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Analysis of the North Fork Valley grasslands in Glacier National Park Montana

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An Analysis of the North Fork Valley Grasslands in Glacier National Park, Montana

by

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Introduction

Of the grassland expanses found in North America, none possess such wide geographical, ecological and vegetational diversities as does the Palouse Prairie grasslands originally described by Weaver (1917). These grasslands occurring in the northern intermontane region are effectively isolated from most other grassland types by deserts or mountains. Within the Palouse Prairie region, or that area occupying the basins of the Columbia and Snake drainage systems (Shelford, 1963), grassland vegetation is restricted to the drier localities, particularly the intermontane valleys where low amounts of precipitation during the growing season prevent the forest from occupying these valleys within this region. The valley of the North Fork of the Flathead River on the western boundary of Glacier National Park supports a series of generally undisturbed grassland communities.

These grasslands in Glacier National Park are of interest for two reasons. First, they represent an isolated segment in the extreme northeastern corner of the Palouse Prairie region and therefore possess the potential for depicting whether phytogeographical diversity occurs within the region. Information gathered from these grasslands would thus aid in a more complete understanding of the Palouse Prairie in addition to the vegetation of Glacier National Park. Secondly, quantitative analyses of the grassland vegetation in this area has never been undertaken.

Several unique features of these North Fork Valley grasslands are readily apparent and deserve special mention. Perhaps the most remarkable feature is their very existence within an otherwise heavily forested valley. What allows them to persist, and why has the very narrow prairie-forest ecotone surrounding them remained stable for nearly a century? Floristically, the most unique features are the presence of Danthonia intermedia, a relatively rare species throughout much of the Palouse Prairie region, and their rather depauperate flora.

The specific objectives of this study were: (1) to develop a quantitative description of the composition of the grassland communities, and (2) to establish and interpret the interrelationships between community structure and factors of the physical environment.

Review of the Literature

The level plains and plateaus which surround the western base of much of the northern Rocky Mountains are usually vegetated with various types of desert and grassland species. Early investigators of these communities (Rydberg 1915, Weaver 1917, and Shantz 1924) designated these areas as Palouse or Bunch Grass prairie. Shantz generally considered the bunch grass areas as consisting of the Palouse Prairie in eastern Oregon and Washington and the Pacific Grasslands in western Oregon and Washington and California. Daubenmire (1942) also points out a close climatological and vegetational affinity between these areas.

Shantz (1924) recognizes three communities of the bunch grass vegetation. The wheat grass sod develops in eastern Oregon and Washington (Palouse Prairie) where the annual precipitation is 15-25 inches annually and moisture conditions are more favorable. Agropyron spicatum, Festuca idahoensis, Poa sandbergii and Balsamorrhiza sagittata are the dominant species here. The wheat grass bunch type occurs in the western portion of this region where moisture supply is deficient (15-20 inches per year) or the soil less able to retain available water. This type is dominated by Agropyron spicatum and Poa sandbergii and marks a transition zone between the wheat grass sod and sagebrush desert. The Stipa-Poa bunch grass is found in the Pacific Grasslands of western Oregon and Washington and California.

Daubenmire (1943), in considering this entire region of the Rocky Mountains, generally agrees with Shantz. He describes a prairie characterized by Festuca idahoensis and Agropyron spicatum which borders the forest west of the Rockies from British Columbia to northern Oregon. Southward from central Oregon to northern Arizona the lowland areas are dominated by sage, perennial grasses and several halophytes.

Stoddart (1941) in studying the grasslands of northern Utah pointed out the close similarity in climate between the mid-west grasslands and those of Utah. Dry air and moisture deficiencies during the growing season make the latter region ecologically more arid than the plains or prairie. He pointed out that heavy winter snows occurring there result in deep percolation during the winter and as a result a greater soil leaching per unit of total annual precipitation occurs in these bunch grass soils. This fact, together with the dependence of the plants on stored soil moisture during the growing season, result in the occurrence there of deeper rooted bunch grasses than in the plains or prairie. He described the areas as being "unquestionably true Palouse Prairie belonging to the drier Agropyron consociation." Festuca idahoensis is notably lacking in these grasslands but does occur there in the moister coniferous belt. Artemisia tridentata occurs widely on unplowed land and is believed to be the climax dominant.

Daubenmire (1942) indicated a close correlation between vegetational zones and soil types in southeastern Washington and adjacent Idaho. He recognized three climatic climax associations, viz. (1) Artemisia-Agropyron spicatum, (2) Agropyron spicatum-Poa secunda and

(3) Festuca idahoensis-Agropyron spicatum. The more xerophytic types, Artemisia-Agropyron spicatum and Agropyron spicatum-Poa secunda, occupy areas from which much of the pre-glacial loess, which covered the entire region, was scraped away by the glaciers, thus creating a drier ecological environment.

Tisdale (1947), working in British Columbia, also described the three vegetational zones found by Daubenmire in Washington and Idaho. However, he did not speculate that the distinct zones are correlated with soil types. In British Columbia, Agropyron spicatum is the chief species with Festuca scabrella often of equal abundance. Festuca idahoensis is relatively unimportant. Because of the importance of Festuca scabrella in British Columbia there seems to be a link with the grasslands of Alberta as described by Moss (1944).

The studies of Moss (1944, 1952) in the Fescue Grasslands of Alberta indicate a very marked dissimilarity with the grasslands as described by Weaver (1917) and Daubenmire (1942), however some elements of the Palouse Prairie are present. They presumably reached the northern areas from the south or migrated through the northern mountains from the west. These species include Agropyron spicatum, Festuca idahoensis, Stipa columbiana, Geranium viscosissimum and Balsamorrhiza sagittata.

Mitchell (1958) in studying the grassland vegetation surrounding Missoula, in western Montana, characterized two association types. The Agropyron type is found on the drier sites and is dominated by

Agropyron spicatum with Poa secunda occurring as an important secondary species. The Festuca type is found on the wetter sites and is dominated by Festuca idahoensis or Festuca scabrella or both with Agropyron spicatum and Koeleria cristata as minor constituents. He recognizes two phases within the Festuca type. The more mesic phase is dominated by Festuca scabrella and the drier phase is dominated by Festuca idahoensis. The two grassland types were found to readily grade into one another and not to exist as well-defined zones. The intergrading of types was due to varying climatic conditions as modified by edaphic factors and those of exposure, slope, elevation and valley width.

Lynch (1955) studied the aspen groveland and associated vegetation in Glacier County, Montana, and found the grassland to be dominated by Festuca scabrella. Stipa columbiana and Festuca ovina occurred as minor components within his Festucetum scabrella association.

Blinn (1966) in studying microenvironmental conditions on morainal mounds in the Upper Blackfoot Valley in western Montana recognized communities as belonging to a single Festuca-Agropyron type.

Wright and Wright (1948) studied a tension zone between the bunch grass and short grass prairies of the Great Plains in south-central Montana. They recognized five grassland types which intermingled as a result of variations in the soil and the climatic variations produced by the rough and broken topography of the area. They found a striking resemblance between their Festuca idahoensis type and the

Festucetum association of southeastern Washington and adjacent Idaho as described by Daubenmire (1942).

Studies on Agropyron spicatum conducted by Heady (1950) led to his discovering elements of the Palouse Prairie surrounded by short grass prairie in central Montana. He concluded that the optimum conditions for the development of Palouse Prairie in central Montana occurred at an elevation of approximately 5,000 feet. At these higher elevations the most important species associated with Agropyron spicatum were found to be Festuca idahoensis, Poa ampla and Stipa occidentalis.

Description of Study Area

Location:

From Apgar, Montana northwestward to the international boundary there is a broad trough between the rugged Livingston Range of Glacier National Park on the northeast and the Whitefish Range on the southwest. This valley is about 32 miles long with an extreme width of 4 miles (approximately 100 square miles in area). The North Fork of the Flathead River follows this trough, known as the North Fork Valley, for more than 20 miles.

The North Fork is fed by numerous streams headed in the Livingston Range and between them are interstream ridges several hundred feet in height which extend southwestward from the mountain flank and the sides of which are terraced to a height of about 200 feet above the valley floor. When this trough is viewed in cross-section these ridges appear to merge into a plain at its bottom.

The principal areas of investigation are isolated patches or grassland mosaics on the valley floor. These areas are located east of the river within the boundary of Glacier National Park (See Figure 1). They roughly follow a moisture gradient going from xeric-mesic in the north to mesic-hydric in the south. Four such areas were selected for study. They were: Round Prairie, Big Prairie, Lone Pine Prairie and Dutch Creek Prairie.

Round Prairie is a grassland outlier about one-half mile long by

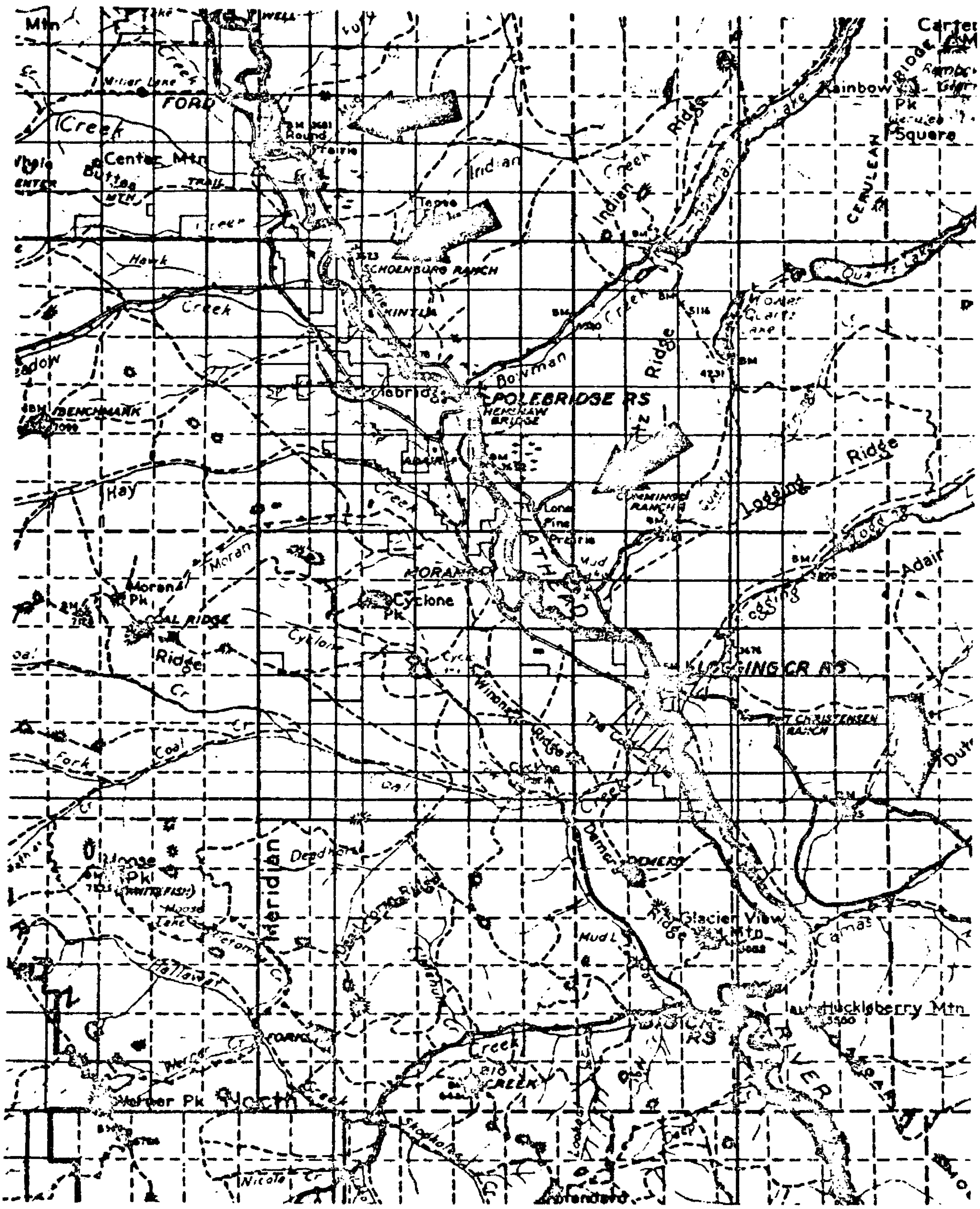


Figure 1. The North Fork Valley.

three-fourths mile wide located approximately 35 miles north of Apgar, Montana. It is the most northerly one studied and has an altitude of about 3,680 feet. It is completely surrounded by lodgepole pine (Pinus contorta) and an occasional patch of aspen (Populus tremuloides). Big sage (Artemisia tridentata) is locally very abundant.

Big Prairie is a grassland mosaic 4 to 5 miles long by 1 mile wide located approximately 30 miles north of Apgar. The forest species surrounding this area are lodgepole pine and occasionally aspen. Big sage is somewhat less abundant and is isolated at the southern end of the area. The altitude here is about 3,600 feet.

Lone Pine Prairie is a small grassland outlier one-quarter mile long by one-half mile wide located approximately 23 miles north of Apgar. This is a luxuriant grassland outlier surrounded by lodgepole pine, aspen and an occasional spruce (Picea engelmannii). The prairie is about 3,690 feet above sea level.

Dutch Creek Prairie is a small grassland outlier one-quarter mile long by one-half mile wide located approximately 12 miles north of Apgar. This is the most southerly one studied and consequently the most mesic-hydric. It is about 3,700 feet above sea level.

Geology:

The approximate plain or bottom of the North Fork Valley was developed in late Tertiary and early Pleistocene time by the truncation of faulted and upturned Tertiary beds and by the deposition of glacial drift during the Wisconsin stage and earlier. Several scarps have exposed these stratified deposits (consisting chiefly of gray sand clay and gray sandstone) which dip northeasterly and are covered by 15 to 65 feet of coarse gravel and boulders.

