situation approaches the commonly observed "dog-hair" stands that develop after a fire (Horton 1956, Smithers 1961).

The _Abies lasiocarpa_ show about a 10 year or more lag period with respect to the _Pinus contorta_ in most areas. The growth rate is variable, depending to some extent on density. In areas where the density exceeds 1500 trees per acre, the average yearly diameter increase is less than 0.1 inch. The areas having the largest _Abies lasiocarpa_ have the highest average growth rate, this being over 0.2 inch per year. Some caution is necessary in interpreting this since, in most cases, the largest trees of an area were chosen to be sampled. There are several instances in which the largest _A. lasiocarpa_ of an area had much slower growth rates than some of the smaller trees.

The oldest and largest trees in the study area, some exceeding 36

TABLE XII. DIAMETER AND AGE CHARACTERISTICS OBTAINED BY INCREMENT CORE ANALYSIS OF PINUS CONTORTA (P.c.), ABIES LASIOCARPA (A.l.) PSEUDOTSUGA MENZIESSII (P.m.) AND POPULUS TREMULOIDES (P.t.) IN DIFFERENT AREAS (A).

A*	T	No.	Dia. range	Ave. dia.	Age range	Median age	Ave. age	Ratio# range	Ave. ratio
1	P.c.	10	6.9-13.8	9.7	50- 70	60.0	62.9	0.109-0.232	0.156
2	P.c.	7	6.9- 9.6	7.9	35- 68	51.5	55.0	0.115-0.211	0.149
3	P.c.	9	4.6-15.2	9.4	67-131	99.0	90.4	0.068-0.170	0.101
4	P.c.	4	8.0-12.5	9.4	25- 34	29.5	28.8	0.300-0.524	0.365
5	P.c.	9	7.4-13.6	11.0	61- 87	74.0	71.6	0.104-0.187	0.155
6	P.c.	10	6.7-12.5	9.4	59- 77	68.0	69.4	0.094-0.184	0.135
7	P.c.	10	8.5-16.6	11.1	67-148	112.5	101.6	0.060-0.190	0.119
8	P.c.	16	5.1-14.0	9.0	38- 59	48.5	50.5	0.108-0.259	0.175
9	P.c.	7	14.9-21.5	19.1	74-147	110.5	89.8	0.146-0.270	0.220
10	P.c.	4	6.4- 7.9	7.0	32- 40	36.0	37.5	0.164-0.230	0.193
11	P.c.	8	11.2-19.9	14.4	92-103	97.5	96.3	0.113-0.214	0.150
12	P.c.	5	9.3-12.7	10.6	85- 95	90.0	89.6	0.098-0.122	0.118
13	P.c.	9	6.5-15.1	8.6	30- 94	62.0	56.0	0.119-0.236	0.165
14	P.c.	6	7.2-14.2	10.8	119-221	170.0	176.0	0.042-0.074	0.062
15	P.c.	10	2.9- 8.9	5.7	73- 81	77.0	76.5	0.039-0.115	0.075
16	P.c.	12	5.8-21.1	12.2	62-104	83.0	79.4	0.083-0.207	0.152
17	P.c.	3	12.5-16.4	14.7	46-171	108.5	128.8	0.091-0.272	0.153
18	P.c.	5	9.9-13.5	11.9	74- 83	78.5	77.3	0.132-0.182	0.155
19	P.c.	14	4.7-11.6	8.3	63- 83	73.0	76.0	0.067-0.166	0.110
20	P.c.	14	3.6-10.6	6.4	58- 83	70.5	72.4	0.057-0.133	0.088
21	P.c.	11	4.5-14.8	7.6	63- 72	67.5	65.3	0.069-0.214	0.115
22	P.c.	10	3.2- 6.7	5.4	62- 80	71.0	72.8	0.040-0.093	0.074
23	P.c.	4	13.5-21.6	18.5	62-149	105.5	85.5	0.145-0.264	0.210
24	P.c.	5	12.0-15.0	13.1	143-168	155.5	154.6	0.067-0.101	0.088
25	P.c.	10	4.4-13.9	9.2	52-223	137.5	102.2	0.055-0.170	0.100
26	P.c.	5	1.5-14.5	5.5	45-151	98.0	70.0	0.033-0.096	0.071
27	A.l.	2	14.0-14.5	14.3	57- 92	74.5	74.5	0.158-0.246	0.202
28	A.l.	2	9.3-14.3	11.8	84- 89	86.5	86.5	0.104-0.170	0.137
29	A.l.	5	8.1-12.4	9.7	61- 95	78.5	74.7	0.113-0.155	0.131
30	A.l.	5	9.7-13.5	11.5	119-157	138.0	129.4	0.070-0.104	0.090
31	A.l.	5	19.9-23.9	21.8	81-106	93.5	98.6	0.203-0.247	0.223
32	A.l.	5	7.2- 8.8	8.1	56- 75	65.5	69.8	0.105-0.129	0.115
33	A.l.	2	16.3-19.2	17.8	66- 72	69.0	69.0	0.247-0.267	0.257
34	A.l.	10	4.2-20.6	11.6	38-154	96.0	82.2	0.056-0.238	0.141
35	A.l.	5	2.7- 7.8	5.9	49- 80	64.5	62.8	0.051-0.159	0.097
36	P.m.	6	18.4-27.0	24.2	86-187	136.5	140.1	0.102-0.280	0.189
37	P.m.	5	12.8-22.0	17.5	112-169	140.5	145.6	0.088-0.150	0.121

