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Analysis of Subalpine Grasslands in Western Montana

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INTRODUCTION

The occurrence of treeless grassland areas in the subalpine forests of the temperate zone has long been recognized as being an unusual phenomenon. Many people have speculated on the origin of these predominantly grassy sites and the forces that maintain them. In a forested region trees are the dominant climax vegetation and, of course, one would expect to find trees invading those sites seemingly suitable for their development. On these sites, however, invasion does not appear to be taking place, and the question often asked is "why?".

In spite of many apparent inconsistencies from site to site, the majority of these grasslands are well-drained, upland areas, variously referred to as "balds" or "mountain parks." Although the term "subalpine meadow" has also been used by some in this connection, this term is usually used to refer to the wet meadows found in high mountain valleys, where sedges predominate. Such wet meadows are not included in this study.

Recent attention has been focused on the grassland balds occurring in the Great Smoky Mountains of North Carolina and Tennessee. For example, Wells (1936a, 1936b, 1937, 1946, 1956, 1961) believes the balds were established by the local Cherokee Indians who, according to him, maintained them to attract wild game which they hunted. Some mountain sites which were cleared by white settlers to grow crops and provide pastureland for their stock have become bald-like, but according to

Camp (1931), the soil development indicates that the balds were in existence long before white man's settlements. Mark (1958) and others think their occurrence is a natural one. Extensive studies have been conducted to determine how the Appalachian balds originated and how they are maintained.

The grassy balds of the Rocky Mountains, however, have received little serious attention and little is known about their occurrence. The primary objectives of this study were twofold: (1) to collect, preserve and identify the plants found on these grassy sites and to establish the distributional patterns formed by their communities, correlating these associations with slope, exposure, surface and soil temperatures, and soil moisture regimes; and (2) to establish the stability of the balds by determining if they are being invaded by forest species.

Review of the Literature:

The grassy balds found as islands within the subalpine spruce-fir forest have a variability of composition and structure. This variability has led to numerous investigations concerned with the origin and maintenance of these grassy balds.

One of the earliest investigators to consider this question was Rydberg (1915). Although he felt that the soil could be too alkaline or too saline for tree growth, he found that this explanation was not always adequate. He concluded that once the grasses became established as pioneers following forest destruction by fire, etc., they could inhibit the establishment of the forest, even where soil and moisture regimes were favorable for seedling establishment.

Wells (1937) also advanced the theory that competition is a major factor in the maintenance of grassy balds. In his Appalachian Mountain study areas, he believed that the competition of *Danthonia compressa* was sufficient to prevent the invasion of tree species.

Wells has a different opinion, however, on the origin of the balds. He believes (1936a, 1936b, 1937, 1946, 1956, 1961) that these grassy areas were originally created by the Cherokee Indians, who destroyed sections of the forest as a means of luring the grazing deer and elk which were their livelihood.

Others have also speculated about the influence of man on the balds, suggesting that the early settlers destroyed the forest along Appalachian ridges in order to create a grazing range for their livestock (Camp, 1931). Although Camp admits that grazing and fire have significantly changed these balds, he believes that not they but men were the causal agents.

Cain (1931) concluded that the soils are so well developed that they probably could not have been created since the beginning of white settlement. Camp (1931) agrees, but goes on to present the hypothesis that these balds were originally more heath-like than grassy. He points out that some heath balds occur within the limits of the spruce-fir zone but on more northeastern exposures than the southwest grassy balds.

The overall climate of these balds is favorable for the development of trees, but occasional periods of extreme drought in midsummer terminate the development of tree seedlings, thereby limiting the character of the grassy balds (Camp, 1931).

In 1936 Clements makes a distinction between the Appalachian "balds" and the "parks" of the Rockies. He suggests that fire is the underlying factor which has maintained the Appalachian balds. On the other hand, he describes the Rocky Mountain parks as being "well-developed on warm, dry slopes where compensation is usually afforded by a sandy or rocky soil."

Brown (1941) in his analysis of the vegetation of Roan Mountain [Appalachians] stresses the importance of periodic drought. He points out that there have been floristic changes quite recently and attributes the invasion of rhododendron, conifers and alders to a "shortening of dry periods at critical times." Brown also recognized the possible importance of domestic grazing as being a factor in the expansion of the balds.

Daubenmire and Slipp, in their 1943 study of plant succession on talus slopes in northern Idaho, conclude that the xeric condition of the southern exposure prevents the invasion of spruce and fir. Moreover, they point out that the dryness of the southern slopes reflects very little snow accumulation and high surface temperature. Since these southern slopes are bare for a greater period of time, they become very dry.

Soil temperature may also be significant. Daubenmire (1943) suggests that where the soil is fine-textured or compacted the physical characteristics of the soil may prevent the rapid penetration of seedling roots. And, he believes, "the progressive drying out of the soil from the surface downward overtakes the root tips before they reach a relatively permanent supply of moisture contained in the subsoil." However, where the soils are coarse, over-drainage may be the problem. Daubenmire also claims in the same study that studies in grassy balds dominated by _Agropyron spicatum_ and/or _Festuca idahoensis_ in the Bitterroot Mountains have shown that the moisture content of these soils is below the wilting coefficient for a long period in summer, although the soils in the adjacent forests remain more mesic during most if not all of the year.

An experiment to see if grassy balds would support trees was conducted by Brown (1953) on his Roan Mountain study areas. He transplanted blocks of soil containing well-established spruce and fir seedlings to the summit of Round Bald in the Appalachian Mountains. Barriers were constructed around half of the transplants, preventing mechanical injury by livestock. After several years Brown concluded that Round Bald was capable of supporting both spruce and fir and that the seedlings protected from livestock and shielded from the wind did significantly better.

According to Whittaker (1956) the south-facing orientation of the Appalachian balds suggests that climatic factors are critical. In fields which have been cleared, invasion is better along the north and east ridges. Water runoff, exposure and strong winds from the west contribute to the unfavorable moisture-balance which has eliminated trees from the grassy balds.

Billings and Mark (1957) allege that all grassy balds occur near the upper or lower altitudinal limits of a forest type zone. The balds, they contend, have an ecotonal status, and along such a marginal zone tree seedlings do not easily become established once the forest has been destroyed. In addition, competition, climatic extremes, inadequate seed source and grazing have all helped to maintain these sites as grassy balds.

Mark (1958), who has done the most comprehensive study on the origin and maintenance of grassy balds of the Appalachian Mountains, refutes the hypothesis that periodic drought is responsible for their existence. He states that "published observations...indicate that the herbaceous vegetation is much more vulnerable to drought than are the trees growing either as regeneration on the balds or as mature trees in the adjacent forest." The soils of the balds and adjacent forest, according to Mark, are chemically and physically similar; comparisons of environmental data from balds and recently cleared forest are not substantially different. According to Mark, a post-Wisconsin xerothermic climate fluctuation moved the hardwood-conifer ecotone upward 300-1,000 feet above its present position. Then, subsequent cooling seemed to have caused a bald-susceptible zone along the ecotone. He also suggested that previous "biotype depletion" in spruce and fir may have hindered the invasion of these species into relatively open land left by climatic degeneration of the upper deciduous forest.

The maintenance of these balds is complex and includes the influence of the severe, open climate, the lack of conifer seed source, the elimination of conifers capable of migrating to more xerothermic sites, and the grazing by native and domestic stock (Mark, 1958).

Secor (1960) tried to determine the possible influence of volcanic ash upon bald distribution of Gisborne Mountain in the Kaniksu National Forest, Idaho. It had been suggested that the strong winds in the area might be making the habitat too xeric for spruce and fir by drying out the soil; it was also known that the volcanic ash had been unevenly distributed in the area. The effect of this important soil constituent was found to be negative: no correlation between volcanic ash content of the soil and bald occurrence was found.

In his study of the grassy balds of the Bunya Mountains, Australia, Webb (1964) has rejected the hypothesis which many hold that the balds are man-caused. Many have attributed the Australian balds to the regular burning of the forest by Aborigines when they roasted Bunya nuts each fall during their annual festival. Instead, Webb states that there has been a climatic change. The previous cool-moist climate has changed to a more xerothermic one. The original temperate rain forest has survived with drastic floristic modification only in sheltered gullies moistened by fog-drip.

Patten (1963) conducted a study to determine the "influence and interaction" of light and temperature on the germination of Engelmann spruce (*Picea engelmannii*) seed and to relate species position to forest advance into subalpine grassy balds. He found that there was a differential germination response to increasing temperature. He was surprised, however, to find an increased spruce germination in light since it requires no light for germination. Patten speculates that the light may be converted into heat within the seed or that the light may speed a conversion of some reactant, by way of a red-absorbing pigment, that stimulates germination. While spruce seedlings can germinate in darkness if temperatures are optimum, they are apt to die within the forest where it is cool as well as dark. But on the forest margin where there is adequate light and the soil temperatures are more favorable, they survive best.

It can be seen from the opinions set forth above that, while there is agreement on some factors (namely temperature and drought) involved in the origin and maintenance of grassy balds, there is no common belief in a single set of causal factors.

DESCRIPTION OF STUDY AREA

Location:

The study area consisted of 19 grassland sites concentrated in three separate locations in the Bitterroot Mountains, which run along the Idaho-Montana border west of Missoula, Montana (see Figure 1). All the sites were within Lolo National Forest.