During the Wisconsin and earlier stages of the Pleistocene glaciation, an enormous glacier advanced southeastward across the present international boundary extending from the Kootenai River Valley to the Continental Divide. A large part of the ice, what was perhaps the main flow, crossed the Tobacco Plains east of the river and continued southeastward along part of the small Tobacco River. This great glacier, known as the Flathead Glacier, advanced southeastward down the part of the continuous Rocky Mountain Trench that is now drained by the Stillwater River and joined a great tributary flow from the North Fork Valley (See Figure 2). Forty to fifty miles south of the boundary, this great ice mass entered the Flathead basin south of Whitefish and Columbia Falls, in what is now Flathead Lake. The Flathead Glacier, both north and south of the boundary, was joined by numerous tributary glaciers headed in the Galton and Whitefish Ranges on the east. It has been estimated that the maximum thickness of the ice in the vicinity of the boundary was about 5,000 feet, completely overtopping the peaks of the Whitefish Range here (Alden, 1953).

Great glaciated gorges gashed the east flank of the Galton and Whitefish Ranges west of the North Fork of Flathead River and also

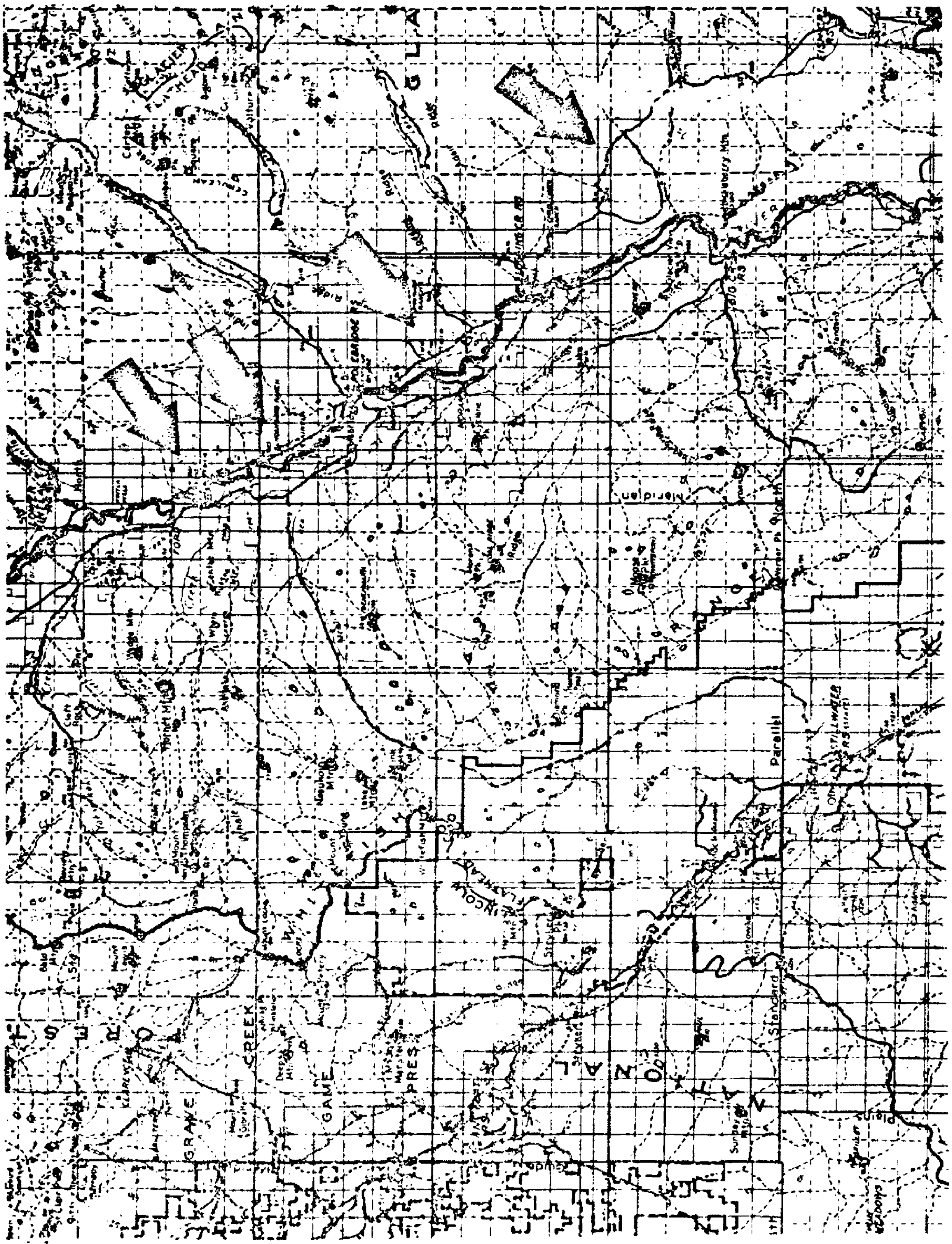


Figure 2. The North Fork Valley and vicinity.

the west flanks of the Livingston Range and all the other mountains of Glacier National Park west of the Continental Divide. During the maximum stages of glaciation the mountain glaciers headed high up the flanks of the Livingston Range in the western part of the Park were tributaries of a great branch glacier which filled the North Fork Valley from side to side and overtopped most of the ridges on the west.

Early History and Description:

Earliest description of the area (Ayers, 1900) states that the bottomlands of the North Fork were forested by irregular patches of Populus trichocarpa, Populus tremuloides, Picea engelmannii and Pinus contorta. In the drier areas, which were severely burned, young growth of lodgepole pine prevailed. In general, the entire valley seemed unfavorable for forest growth and reproduction due to the prevalence of gravelly subsoils.

Evidence of extensive fires in the area prompted Ayer to note "actual prairie making has been accomplished." Fires at times were so severe that they gave the land a "desert-like" appearance. Early observers of these barren grounds said of the destruction, "it has been so severely and so repeatedly burned that it will no longer grow vegetation." By 1900, however, the land was revegetated by lodgepole pine, with some larch (Larix occidentalis) and spruce.

Ayer describes the discovery of several homestead cabins in the

North Fork, only a few of which were occupied or kept in repair. Mining, agricultural and lumbering potential were probably the main reasons for early settlement, at least in the upper valley. However, these prospects failed to develop and today many abandoned homesteads can be seen throughout the valley.

A miner working for a Butte Company came into the Big Prairie areas in 1905-1906 looking for signs of ore. He found most of the available range land under cultivation or being hayed. Old seed drills found at some of the abandoned homesteads today indicate the intensity of cultivation at this time. The land was mostly used to raise cereal crops that were fed to livestock. The majority of the early homesteaders were actively engaged in the cattle industry but because of the remoteness of the area and dry years this practice was gradually given up. It was not until about 1930, however, that all grazing practices were completely abandoned.

Because of the intensified grazing practices at this time, big sage became a dominant over the Big Prairie area. According to Mrs. W. C. Rae, whose parents homesteaded the area, "my mother would never have to worry about putting up a clothes line to dry clothes, but would sling them over large sage plants." Big sage is still a conspicuous feature of the landscape although its abundance has declined in recent years.

Climate:

The climate of western Montana is greatly influenced by the Pacific Ocean and the Continental Divide. The most important source of precipitation are the moisture-laden air masses moving inland from the Pacific Ocean following storm tracks which approximately follow the international boundary. Considerable amounts of their moisture are dropped on the west slopes of the Coastal and Cascade Mountain Ranges as they are forced to ascend and cool. Considerable moisture is retained, however, and is carried farther inland to the Rocky Mountains and the Continental Divide. The higher mountain ranges of the western Rockies intercept these cool, moist air masses forcing them to drop their moisture on the windward (western) slopes and thus the leeward (eastern) slopes receive little moisture, which produces a rain shadow effect. Some of the air masses are not intercepted and penetrate to the Continental Divide before their moisture is dropped.

The Continental Divide, in addition to barring the Pacific air masses from reaching farther inland, generally prevents the colder Arctic air masses from spilling over into western Montana. As a result, this area has warmer winters, cooler summers, greater precipitation, less wind and a shorter growing season than eastern Montana.

Precipitation in the North Fork Valley is generally uniform although local variations occur due to slope and exposure. Average precipitation is about 25 inches per year, which is generally considered enough to support a forest vegetation. There tends to be a slight increase southward which is probably due to a decreased elevation of the southern Whitefish Range with the consequence that the moisture-laden clouds do not drop their contents on the western slopes of the Livingston Range but carry it over into the valley. A slight rain shadow effect thus appears to exist in the more northern parts of the North Fork Valley.

As is typical of northwestern Montana most of the moisture falls as snow during the months of October through March. According to Shantz (1924), this weather pattern is largely responsible for the development (and possibly the maintenance) of the bunch grass prairie in the Northwest. He states two principal reasons for this: (1) an insufficient moisture supply for the development of a dense stand during the growing season, and (2) the presence of considerable moisture to a depth of several feet at the beginning of the growing season. Consequently if the precipitation were more confined to the growing season, short grass vegetation would develop and if a greater proportion fell during the winter months, vegetation would give way to sagebrush.

Climatological data was extracted from partially complete records kept at the Polebridge Ranger Station since 1953 (Tables VII and VIII). Although the station itself is located immediately adjacent to the river in a lodgepole pine stand, the information collected is considered valid for characterizing the climate of the area. Annual precipitation at the station is 21.7 inches, but the prairie near the weather station most probably receives lesser annual amounts since it is unable to support forest growth as found at the station site.

Methods and Procedures

Field Procedure:

During June, July, August and September of 1967 a field study of four isolated grassland areas in the North Fork Valley was conducted. Location of suitable study sites within these grasslands did not prove to be difficult since these areas have been free from major disturbance since 1930. Minor disturbances caused by natural grazing of white tail deer (*Odocoileus virginianus*) and elk (*Cervus canadensis*) were overlooked in selecting study sites.

A total of 40 prairie communities were selected for study. In addition 5 nearby stands dominated by big sagebrush (*Artemisia tridentata*) were also studied. Field sampling of these stands was done employing Daubenmire's (1959) canopy coverage method. Stand homogeneity was assessed visually by observing both site characteristics and distribution of community dominants.

A tenth meter square (20 X 50 cm.) quadrat was used to obtain frequency and canopy coverage data for each species in all selected stands except the sagebrush stands. The latter were sampled by meter square quadrats placed at 3 foot intervals along two 50 foot lines laid out through each stand. Twenty quadrats per stand were tallied in both sagebrush and prairie stands.

Species occurring in each quadrat were recorded on field data sheets. Canopy coverage by each species in each quadrat was estimated on the basis of the six following classes:

Class 1 - less than 5% coverage
Class 2 - between 5% and 25% coverage
Class 3 - between 25% and 50% coverage
Class 4 - between 50% and 75% coverage
Class 5 - between 75% and 95% coverage
Class 6 - between 95% and 100% coverage

A plant was considered as contributing to the coverage if any part of it extended into the quadrat. The average percentage cover of each species in each stand was calculated by totalling the mid-points of each class and dividing by 20.

Several of the original sites were selected for additional field study in late June before analysis of the vegetation was undertaken. An attempt was made in selecting them to include a variety of plant communities exhibiting noticeable differences in dominant species. Field soil moisture readings were recorded for 26 of these selected sites at approximately one month intervals between July and October. In addition to field soil moisture, air temperature and soil temperature data were collected on the same days. Measurement of soil temperatures were taken at the surface and at a depth of 3 inches.

Soil samples were collected in each of the 45 stands and placed in plastic quart bags. The soils were allowed to air dry and then screened through a 2 mm sieve. A portion of each sample was sent to the University of Wisconsin Soil Testing Laboratory where the following procedures were conducted to determine chemical makeup of the soil (Blinn, 1966):

1. Calcium and magnesium were extracted with 1N NH_4OAc and determined with a Coleman Model 21 flame photometer.

2. Phosphorus and potassium were both extracted with Bray P_1 solution. Phosphorus was determined colorimetrically using ammonium molybdate to develop the color. Potassium was determined by flame photometric procedures.

3. Organic matter was determined by modified wet digestion using a $NaCr_2O_7$ - H_2SO_4 mixture. Final analysis of the chromate color was made colorimetrically.

4. Nitrate was extracted with water and determined semi-quantitatively with the visual brucine-yellow color.

5. Ammonium was extracted with 0.3N HCL and determined semi-quantitatively using visual color developed with Nessler's reagent.

Further tests were conducted in the laboratory on the remaining soil of each sample. Water holding capacity and permanent wilting percent were calculated in the soils lab of the University of Montana Forestry School. Available soil moisture was determined by subtracting the value found for the permanent wilting percent from that of the water holding capacity. Soil texture (mechanical analysis) for each sample was analyzed using the Bouyoucos hydrometer method.

Plants encountered in the field were later identified or verified in the laboratory. Nomenclature follows that of Hitchcock and Chase (1950) for the Gramineae, Hitchcock et al. (1955, 1959, 1961, 1964) for the Dicotyledoneae and Moss (1959) for the Monocotyledoneae.

Laboratory treatment of the data:

Data compiled during the summer of 1967 were transferred to specially adapted post-index sheets. Quadrat frequency for each species in each stand was tabulated from the field data sheets and transcribed onto the special forms. Soil data were also placed on these sheets. Canopy coverage for each species in each stand was calculated and was placed on separate sheets.

Data on the post-index sheets were used to construct an ordination following the methods described by Bray and Curtis (1957) and Beals (1960). When the two-dimensional ordination was complete it was decided that use of the third, Z, axis would not be needed for further stand separation. Species frequency and environmental data were plotted into the two-dimensional ordination by means of the quartile technique (Bray and Curtis, 1957).

Further extraction of information from the ordination involved the arrangement of stands along the X axis at objectively determined intervals. This axis was divided into 5 segments, each of 20 axis units. Percent frequency, canopy coverage for each species in each stand, as well as environmental data collected at each stand was summed and averaged for each of the 5 gradient segments.

Results

Vegetational Analysis:

Approximately 50 species of vascular plants were found in the North Fork grasslands. All are included in the compositional gradient (Tables 5 and 6), which includes both average frequency and percent coverage values. Frequency values for 18 representative species have been plotted in the ordination using 5 classes (1 - 20%, 21 - 40%, etc.) each represented by 5 different sized circles. The smallest class is represented by the smallest sized circle and the largest by the largest circle. Limitations and distributional patterns of species can be seen in the ordination by observing limitations and clumping of these circles (Figures 4, 5 and 6).