TABLE XII. Continued.

A*	T	No.	Dia. range	Ave. dia.	Age range	Median age	Ave. age	Ratio# range	Ave ratio
38	P.m.	6	15.0-18.0	16.6	52- 68	60.0	62.6	0.230-0.323	0.270
39	P.m.	3	21.3-22.2	21.9	132-245	188.5	186.0	0.087-0.168	0.125
40	P.m.	2	17.0-22.3	19.7	128-148	136.0	136.0	0.137-0.151	0.144
41	P.t.	10	8.5-13.3	10.8	62- 85	73.5	75.3	0.108-0.179	0.144

* See Table XIII for area specifications.

\# Diameter/age ratio.

TABLE XIII. LOCATIONS OF AREAS FROM WHICH THE INCREMENT SAMPLES LISTED IN TABLE XII WERE TAKEN.

No.	Location of area
1.	Outcroppings east of Burnt Ridge.
2.	Outcroppings east of Burnt Ridge.
3.	Outcroppings east of Burnt Ridge.
4.	Northeast ecotone of Burnt Ridge.
5.	Outcroppings east of Burnt Ridge.
6.	Outcroppings east of Burnt Ridge.
7.	Outcroppings east of Burnt Ridge.
8.	Outcroppings east of Burnt Ridge.
9.	East side of Artemisia arbuscula park near Pilgrim Creek.
10.	In the Artemisia arbuscula park near Pilgrim Creek.
11.	West side of Artemisia arbuscula park near Pilgrim Creek.
12.	West side of the Artemisia arbuscula park but farther into the forest than No. 11.
13.	In the Artemisia arbuscula park.
14.	West-northwest slope of Burnt Ridge with dense tree growth.
15.	Jackson Lake Moraine west from Mt. Moran turnout, dense growth.
16.	East of Bison pasture.
17.	Near center of Timbered Island.
18.	Southwest side of Burnt Ridge.
19.	West part of Burnt Ridge.
20.	Dense tree growth on southwest side of Burnt Ridge.
21.	In the Spalding Bay area near look-out tower.
22.	Dense tree growth on the east side of Burnt Ridge.
23.	Jackson Lake moraine, west of Mt. Moran turnout.
24.	North end of Timbered Island.
25.	Pinus contorta/Shepherdia canadensis Community near the middle of Timbered Island where there were a lot of Abies lasiocarpa.
26.	Dense tree growth on Timbered Island.
27.	East side of Artemisia arbuscula park.
28.	West side of Artemisia arbuscula park.
29.	Farther in on the west side of the Artemisia arbuscula park than No. 28.
30.	West-northwest, 35% slope on Burnt Ridge.
31.	Near middle of Timbered Island, near swampy area.
32.	Southwest side of Burnt Ridge.
33.	In Spalding Bay area, west of look-out tower.
34.	Pinus contorta/Shepherdia canadensis Community near the middle of Timbered Island, with a lot of Abies lasiocarpa.
35.	Dense tree growth on Timbered Island.
36.	East side of Artemisia arbuscula park.
37.	West-northwest, 35% slope on Burnt Ridge.
38.	Southwest side of Burnt Ridge.
39.	Jackson Lake moraine west of Mt. Moran turnout.
40.	Tree outcroppings east of Burnt Ridge.
41.	Populus tremuloides stand on northwest-face of Signal Mountain.

inches diameter at breast height (dbh), are Pseudotsuga menziessii, probably because they were able to survive one or more fires that eliminated the other trees. The ages of the largest trees could not be determined because the increment borer employed in this study was not long enough to reach the center. The growth rates are very nearly the same in different areas except that the best growth occurs in trees located in open areas and the slowest growth in dense situations. There are some P. menziessii scattered in the outwash plain southeast of Burnt Ridge that are about 63 years of age on the average and are 17 inches dbh giving them an average growth rate of 0.27 inch per year. That P. menziessii seems to tolerate crowding better than some other conifers is indicated by data from one area with a density of about 1500 trees per acre, where the P. menziessii had a diameter to age ratio of 0.12 while Abies lasiocarpa had a ratio of 0.09 and Pinus contorta had a ratio of 0.06.