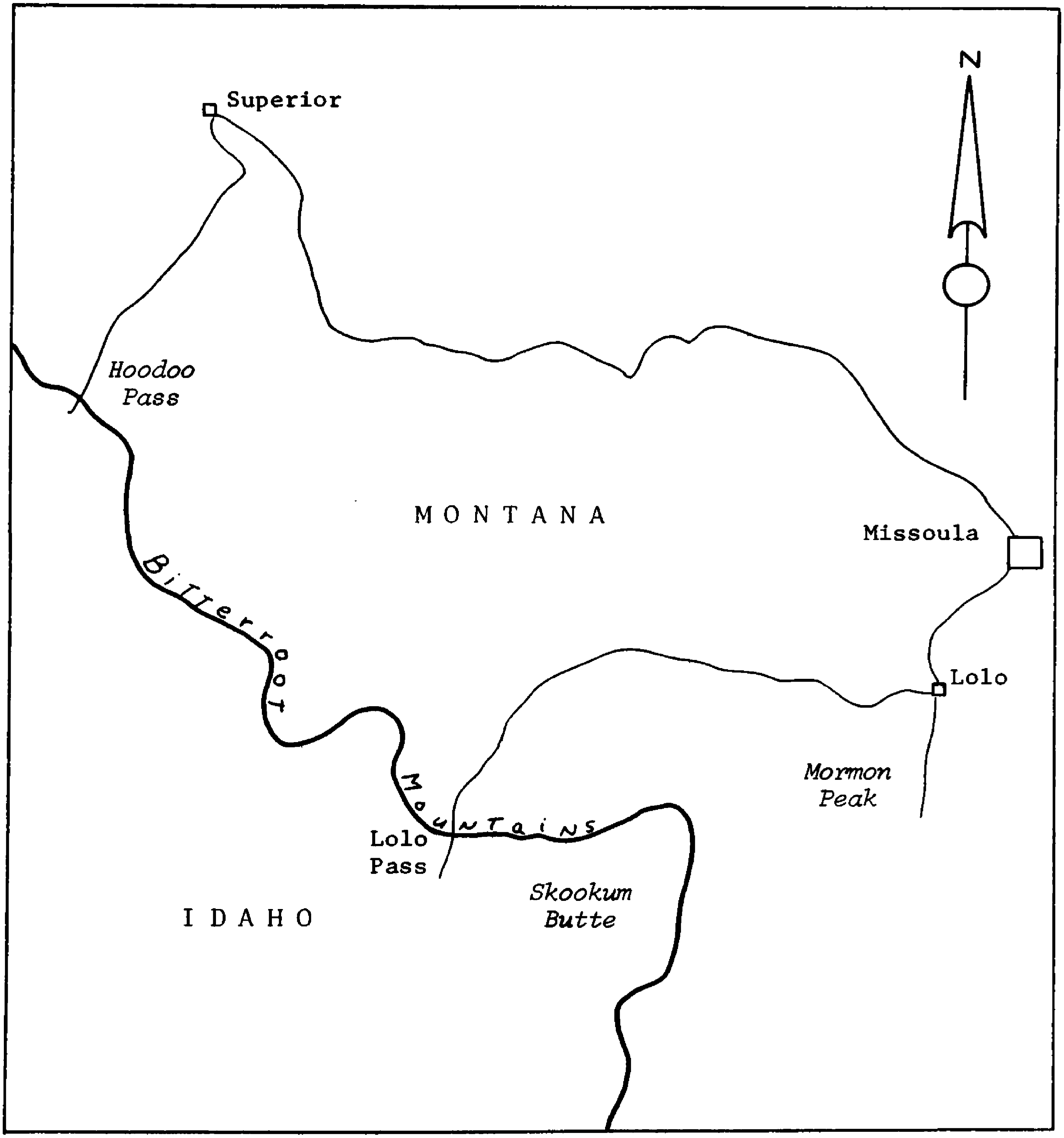
The first of these general locations was in the vicinity of Skookum Butte, along the Elk Meadows Road at the Idaho-Montana border 15 miles west of Lolo, Montana. Of the ten grassland stands studied here, three were about a mile distant from the other seven.

The second general location, consisting of seven grassland stands, was just below the Mormon Peak Lookout Tower (elevation 6,100 feet), 12 miles west of Lolo, Montana, on the Mormon Peak Road.

The third area, north of the other two, was west of Superior, Montana in the vicinity of Hoodoo Pass (elevation 6,250 feet). Two grasslands were found here: one two miles from Hoodoo Pass on the Trout Creek Road, and the other on a spur road leading to the Gildersleeve gold mine.

The study areas fall within the subalpine forest zone (5-7,000 feet). This zone is characterized by forests composed of Engelmann spruce (Picea engelmannii), subalpine fir (Abies lasiocarpa), the climax species--and by western larch (Larix occidentalis), lodgepole pine

Figure 1. Map of the Study Areas.



(Pinus contorta), whitebark pine (Pinus albicaulis), ponderosa pine (Pinus ponderosa), and Douglas fir (Pseudotsuga menziesii) which function as seral or subclimax species, depending on the site and amount of disturbance.

Geology:

The Bitterroot Mountains, location of the study areas, were formed by massive vertical movements of the earth. In these movements, known as "block faulting," huge sections of land were displaced thousands of feet higher or lower than adjoining sections. As the rocks were broken the general trend of the faults was approximately south to north, thus forming the mountain ranges which are part of western Montana's topography today. It is seldom that one can see the actual planes of the faults, because layers of alluvial matter have filled in and hidden most of the signs of breakage. The Bitterroot Range, as part of these block-fault mountains, was formed mostly during the middle Tertiary Period, although the movements of the earth are believed to have continued into the late Tertiary and even into the early Pleistocene Period (Perry, 1962).

Interestingly, the soils of each of the three general study areas have been formed from different parent materials. The Mormon Peak balds are part of the Ravalli Formation, consisting mostly of quartzite or sandstone and thin-bedded argillites. Characteristic of this formation are steep slopes covered with rough broken stones (Perry, 1962).

The Hoodoo stands are located in what is called the Newland Formation, part of the same collection of sediments as the Ravalli Formation. It is characterized by thin-bedded siliceous and calcareous shales, and by limestones which form "molar-tooth structures" on weathered surfaces (Perry, 1962).

The Skookum Butte stands differ from the others in being underlain by igneous rocks, batholiths chiefly of quartz monzonite (Perry, 1962).

Climate:

General comments about the climate of the subalpine zone can be misleading. The subalpine is a mountainous zone containing abrupt changes in the topography which create a mosaic of microclimates. Factors such as slope steepness and exposure to the sun vary greatly from site to site, and these variations are what create the individual microclimates. For example, on northern slopes snow is apt to melt much more slowly in spring than on southern slopes which receive more direct insolation. Thus on the northern side of a mountain peak, water is more plentiful because of the slower rate of snow melt and the cooler ambient temperatures.

Accurate information on the climate of specific study areas was difficult to find, because the nearest weather stations (Lolo Hot Springs and Superior) were situated below the subalpine zone. However, in the general study areas the mean minimum temperatures for January and July are 12° and 46° F. respectively; the mean maximum temperatures for the same months are 32° and 82° F.

The average precipitation for the Mormon Peak stands is approximately 20 inches per year; for the other stands the precipitation is much higher--approximately 60 inches per year (U.S. Weather Bureau, 1963). The subalpine is characterized as a zone of abundant snow accumulation--the snow covers the ground early in the fall and usually prevents the development of a deep frost. Temperatures above the snow, however, often fall below zero, and evidence of winter pruning can be seen on many of the shrubs which protrude above the snow.

Description of Balds:

The balds appeared as isolated grassland islands partially or completely surrounded by forest. The Mormon Peak balds were the most open, extending hogback fashion out of the forest.

Each bald was situated on a more or less south-facing slope. Slope steepness varied from 5 to 40 degrees. With the exception of two sites (one at Hoodoo Pass and one at Skookum Butte), there were patches of bare ground in the meadows and large rock outcroppings were common. It was noticed that, with the exception of the Mormon Peak balds, alder swales and the abundant water associated with them were adjacent to, or extending into, most of the dry grassland areas. Interestingly, several balds were situated below alder swales, without any apparent vegetational pattern indicating an increase in the amount of available moisture.

In many of the areas a narrow transition zone of low shrubs and other intermediate vegetation separated the grassland from the forest.

The forest itself varied to some extent from location to location. For example, at the Skookum Butte area the forest vegetation was the most typically subalpine. The surrounding area was covered with large Engelmann spruce and subalpine fir, interspersed with whitebark pine and lodgepole pine. The transition zone between the forest and the bald was predominantly *Xerophyllum tenax* and *Vaccinium spp.*

The Hoodoo Pass area was similar to the Skookum Butte area, except that there were large stands of western larch mixed in with the spruce, fir and pine. The transition zone was mostly *Vaccinium spp.*

Mormon Peak was the most open and park-like of the three areas. The sandy texture of the soil and the climax of ponderosa pine on the periphery of the southern slope made the overall appearance of this area quite different from the others along the stateline, and indicated that this was actually an upward extension of xeric forest zone communities. The soil was noticeably hot and the occurrence of trees almost exclusively along the drainage pattern immediately gave the impression that this was a dry site in midsummer.

METHODS AND PROCEDURES

Field Methods:

During the period of July, August and September, 1967, a study of the vegetation and microenvironment of subalpine grassy balds in the Rocky Mountains was conducted.

The location of suitable stands was a problem. One important requisite of the balds was that they be ungrazed by domestic animals, at least within recent years. Since it has been common practice for ranchers to pasture their cattle in the subalpine during the summer months, several otherwise suitable sites were not included in the study because they had obviously been grazed. Most of the balds studied were in places where cattle did not have easy access, or on steep slopes where grazing would have been difficult.

It was originally hoped that a sufficient number of balds could be located which were completely surrounded by forest, making them grassland islands within the forest. Although most of the balds did meet this criterion, there were some that did not. However, since these areas were surrounded on three sides by trees and sparsely on the fourth, they were considered similar enough to be included with the others.