Many species were encountered that contributed less than 1.0% to the vegetational cover and were therefore relatively unimportant to the total vegetational cover. In this group of species, only Lithospermum ruderale and Berberis repens are exclusively found in the first 3 gradient segments. The following occurred in the 3 medial segments: Campanula rotundifolia, Zigadenus elegans, Melica spectabilis, Tragopogon pratense, Taraxacum officinale, Agropyron smithii, Antennaria rosea, Senecio triangularis and Agrostis scabra. Several species including Heuchera cylindrica, Stipa columbiana, Potentilla diversifolia, Smilacina racemosa, Penstemon confertus and Equisetum fluvatile are restricted to segments 4 and 5.

It was found that most of the abundant species show no distributional restrictions within the ordinational segments. A few species are limited to 3 segments of the compositional gradient, but none are so highly restricted that they occur only in 1 of the segments. Many are limited to 4 of the segments but most are found in all five segments.

Of the most highly restrictive species, only two, Grindelia squarrosa and Sedum stenopetalum are restricted to segments 1, 2 and 3 and the former is restricted to the first 2 segments and reaches its highest values in the first. Several other species, including Poa pratensis, Potentilla gracilis, Anemone multifida, Fragaria virginiana, Geranium viscosissimum and Stipa richardsonii are restricted to segments 3, 4 and 5.

Many of the species showing limitations in their distribution are absent in only 1 segment. Agropyron spicatum, Poa compressa and Calochortus apiculatus represent species found in all segments except segment 5. Arctostaphylos uva-ursi, Lupinus sericeus, Geum triflorum, Danthonia intermedia and Festuca scabrella are found in all segments except the first.

Among the most ubiquitous species, several patterns occur. Rosa acicularis and Arenaria congesta reach their greatest prominence within segments 1 and 2 and decline along the primary axis. Several species including Arnica fulgens, Antennaria parviflora, Achillea millefolium and Festuca idahoensis are of greater importance within the medial segments and are somewhat less important in the extreme segments. Phleum pratense and Potentilla glandulosa display a greater vigor in segments 3, 4 and 5 than in segments 1 and 2 while Koeleria cristata is almost equally persistant throughout the segments except for a small decline in the fifth. Galium boreale, on the other hand, shows a steady increase from segment 1 through 5.

Species within segment 1 combine to cover only 39.1% of the ground. The relative percent coverage of Agropyron spicatum is 55% there while Grindelia squarrosa, Festuca idahoensis and Eriogonum flavum combine to cover another 31%. None of the remaining species contribute more than 1.0% except Sedum stenopetalum, which contributes 1.3% to the total ground surface covered. Grindelia squarrosa, Lithospermum ruderale, Agropyron spicatum, Poa compressa and Eriogonum flavum all reach their highest coverage values within segment 1.

Total percent coverage of all species in segment 2 communities averages 45.6% of which Agropyron spicatum contributes 35% of the relative coverage. Danthonia intermedia and Festuca idahoensis are the most conspicuous secondary species and they combine to form 24.0% of the cover. Several species which contribute more than 1.0% to the total include: Sedum stenopetalum, Eriogonum umbellatum, Eriogonum flavum, Antennaria parviflora, Achillea millefolium, Geum triflorum, Festuca scabrella and Danthonia unispicata. Species reaching their highest values within this segment are Sedum stenopetalum, Rosa acicularis, Arenaria congesta and Danthonia unispicata.

The total percent coverage value in segment 3 was found to increase by 8.2% over segment 2 and to reach an average of 53.8%. Three species, Phleum pratense, Festuca idahoensis and Agropyron spicatum are the most prominent species contributing 44% relative coverage. Several species were found to contribute greater than 1.0% to the total coverage. These include: Arnica fulgens, Eriogonum umbellatum, Antennaria parviflora, Achillea millefolium, Lupinus sericeus, Danthonia intermedia, Festuca scabrella, Danthonia unispicata, Monarda fistulosa, Poa pratensis, Fragaria virginiana, Geranium viscosissimum and Stipa richardsonii. Species attaining their highest values here are Phleum pratense, Arnica fulgens, Koeleria cristata, Festuca idahoensis, Lupinus sericeus, Campanula rotundifolia, Monarda fistulosa, Poa pratensis, Anemone multifida, and Geranium viscosissimum. Agrostis scabra, Antennaria rosea, Senecio triangularis and Agropyron smithii were found to be restricted exclusively to this segment.

Species within segment 4 show an increase of 11.4% coverage over those of segment 3. Of the 65.2% total plant coverage here the relative coverage of Fragaria virginiana, Festuca scabrella, Danthonia intermedia and Festuca idahoensis make up 44%. Stipa richardsonii and Poa pratensis, two of the most abundant secondary species, contribute 15%. Those species contributing greater than 1.0% include Agropyron spicatum, Phleum pratense, Arnica fulgens, Potentilla glandulosa, Eriogonum umbellatum, Galium boreale, Antennaria parviflora, Achillea millefolium, Arctostaphylos uva-ursi, Geum triflorum, Bromus pumpellianus, Potentilla gracilis and Geranium viscosissimum. Those species reaching their highest values in segment 5 include Galium boreale, Arctostaphylos uva-ursi, Geum triflorum, Festuca scabrella and Stipa richardsonii.

Of the major grass species occurring in these grasslands, Agropyron spicatum is the most dominant in terms of coverage; however, its overall frequency is low which indicates its restricted appearance. Agropyron spicatum averages about 7.1% coverage in all stands of these North Fork sites and has an average frequency of 36%. Agropyron spicatum reaches its highest coverage and frequency values in segment 1 and gradually becomes less conspicuous along the compositional gradient on which it reaches its lowest values in segment 4. It is entirely lacking in stands of segment 5. It reaches its highest coverage/frequency value in stand 18 where it was found in 100% of the sample quadrats and covered 28.4% of the ground surface.

Festuca idahoensis, a common associate with Agropyron spicatum in the Palouse Prairie region, attains a 6.2% coverage value for all stands; however, its frequency value (53%) indicates it is more widely dispersed than Agropyron spicatum. This species occurs in all segments of the gradient and is the most frequently encountered one in these grasslands. Although it reaches its highest coverage values in segment 3 (7.9%) its frequency values are highest in segment 2 (82%). This species occurs almost equally in the first 4 segments of the gradient but there is a marked decrease in both coverage and frequency values in segment 5. Festuca idahoensis reaches its highest coverage/frequency value in stand 37 where it appeared in 75% of the quadrats and covers 24.5% of the ground.

Danthonia intermedia is also commonly found (average frequency 51%) throughout the study area although it was not found to contribute as greatly to the canopy coverage (4.9%) as the other major grass species. It reaches its highest coverage value in segment 4 (7.0%); however, it is more frequent in segment 5 (74%) although its increase in frequency over segment 4 (72%) is slight. This species is absent from segment 1 communities but in segment 2 stands it attains a disproportionately high coverage value of 5.2%. The frequency, however, which it displays is consistent with the general increasing trend along the compositional gradient to segment 4. There is a slight decrease in Danthonia coverage in segment 5. Danthonia intermedia reaches its highest coverage/frequency value in stand 1 where it was found in 100% of the quadrats and covered 35.6% of the ground.

Festuca scabrella, much like Agropyron spicatum, has a low overall average frequency (35%) indicating a rather restricted distribution in these grasslands. Both Agropyron spicatum and Festuca idahoensis contribute more to the total ground cover than does Festuca scabrella, but rough fescue covers 0.8% more ground surface than does Danthonia intermedia. It reaches its highest coverage and frequency values in segment 5. It is absent from segment 1 and only of minor importance in segments 2 and 3. Festuca scabrella reaches its highest coverage/frequency value in stand 40 where it attained a frequency value of 100% and covered 50.1% of the ground.

It is of interest to summarize the distributional patterns of the four major grass species displayed along the compositional gradient.

As stated earlier, there are no natural breaks or dividing lines evident along this gradient. In segment 1, Agropyron spicatum exists almost to the exclusion of the other three grass dominants. Festuca idahoensis does occur, but is only one-third as frequent; it displays an inability to develop luxuriant foliage in stands so completely dominated by Agropyron spicatum.

In the second segment Agropyron spicatum becomes less conspicuous in both stature and abundance. while Festuca idahoensis increases. Festuca idahoensis becomes more frequent than Agropyron spicatum; however, it is still unable to produce more vegetative growth than Agropyron spicatum. Danthonia intermedia and Festuca scabrella make their first appearances in this segment, but both are unimportant in terms of both coverage and frequency in this portion of the gradient.

In segment 3 Agropyron spicatum remains a major species contributing much of the total plant cover, but Festuca idahoensis becomes much more frequent in addition to contributing greater coverage. Danthonia intermedia, although contributing in only a minor way to the total vegetational cover, is actually more frequent than Agropyron spicatum. Festuca scabrella still does not attain high values in this segment and has increased in frequency and cover only slightly from segment 2.

In the fourth segment communities Agropyron spicatum displays minor importance and contributes only fractionally to the coverage. Festuca scabrella is the most luxuriant species in this segment covering 7.2% of the ground, but Danthonia intermedia and Festuca idahoensis are almost of equal importance covering 7.0% and 6.9% respectively. Danthonia intermedia, however, is by far the most frequent species in this portion of the gradient (72%) while Festuca scabrella and Festuca idahoensis occur (46% and 43%) less commonly.

The fifth segment is completely dominated by Festuca scabrella. Agropyron spicatum is lacking and Festuca idahoensis is noticeably reduced. Danthonia intermedia is nearly as common (74%) as Festuca scabrella (90%) but shows a reduction in coverage from segment 4, which may be due to Danthonia being unable to compete strongly with rough fescue.

Stipa richardsonii is an important constituent of the plant communities of segments 4 and 5. In segment 4 it is second in importance to Danthonia intermedia in its frequency; however, both Festuca idahoensis and Festuca scabrella as well as Danthonia intermedia contribute more to the ground coverage. In segment 5 Stipa was found to attain higher frequency and canopy coverage values with Festuca scabrella than was Danthonia intermedia. Both Danthonia and Stipa occurred 74% of the time in these stands but Stipa outproduced Danthonia 13.5% to 5.5% in canopy coverage values.

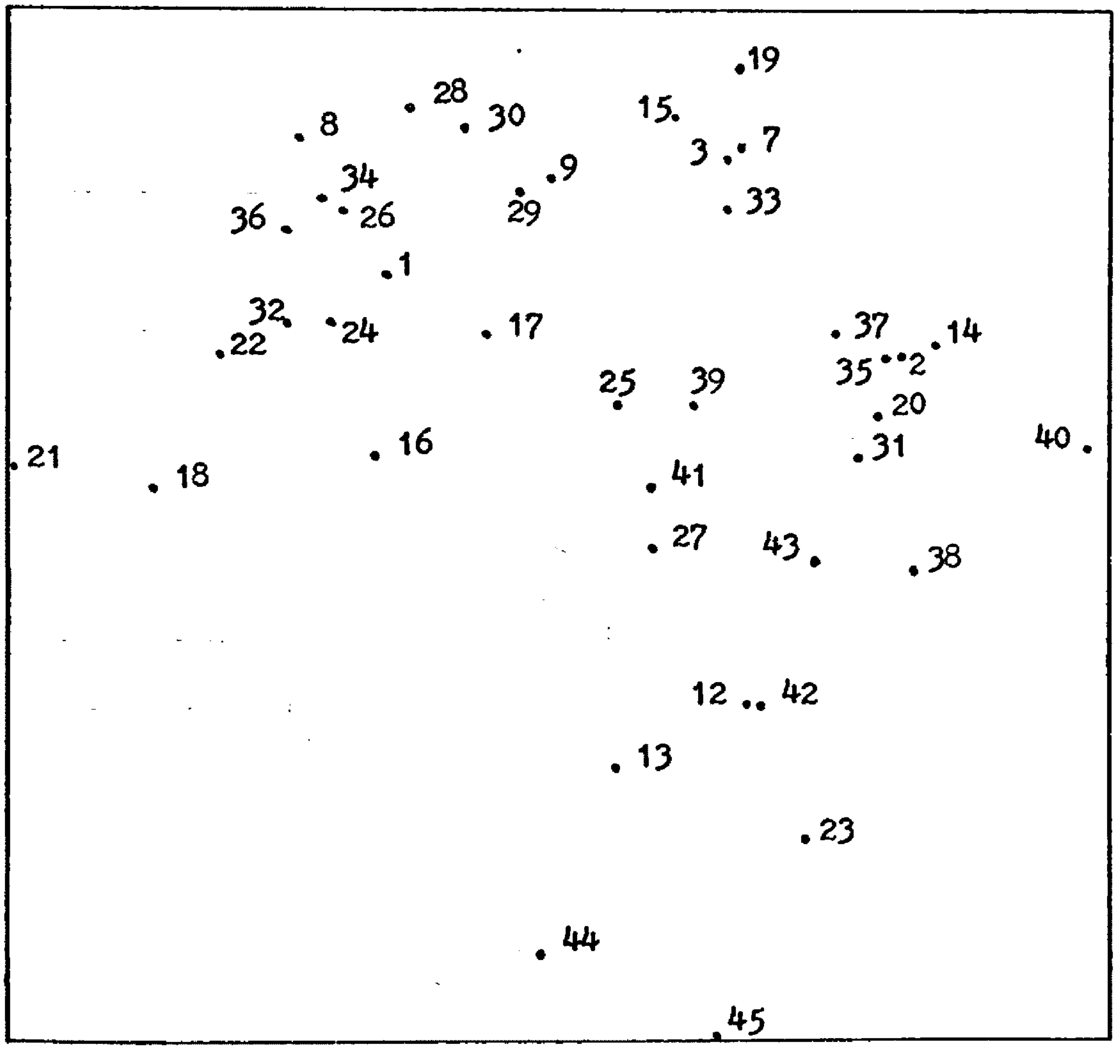


Figure 3. Distribution of stands in two-dimensional ordination.