There was only one area where sufficient samples were taken from Populus tremuloides to yield an indication of the growth rate of the taxon because, in other areas, common occurrence of heart rot made age determination impossible. In the "aspen island" on Signal Mountain, the largest trees are between 62 and 85 years old and have an average yearly diameter increase of 0.14 inch (Table XII).

Determination of Fires

Only one fire was accurately dated by increment samples from fire-scarred Pseudotsuga menziessii and this was the fire which occurred in 1879 and affected most of Jackson Lake moraine, including the Spalding Bay area. The approximate dates of other fires were determined by finding the age of stands and adding 10 years to compensate for the usual lag in regeneration of trees following a burn (Smithers 1961). The dates are as follows: a severe fire occurred on Timbered Island about 1765; the Wild Life Refuge near the Oxbow was burnt over about 1865; the Jackson Lake moraine was burnt in 1879; and a fire extending from the south end of Timbered Island, across Burnt Ridge and the outwash plain to the east to Signal Mountain occurred about 1890. This does not exclude other fires that may have occurred in these areas before the dates given since these dates are derived from the oldest trees now inhabiting the areas. Burnt Ridge and Jackson Lake moraine conceivably could have been burnt over at the same time that Timbered Island was in 1765 because some trees in the outwash to the west of Burnt Ridge are 180 to 190 years old.

Dendrometric Growth Analysis

Four *Pinus contorta* of different diameters, 6.8, 8.2, 20.3 and 22.2 inches dbh, were selected at the Biological Research Station on 30 May 1965 for detecting increase of diameter with a dial gauge dendrometer (Table XIV). The measurements were taken between the hours of 0545 and 0600 periodically throughout the summer. It is possible that the seasonal growth of the trees began before the dendrometer measurements were initiated; Crossley, according to Smithers (1961), found growth of *P. contorta* to begin around 1 May in Kananaskis, Alberta and continued to 15 August. In the present study, the trees showed a decline of growth rate beginning about 4 August but then two of the trees showed an increase in growth at a

TABLE XIV. MEASUREMENTS MADE WITH A DIAL GAUGE DENDROMETER ON FOUR *PINUS CONTORTA* LOCATED AT THE BIOLOGICAL RESEARCH STATION, MORAN, WYOMING.

Date	Diameter of tree by tape at breast height			
	6.8"	8.2"	20.3"	22.2"
	Dendrometer readings*, in inches			
31 May	0.021	0.027	0.041	0.028
15 June	0.030	0.047	0.050	0.034
16 June	0.031	0.037	0.049	0.034
17 June	0.031	0.040	0.051	0.036
21 June	0.033	0.036	0.050	0.038
23 June	0.037	0.037	0.052	0.040
8 July	0.054	0.050	0.064	0.056
15 July	0.061	0.059	0.069	0.068
22 July	0.068	0.063	0.072	0.072
29 July	0.075	0.068	0.076	0.080
4 Aug.	0.077	0.070	0.080	0.083
7 Aug.	0.077	0.069	0.080	0.084
10 Aug.	0.077	0.068	0.080	0.083
24 Aug.	0.084	0.069	0.084	0.085
28 Aug.	0.084	0.068	0.083	0.085
	Difference between maximum and minimum measurements			
	0.063	0.041	0.042	0.057

* All readings were made at between 0545 and 0600 hours.

later time. The diameter increase of the trees over the period 31 May to 28 August, based on the highest values obtained in August, varied from 0.042 to 0.063 inch which is less than the expected average yearly increase. The number of samples used in this study is insufficient to draw any firm conclusions but does indicate possible trends.

Bryophyte and Lichen Flora

Several mosses, lichens and a few liverworts were collected in various areas throughout Grand Teton National Park. These were identified by W. A. Weber, University of Colorado Museum. Insufficient information was gained to establish their full ecological significance, but several mosses and lichens were found growing on litter whereas others occurred mostly on rock surfaces or in rock crevices. Some were growing on the bare surfaces of the outwash and morainal soils, and some occurred as epiphytes. Seepage channels and small streams shaded by vascular plants possessed the most luxurious moss growth.

Only a few species of mosses, such as Ceratodon purpureus, Pohlia nutans, Polytrichum juniperinum and P. piliferum were found on the outwash soil; however, here they may form mats two, three, or occasionally more, feet in diameter. Peltigera canina, a lichen, forms spherical mats 3 to 5 inches in diameter and several mats may occur together covering much of the area between grass or sagebrush clumps in some places.