The 19 stands sampled were picked as homogeneous units as nearly as could be determined by visual inspection. After the boundaries of each stand had been selected, the spacing of the quadrat samples was determined. Where space permitted, the quadrats were placed at 20-foot intervals along a straight line perpendicular to the slope. A heavy wire frame (20 x 50 cm) quadrat was used in obtaining both frequency percentages and canopy-coverage of each species occurring in the selected stands. Daubenmire's canopy-coverage method (1959) was generally employed.

The quadrats were always placed on the lower side of a 100-foot tape. Whenever the quadrat fell on bare ground, a large rock, or some other irregularity, the station was skipped and another selected. Species occurring in each quadrat were recorded on field data sheets. The canopy-coverage of each species occurring within the quadrat at each station was estimated as one of six classes as indicated below:

Class 1 -- up to 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

The midpoint of each class was used in summarizing the canopy-coverage classes. Class summaries were totaled and divided by the number of quadrats sampled to obtain the average percent canopy-coverage of each stand for each species.

The slope, exposure and elevation of each stand were recorded. An inclinometer was used to measure the slope. Where the aspect was uniform several representative readings were averaged. On slopes not so consistent a series of 4-5 readings were recorded on a freehand sketch of the slope. Exposure and elevation were measured by compass and altimeter respectively.

At every fifth point soil samples and temperature readings were taken. Temperatures were recorded for -4 inches, -1 inch, ground surface and air. Because the midday temperatures in the subalpine differ so markedly from the early morning and evening temperatures, each stand was sampled as nearly as possible at midday to make the readings more comparable. The soil samples were collected at -2 inches to -4 inches below the ground surface, in small airtight jars, for the purpose of determining the soil moisture. Additional soil, representative of each stand, was put into paper bags. These soils were air dried and then sieved through a 2 mm screen.

Laboratory Methods:

A portion of each soil sample was sent to the University of Wisconsin Soils Testing Laboratory where the following procedures were used to analyze the samples (Blinn, 1966):

1. Calcium and magnesium were extracted with 1N NH_4OAc and determined flame photometrically using the Coleman Model 21.
2. Phosphorus and potassium were both extracted with Bray P_1 solution. Phosphorus was determined colorimetrically using ammonium molybdate to develop color. Potassium was determined by flame photometric procedures.

3. Organic matter was determined by modified wet digestion using a $Na_2Cr_2O_7$ - H_2SO_4 mixture. Final analysis was made colorimetrically for the chromate color.
4. Nitrate was extracted with water and determined semiquantitatively with the visual brucine-yellow color.
5. Ammonium ion was extracted with 0.3N HCl and determined semiquantitatively using visual color developed with Nessler's reagent.

Soil moisture measurements were determined using the pressure membrane technique in the soil laboratory of the University of Montana School of Forestry. Water holding capacity (WHC) was measured at 1/3 atmospheric pressure and the "permanent wilting percentage" was determined by subtracting the "permanent wilting percentage" from the water holding capacity. A mechanical analysis of the soils was done by the hydrometer technique to determine the proportion of sand, silt and clay in the soils. Soil particles larger than 2 mm were discarded.

The quadrat data were used to determine frequency values for each species in each of the stands. Average coverage percentages were also calculated. Post-index forms were employed in summarizing the data from each stand.

Initial efforts in analyzing these community data involved the use of the ordination methods described by Bray and Curtis (1957) and Beals (1960). In developing this ordination, indices of similarity were calculated using all species that occurred in two or more of the study areas. A two-dimensional arrangement of the stands was developed and further effort was directed towards discovering and interpreting community/environment interrelationships.

Several of each of the species found in the stands and in the immediate vicinity were collected as voucher specimens. The nomenclature follows that of Hitchcock *et al*. (1955, 1959, 1961, 1964) for the Dicotyledoneae and Hitchcock and Chase (1950) for the Gramineae. The rest of the Monocotyledoneae follow Davis (1952) or Moss (1959).

RESULTS

Vegetational:

Approximately 125 species of plants were encountered on the grassy balds. Many of these species were found only once or twice and are therefore thought to have only a limited importance to the communities in which they were found. Frequency percentages for 60 representative species occurring in more than one stand were used to construct a two-dimensional ordination of the 19 study stands, following the methods described by Bray and Curtis (1957). Total frequency (100%) was divided into five classes of 20% each (1-20%, 21-40%, etc.) and a series of appropriate circles were selected to aid in the graphical representation of frequency values for each species. These quartiled frequency values were plotted within the ordination as an aid in interpreting species distribution patterns (see Figure 2).

The ordination method employed is used by ecologists to arrange plant communities on the basis of their vegetational similarity and dissimilarity. Ordering in this way arranges the stands along axes so that the most dissimilar stands are spatially the most distant and the remaining stands are distributed between these. This ordinational procedure can be repeated until the stands form a 2- or 3-dimensional array, whichever is appropriate. Climatic, edaphic and successional features, which are reflected in the community composition, can often be more fully understood and better interpreted and illustrated when they have been objectively ordinated. Such an analysis is valuable for its insight into factors determining or controlling the kinds and abundance of the species composing a series of communities.

Soil moisture appears to be highly correlated with the primary axis of the ordination. The Mormon Peak stands, which receive only about 20 inches of annual precipitation (U.S. Weather Bureau, 1963), are on the dry end at the left. The more mesic end of this primary axis is occupied by a stand at Skookum Butte. This latter stand, which was clearly unusual, was flanked on the top and one side by Alnus communities. The soil in this stand contained nearly double the moisture of those soils on adjacent bald sites (8.3% for the end stand as opposed to 4.2% for the other bald sites). The alder site and grass bald met with no apparent transition zone. It was apparent, however, that since the alders were adjacent to the bald, there was possibly some seepage of water from the swale into the bald.

If the Mormon Peak stands are eliminated from the ordination because they represent the extension of the Palouse Prairie, the remaining stands align themselves along the Y-axis. Comparisons with environmental and soil data do not reveal what this axis represents, although it does seem to reflect internal variation among the Stateline stands. It is probably a composite of environmental factors.

Ubiquitous species have a wide range of environmental tolerance and consequently may occur in many different habitats. Species found in at least 60% of the stands of both Mormon Peak and the Stateline stands were considered ubiquitous. Those exhibiting this type of distributional pattern were: *Achillea millefolium*, *Agropyron spicatum*, *Arenaria congesta*, *Festuca idahoensis*, and *Hieracium albertinum*.

While some species can be found in a variety of locations, others were restricted to a limited number. Those species found only on Mormon Peak are the following: *Agoseris glauca*, *Allium cernuum*, *Arnica fulgens*, *Artemisia dracunculus*, *Artemisia ludoviciana*, *Balsamorrhiza sagittata*, *Bromus tectorum*, *Collomia linearis*, *Danthonia unispicata*, *Koeleria cristata*, *Orthocarpus tenuifolius*, *Phacelia lineralis*, *Poa secunda*, *Sisymbrium altissimum*, *Stipa williamsii* and *Tragopogon dubius*.

An even larger number of species were restricted to the Stateline stands and are as follows: *Agrostis diegoensis*, *Amelanchier alnifolia*, *Aster intergrifolius*, *Berberis repens*, *Calamagrostis canadensis*, *Calamagrostis rubescens*, *Calochortus elegans*, *Carex geyeri*, *Danthonia intermedia*, *Elymus glaucus*, *Erigeron peregrinus*, *Eriogonum flavum*, *Erythronium grandiflorum*, *Juncus parryi*, *Melica spectabilis*, *Penstemon albertinus*, *Phlox caespitosa*, *Polygonum phytolaccaefolium*, *Senecio integerrimus*, *Spiraea betulifolia* and *Xerophyllum tenax*.

In the study areas, some species occurred in only a few stands while others occurred in a majority of the stands. At Mormon Peak the species found in the majority of the stands were: *Achillea millefolium*, *Agropyron spicatum*, *Antennaria umbrinella*, *Arenaria congesta*, *Balsamorrhiza sagittata*, *Bromus tectorum*, *Collomia linearis*, *Erigeron speciosus*, *Festuca idahoensis*, *Koeleria cristata*, *Lupinus spp.*, *Orthocarpus* tenuifolius and Tragopogon dubius.

At the Stateline stands the following species were found in a majority of the stands: Agropyron spicatum, Carex geyeri, Erigeron peregrinus, Phlox caespitosa and Polygonum phytolaccaefolium.

The distributional patterns of Polygonum phytolaccaefolium and Xerophyllum tenax demonstrate how comparatively large, transition zone species may occur in the sampling. Xerophyllum is an important understory species in the spruce-fir forest. It is capable of extending itself into more xeric habitats than either the spruce or fir and for that reason it is an important component of the transition zone. Where suitable microhabitats occur within the balds Xerophyllum may also be found. Polygonum and Xerophyllum were encountered in the sampling even though these species do not have a high frequency within the balds. The canopy-coverage whenever they were encountered was high.

It should be mentioned that Agrostis diegoensis occurred in stand #10 at Hoodoo Pass. This species was not included in the ordination because it was only found in one stand. At this site, however, it was the dominant grass with a frequency of 90% and canopy-coverage of 55.3%. It was previously mentioned that in many of the stands as much as 1/3 of the ground was bare. Where Agrostis diegoensis was found, however, there was a large accumulation of ground litter. The litter formed an estimated 2-4 inch mat above the soil throughout the entire bald. It was only with much labor that this litter layer was penetrated so that soil samples could be obtained. This litter must have taken many years to accumulate to such a depth and probably this area had not been burned for a number of years.