Ordinational diagrams for representative species are based on frequency classes represented by the following five different sized circles:

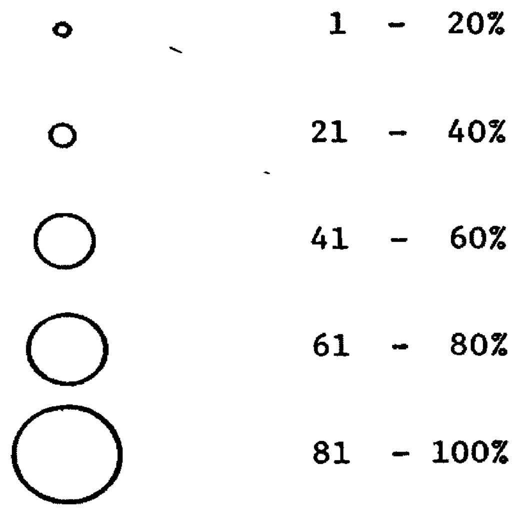


Figure 4. Ordination of six representative species.

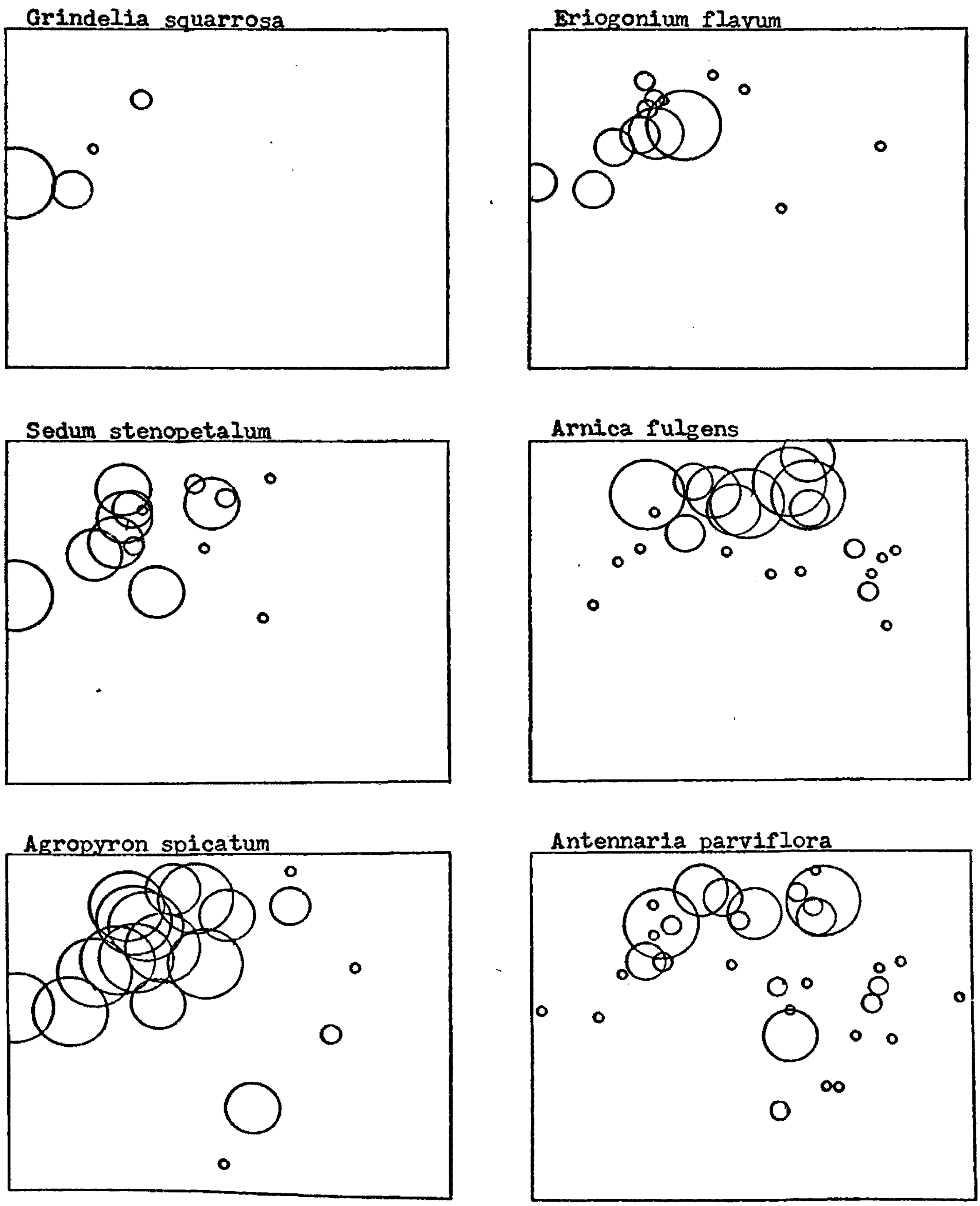


Figure 5. Ordination of six representative species.

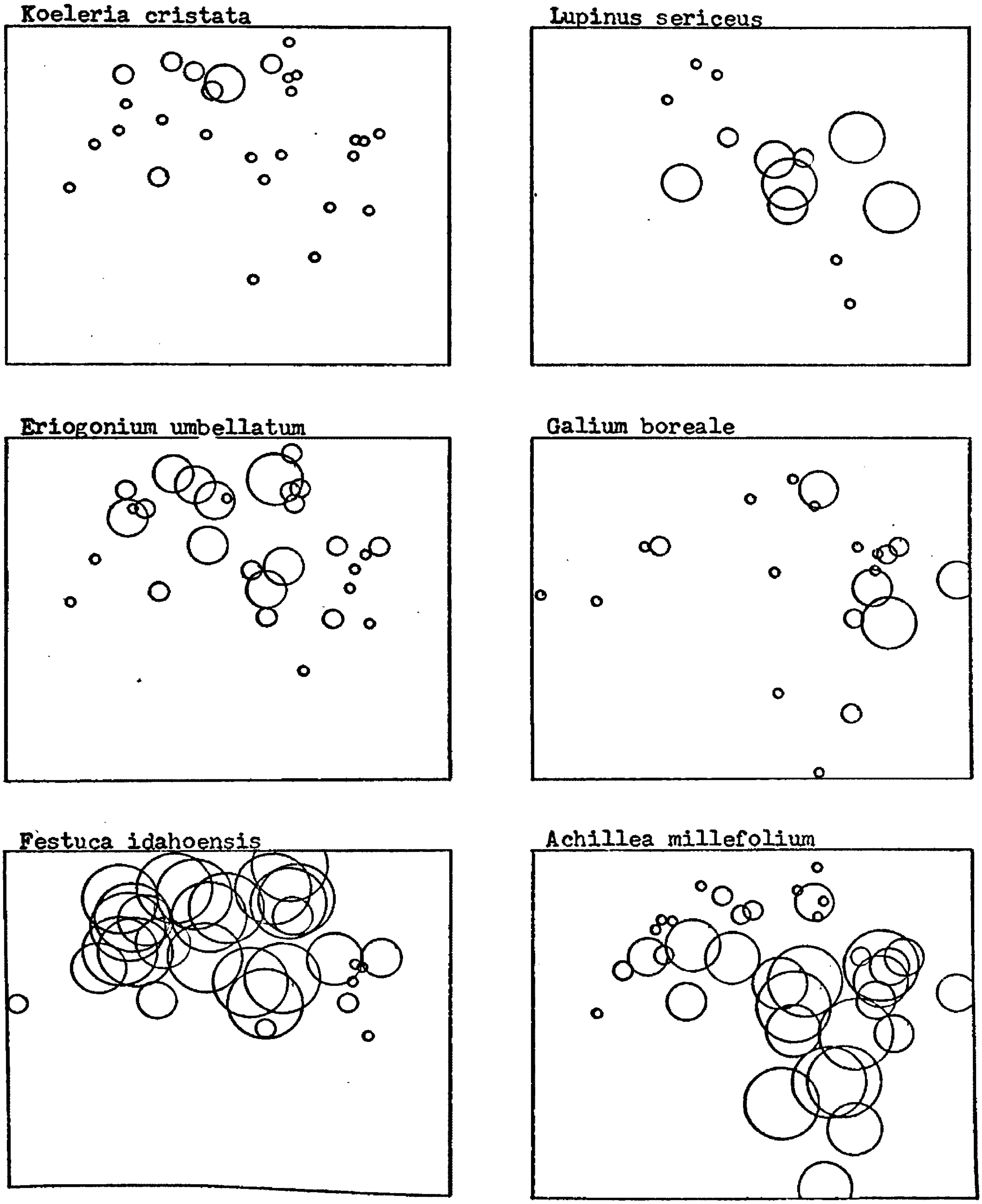
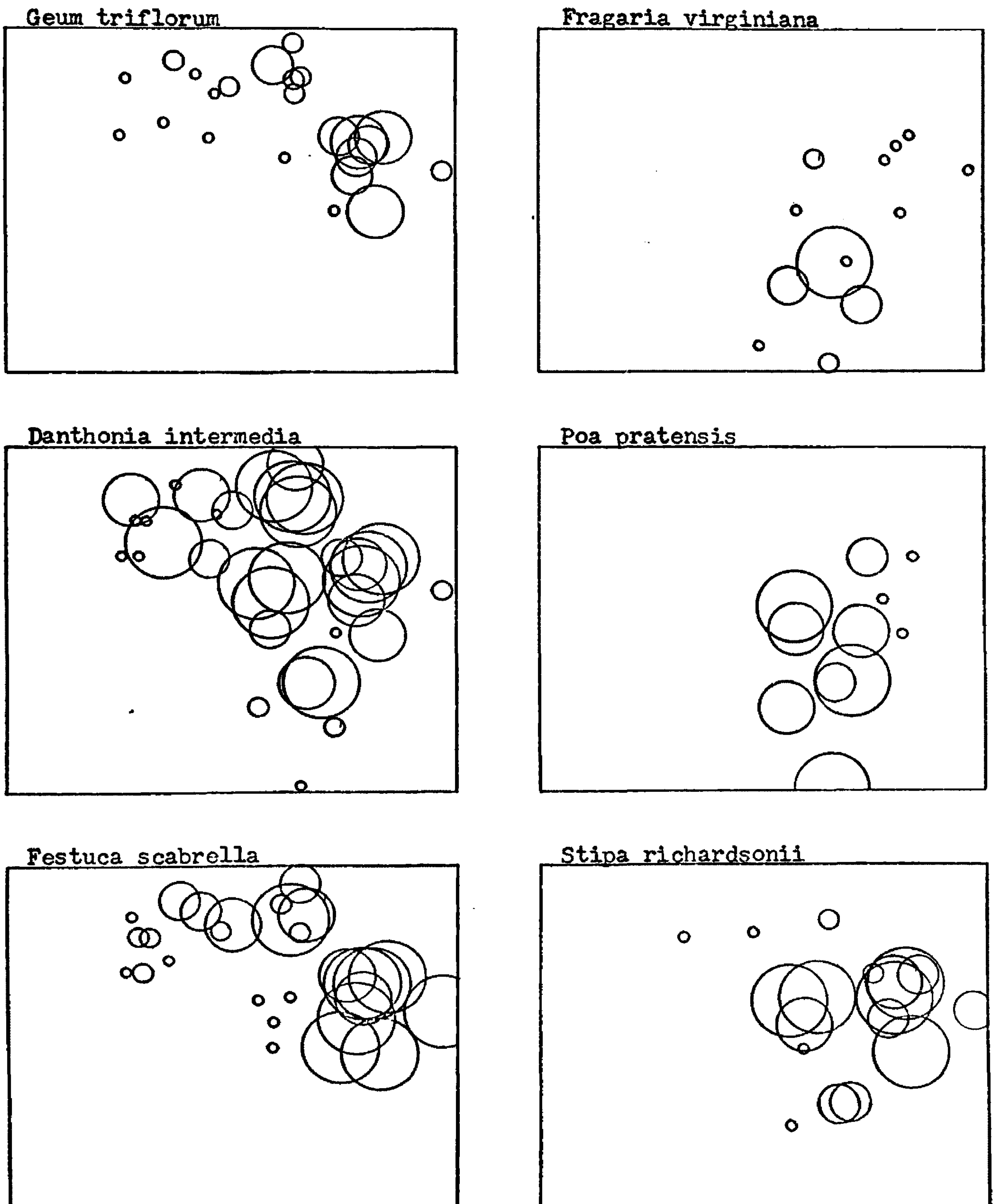


Figure 6. Ordination of six representative species.



Environmental data collected in the field during the study and soils data compiled in the laboratory will be discussed as separate units. They will be considered together in interpreting community compositional and distributional features. All environmental data have been summarized along the compositional gradient to indicate general trends. In selecting sites for collecting environmental field data, stands representative of segments 1 and 5 were not included. Although a wide variety of communities were purposely selected, the extreme stands, being limited in number (3 in segment 1 and 4 in segment 5), were difficult to foresee at the beginning of the field investigations. Therefore field data is only available for communities within the central segments of the compositional gradient.

It is the opinion of the author, based on knowledge of the North Fork area that the extreme stands (those stands falling within segments 1 and 5) do display significant moisture differences in comparison to their adjoining segments. Segment 1 communities are somewhat more xeric than segment 2 stands and segment 5 communities are more hydric than segment 4 sites, but these estimates are not supported by actual field measurements.

Soil Moisture:

Field soil moisture data were taken at approximately 1 month intervals throughout the summer at 26 selected sites which included 20 prairie sites, 4 forested sites and 2 big sage sites. Percent moisture (by weight) of the upper 6 inches of soil was calculated for each of the selected sites (Table 1).

As might be expected, there is a general trend for soil moisture to decrease during the summer and a general resurgence of moisture in early fall. The average increase from September 1 to October 1 is slight, however, due probably to a relatively low amount of precipitation (0.16 inches) during September.

The residual soil moisture which collected during the winter months and early spring is almost exhausted by the first week in September. Soil moisture present in plant communities within segment 2 during the first week in September averages only 0.8%. The highest average (6.2%) was found to occur within segment 4 during the first week in July (Table XV).