The forest litter provides a substrate for many mosses, such as Brachythecium collinum, B. latifolium, Chamberlainia erythrorhiza, and Dicranum scoparium, and lichens, such as Cladonia cariosa, C. cenotea,

C. chlorophaea and Peltigera venosa. Bryoerythrophyllum recurvirostrum, Bryum argenteum, Ceratodon purpureus, Hypnum revolutum, Polytrichum juniperinum and P. piliferum occur in open areas of moraines and slopes of the Teton Mountain Range. The rocks and rock crevices of moraines often possess mosses such as Brachythecium collinum, Chamberlainia albicans, Dicranoweisia crispula, Grimmia affinis, G. alpestris, G. apocarpa, Orthotrichum macounii, Pseudoleskeella tectorum and Tortula norvegica. Several lichens, such as Alectoria glabra, Letharia vulpina f. californica, Parmelia subolivacea and Usnea glabrata, grow on dead branches of conifer trees and Candelaria concolor, Parmelia elegantula, Parmeliopsis ambigua and Xanthoria fallax, occur on the trunks of conifers. Stroemia obtusifolium was the only moss found growing on trunks and branches of trees and it was observed only on living Populus trichocarpa.

By far the greatest diversity of bryophytes occur along seepage channels and small streams. Included in these areas are Atrichum selwyni, Aulacomnium palustre, Brachythecium collinum, Bryum pseudotriquetrum, B. weigelii, Calliergon stramineum, Campylium stellatum, Ceratodon purpureus, Cratoneuron filicinum, Dicranoweisia crispula, Drepanocladus aduncus, D. uncinatus, Hygrohypnum ochraceum, Isopterygium pulchellum, Leptobryum pyriforme, Marchantia polymorpha, Mnium punctatum, Pellia endiviaefolia, Philonotis fontana, Pohlia albicans, P. cruda, P. nutans, P. proligera and Tortula mucronifolia.

DISCUSSION

Community Classification

A random sampling of the shrub and forb layers of the forest communities would probably indicate a preponderance of Calamagrostis rubescens and Carex geyeri with a variable mixture of associated plants because the Calamagrostis rubescens union is the most frequently encountered. On the other hand, if a line transect were run across a moraine the continuum concept would gain support because a demarcation between two unions cannot be clearly established due to diffusion of one union into another. Perhaps part of the vagueness of union demarcation is due to the seral stages presently represented by the forest communities. However, it is felt that the separation of the field layer into unions is justifiable because of the uniqueness and constancy of each union outside of the ecotones. The physiognomy is perhaps the most easily recognized basis for separation of the unions occurring under conifers. The Calamagrostis rubescens union may be recognized by the absence of an abundant shrub growth. Vaccinium scoparium is about half as tall as V. membranaceum and has smaller leaves which distinguishes between these two unions. Spiraea betulifolia, which is relatively abundant in both Vaccinium unions, has a more vigorous growth form in the V. membranaceum union, and therefore, does not hinder separation. Shepherdia canadensis is four to six times the height of Vaccinium membranaceum and is thus easily separated. Floristically, these unions may be distinguished by the presence of the dominant taxon with the exclusion of the dominants of other unions; the subordinant vegetation is mostly a characteristic of the forest and not of any one union with the exception of Carex geyeri which is confined to the Calamagrostis rubescens union. The

Geranium viscosissimum union may be separated either floristically by the large number of grasses and forbs or physiognomically by its unkempt appearance. This method of community analysis has not gained much favor among researchers of central and eastern North America but Daubenmire (1952, 1953) and Langenheim (1962) have found it suitable for vegetational analysis in the Rocky Mountain region.

The Populus tremuloides/Geranium viscosissimum Community occurs at the edges of some moraines and in restricted stands, some of which are relatively extensive. It is associated with a wide variety of soils and moisture regimes from coarse textured, relatively dry soils on southern exposures, to fine textured, wet to almost soggy soils in drainage channels. The regions with soil and moisture conditions between these extremes are generally occupied by coniferous communities. Apparently the outwash soils are too shallow and coarse textured for the community to develop. Populus tremuloides reproduces by "suckering" which may account, in part, for its unique occurrences. Seeds have been observed to germinate in catkins that have fallen on litter but how extensive this is, and whether the seedlings become established, has not been examined. Often suckers, and perhaps seedlings, develop dense populations with up to 4,000 or more per acre in a stand, but browsing by moose, elk and deer along with some pathological conditions reduce them to less than 1000 trees per acre at maturity. Geranium viscosissimum was somewhat arbitrarily selected from a relatively large variety of grasses and forbs to represent the field layer of the Populus tremuloides Community. It is well represented in some stands of the community but almost absent in others. It occurs in some areas without