Environmental:

At the beginning of the study, the Stateline area was still characterized by lingering snow patches and frequent rain showers. In early July, on my initial visit to the Skookum Butte area, the mountain road was still blocked by snow drifts. There was an abundance of snow patches throughout the forest, and while I was there it rained steadily for over an hour. Although this visit was only for orientation, and no environmental data were recorded, I think it is safe to assume that there was an abundance of moisture available to the grassy balds in this area up through June.

Four temperature readings (air, soil surface, -1 inch below surface and -4 inches below surface) were taken weekly at the same six stations in stands #2 and #3. Soil samples were also taken at each station and the percent soil moisture calculated for each. The weekly soil moisture data for these two stands (Figure 3) show that the soil moisture was quite low (4-8%) during the month of July. August is typically the driest month in western Montana, and these data reflect this dryness. Readings for August 24, 31 and September 7 were taken when the forests were officially closed because of the 1967 drought.

For these two stands where weekly soil moisture readings were taken, there appears to be no significant change in percent soil moisture during the dry spell in August, not even when the temperature dropped significantly on August 24 (see Figure 4). The data here also show that the hot, dry season did not terminate because of the rain during the week of September 7-14. Although, as Figure 3 shows, the soil moisture percent rose to 11% for stand #2 during the rain, it quickly dropped below 8% again afterwards.

The soil and surface temperature values for stands #2 and #3 reach their peaks in the second and last weeks in August (see Figure 4). The data demonstrate a soil temperature lag with increasing soil depth. Because soil is a poor conductor of heat (Billings and Mark, 1957), the soil at -4 inches responds more slowly to changes in temperature and thus is more stable with respect to temperature. A comparison of the soil temperatures at these two weekly stands reveals striking similarity for the -4 inch temperatures, as shown in Figure 4. Furthermore, the temperature curve for -4 inches is almost identical even though there are wider differences among the -1 inch and surface temperatures.

Data from stand #2 show that there is a progressive increase in soil moisture from the highest station (5.1% soil moisture) within the stand to the lower stations (6.7%). This progressive increase creates a moisture gradient which seems to be based on the slope of the bald (33°). The lowest station is an exception because it shows a decrease from the 6.7% of the stations immediately above it to 5.8%. This exception in the otherwise consistent gradient may be due to the sharply increased slope (39°), and consequent increase in runoff, at the bottom of the bald; it may also be because the bald dropped off abruptly in cliff-like fashion immediately below this moisture sampling station.

The slopes supporting the grassland balds of the study areas in general varied from 5° to 40°, with an overall average of 18°.

For the remaining 17 stands, soil moisture and temperature readings were taken only at the time of sampling. These data are not comparable, because they were taken on different days and in different places. However, it may be significant to note that average soil moisture for these stands was only 5.9%. The Mormon Peak area receives considerably less precipitation than the subalpine areas farther to the west, and the grassland vegetation is essentially an upward extension of the lower valley grasslands. The lowest soil moisture reading was 1.6% in the Mormon Peak area (on July 24), and the highest was 15.1% at Skookum Butte (on September 13).

One observation which seems important is that, with the exception of the Mormon Peak stands, nearly all of the subalpine balds are adjacent to, or not far from, an alder swale. In the spruce-fir zone, the mountain alder (Alnus sinuata) develops communities only where subsurface and often surface water is abundant. In several cases alder swales were located uphill in relation to the adjacent grassy balds. Soil moisture samples taken in a swale and in an adjoining bald on the same day were substantially different; the swale soil contained nearly 24% water by weight and the bald about 8% water.

The results of the chemical analysis of the soils are listed in pages 44 and 45. These results have been quartiled for each category: the highest value was divided by 4 and each quartile represented by an appropriate circle (see Figure 5).

This analysis of the soils reveals that the Mormon Peak stands are very similar to each other, but generally quite different from the Stateline stands. The Stateline bald sites in general are edaphically similar to the adjacent forest sites. Average soil characteristics of Mormon Peak and Stateline areas have been calculated; the Mormon Peak averages are based on data from stands #4-#9; the Stateline values include stands #1-#3, #10, and #12-#19. One stand, #11, has been omitted from these averages because it is edaphically more like Mormon Peak, yet occurs geographically along the state line.

The data show that calcium, magnesium and potassium reach their highest values at Mormon Peak, where calcium averages 1,775 lb/A, magnesium 648 lb/A and potassium 458 lb/A. These three minerals occur in lower quantities along the Stateline; here calcium is only 1/3 as great (525 lb/A), magnesium is also about 1/3 as great (213 lb/A) and potassium is less than 1/2 as great (208 lb/A).

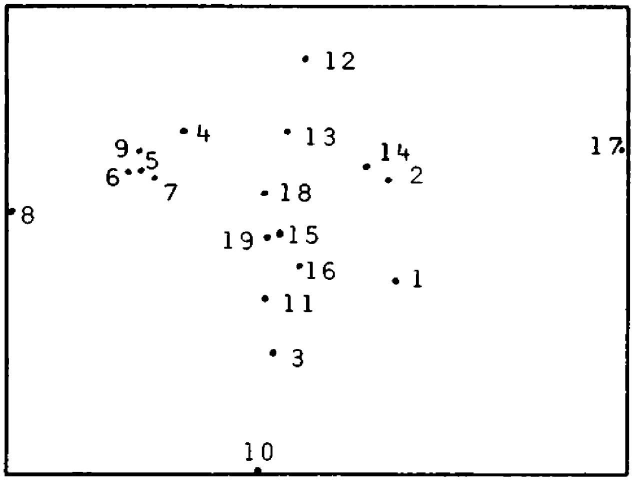
The abundance of calcium, magnesium and potassium is probably a result of the weathering of the parent material (mostly quartzite and sandstone). The "pumping" of calcium by grasses is well known and may in part be responsible for the high concentration of this mineral in the upper soil layers of the study stands. The lower acidity in the Mormon Peak soils compared to the Stateline stands probably is the result of the high cation concentration (especially calcium) in these stands. The high availability of phosphorus among the Stateline stands is thought to be a result of the weathering of a parent material higher in phosphorus than the parent material found on Mormon Peak.

The soils found in the balds are classed as either sands or sandy loams (see Figure 5) (Eyre, 1963). They were, however, very high in organic matter--so much so that some were still dry after they had been "soaked" in water for 48 hours while the "permanent wilting percentage" and the water holding capacity were being determined. Ethanol had to be used as a wetting agent in order to saturate the soils with water. The chemical analysis confirms this high organic matter: the bald soils contained an average of 67 tons/acre organic matter. The organic matter represents approximately 6.7% of the soils with a high of 9.0%, using 1,000 tons as the weight of a surface-acre slice (Lyon, Buckman and Brady, 1952).

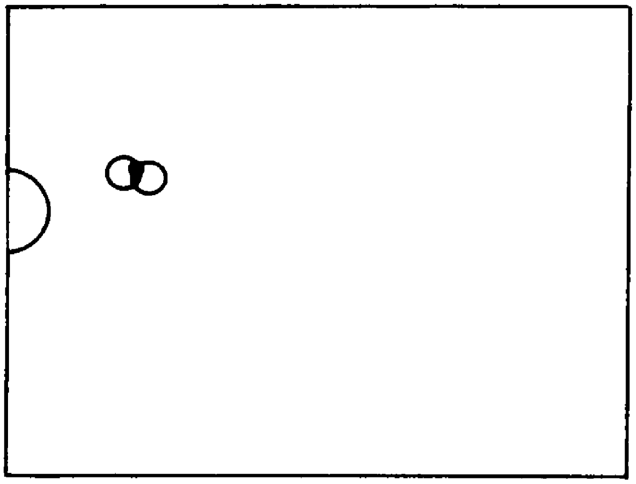
Organic matter is higher among the Stateline study areas (71 tons/A) than in Mormon Peak sites (56 tons/A). The water holding capacity (35.5% for Mormon Peak as opposed to 41.2% for Stateline areas) reflects this difference in organic matter and even though the Stateline soils are more sandy, they are capable of holding more available soil moisture (25.4% for Stateline as opposed to 19.3% for Mormon Peak).

There is not a substantial difference between the amounts of NO_3^- in these two areas except for stand #2, which has about five times more NO_3^- than the others. There is no apparent reason for this difference. The difference in NH_4^+ between Mormon Peak and Stateline is probably not significant: Mormon = 21.7 lb/A and Stateline = 27.5 lb/A.

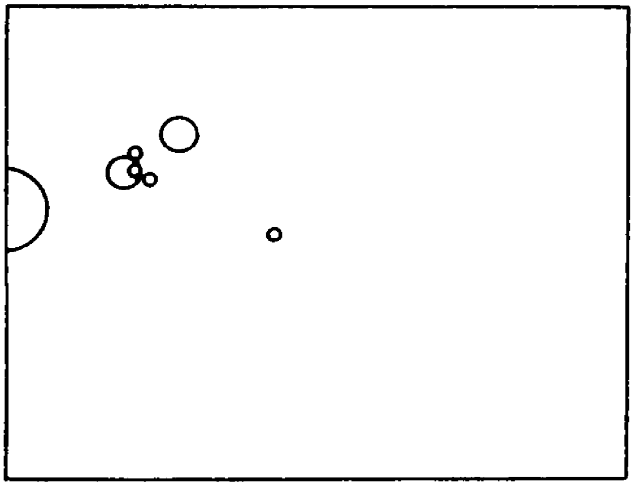
The exposure of the majority of the balds was either south, southeast or east. One might expect the exposure to be southwest, and indeed that might have been the case if more stands could have been located and included. An exposure of northeast, unusual for the balds studied, was encountered at Hoodoo Pass. At this particular site the bald was lens-shaped and occurred below an outcropping which probably prevented the natural runoff of water from above into the bald. An alder swale occurred below this bald.