This trend established in the field data is consistent with those data compiled on the soils in the laboratory. Available soil moisture increases along the X axis from segment 1 to 5 (Table X).

It was found that soil moisture averaged significantly higher in the surrounding forested areas than in the adjacent prairie stands. Available soil moisture was not found to be significantly greater in forest soils (27.8%) than in the prairie soils (26.1%). The latter were found to contain significantly greater amounts of sand (53.2%) than the forest soils (36.1%). Percent clay was not significantly different in either case (19.2% for forest soils and 18.0% for prairie soils).

Thus, it appears that the greater amount of soil moisture is not entirely due to soil texture. Reduced insolation under the forest canopy, a greater snow accumulation and deeper percolation of water during the winter months probably contribute greatly to this difference in soil moisture.

The organic matter content in soils plays a major role in maintaining soil moisture and ultimately plant environments. Because organic matter possesses colloidal properties its water holding capacity is relatively high. Organic matter in prairie soils, chiefly contributed by dead plants and decaying roots, is highest near the surface and therefore this part of the soil profile has the highest water holding capacity. However, the water held in the upper layers is highly vulnerable to evaporation. Because of this property, the incorporation of organic matter into sandy soils results in a tendency for such soils to maintain an unexpectedly high percent of water (Daubenmire, 1962). It is probably true, however, that such soils are not as effective in holding water late into the growing season as are soils possessing high clay contents.

This may be the reason for the appearance of more mesic species such as Festuca scabrella and Danthonia intermedia in stands 8, 24, 26 and 34 of segment 2. Percent sand content in these four stands averages almost 20% greater than the average of all stands included in gradient 2, while organic matter averages almost 20 tons/acre more than the overall average.

Table XV. Community dominant and compositional gradient averages for field soil moisture in the North Fork Valley grasslands.

Location	July 3	August 1	September 1	October 1
Forest	12.4%	7.5%	7.2%	9.3%
Prairie	4.6	2.7	1.7	2.4
Big Sage	5.4	3.8	2.9	2.6

Month	2	3	4
July	2.6%	3.9%	6.2%
August	1.4	2.3	3.7
September	0.8	1.7	2.8
October	1.8	2.1	3.3

Soil and Surface Temperature:

Subsoil, surface and air temperatures were collected at each of the selected sites concurrently with the soil moisture data. Soil temperatures were taken at a depth of 3 inches below the surface. Surface temperatures were taken at the surface; however, when duff or litter matted the surface readings were taken under the debris but not in the soil. All temperatures were collected between 10 a.m. and 2 p.m. on cloudless days when wind movement was at a minimum.

Although air temperature did not establish any patterns when fitted into the gradient, it was found that the highest average temperatures occurred in July and that they decreased through October. As would be expected air temperatures under the forest canopy were lower than those of adjacent grassland communities.

Unlike air temperatures, soil and surface temperatures were found to peak in August, thus displaying the thermal lag in the soils. The increase from July to August was slight in most cases when compared with the decrease from August to September. On the more moist sites included in segment 4 it was found that soil temperature increased from August to September and surface temperatures remained almost unchanged over the corresponding period. The drop in both soil and surface temperature from September to October in all segments was very marked (Table XVI and XVII).

The noticeably higher soil temperatures in segments 2 and 3 are probably due to soil texture. The lighter soils in these segments have

Table XVI. Community dominant and compositional gradient averages for field surface temperatures in the North Fork Valley grasslands.

Location	July 3	August 1	September 1	October 1
Forest	23.3°C	23.3°C	23.2°C	14.4°C
Prairie	38.4	39.9	34.8	24.4
Big Sage	41.1	29.5	23.8	19.8

Month	2	3	4
July	42.8°C	37.5°C	35.0°C
August	43.8	40.3	37.1
September	34.4	35.5	37.0
October	27.0	25.0	22.5

Table XVII. Community dominant and compositional gradient averages for field soil temperatures in the North Fork Valley grasslands.

Location	July 3	August 1	September 1	October 1
Forest	15.6°C	15.9°C	16.0°C	12.1°C
Prairie	25.8	26.3	24.2	18.3
Big Sage	24.9	21.8	18.9	16.3

Month	2	3	4
July	29.3°C	24.9°C	23.6°C
August	29.9	27.1	24.1
September	25.1	24.6	24.3
October	20.1	18.3	17.6

greater porosity and tend to favor an equilibrium between soil and air temperature. Because the greater porosity allows for freer gas exchange and lowers water holding capacity, soils in segments 2 and 3 (as well as 1) warm earlier in spring and thus allow for earlier development of the flora (Daubenmire, 1962). As a result, the water supply collected during the winter in these soils is probably utilized and consequently exhausted earlier than water in soils of segments 4 and 5.

Sandy soils normally carry less organic matter than one of finer texture due probably to their lower moisture content and thus more rapid oxidation than that occurring in the finer soils. In addition the natural vegetative growth is normally less in lighter soils. Thus soil temperature, and its effect on the accumulation of organic matter and on soil moisture, is one of the primary factors controlling the growth and distribution of plants.

Forest surface and sub-soil temperatures also show a thermal lag. Although temperatures are lower for both in the forest the greatest differences in temperatures are found at the surface. This is probably due to the insolating effect of the soils (Tables XVI and XVII).

Soil Analyses:

The soils of this region are principally of the Chernozem Great Group with associations of azonal soils of the alluvial and regosol Great Groups (U.S.D.A., 1964). These soils can be generally classified as sandy loam. Chemical analysis of these soils failed to reveal any striking correlations within the compositional gradient.

Calcium reaches its highest values in segment 3 of the gradient. These values are extremely low in comparison with those of grassland soils of the Upper Blackfoot Valley (Blinn, 1966) where they average nearly 8,500 pounds/acre. In soils of drier regions, calcium carbonate accumulates in a definite zone in the soil profile and the depth of this zone is dependent upon climate. As a general rule the drier the region the nearer to the surface it will be (Trewartha et al., 1961). Since annual precipitation in the Upper Blackfoot Valley is only about 16 inches while in the North Fork grasslands it is about 22 inches, there is an indication that the calcium enriched layer is well below the layer of soil sampled.

In contrast to the distribution of calcium, magnesium and potassium reach their highest average values in segments 4 and 5 although no specific conclusions can be made of this because both also reach high values in segment 1. Phosphorus reaches its highest average value in segment 1 (46 pounds/acre) although stands in segment 4 attain values nearly as high (42.2 pounds/acre). Nitrogen (nitrate and ammonium) shows a general increase from segment 1 to 4 where it peaks (Table X).

The pH of a soil is a general indicator of the availability of nutrients (Daubenmire, 1962). In the soils studied the pH was generally higher in the first 3 segments but also peaked in segment 5. It was suspected that the floor of the North Fork Valley would be slightly basic or circumneutral since the bases replaced by H ions in the upper topographic regions would accumulate at lower levels. The average pH of the prairie soils was found to be 5.9. This average is more acidic than normal for prairie soils and is probably the result of leaching during the winter months when soil moisture is abundant.

Artemisia stands:

Five stands dominated by Artemisia tridentata found in Big Prairie and Round Prairie were sampled using meter square quadrats. Quadrat frequency and canopy coverage data were collected for each stand. The 5 stands were arranged on the basis of increasing sagebrush dominance (Tables XII and XIII). Stands 6, 11, 5, 4 and 10 were aligned along the gradient and ranged in dominance from 11.9% in stand 6 to 58% in stand 10. Stands 10 and 11 were located in Big Prairie and are thought to have had a more recent history of disturbance due to natural grazing.

The first four stands possess only minor differences in the abundance of Artemisia tridentata and consequently do not display major differences in species. The abundance of big sage in stand 10, however, is significantly greater (over twice the coverage value of stand 4) than any of the other stands. Stand 10 was also found to display a greater number of species than all other big sage stands.

A significant reduction in the number of species was found in big sage stands in comparison with the prairie stands. Antennaria rosea, Arctostaphylos uva-ursi, Berberis repens, Bromus pumpellianus, Danthonia unispicata, Eriogonum flavum, Equisetum fluviatile, Geranium viscosissimum, Grindelia squarrosa, Lithospermum ruderale, Melica spectabilis, Monarda fistulosa, Potentilla diversifolia, Potentilla gracilis, Senecio triangularis, Smilacina racemosa and Tragopogon pratensis did not occur in the big sage stands, but were commonly present in prairie stands. Only one species, Lomatium simplex, occurred in the sagebrush stands but not in the prairie stands.

Species flourishing under the canopy of big sage in stand 6 include Festuca idahoensis, Achillea millefolium and Agropyron spicatum. These species together constitute 60% relative coverage of the understory species. Festuca scabrella and Eriogonum umbellatum are also important species contributing another 20% of the understory cover.

In stand 11 Agropyron spicatum and Festuca idahoensis together contribute 59% of the relative coverage of understory species. Few other species reach prominence in this stand, only Festuca scabrella and Galium boreale attaining values greater than 3%.

Festuca idahoensis and Festuca scabrella were found to be the major understory species of stand 5 combining to contribute 57% of the relative coverage of all understory species. Achillea millefolium, Antennaria parviflora, Eriogonum umbellatum and Calochortus apiculatus are other important species which contribute greater than 3.0% to the total coverage of understory species.

In stand 4, Festuca idahoensis and Festuca scabrella again are the two major understory species; however, they contribute less to the relative coverage (47%) than in stand 5. Several species including Arnica fulgens, Danthonia intermedia, Antennaria parviflora and

Agropyron spicatum each contribute nearly 10% to the total coverage while Achillea millefolium and Calochortus apiculatus contribute greater than 3.0% to the understory cover.

Poa compressa was found to be the major understory species in stand 10, singly contributing 38% of the relative coverage. Fragaria virginiana, Agropyron spicatum, Poa pratensis, Achillea millefolium, Eriogonum umbellatum and Anemone multifida were found to contribute greater than 3.0% coverage in this segment. Agrostis scabra, Fragaria virginiana, Lupinus sericeus, Penstemon confertus and Stipa columbiana were found to be restricted to this segment.

Festuca idahoensis, Agropyron spicatum and Festuca scabrella were all found to attain higher average coverage values in the Artemisia stands than in the prairie stands, while Danthonia intermedia displayed a lower average cover. Festuca idahoensis showed the greatest increase in overall average (6.2% for prairie stands and 16.2% for sage stands) while Agropyron spicatum and Festuca scabrella increased only slightly in the big sage stands.

Vegetational patterns demonstrated by species in the Artemisia stands are similar to those along the grassland compositional gradient. Sedum stenopetalum, Arenaria congesta, Agropyron spicatum and Eriogonum umbellatum show a gradual decreasing trend from segment 1 to 5 in prairie stands and from stand 6 to stand 10 in big sage stands. Achillea millefolium and Festuca idahoensis appear generally of equal importance under all degrees of dominance by big sage although Festuca does decrease sharply in stand 10. *Festuca scabrella*, *Calochortus apiculatus*, *Geum triflorum*, *Antennaria parviflora*, *Arnica fulgens*, *Danthonia intermedia* and *Koeleria cristata* reveal an increasing trend from segments 1 to 5 in prairie stands and from stand 6 to stand 10 in big sage stands.

Field soil moisture was found to be higher in the sagebrush stands than in prairie stands; however, these stands were significantly lower than the selected forest sites. There was a general decrease throughout the summer but a replenishment of soil moisture in October was not found in the two *Artemisia* stands selected for field study.

Surface and subsurface temperatures were generally cooler in the sagebrush sites than in the prairie areas; however, these soils were generally much warmer than nearby forest soils. Surface temperatures were found to be higher in July and decreased steadily throughout the summer. No increase in temperature was found from July to August as was found for both prairie and forest soils. Subsoil temperatures followed the same trend as surface temperature.

Air temperatures, taken at approximately 2 feet above the ground, in big sage stands were found to be highest in July and decreased steadily throughout the summer. They were much higher than those of forested stands and only slightly cooler than in the prairie stands.

The *Artemisia* dominated stands were found to have lower phosphorus, potassium, nitrate and ammonium averages than both prairie and forest communities (Table XIV). Organic matter was slightly higher than in forest soils but averaged 12 tons/acre less than in the prairie soils. Calcium in the sagebrush areas was found to be higher on the average than in the forest soils, but about 350 pounds/acre less than in prairie soils. Magnesium was found to be slightly higher than in forest soils and almost identical with that of prairie soils. Hydrogen ion values averaged about 5.9, the same as for prairie soils; however, forest soils were found to be more acidic (5.4).

Big sage stands were found to exist on the more sandy sites, averaging 61.6% sand as compared with 53.2% for prairie stands and 36.1% for forest stands. Clay content was correspondingly low, averaging 11.4% as compared with 18.0% and 19.2% for prairie and forest stands respectively.

Discussion

The total environmental complex as reflected in the compositional and distributional patterns of individual species reveals that soil moisture is probably the most important factor operating in the North Fork Valley grasslands. Soil moisture, however, must be viewed as a complexity of factors. Winter and summer precipitation add directly to the soil moisture supply but many indirect factors such as organic matter, surface temperature, subsoil temperature and soil texture are important in maintaining it.

It is difficult to believe that summer precipitation contributes greatly to vegetational patterns primarily because only minor variation from site to site would be expected within the study areas. It appears much more likely that the many indirect factors acting as regulators of the soil moisture supply during the hot, dry summer are responsible for vegetational patterns.

Arrangement of environmental data (Table X) along the compositional gradient reveals a general increase in available soil moisture from segment 1 to segment 5. Further, the general trend established by soil texture is for percentage clay and silt to increase while the percentage of sand decreases from segment 1 to 5. Organic matter content also increases along the compositional gradient peaking in segment 4 and then becoming reduced in segment 5. The gradient, therefore, ranges from communities where soil moisture is relatively limiting, sand content high and clay content and organic matter low to sites where soil moisture is much more available (nearly a two-fold increase), sand content low and clay content and organic matter are high.