P. tremuloides, but it is more nearly confined to the community than any other field-layer taxon.

The coniferous communities, for the most part, are dominated at the present time by Pinus contorta var. latifolia, probably due to its enhanced growth after fires. A few relict stands of Pseudotsuga menziessii remain and appear to be maintaining themselves and even advancing into the Pinus contorta communities in some places. Abies lasiocarpa, if abundant at some earlier time, was almost completely eliminated by fires, but at least a few seeds apparently escaped destruction by each fire and were able to reestablish the taxon. Several A. lasiocarpa over 100 years old, the oldest 157 years, occur in areas believed to have been burnt more recently so they apparently survived fire, and could contribute seeds important in reestablishment. A seed source is also provided by A. lasiocarpa occurring on the slopes of the Teton Mountain Range above the moraines, and it is conceivable that seed could be blown across the snow surface during the winter and reestablish the taxon on the moraines. At the present time, A. lasiocarpa is the most abundant taxon in the arboreal reproductive layers except in a few places where Pseudotsuga menziessii dominates. Some relatively open Pinus contorta stands have high percentages of P. contorta in the reproductive layers but they are insignificant when considering the forested areas in entirety. In view of these considerations it may be justifiable to name at least some of the coniferous unions after Abies lasiocarpa instead of Pinus contorta; however, it is felt that as the Abies lasiocarpa gains maturity and dominance, the subordinate vegetation will consequently change and a different nomenclatural scheme may be necessary in describing the

the forest vegetation. Also recurrent fires may be considered to have been a part of the normal environment in the past, leaving Pinus contorta as a "pyroedaphic climax" taxon (Daubenmire 1959) but the current fire-control measures are allowing Abies lasiocarpa to gain dominance. Therefore, under the present circumstances, Pinus contorta is used to name the segments of the forest communities except where Populus tremuloides and Pseudotsuga menziessii are more abundant in the mature stratum.

The Calamagrostis rubescens union occurs at the periphery of the moraines, except in some areas where the Populus tremuloides/Geranium viscosissimum Community occurs, and forms a relatively wide band in most cases. Representations of the union may also be found on tops of some ridges and on some east and south slopes of the moraines. Generally it is associated with the coarse-textured and shallow morainal soils. The associated forbs are more diverse in this union than in any other except the G. viscosissimum union, with a relatively high number having low frequency values indicating an immature stage of community development. Calamagrostis rubescens appears to exhibit its best growth when partially shaded. Treeless areas on moraines usually have C. rubescens growing only near the edges that are partially shaded during the hot period of the day. However, dense forested areas, having more than about 2,000 trees per acre, also have a very sparse growth of C. rubescens. Carex geyeri, the main associate of this union, is somewhat more tolerant of both the open and dense situtations but is also limited by both extremes.

The Calamagrostis rubescens union grades into the Vaccinium scoparium union in most places toward the middle of morainal forests. The latter taxon is generally associated with a greater accumulation of fine-textured substrate material and can tolerate a more dense arboreal cover than the Calamagrostis rubescens union, although it sometimes is present under a sparse tree growth. The number of associated taxa of this and the subsequent unions are relatively few with some having low frequency values. Spiraea betulifolia is a common associate having relatively high frequency values but most individuals show poor vigor.

The next union encountered as one approaches the center of a moraine is the Vaccinium membranaceum union. In some areas where the V. scoparium union is absent, the V. membranaceum union is adjacent to the Calamagrostis rubescens union and in some areas the Vaccinium membranaceum union and the Calamagrostis rubescens union are separated by a C. rubescens-V. scoparium-V. membranaceum ecotone. The substrate associated with the Vaccinium membranaceum union is commonly deeper and less rocky than that of the other unions mentioned. The best development of the union is on northern and western slopes where there are few associated taxa. Spiraea betulifolia is a common associate and provides a relatively high proportion of cover due to its vigorous growth form.

On most moraines, such as Burnt Ridge and the Jackson Lake moraine, the Vaccinium membranaceum union is the last one encountered. However, on moraines such as Timbered Island and parts of Signal Mountain where there is a relatively deep (4 to 6 feet) accumulation of aeolian material or volcanic ash the Shepherdia canadensis union occurs. A S. canadensis bush may attain a height of three to five, or occasionally more, feet and cover an area up to about 12 feet in diameter. Some areas have a nearly continuous cover of S. canadensis while in others they may be relatively sparse. The associates are other woody plants such as Spiraea betulifolia, Vaccinium membranaceum and V. scoparium.