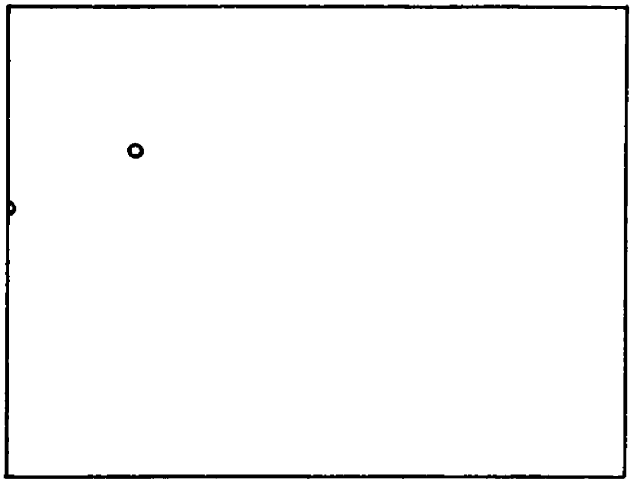
Poa secunda



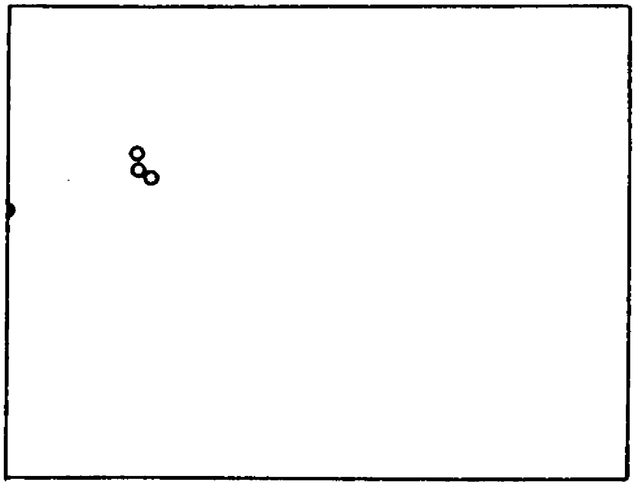
Antennaria umbrinella



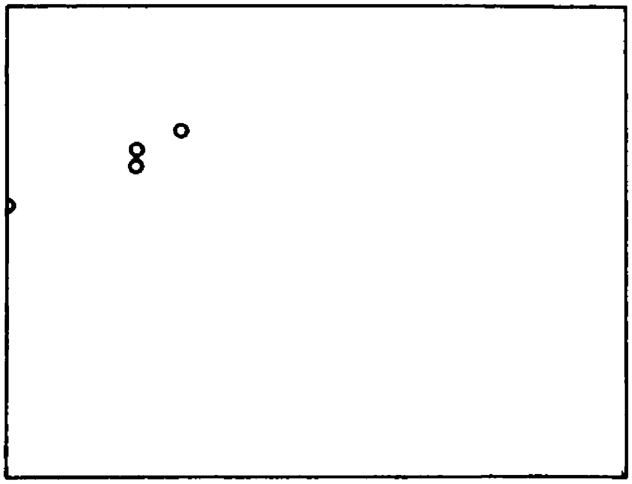
Potentilla recta



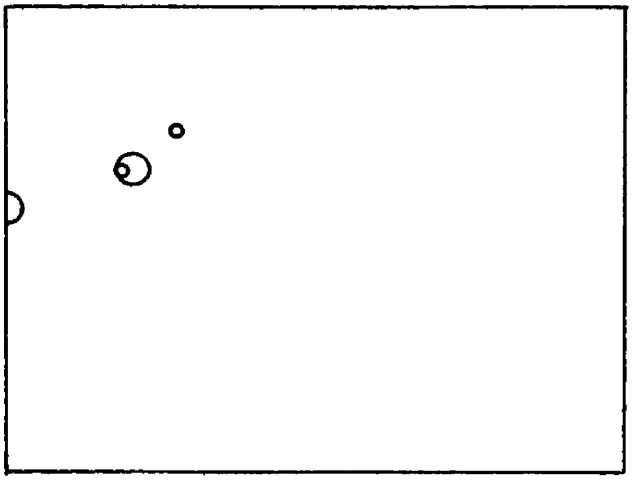
Phacelia lineralis



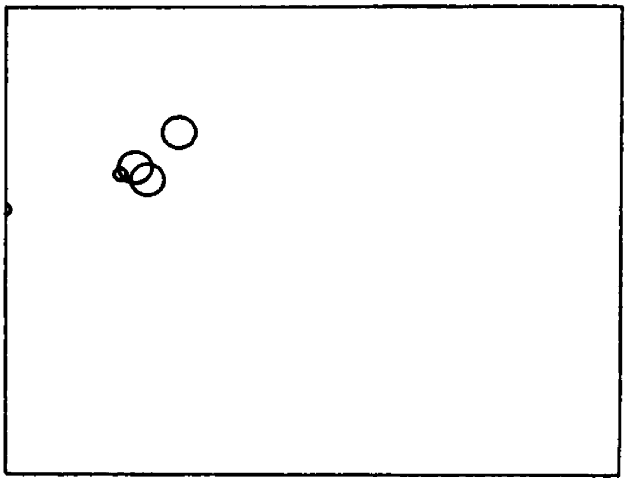
Stipa williamsii



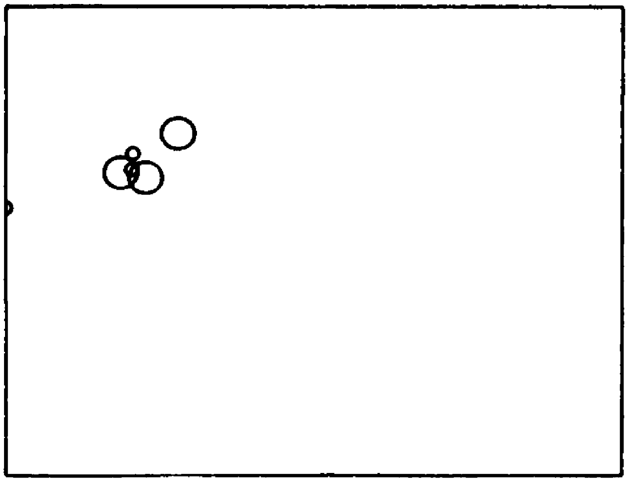
Arnica fulgens



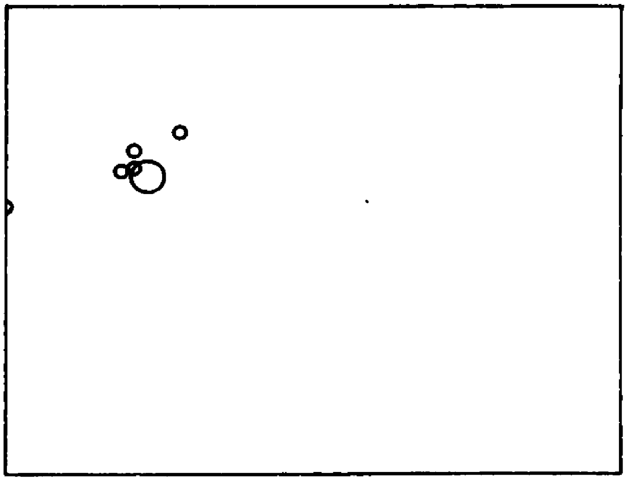
Bromus tectorum



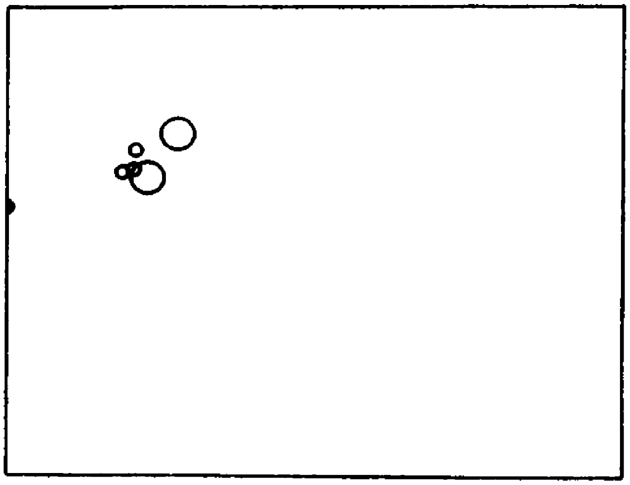