Organic matter content of soils in segments 1 and 5 was found to be lower than in the medial gradient segments. The low organic matter associated with segment 1 is probably caused by the lower vegetative cover in the communities of this segment with a consequent reduction in litter production. Soil texture in stands of the first segment is so coarse that moisture is not generally available for luxuriant plant growth. Plant coverage values for stands of segment 1 are low and this no doubt contributes to higher surface and soil temperatures which further reduce soil moisture.

The soils in stands included in segment 5 are also relatively low in organic matter; however, in each of the stands large amounts of litter remain undecomposed on the ground surface. These stands are situated near the forest margins on soils with relatively high moisture contents. It may be that the high soil moisture combined with factors related to soil aeration is sufficient enough to have a retarding effect on the rate of decomposition of dead plant tissue here.

Organic matter influences the soil moisture supply far out of proportion to the small quantity present (Buckman and Brady, 1960). The available soil moisture for example of stand 12 is approximately 13% greater than that of stand 15 although both stands have nearly identical soil textures. Apparently an increase of 7 tons/acre organic matter in stand 12 accounts for this major difference in the soil moisture supply. Similarly, an increase of 16% available soil moisture in stand 38 over stand 21 is presumably due to a 10 tons/acre increase in organic matter in stand 38.

Soil texture was also found to play an important role in influencing the soil moisture supply. Although soils of stands 15 and 30 have the same measured organic matter content, the available soil moisture is 9% greater in stand 15. Stand 15, however, has a higher clay and a lower sand content than does stand 30. Similarly, an increase of 16% available soil moisture in stand 7 over stand 21 is presumably due to a higher silt and clay content than is found in stand 7.

The increase of available soil moisture along the compositional gradient is probably due to a complex of intimately related factors, each contributing greater or less influences on the communities in each segment. Availability of moisture in soils of segment 1 is relatively low; however, these soils are heavier (difficult to work) and richer in chemical constituents, except nitrogen and organic matter than those of segment 2. The amount of organic matter and the availability of soil moisture are undoubtedly dominant environmental features controlling vegetation; however, assessing their importance as separate factors is difficult. Although organic matter will improve moisture conditions in the soil, certain minimum levels of soil moisture must be available in order for sufficient amounts of plant material to be produced to be decomposed into humus. Coverage values averaging less than those of all other segments and direct insolation probably account for much of the water loss in the stands of segment 1.

Stands included in segment 2 can be characterized by their locations on low ridges near forested areas or on north-facing ridges within the prairie landscape. Apparently the soil moisture supply on such sites persists farther into the growing season and thus results in a denser vegetative cover. During the ensuing dry summer much of the plant remains of the litter begins to be incorporated into the humus layer. The relatively sandy soil conditions and/or the exposures of these stands probably retard the development of an even more profuse vegetative growth.

Segment 3 communities were found to have heavier soils than all other segments except the fifth. A relatively small increase in organic matter content and a more substantial increase in clay content in the soils of these stands over those of segment 2 has resulted in a very slight increase in available soil moisture.

Although the organic matter content of soils in segment 4 remains about the same as that found in soils of segment 3 and they are found to be somewhat lighter than those of segment 3 available soil moisture continues to increase along the gradient. The explanation for this increase in available soil moisture is difficult since this figure indirectly results from soil texture and organic matter content. Actual increase in field soil moisture is probably best explained in terms of the reduction in exposed surface and the soil temperature under the greater vegetative coverage.

In segment 5 organic matter content was found to be lowest of all segments; however, the soils are much heavier than those of the other four segments. Presumably the higher clay and silt content of soils in this segment are responsible for attaining the highest available soil moisture value in the gradient.

The soil moisture complex suspected in establishing species relationships in the prairie communities are also probably important in species relationships under the canopy of Artemisia tridentata. Only slight differences in the organic matter content in the soils of these stands were found and they are probably not a major factor in the species distribution.

Available soil moisture in stand 6 is relatively low (18.0%) despite a moderately high clay (8.5%) and organic matter (54 tons/acre) content. The lack of cover which results in higher soil temperatures and higher evaporation of moisture from this sandy soil is probably the most important factor contributing to this reduced soil moisture supply.

Available soil moisture in stand 4 is 28.0% (about twice that of segment 1) although soil of this segment is lower in both clay (6.4%) and organic matter content (49 tons/acre). Presumably it is again the lower surface and soil temperatures caused by a greater vegetative cover which contribute to the higher moisture supply.

The general pattern established by the community structure reveals a gradual increase in the number of species from segment 1 to segment 5. These prairie communities, however, display a relatively impoverished landscape devoid of species diversity in comparison to the other Palouse Prairie grasslands. Moss and Campbell(1947) reasoned that a richer flora in the southern areas of the Fescue Grasslands in Alberta may be explained in terms of a time element; insufficient time has elapsed since glaciation for many species to have reached the northern areas. They found approximately 150 species in the southwestern areas of Alberta in the Fesuce Grasslands as compared with only 50 species found in the North Fork grasslands which are located slightly south of the Canadian Fescue Grasslands. Thus, the time element seems improbable as a factor in the limited number of species found in this area since richer floristic areas are found farther north.

Ramaley (1919) found a reduction of species roughly corresponding to an increase in altitude in Colorado grasslands. Tisdale (1947) reported a greater cover, higher production and a generally richer flora in his most mesic grasslands in central British Columbia. Both investigators describe a trend of increasing numbers of species correlated with an increase in precipitation or moisture supply. Some of the North Fork grasslands occur in areas that could be classed as mesic, and therefore would be expected to display a rich flora. They, however, do not do so.

Seasonal distribution of precipitation, exerting a selective influence upon the immigration of species into the areas, is probably a critical factor. Even where the normally closed prairie community is disturbed by rodent mounds, exotic species do not invade. In addition, these areas are characterized by rather uniform edaphic and climatological conditions associated with a rather flat, rolling topography. Monotonous environmental and topographic areas do not favor the establishment of a wide variety of migrant species simply because a diversity of niches is not available.

Revegetation of the North Fork Valley since glaciation has suffered many setbacks. Virtually the entire valley was denuded of vegetation by recurring forest fires before 1900, but reforestation has almost completely covered the entire valley today. A few prairie communities have somehow been able to resist this forest invasion and formed outliers completely surrounded by the forest.

Rydberg (1915) suggested that great amounts of snow accumulates during the winter in these Rocky Mountain valleys and that it melts so slowly during the growing season that tree seedlings are suffocated. Some investigators (U.S.D.A., 1964) in the western United States have found that the balance between low precipitation and high temperatures during the growing season favors grassland and/or the high base status of soils due to incomplete leaching. Daubenmire (1942) concluded that seasonal distribution of precipitation in eastern Washington and adjacent Idaho acts as a selective influence upon the invasion of species onto the unforested plains.

Probably the ultimate factor in the maintenance of these grassy areas is an insufficient amount of available moisture especially during the late growing season for the establishment of tree seedlings. A rain shadow effect of the Whitefish Range to the west may contribute to the establishment of isolated "islands" of low precipitation that allow for the perpetuation of these prairie outliers. Although macro environmental differences produced by a rain shadow effect probably do not exist here, minor differences can be suspected to contribute to the maintenance of prairie communities.

Drainage systems underlying the glacial deposits in the North Fork Valley may also be suspected as contributors to local areas of reduced soil moisture. Wherever these strata closely underly the surface, a thin glacial veneer may not be of sufficient depth to hold enough soil moisture for sustained tree growth late in the growing season. Geological evidence of the underlying strata of this area is not available however.

In general, grasslands are found on the sandy to sandy loam bottomlands of the North Fork Valley while lodgepole pine, the most conspicuous tree species surrounding the grasslands, occupies the loamy terraces. The ecotone between them is very narrow, often less than 2 or 3 feet. Only limited reproduction of lodgepole pine seedlings can be found near the prairie-forest edge and wherever tree seedlings have made advances, presumably during wetter years, they usually perish during subsequent drier years.

There is an indication that soil texture, coupled with seasonal distribution of precipitation, the possible existence of local "pockets" of reduced precipitation and underlying rock strata, may be very important in maintaining the ecotone.

In addition, since game animals are under park protection in this area, wildlife disturbance may play a very minor role in thinning out and destroying the tree seedlings that do become established within the grasslands.

Although the occurrence of Danthonia intermedia is not unusual in the Palouse Prairie region it is rarely found as a major dominant species. Danthonia intermedia is known to occur in this region, however, whenever grassland vegetation is found at higher, even alpine, elevations. Choate (1963) found Danthonia intermedia on Logan Pass in Glacier National Park in Montana at an altitude of about 6,664 feet above sea level. Mueggler (1967) studying grassy balds in southwestern Montana also encountered this species.

Moss (1944) indicates that Danthonia intermedia is present throughout the Fescue Grasslands of Alberta but that it is rare. Ramaley (1919) found Danthonia intermedia in Utah at about the 6-7,000 foot level although it did not contribute greatly to the total vegetational cover. Blinn (1966) found rare occurrences of Danthonia intermedia in the Upper Blackfoot Valley but it was not encountered on the glacial mounds that he studied.

Summary

The objectives of the study were to determine the vegetational patterns on four intact grassland communities in the North Fork Valley of Glacier National Park and to relate these patterns to factors of the physical environment.

Forty-five stands, encompassing a wide variety of community characteristics, were selected for vegetational analysis in these grasslands. Frequency and canopy coverage values were recorded for each stand. Soil samples were also collected to determine their physical and chemical properties.

In addition, 26 of the selected stands were also chosen for additional field study. Soil moisture, surface and soil temperatures were recorded for each of these sites at one month intervals.

An ordination was initially constructed to reveal vegetational patterns and their interrelationship with environmental aspects. A compositional gradient was finally constructed to indicate plant-environmental relationships in a more quantitative manner.

Results indicate that the distribution of species in the North Fork Valley grasslands is primarly controlled by a complexity of factors all intimately related to soil moisture. The drier aspect of these communities is characterized by species such as *Agropyron spicatum*, *Grindelia squarrosa*, *Eriogonum flavum* and *Sedum stenopetalum* which reach their highest frequency and coverage values in segments 1

or 2 of the compositional gradient. The more mesic communities are characterized by such species as Festuca scabrella, Stipa richardsonii, Geum triflorum, Galium boreale and Danthonia intermedia which reach their highest frequency and coverage values in segments 4 or 5 of the compositional gradient.

Generally interesting features are discussed including conjecture about the presence of these grasslands and their stability. The present paper points out a need for further investigation in this respect.

Literature Cited

Alden, W. C. 1953. Physiography and glacial geology of western Montana and adjacent areas. U.S. Geological Survey Prof. Paper No. 231: 200 pp.

Ayres, H. B. 1900. The Flathead Forest Reserve. 20th Ann. Rep. U.S. Geol. Sur., Part 5:245-316.

Beals, Edward. 1960. Forest Bird Communities in the Apostle Islands of Wisconsin. The Wilson Bulletin 72(2):156-181.

Blinn, Dean W. 1966. Analysis of the vegetation on the glacial moraines in the Upper Blackfoot Valley, Montana. Unpublished M.A. thesis, University of Montana. 90 pp.

Bray, J. R. and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monog. 27: 325-349.

Buckman, H. O. and N. C. Brady. 1960. The Nature and Properties of Soils. 6th Edition. The MacMillan Co., New York. 544 pp.

Clements, F. E. 1910. Life history of lodgepole pine burn forests. U.S. Forest Serv. Bul. 79. 56 pp. Illus.

Daubenmire, R. F. 1942. An ecological study of the vegetation of southeastern Washington and adjacent Idaho. Ecol. Monog. 12: 53-79.

__________. 1943. Vegetational zonation in the Rocky Mountains. Bot. Rev. 9:325-393.

__________. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33(1):43-64.

__________. 1962. Plants and Environment.

Hitchcock, A. S. and Agnes Chase. 1950. Manual of the Grasses of the United States. Government Printing Office, Washington. 1051 pp.

Hitchcock, C. L., Arthus Chronquist, Marion Ownbey, and J. W. Thompson. 1955. Vascular Plants of the Pacific Northwest. Part 5. Compositae. University of Washington Press. 343 pp.

__________. 1959. Vascular Plants of the Pacific Northwest. Part 4. Ericaceae through Campanulaceae. University of Washington Press. 510 pp.

__________. 1961. Vascular Plants of the Pacific Northwest. Part 3. Saxifragaceae to Ericaceae. University of Washington Press. 613 pp.

__________. 1964. Vascular Plants of the Pacific Northwest. Part 2. Salicaceae to Saxifragaceae. University of Washington Press. 597 pp.

Heady, H. F. 1950. Studies on blue-bunch wheatgrass in Montana and height-weight relationships of certain range grasses. Ecol. Monog. 20:55-81.

Lynch, Brother Danial. 1955. Ecology of the aspen groveland in Glacier County, Montana. Ecol. Monog. 25:321-344.

Mitchell, Warren. 1957. An ecological study of the grasslands in the region of Missoula, Montana. M. A. thesis, University of Montana. 111 pp.

Moss, E. H. 1944. The prairie and associated vegetation of southwestern Alberta. Can. Jour. Res. C. 22:11-31.

__________. 1959. Flora of Alberta. University of Toronto Press, Toronto, Canada. 546 pp.

__________ and J. A. Campbell. 1947. The fescue grassland of Alberta. Can. Jour. Res. C. 25:209-227.

Mueggler, W. F. 1967. Response of mountain grassland vegetation to clipping in southwestern Montana. Ecology 48(6):942-949.

Ramaley, Francis. 1919. Xerophytic grasslands at different altitudes in Colorado. Bull. of the Torrey Bot. Club. 46:37-52.

Regional Publication, U.S.D.A. 1964. Soils of the western United States. Washington State University. 66 pp.

Rydberg, P. A. 1915. Phytogeographical notes on the Rocky Mountain Region. V. Grasslands of the subalpine and montane zones. Torrey Bot. Club Bulletin 42(2):629-642.

Shantz, H. L. 1924. Natural vegetation; grassland and desert shrub. U.S.D.A. Atlas Am. Agr., Part I, Sec. E:15-29.

Shefford, V. E. 1963. The Ecology of North America. University of Illinois Press. 494 pp.

Stoddart, L. A. 1941. The palouse grassland association in northern Utah. Ecology 22:158-163.