Statistical Analysis and Interpretation

A method of estimating the degree of floristic maturity of a well-established plant community, which involves the calculation of the average frequency of the taxa occurring in a community, was proposed by Pichi-Sermolli (1948). The values may range from 0 to 100; the higher the number, the more mature the community is. Application of this method to the communities of this study (Table XV) which provided values ranging from 15 to 50 with an average of 27 indicate that all the communities are immature. The Pinus contorta/Vaccinium scoparium Community with a density of 500 to 750 trees per acre in the upper stratum and with a high ratio of P. contorta to Abies lasiocarpa is the most mature with a maturity index of 50.

Another method of estimating floristic maturity is by the relative abundance of arboreal taxa occuring in the reproductive layer. The data presented in Tables II, IV, VI, VII and IX reveal a consistent invasion by Abies lasiocarpa in all the presently Pinus contorta-dominated communities and, therefore, these communities would be considered immature because the dominant taxon is not reproducing itself. The Pseudotsuga menziessii/Vaccinium membranaceum Community evidences more stability since the dominant taxon is also abundant in the reproductive layer.

Several methods of determining a coefficient of relation between two communities have been proposed (Gleason 1920, Jaccard 1912, Kulczynski 1937)

TABLE XV. COMMUNITY COEFFICIENTS AND MATURITY INDEX VALUES CALCULATED ACCORDING TO THE METHODS OF KULCZYNSKI (1937) AND PICHI-SERMOLLI (1948) RESPECTIVELY. ARRANGED ACCORDING TO THE DENSITY OF THE UPPER STRATUM AND THE RELATIVE PROPORTIONS OF PINUS CONTORTA TO ABIES LASIOCARPA (Pc:Al).

Community[1/]	Density of upper stratum	Pc:Al[2/]	Pc/Cr 550-650 h	Pc/Cr 650-750 h	Pc/Cr 750-950 h	Pc/Cr 1500-3000 h	Pc/Vs 500-750 h	Pc/Vs 750-1000 h	Pc/Vm 600-850 h	Pc/Vm 500-700 l	Pc/Sc 650-800 h	Pc/Sc 650-800 l	Pm/Vm 1000-1500	Pt/Gv 400-600
Pc/Cr	550-650	h												
	650-750	h	71											
	750-950	h	55	76										
	1500-3000	h	29	45	55									
Pc/Vs	500-750	h	56	63	49	22								
	750-1000	h	32	51	61	33	94							
Pc/Vm	600-850	h	22	32	42	29	38	39						
	500-700	1	15	23	29	21	34	28	87					
Pc/Sc	650-800	h	36	51	51	44	42	42	65	50				
	650-800	1	55	58	62	53	48	48	58	44	83			
Pm/Vm	1000-1500		54	59	53	27	65	42	54	45	50	54		
Pt/Gv	400-600		29	33	27	19	26	20	18	13	20	27	27	
Maturity Index			39	20	16	15	50	25	20	24	19	22	40	36

1/ Pc/Cr = Pinus contorta/Calamagrostis rubescens Community.
Pc/Vs = Pinus contorta/Vaccinium scoparium Community.
Pc/Vm = Pinus contorta/Vaccinium membranaceum Community.
Pc/Sc = Pinus contorta/Shepherdia canadensis Community.
Pm/Vm = Pseudotsuga menziessii/Vaccinium membranaceum Community.
Pt/Gv = Populus tremuloides/Geranium viscosissimum Community.

2/ Pc:Al = Pinus contorta:Abies lasiocarpa.
h = high, 1 = low.

based on frequency, occurrence of frequency percent. Table XV contains the community coefficients of the recognized forest communities occurring in Grand Teton National Park based on the frequency percent proposed by Kulczynski according to Mueggler (1965). The formula of the community coefficient, C, is:

$$C = 2w/(a + b) \times 100$$

where a = the sum of frequency values from community A

b = the sum of frequency values from community b

w = the sum of the lower of the frequency values for all species common to both A and B.

The higher the coefficient, the more nearly the two communities are related floristically. The data presented in Table XV indicate that perhaps the dominant shrub taxon produces the greatest influence on community correlation, because when the communities are divided either according to tree density or relative proportions of arboreal taxa occurring in the upper stratum, the highest correlations occur in the Pinus contorta/Vaccinium scoparium, P. contorta/V. membranaceum and P. contorta/Shepherdia canadensis Communities. This tendency was expected; however, some compensation for shrub growth by dense tree growth was also expected but not realized. Perhaps a greater competition for available water and nutrients than for insolation is indicated.