Collomia linearis



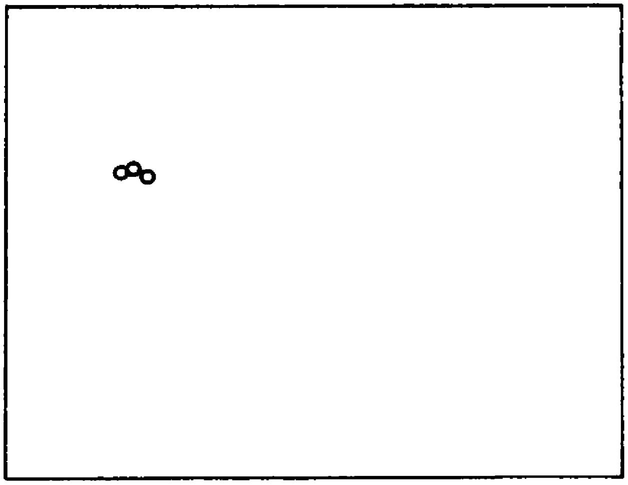
Tragopogon dubius

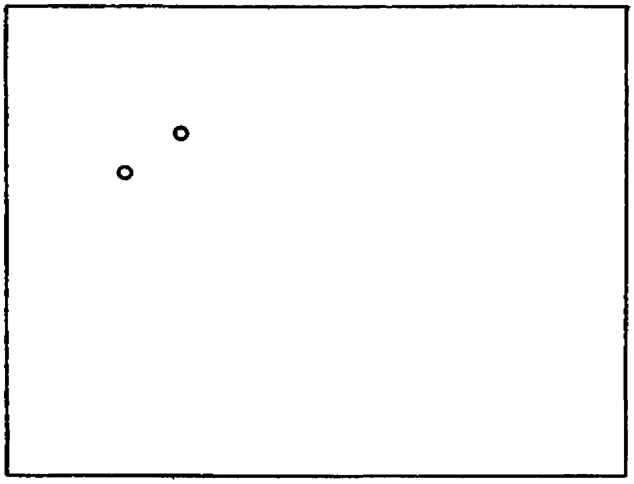


Koeleria cristata



Sisymbrium altissimum

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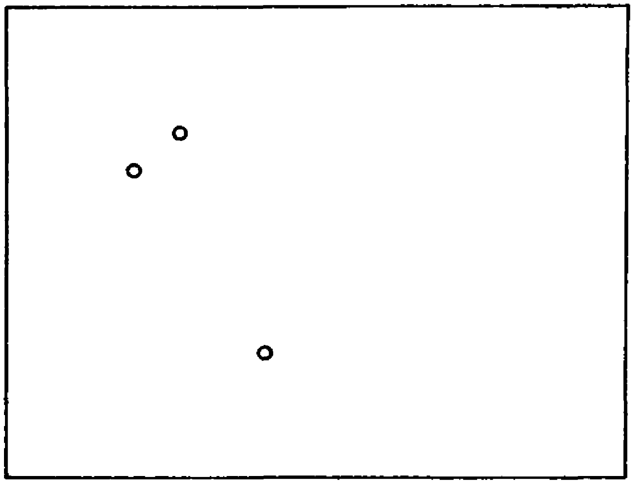
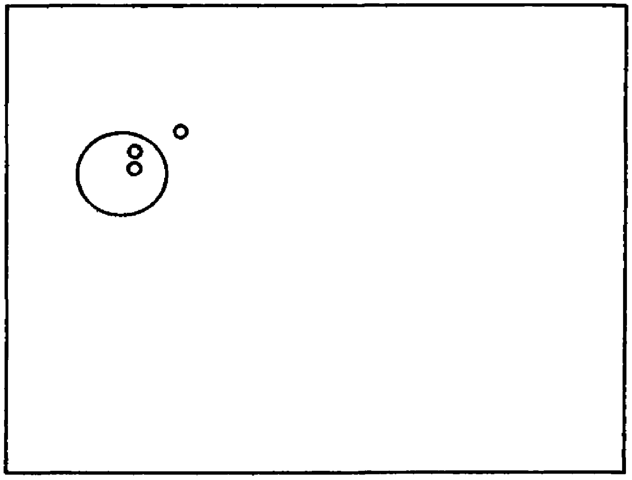
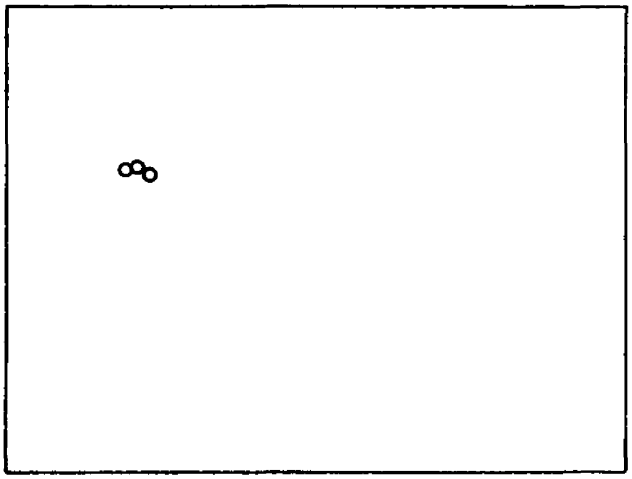
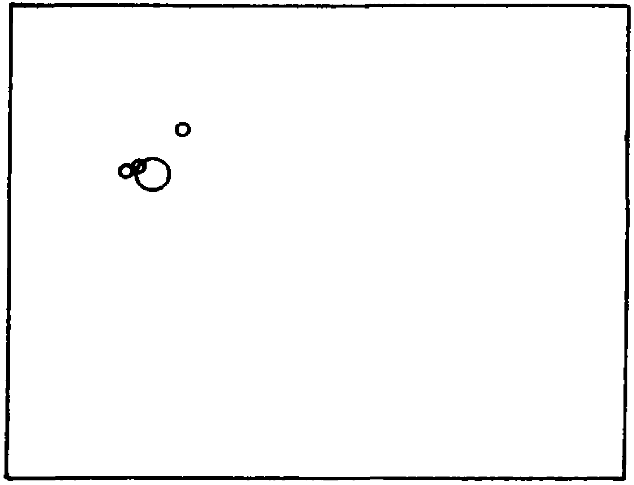
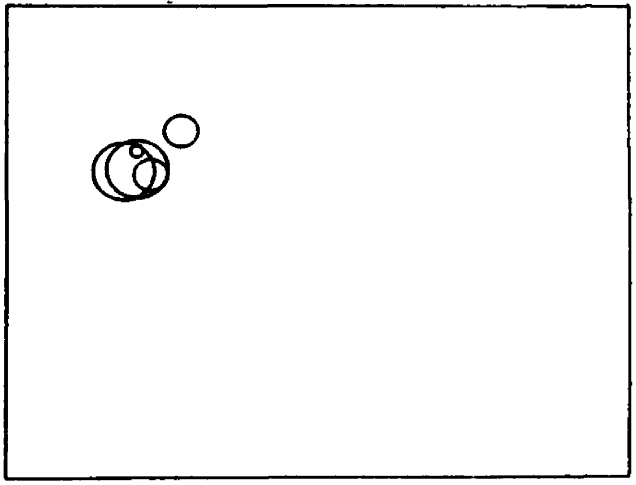