Tisdale, E. W. 1947. The grasslands of the southern interior of British Columbia. Ecology 28:346-382.

Trewartha, G. T., A. H. Robinson, and E. H. Hammond. 1961. Fundamentals of physical geography. McGraw-Hill Book Company, Inc. 394 pp.

Weaver, J. E. 1917. A study of the vegetation of southeastern Washington and adjacent Idaho. Univ. of Neb. Studies 17:1-114.

Wright, J. C. and E. A. Wright. 1948. Grassland types of south central Montana. Ecology 29:449-460.

Table I. Field Soil Moisture Data

Location	July 3	August 1	September 1	October 1
RP - F*	9.0%	8.9%	6.5%	9.9%
8	1.7	1.3	0.6	1.5
5	5.7	3.2	1.8	1.8
BP - F**	12.9	7.0	3.4	7.0
9	1.7	1.1	0.8	3.2
10	5.1	4.5	3.9	3.5
12	4.8	3.4	1.8	1.9
16	6.1	2.7	1.2	3.5
24	2.2	1.5	0.7	2.9
25	3.1	2.9	1.2	1.7
26	2.8	1.4	1.1	0.9
27	7.5	4.8	4.4	3.1
29	2.1	1.6	1.1	1.3
30	0.9	0.8	0.6	0.9
31	4.8	4.4	2.4	1.2
32	1.6	1.5	0.7	0.9
33	4.7	1.9	1.1	0.8
34	1.4	0.5	0.4	0.9
35	1.7	0.6	0.8	1.6
41	8.4	2.4	2.0	2.4
42	5.8	2.5	1.8	2.1
LPP - F***	8.3	4.2	6.5	5.6
43	3.9	2.7	1.1	2.1
44	66.9	13.7	7.2	9.5
DCP - F****	19.3	9.7	12.5	14.7
45	17.8	10.6	10.3	13.3

* RP - F indicates forested station near Round Prairie.
** BP - F indicates forested station near Big Prairie.
*** LPP - F indicates forested station near Lone Pine Prairie.
**** DCP - F indicates forested station near Dutch Creek Prairie.

Table II. Field Soil Temperature Data

Surface Temperature

Location	July 3	August 1	September 1	October 1
RP - F	27.7°C	26.2°C	16.1°C	16.1°C
8	46.1	40.5	27.9	29.5
5	38.1	36.6	17.4	18.3
BP - F	27.8	30.6	19.5	15.2
9	47.8	48.5	38.9	31.5
10	54.1	22.4	30.2	21.3
12	43.5	29.0	42.0	26.1
16	42.4	35.1	31.3	32.1
24	48.2	41.5	38.2	22.4
25	40.9	46.8	36.1	27.9
26	40.0	48.2	37.9	28.4
27	32.9	40.2	36.0	27.5
29	39.5	46.1	37.2	23.9
30	39.9	44.2	38.2	25.0
31	35.4	36.1	36.4	22.5
32	42.5	46.4	37.2	25.6
33	31.5	42.4	38.2	22.1
34	43.8	45.5	34.1	24.1
35	33.2	42.3	30.6	21.2
41	43.0	43.8	26.7	30.1
42	43.0	42.4	32.9	27.9
LPP - F	20.5	15.1	30.1	13.7
43	36.8	37.9	42.5	18.3
44	24.1	16.1	27.2	14.6
DCP - F	17.0	21.2	26.8	12.5
45	22.0	29.6	36.5	19.1

Table III. Field Soil Temperature Data

Location	July 3	August 1	September 1	October 1
	Soil Temperature			
RP - F	16.5°C	16.1°C	13.3°C	13.6°C
8	31.5	31.6	19.7	21.1
5	29.1	26.2	14.8	15.1
BP - F	18.1	19.1	17.3	12.3
9	23.2	28.9	28.7	19.6
10	20.7	17.4	23.1	17.4
12	22.0	18.2	25.5	18.1
16	24.6	19.8	26.2	19.5
24	30.0	37.1	26.3	21.1
25	31.2	33.0	25.0	20.7
26	29.1	21.1	29.8	21.3
27	27.1	25.8	21.2	17.3
29	26.7	32.2	26.4	20.8
30	27.7	30.9	27.1	19.1
31	21.1	26.0	23.4	17.7
32	31.3	29.6	26.1	19.2
33	25.9	27.8	26.3	20.5
34	29.8	30.2	22.8	18.7
35	27.9	27.8	20.3	18.5
41	26.8	29.2	20.1	18.1
42	29.4	27.2	19.5	19.0
LPP - F	13.8	11.9	18.6	11.9
43	21.2	19.2	32.1	14.8
44	13.9	12.1	19.7	12.8
DCP - F	13.8	16.4	17.2	10.7
45	17.0	23.1	23.4	14.8

Table IV. Field Air Temperature Data

Location	July 3	August 1	September 1	October 1
RP - F	27.9°C	25.4°C	15.5°C	17.3°C
8	30.2	28.1	20.4	18.8
5	30.7	27.9	20.1	18.2
BP - F	25.8	25.4	16.3	16.4
9	25.1	29.9	32.0	18.3
10	25.1	26.8	34.2	19.6
12	26.2	26.0	33.6	20.1
16	28.0	28.3	29.8	19.1
24	25.8	26.2	28.1	15.8
25	26.6	27.8	24.5	19.1
26	26.4	28.1	25.1	19.5
27	27.2	27.5	23.8	18.2
29	27.5	27.8	27.2	18.1
30	26.3	29.1	27.4	17.8
31	28.2	28.7	25.9	18.1
32	28.3	29.2	26.3	18.7
33	29.1	28.9	27.3	17.1
34	31.5	29.8	23.9	19.2
35	31.5	28.7	23.5	19.1
41	28.0	29.1	22.1	20.1
42	33.0	28.2	21.3	18.3
LPP - F	22.6	21.2	22.1	14.0
43	26.3	26.9	33.6	15.4
44	23.3	21.8	31.8	18.2
DCP - F	20.0	23.2	21.6	13.1
45	23.0	25.8	29.8	15.2

Table V. Average quadrat frequency values for all species occurring within the stands of each gradient segment in the North Fork Valley grasslands.

	Compositional Gradient Segments				
Species	I	II	III	IV	V
Grindelia squarrosa	55	4	0	0	0
Sedum stenopetalum	52	59	12	0	0
Lithospermum ruderale	5	0	1	0	0
Berberis repens	5	0	2	0	0
Agropyron spicatum	98	78	37	12	0
Poa compressa	17	4	3	4	0
Calachortus apiculatus	t	4	5	1	0
Rosa acicularis	t	6	3	0	t
Phleum pratense	3	0	25	26	3
Arenaria congesta	5	16	11	18	10
Arnica fulgens	5	30	41	23	11
Potentilla glandulosa	8	0	12	11	6
Eriogonium umbellatum	12	24	34	26	10
Galium boreale	3	3	4	13	51
Eriogonium flavum	70	38	6	0	5
Koeleria cristata	20	18	21	15	5
Antennaria parviflora	10	36	35	26	5
Achillea millefolium	18	31	49	69	56
Festuca idahoensis	33	82	61	43	21
Arctostaphylos uva-ursi	0	t	0	3	23
Lupinus sericeus	0	8	29	9	16

Table V. (continued)

Species	Compositional Gradient Segments I	II	III	IV	V
Geum triflorum	0	8	13	28	59
Danthonia intermedia	0	26	38	72	74
Festuca scabrella	0	20	21	46	90
Campanula rotundifolia	0	3	9	2	0
Zigadenus elegans	0	t	t	0	0
Danthonia unispicata	0	12	9	0	0
Monarda fistulosa	0	6	34	0	0
Melica spectabilis	0	0	t	1	0
Tragapogon pratensis	0	0	t	t	0
Taraxacum officinale	0	0	3	t	0
Bromus pumpellianus	0	0	3	12	0
Agrostis scabra	0	0	1	0	0
Antennaria rosea	0	0	1	0	0
Senecio triangularis	0	0	4	0	0
Agropyron smithii	0	0	2	0	0
Poa pratensis	0	0	27	28	5
Potentilla gracilis	0	0	7	14	20
Anemone multifida	0	0	7	3	4
Fragaria virginiana	0	0	8	21	14
Geranium viscosissimum	0	0	9	11	6
Stipa richardsonii	0	0	14	53	74
Heuchera cylindrica	0	0	0	t	0
Stipa columbiana	0	0	0	3	0

Table V. (continued)

Species	Compositional Gradient Segments I	II	III	IV	V
Potentilla diversifolia	0	0	0	7	0
Smilacina racemosa	0	0	0	4	5
Penstemon confertus	0	0	0	3	5
Equisetum fluvatile	0	0	0	5	8

t = 0.05% or less

Table VI. Average quadrat coverage values for all species occurring within the stands of each gradient segment in the North Fork Valley Grasslands.

Species	Compositional Gradient Segments				
	I	II	III	IV	V
Grindelia squarrosa	4.7	0.4	0	0	0
Sedum stenopetalum	1.3	1.6	0.5	0	0
Lithospermum ruderale	0.1	0	t	0	0
Berberis repens	0.1	0	0.1	0	0
Agropyron spicatum	21.5	16.0	7.2	1.3	0
Poa compressa	1.0	0.6	0.1	0.3	0
Calachortus apiculatus	t	0.1	0.1	t	0
Rosa acicularis	t	0.2	0.1	0	t
Phleum pratense	0.1	0	8.5	2.5	0.1
Arenaria congesta	0.1	0.8	0.3	0.4	0.4
Arnica fulgens	0.1	0.8	1.2	1.1	0.3
Potentilla glandulosa	0.2	0	0.8	1.5	0.8
Eriogonium umbellatum	0.3	2.2	2.0	2.5	1.3
Galium boreale	0.3	0.2	0.3	1.1	1.9
Eriogonium flavum	3.2	2.5	0.1	0	0.3
Koeleria cristata	0.5	0.4	0.6	0.4	0.1
Antennaria parviflora	0.6	1.2	1.3	2.1	0.1
Achillea millefolium	0.7	1.3	1.8	2.9	2.1
Festuca idahoensis	4.3	5.8	7.9	6.9	1.7
Arctostaphylos uva-ursi	0	t	0	2.1	6.4
Lupinus sericeus	0	0.6	1.2	0.5	0.6

Table VI. (continued)

Species	Compositional Gradient Segments				
	I	II	III	IV	V
Geum triflorum	0	1.1	0.4	1.8	5.3
Danthonia intermedia	0	5.2	2.5	7.0	5.5
Festuca scabrella	0	1.1	1.4	7.2	26.0
Campanula rotundifolia	0	0.2	0.3	t	0
Zigadenus elegans	0	t	t	0	0
Danthonia unispicata	0	2.6	1.4	0	0
Monarda fistulosa	0	0.7	2.4	0	0
Melica spectabilis	0	0	t	t	0
Tragapogon pratensis	0	0	t	t	0
Taraxacum officinale	0	0	0.1	t	0
Bromus pumpellianus	0	0	0.1	2.1	0
Agrostis scabra	0	0	t	0	0
Antennaria rosea	0	0	0.1	0	0
Senecio triangularis	0	0	0.2	0	0
Agropyron smithii	0	0	0.6	0	0
Poa pratensis	0	0	3.9	3.8	0.5
Potentilla gracilis	0	0	0.2	1.4	1.2
Anemone multifida	0	0	0.5	0.2	0.4
Fragaria virginiana	0	0	1.1	7.6	0.7
Geranium viscosissimum	0	0	2.4	1.5	1.2
Stipa richardsonii	0	0	2.1	5.8	13.5
Heuchera cylindrica	0	0	0	t	0
Stipa columbiana	0	0	0	0.1	0

Table VI. (continued)

Species	Compositional Gradient Segments I	II	III	IV	V
Potentilla diversifolia	0	0	0	0.9	0
Smilacina racemosa	0	0	0	t	0.1
Penstemon confertus	0	0	0	t	0.1
Equisetum fluvatile	0	0	0	0.2	0.2

t = 0.05% or less

Table VII. Results of Laboratory Treatment of Soil Samples.