There is floristic relationship within the P. contorta/Calamagrostis rubescens Community depending on tree density. Any two adjacent groups of tree densities are more closely related vegetationally than groups separated by one or two groups, a phenomenon which would be expected. The interrelationships between two different coniferous communities are inconsistent with respect to tree density with the possible exception of P. contorta/C. rubescens and P. contorta/Vaccinium scoparium Communities. The P. contorta/V. membranaceum Community is poorly correlated floristically with the P. contorta/Calamagrostis rubescens and P. contorta/Vaccinium scoparium Communities but relatively well correlated with the P. contorta/Shepherdia canadensis and Pseudotsuga menziessii/Vaccinium membranaceum Communities. The Pinus contorta/Shepherdia canadensis and Pseudotsuga menziessii/Vaccinium membranaceum Communities are relatively well correlated floristically with all the coniferous communities with the exception of the latter community and the Pinus contorta/Calamagrostis rubescens Community with high densities.

The Populus tremuloides/Geranium viscosissimum Community is poorly correlated floristically with any of the coniferous communities which is expected because of the more open and deciduous nature of the P. tremuloides. The ecotonal position commonly occupied by the community may further contribute to its diversity from the coniferous communities.

Various methods have been proposed for calculating correlation coefficients between two taxa (Cole 1949, de Vries 1954, Kershaw 1964) and each method appears to have limitations of adaptability. The method selected for the present study is the one proposed by de Vries according to Phillips (1959). This involves establishing a 2 X 2 contingency table for each pair of taxa and calculating the correlation coefficient, r, by:

$$r = \sin (T \times 90^{\circ})$$

where $$T = AD - 3C/(P \times Q \times R \times S)^{\frac{1}{2}}.$$

The relationships of A, C, D, P, Q, R and S are presented in Figure 11. The more frequent taxon was always placed at the top of the contingency

		more frequent taxon: present	more frequent taxon: absent	
less frequent taxon	present	A	B	P = A + B
	absent	C	D	Q = C + D
		R = A + C	S = B + D	n = R + S or P + Q

Figure 11. Contingency table employed for determining the correlation coefficient between two taxa.

table in compliance with the specifications of Cole (1949) for determining the standard error. Reversing the order would yield slightly higher correlation coefficient values unless both taxa had the same frequency. The formula used in calculating the standard error depends on the relationships of A, B, C and D and is as follows, using the notations of Figure 11:

if $AD \geq BC$ then,

$$\sigma = (RQ/nPS)^{\frac{1}{2}},$$

if $AD < BC$ and $A \leq D$ then,

$$\sigma = (SQ/nPR)^{\frac{1}{2}},$$

and if $AD < BC$ and $A > D$ then,

$$\sigma = (PR/nSQ)^{\frac{1}{2}}.$$

Correlation coefficients were calculated among all shrub and forb taxa of the coniferous communities with a combined frequency of 30 or more, as suggested by de Vries (1954), considering each 2 X 5 dm quadrat as a sample. The values may range from zero, indicating no correlation, to one, indicating perfect correlation. The values obtained from seven taxa are presented in Table XVI. Most values are lower than expected but this is probably due to the small size of the quadrat used and an insufficient number of quadrats, in terms of the calculations, in at least some communities. Relatively high correlations occur among Arnica cordifolia, Calamagrostis rubescens and Lupinus parviflorus. Carex geyeri is well correlated with Arnica cordifolia and Lupinus parviflorus but not with Calamagrostis rubescens. The reason for the poor correlation between Carex geyeri and Calamagrostis rubescens is perhaps due to their growth form. They often occur in relatively large clumps and in many cases the quadrat frame would only encompass one, or a part of one clump.

For the conditions of measurement, reasonably good correlations occur between Vaccinium scoparium and Calamagrostis rubescens and among Vaccinium scoparium, V. membranaceum and Spiraea betulifolia. These correlations support the proposed community classification by indicating a diffusion of the Calamagrostis rubescens union into the Vaccinium scoparium union and the V. scoparium union into the V. membranaceum union, with but a small correlation between the Calamagrostis rubescens union and the Vaccinium membranaceum union, indicating that they are separate. A similar trend occurs between the V. membranaceum union and the Shepherdia canadensis union. Spiraea betulifolia shows identical correlations between the two Vaccinium unions but the individual plants are better developed in the V. membranaceum union than in the V. scoparium union.

TABLE XVI. CORRELATION COEFFICIENTS* BETWEEN TAXA WHICH HAD OCCURRENCE VALUE OF THIRTY OR MORE CONSIDERING EACH 2 X 5 dm QUADRAT AS A SAMPLE, IN CONIFEROUS FOREST COMMUNITIES.