Microseris nutans

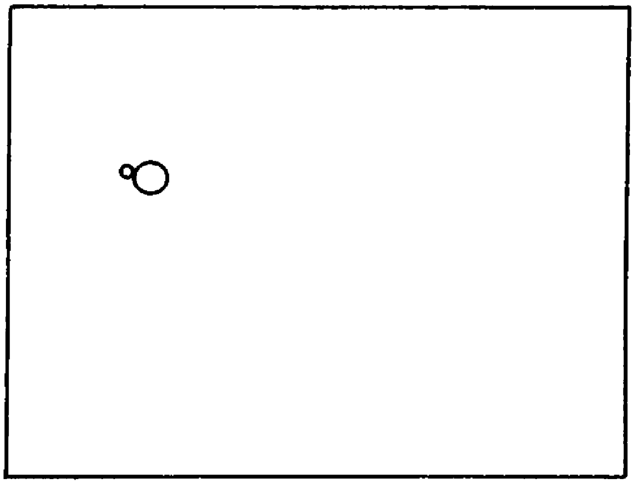

Danthonia unispicata


Allium cernuum

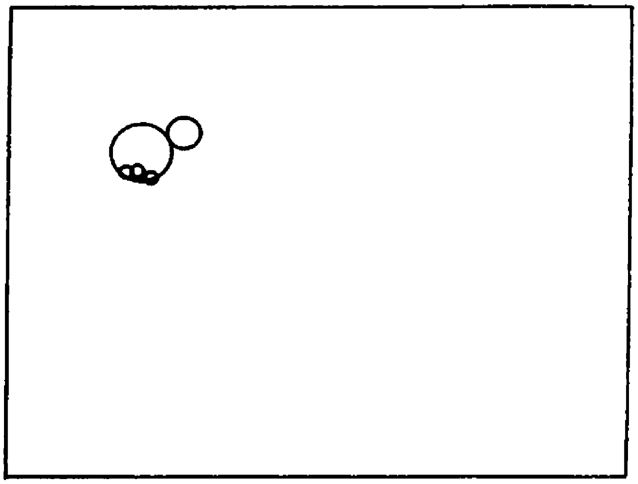

Agoseris glauca


Orthocarpus tenuifolius

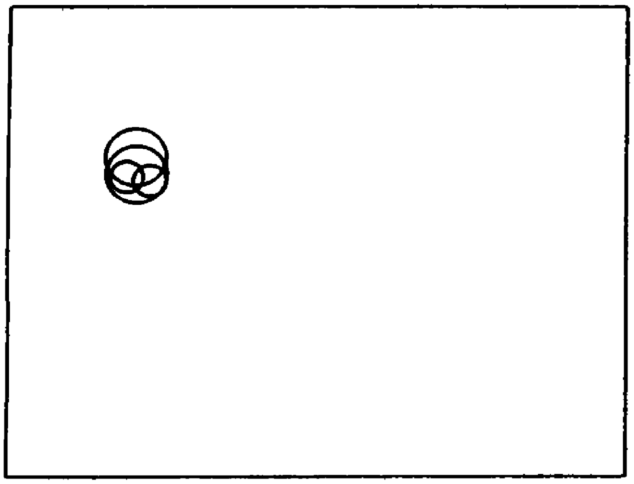
Artemisia dracunculus



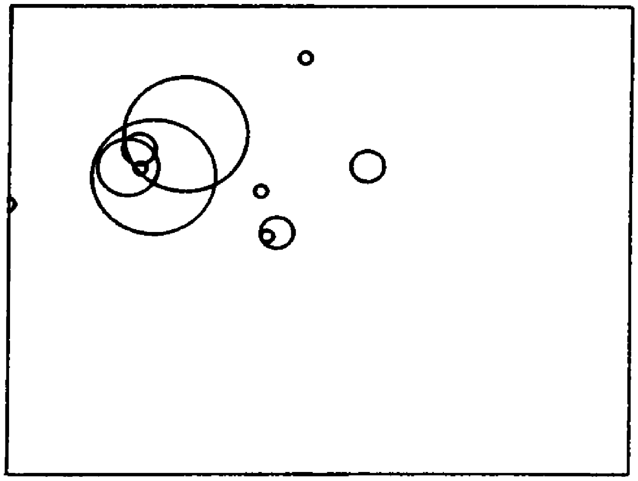
Balsamorrhiza sagittata



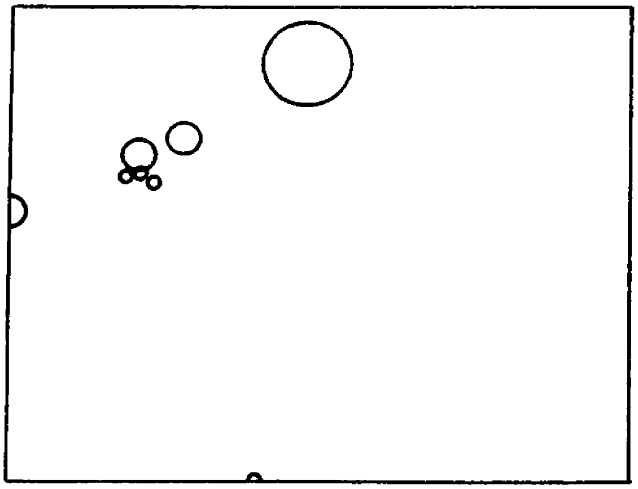
Artemisia ludoviciana



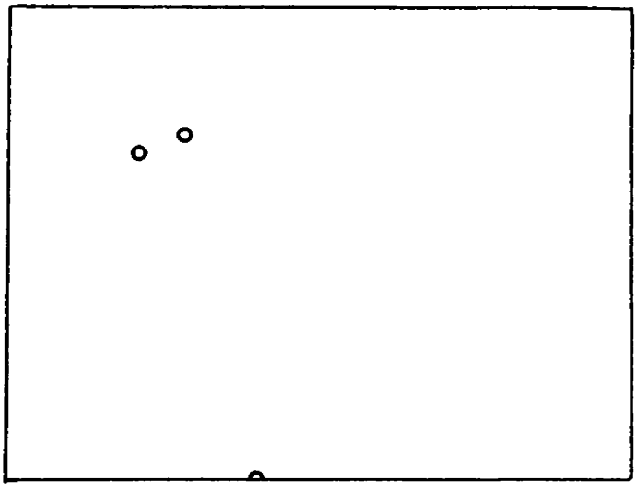
Lupinus spp.



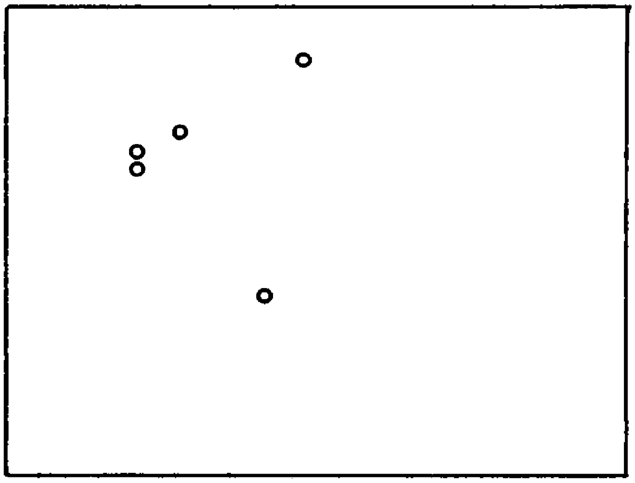
Erigeron speciosus



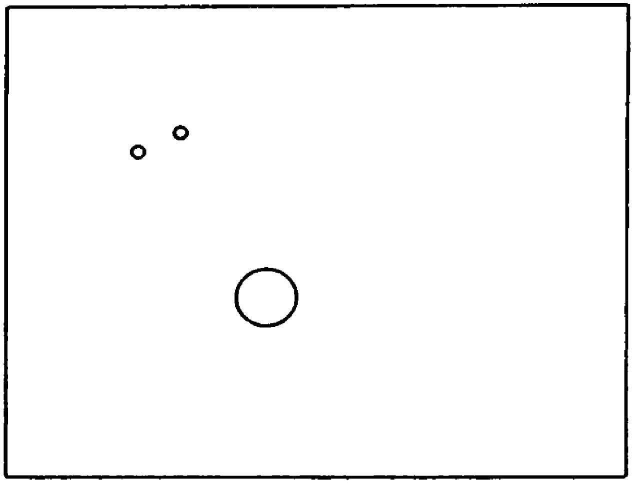
Perideria gairdneri



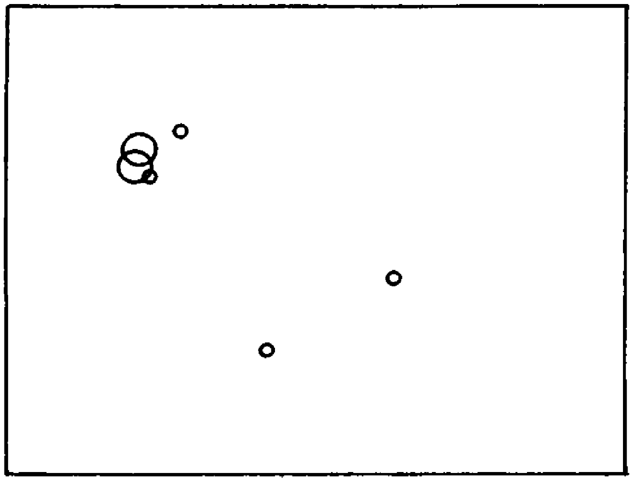
Castilleja spp.



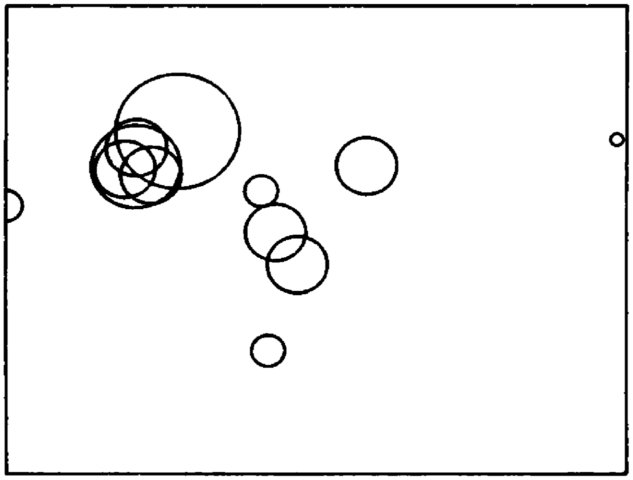
Campanula rotundifolia



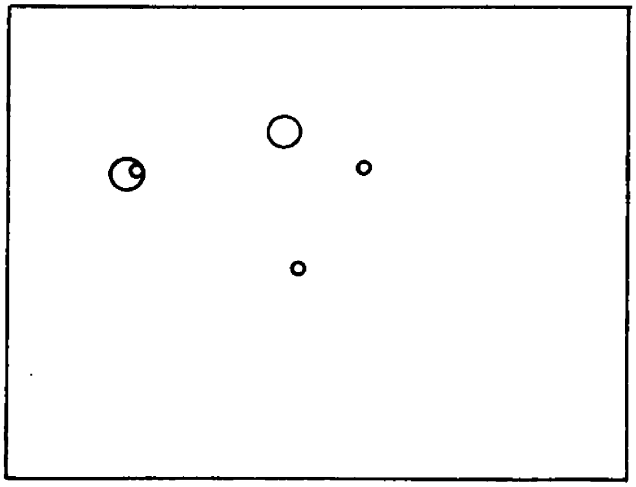
Potentilla glandulosa



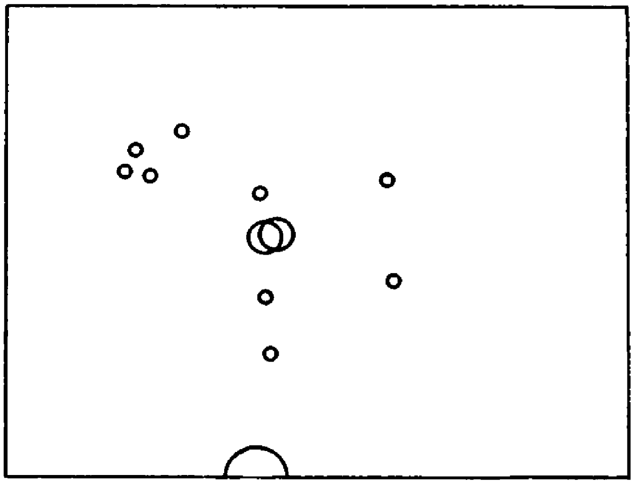
Arenaria congesta



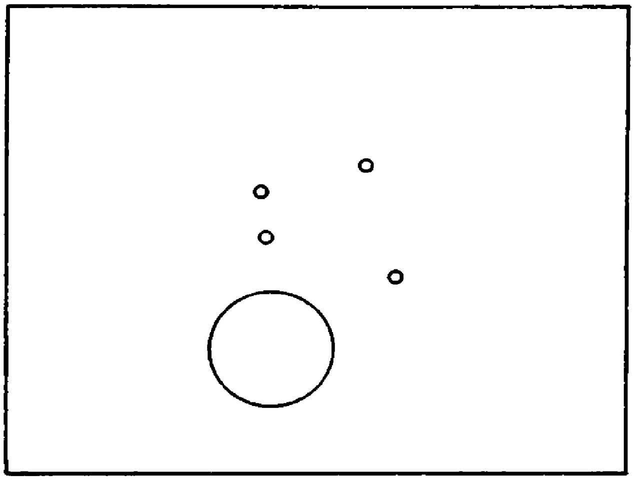
Delphinium spp.