Stand No.	WHC	PWP	ASM	% Sand	% Silt	% Clay	Classification
RP - F	54.9	16.6	38.2	29.4	43.5	27.1	Clay loam
1	17.8	7.2	10.6	86.9	9.1	4.0	Sand
2	38.7	10.6	28.1	26.4	50.2	23.4	Silt loam
3	31.7	10.7	21.0	73.8	20.7	5.5	Sandy loam
4	38.3	10.1	28.2	75.9	17.7	6.4	Sandy loam
5	24.0	7.0	16.9	76.0	17.0	7.0	Sandy loam
6	28.1	10.1	18.0	60.2	31.3	8.5	Sandy loam
7	43.1	9.0	34.1	52.9	36.5	10.6	Loam
8	31.6	12.6	19.0	77.7	16.2	6.1	Loamy sand
BP - F	16.8	5.7	11.1	51.9	33.4	14.7	Loam
9	44.4	13.4	31.0	40.5	49.9	9.6	Silt loam
10	39.6	9.0	30.5	53.4	31.4	15.2	Sandy loam
11	38.2	9.0	29.3	42.9	37.3	19.8	Loam
12	38.3	10.5	27.9	54.1	33.7	12.2	Sandy loam
13	42.1	13.1	28.9	32.7	42.9	24.4	Loam
14	47.0	13.2	33.8	49.1	39.1	11.8	Loam
15	24.9	10.1	14.8	54.5	32.9	12.6	Sandy loam
16	52.3	14.9	37.3	63.4	31.7	4.9	Sandy loam
17	32.7	14.8	17.9	43.9	31.5	24.6	Loam
18	36.5	14.6	16.9	53.9	36.1	10.0	Sandy loam
19	41.1	10.6	30.5	74.8	18.9	6.3	Sandy loam
20	44.0	11.9	32.0	59.9	26.3	13.8	Sandy loam
21	26.0	7.8	18.2	64.2	27.2	8.6	Sandy loam
22	27.7	9.5	18.2	55.2	32.3	12.5	Sandy loam
23	40.7	14.3	26.4	50.6	35.3	14.1	Loam
24	34.8	13.9	20.8	72.9	25.9	1.2	Loamy sand
25	54.0	15.2	38.8	50.6	42.9	6.5	Sandy loam
26	52.7	16.6	36.1	66.2	28.6	5.2	Sandy loam
27	36.4	12.3	24.2	52.1	31.1	16.8	Loam
28	34.3	10.4	23.9	64.8	24.7	10.5	Sandy loam
29	33.6	8.7	24.9	31.9	49.1	19.0	Loam
30	16.4	10.7	5.8	59.3	32.5	8.2	Sandy loam
31	38.5	12.0	26.6	45.0	38.9	16.1	Loam
32	30.0	7.2	22.8	65.9	21.1	13.0	Sandy loam
33	34.2	10.8	23.4	49.5	38.6	11.9	Loam
34	28.6	8.4	20.2	85.4	9.3	5.3	Loamy sand
35	26.0	9.5	16.5	43.8	43.0	13.2	Loam
36	27.4	6.6	20.8	49.0	42.8	8.2	Loam
37	71.1	21.8	49.3	36.9	55.4	7.7	Silt loam
38	45.1	10.9	34.2	68.0	23.1	8.9	Sandy loam
39	74.8	24.1	50.7	36.7	49.4	13.9	Loam
40	42.6	13.5	29.1	15.5	66.0	18.5	Silt loam
41	31.7	11.0	20.6	71.9	21.5	6.6	Sandy loam
42	41.6	11.4	30.2	41.2	44.7	14.1	Loam
LPP - F	41.9	16.1	25.7	34.8	51.0	14.2	Silt loam
43	38.6	23.6	15.0	44.6	49.8	5.6	Sandy loam
44	66.0	27.4	38.6	46.6	43.7	9.7	Loam
DCP - F	46.1	9.8	36.3	28.6	50.6	20.8	Silt loam
45	65.1	27.0	38.1	18.8	49.4	31.8	Silt loam

Table VIII. Polebridge Weather Data

Average Temperature

Year	January Maximum	January Minimum	July Maximum	July Minimum
1953	30.3	28.9	80.8	47.0
1954	18.2	15.2	81.8	42.5
1955	30.4	9.1	75.7	
1956	28.0	10.1	83.6	40.1
1957	14.8	-6.8	83.1	38.5
1958	33.9	22.1	82.9	45.7
1959	28.1	11.8	88.5	37.2
1960	25.4	5.5	90.6	45.5
1961	32.1	13.2	81.2	46.5
1962	20.2	-1.8	70.3	35.2
1963	17.7	-9.9	79.8	35.9
1964	31.9	15.5	82.9	41.4
1965	33.7	19.8	83.7	39.4
1966	30.4	12.7	83.4	39.6
1967	35.6	16.1	89.8	37.6
Average	27.4	10.8	82.5	40.8

Average Extreme Temperature

Year	January Maximum	January Minimum	July Maximum	July Minimum
1953	40	-10	96	34
1954	40	-42	95	28
1955	40	-12	93	23
1956	40	-28	95	31
1957	33	-44	95	28
1958	40	- 5	93	36
1959	44	-42	100	27
1960	47	-24	103	36
1961	44	-11	90	34
1962	48	-40	93	22
1963	40	-28	93	26
1964	44	- 8	96	30
1965	45	- 5	94	27
1966	44	-32	96	30
1967	49	-12	99	29
Average	43	-23	95	30

Table IX. Polebridge Weather Data

Percipitation

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1953	5.45	1.72	.80	2.41	1.75	2.93	.02	1.14	.81	.38	2.49	3.85	23.75
1954	7.21	2.26	1.94	2.77	.72	1.67	1.82	4.83	.97	1.01	1.51	.39	27.10
1955	.51	1.60	1.56	.54	1.08	1.34	1.93	.01	1.48	2.59	3.18	4.43	19.25
1956	1.88	1.73	2.05	1.76	1.41	2.23	1.90	1.04	1.10	1.24	.48	4.64	21.46
1957	1.99	4.78	.82	.87	2.30	3.72	1.13	.31	.30	2.49	.53	2.44	21.78
1958	1.93	2.60	1.09	1.78	1.12	3.03	1.76	.55	2.11	1.56	4.41	2.38	24.32
1959	4.48	2.40	.46	1.92	3.10	1.35	.08	1.23	4.18	2.20	4.97	1.41	27.78
1960	1.45	.47	1.63	.85	2.05	.51	.62	1.62	.37	.97	3.99	1.09	15.12
1961	1.62	3.38	.65	1.67	3.26	.49	.38	.31	1.77	2.72	1.11	3.34	20.70
1962	1.14	1.12	1.29	1.50	1.75	.29	1.41	.73	.58	1.12	1.04	4.00	15.97
1963	.63	1.94	1.32	1.50	1.75	2.15	.61	1.13	1.64	1.26	1.70	1.84	17.47
1964	2.70	.75	2.40	.47	2.80	3.78	.94	1.19	1.62	1.58	3.83	4.81	26.87
1965	2.95	2.40	.62	2.85	1.12	2.63	1.14	1.85	2.43	.32	1.91	2.16	22.38
1966	3.53	.63	1.66	1.04	1.30	5.23	1.71	.94	.86	2.11	4.15	2.18	25.34
1967	3.92	1.39	1.54	.54	.73	.94	.06	.02	.16	2.99	1.32	2.79	16.40
Ave.	2.76	1.94	1.32	1.50	1.75	2.15	1.03	1.13	1.36	1.64	2.41	2.79	21.71

Table X. Average values for environmental Data occurring within the stands of each gradient segment in the North Fork Valley grasslands.

	Compositional Gradient Segments				
	I	II	III	IV	V
Calcium*	1816.6	1705.5	1983.3	1756.6	1562.5
Magnesium*	500.0	439.8	533.3	485.3	585.0
Organic Matter**	53.0	62.2	62.7	62.5	51.5
Potassium*	231.7	164.4	197.7	241.7	241.3
Phosphorus*	46.0	26.2	34.4	42.2	34.0
Nitrate*	1.3	3.1	4.4	5.9	3.3
Ammonium*	20.0	22.2	23.3	23.7	20.0
Clay#	10.4	6.5	14.6	12.2	15.7
Silt#	31.9	33.2	37.8	37.4	44.6
Sand#	57.8	70.2	45.8	50.3	39.8
pH	6.0	5.9	6.1	5.3	5.9
Water Holding Capacity#	30.1	34.4	38.9	44.0	43.4
Permanent Wilting Percent#	10.6	10.9	14.0	14.5	12.1
Available Soil Moisture#	17.7	23.5	25.0	29.5	31.3

* indicates values expressed in pounds/acre

** indicates values expressed in tons/acre

# indicates values expressed in percent

Table XI. Results of Chemical Analysis of Soil Samples.

Stand No.	Ca	pH	OM	P	K	Mg	NO_3	NH_4
RP - F	1200	4.9	55	150	150	590	2	25
1	1400	6.0	50	30	160	380	1	20
2	1350	5.7	42	52	230	510	2	15
3	1500	5.2	60	22	175	450	2	20
4	1600	5.7	49	15	150	450	2	15
5	1150	5.7	46	25	140	400	1	20
6	1250	5.7	54	23	150	400	2	20
7	950	5.4	42	32	175	400	1	15
8	2000	5.8	66	18	150	400	3	25
BP - F	900	6.0	13	130	295	430	25	20
9	2400	6.3	61	14	160	450	5	25
10	1600	5.9	48	20	150	530	5	20
11	1600	6.6	46	15	150	700	10	20
12	1600	6.0	54	29	225	600	15	20
13	2100	7.1	50	13	240	670	5	20
14	1600	6.2	59	25	250	620	5	25
15	1400	6.1	47	25	185	580	15	25
16	2000	6.5	70	25	295	500	15	25
17	1700	6.1	70	35	200	490	10	25
18	1600	5.8	60	68	265	500	3	15
19	1600	5.8	60	21	175	500	1	20
20	1800	5.7	60	46	265	600	1	25
21	2000	6.5	42	28	220	490	1	25
22	1850	5.8	57	42	210	510	2	15
23	1650	5.9	59	122	475	500	1	20
24	2450	6.1	90	27	150	500	1	25
25	1300	5.8	78	51	175	380	2	25
26	1500	5.6	100	35	195	410	1	25
27	1600	5.7	59	79	350	510	3	20
28	1350	5.8	50	27	165	450	3	20
29	1400	6.0	37	30	150	500	2	20
30	1000	5.8	47	25	150	400	3	25
31	1600	5.7	55	41	260	510	2	25
32	1600	6.0	35	25	100	500	3	20
33	1400	5.8	50	16	150	510	3	25
34	2200	6.3	65	14	130	410	3	25
35	2900	6.6	39	10	115	600	3	20
36	850	5.8	34	35	135	400	3	15
37	2000	6.1	85	35	265	580	2	20
38	1600	5.7	54	45	290	510	15	20
39	1200	5.8	75	65	260	400	5	40
40	1700	6.0	51	14	195	700	1	20
41	1300	5.8	65	55	225	410	1	40
42	950	5.5	58	55	275	420	2	25
LPP - F	800	5.5	55	300	400	400	1	40
43	2400	5.5	100	68	225	600	2	20
44	4950	6.3	115	38	170	820	3	25
DCP - F	1300	5.7	49	74	285	400	1	20
45	3500	5.8	75	16	350	200	1	20

Table XII. Average quadrat frequency values for all species occurring within Artemisia tridentata stands in the North Fork Valley grasslands.

Species	I	II	III	IV	V
Artemisia tridentata	70	95	100	95	100
Rosa acicularis	5	0	0	0	0
Galium boreale	0	30	0	0	0
Zigadenus elegans	10	0	0	5	0
Festuca scabrella	95	35	100	100	0
Sedum stenopetalum	70	80	10	35	0
Calachortus apiculatus	100	70	100	75	0
Lomatium simplex	10	15	10	10	0
Geum triflorum	5	45	10	50	0
Heuchera cylindrica	0	0	5	0	0
Arenaria congesta	0	80	20	5	0
Campanula rotundifolia	15	0	10	0	15
Festuca idahoensis	100	100	100	100	10
Achillea millefolium	90	60	65	60	100
Agropyron spicatum	95	95	80	100	70
Eriogonium umbellatum	95	80	80	60	45
Antennaria parviflora	55	60	65	90	55
Arnica fulgens	75	60	65	95	45
Danthonia intermedia	15	5	55	95	65
Koeleria cristata	15	20	20	40	25
Stipa richardsonii	0	75	0	15	35

Table XII. (continued)

Species	I	II	III	IV	V
Poa pratensis	0	10	0	0	60
Poa compressa	0	30	0	0	100
Phleum pratense	0	10	0	0	95
Potentilla glandulosa	0	65	40	0	15
Taraxacum officinale	0	0	5	0	5
Anemone multifida	0	0	5	0	65
Stipa columbiana	0	0	0	0	5
Penstemon confertus	0	0	0	0	55
Lupinus sericeus	0	0	0	0	10
Fragaria virginiana	0	0	0	0	60
Agrostis scabra	0	0	0	0	5

Table XIII. Average quadrat coverage values for all species occurring within Artemisia tridentata stands in the North Fork Valley grasslands.

Species	I	II	III	IV	V
Artemisia tridentata	11.9	17.3	25.3	28.0	58.0
Rosa acicularis	0.1	0	0	0	0
Galium boreale	0	3.3	0	0	0
Zigadenus elegans	0.3	0	0	0.1	0
Festuca scabrella	6.8	3.5	10.4	23.1	0
Sedum stenopetalum	1.7	2.0	0.3	1.5	0
Calachortus apiculatus	2.5	1.7	3.1	3.2	0
Lomatium simplex	0.3	0.1	0.3	0.3	0
Geum triflorum	0.1	1.1	0.3	2.5	0
Heuchera cylindrica	0	0	0.1	0	0
Arenaria congesta	0	2.2	1.0	0.1	0
Campanula rotundifolia	0.4	0	0.3	0	0.4
Festuca idahoensis	16.3	12.8	26.4	25.0	0.3
Achillea millefolium	10.9	2.1	6.0	6.4	3.8
Agropyron spicatum	9.1	28.4	2.0	8.1	4.9
Eriogonium umbellatum	5.5	2.0	3.3	2.8	3.6
Antennaria parviflora	3.3	2.1	4.1	8.5	2.0
Arnica fulgens	2.5	1.5	1.6	9.9	1.3
Danthonia intermedia	0.4	0.1	2.0	9.8	2.3
Koeleria cristata	0.4	0.5	0.5	1.6	0.5
Stipa richardsonii	0	2.5	0	0.1	0.9

Table XIII. (continued)

Species	I	II	III	IV	V
Poa pratensis	0	0.3	0	0	4.0
Poa compressa	0	1.4	0	0	25.5
Phleum pratense	0	0.3	0	0	3.0
Potentilla glandulosa	0	1.6	2.2	0	0.1
Taraxacum officinale	0	0	0.1	0	0.1
Anemone multifida	0	0	0.1	0	3.5
Stipa columbiana	0	0	0	0	0.1
Penstemon confertus	0	0	0	0	1.4
Lupinus sericeus	0	0	0	0	0.9
Fragaria virginiana	0	0	0	0	7.6
Agrostis scabra	0	0	0	0	0.1

Table XIV. Overall environmental averages for three community dominants in the North Fork Valley grasslands.

	Forest Ave.	Prairie Ave.	Big Sage Ave.
Organic Matter	43.0	60.6	48.6
Phosphorus	163.5	36.1	19.6
Potassium	316.5	212.5	148.0
Calcium	1050.0	1786.5	1440.0
Magnesium	475.5	497.5	496.0
Nitrate	4.8	4.3	4.0
Ammonium	26.2	22.6	19.0
pH	5.4	5.9	5.9
Permanent Wilting Percent	12.1	10.5	9.0
Water Holding Capacity	39.9	36.6	33.6
Available Soil Moisture	27.8	26.1	24.5
Sand	36.1	53.2	61.6
Silt	44.6	28.8	26.9
Clay	19.2	18.0	11.4