Taxon	*Calamagrostis rubescens*	*Carex geyeri*	*Vaccinium scoparium*	*Vaccinium membranaceum*	*Spiraea betulifolia*	*Lupinus parviflorus*
C. geyeri	.26 ± .06					
V. scoparium	.35 ± .20	.16 ± .21				
V. membranaceum	.14 ± .09	.05 ± .20	.31 ± .06			
S. betulifolia	.29 ± .09	.17 ± .09	.34 ± .14	.34 ± .15		
L. parviflorus	.59 ± .09	.49 ± .09	.31 ± .15	.02 ± .15	.32 ± .07	
A. cordifolia	.46 ± .15	.45 ± .07	.31 ± .09	.12 ± .22	.28 ± .10	.56 ± .09

* Calculated according to the method of de Vries, according to Phillips (1959).

Fire Determinations

The difficulty of dating fires from increment-core samples lies in finding trees that have fire scars large enough to suppress the growth of the tree for a period of years but small enough to not allow severe damage by decay organisms. Also, the borer must be inserted at the proper position in relation to the scar. It is necessary to confirm an indicated date on one tree with other trees because apparently microenvironmental factors may suppress growth of one tree for a period of a few years and this will give a false indication.

About the only other way of dating fires is to determine the ages of trees that have populated the area since the fire but this has many complications. There is commonly a lag period of six or more years after a fire before the establishment of new trees (Horton 1956, Smithers 1961), an observation that has been confirmed by investigating the trees in areas where the date of burn is known. The establishment in most areas occurs over a period of five or more years so that all trees in a stand are not the same age, even if one chooses only the largest trees to sample. In general, the first _Pinus contorta_ to enter after a fire are not self-pruned (Smithers 1961) but investigations indicate that this diagnostic feature can not be relied upon.

Forest Pathology

Several pathological conditions occur in the forest communities which are worthy of mention. The only condition observed to be affecting _Abies lasiocarpa_ was yellow witches' broom, caused by the rust fungus _Melampsor-_

ella caryophyllacearum, whose alternate hosts are species of Cerastium and Stellaria. This rust infestation has not attracted much consideration in North America because of its low occurrence rate (Mielke 1957; Peterson 1964). The witches' broom appears to have very little or no effect on the growth rate of host trees but occasionally cankers are formed on trunks causing deformities undesirable in the timber industry.

Perhaps the most important organism infecting Populus tremuloides is the heart rot fungus, Fomes igniarius (Baxter 1943). Several other fungi have been found to cause cankers and Hypoxylon pruinatum causes weakened spots in the stem which allow easy breakage. The aspen leaf miner, Phyllacnistis populiella, has been observed on almost every Populus tremuloides specimen investigated in the study area, but apparently no serious harm to the tree results from this organism (Keen 1952).

Pinus contorta is host to a greater variety of diseases than the other conifers in the study area. Comandra blister rust, caused by Cronartium comandrae, occurs to a very limited extent and apparently only causes concern in epidemic areas (Mielke 1961). Dwarf mistletoe, Arceuthobium americanum, is rather wide spread in the study area and causes witches' brooms and cankers on Pinus contorta. The main concern with this infestation is by the timber industry (Gill and Hawksworth 1964, Cohen 1965). Western gall rust, Peridermium harknessii, occurs in the vicinity but was not observed in the study area. The cankers produced by it have ornamental value (Peterson 1961).

The infestation causing by far the most concern in Jackson Hole is that of the mountain pine-bark beetle, Dendroctonus monticolae. A large expenditure of manpower, horsepower and money has gone into supposed control of the beetle in recent years with a return of very limited benefits. The present control measures involve spraying infected trees with a poison, usually ethylene dibromide, in a diesel fuel carrier, the combination of which not only kills the sprayed trees but also the vegetation under the trees. The extended use of such control measures without investigation into their immediate and long range effects is unfortunate. Secondary effects have resulted in the redistribution of the elk and moose populations and have affected their reproductive cycles according to Altmann (personal communications 1964, 1965). These effects may in turn affect the vegetation because some areas may be overgrazed and others may be scarcely touched. There are indications that squirrel and some bird populations have been reduced since the initiation of extensive spraying (Clark and Diem, personal communications 1964, 1965). Reid (1955, 1957a, 1957b, 1958a, 1958b, 1961, 1962a, 1962b, 1963) has presented a detailed documentation of the life-cycle of *Dendroctonus monticolae* and, although control measures are not his primary concern, several possible avenues for research are opened.

Successional Features

The outwash soils possess a sagebrush-grassland type of vegetation which was not thoroughly investigated in this study except in ecotonal areas where it abuts the forest communities. However, there are some occurrences of trees in the outwash which should be mentioned (Figures 12 and 13). Most of these areas are "potholes" that have accumulations of