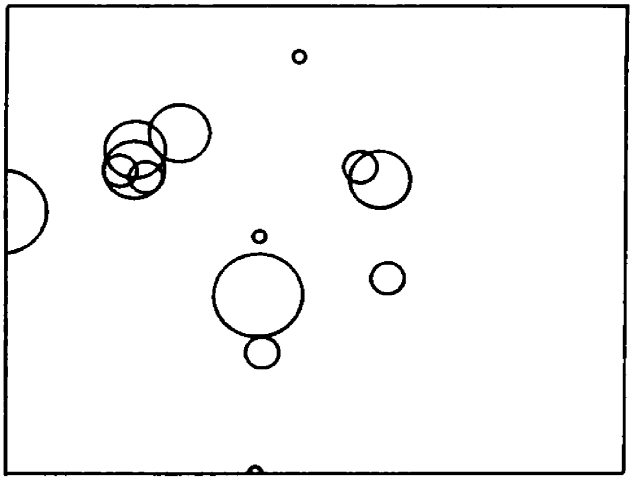
Hieracium albertinum



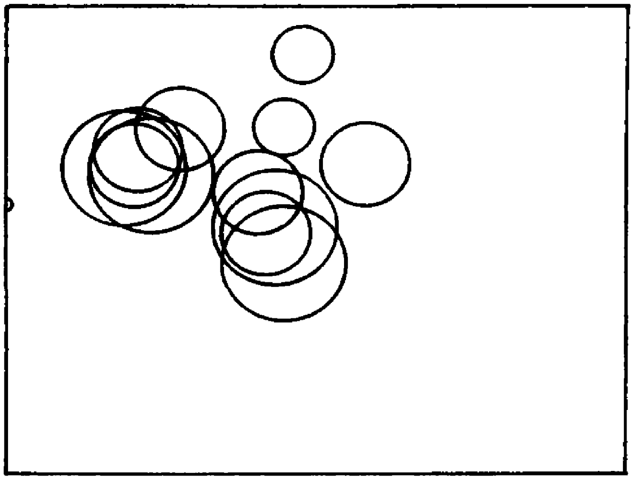
Calamagrostis rubescens



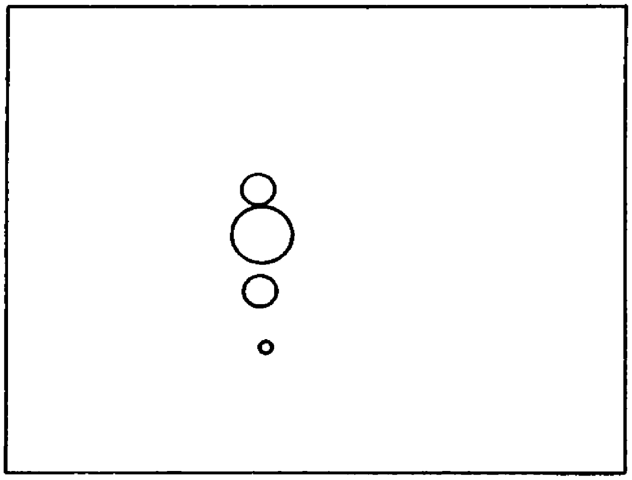
Achillea millefolium



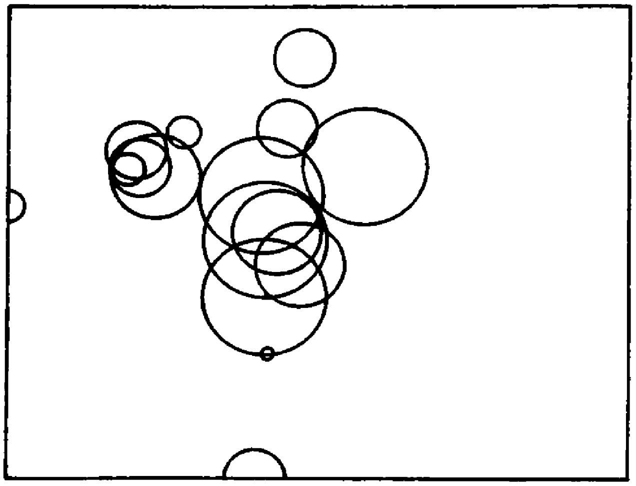
Festuca idahoensis



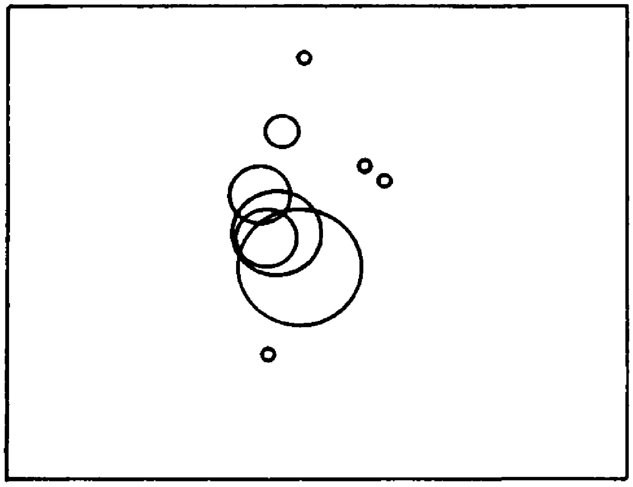
Aster intergrifolius

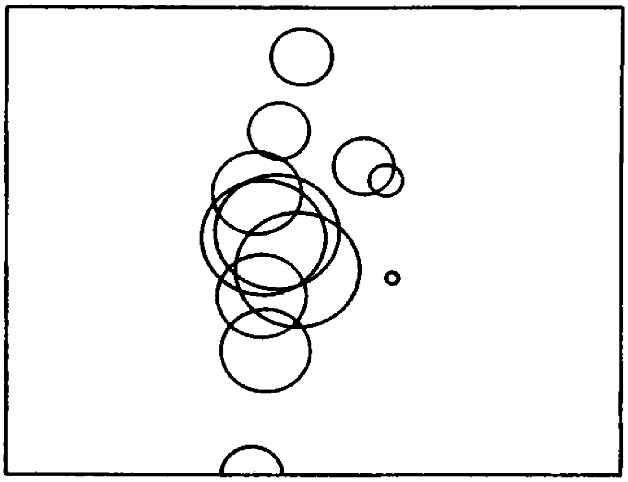


Agropyron spicatum



Phlox caespitosa

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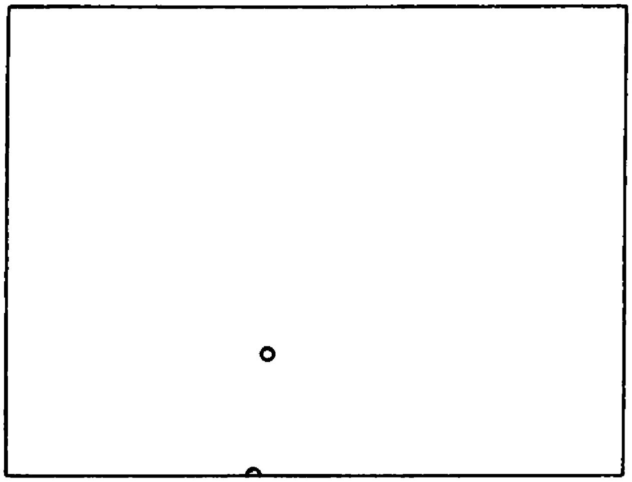
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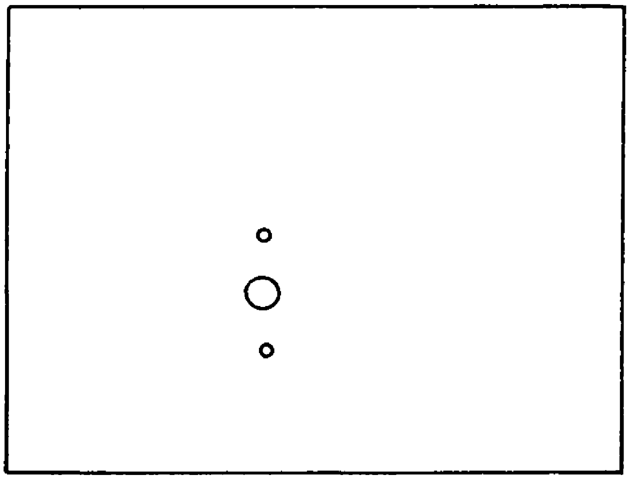
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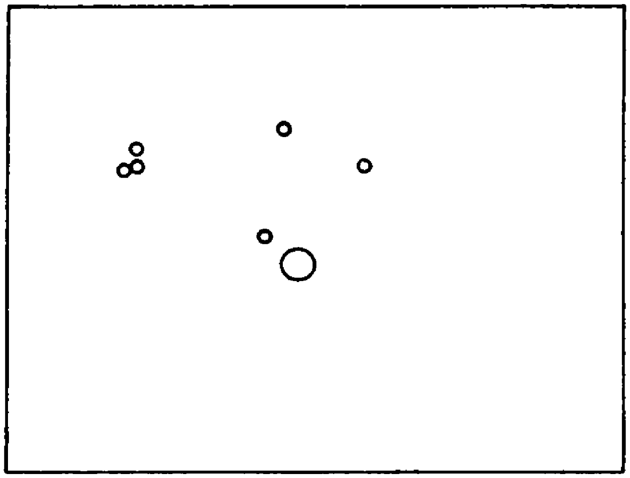
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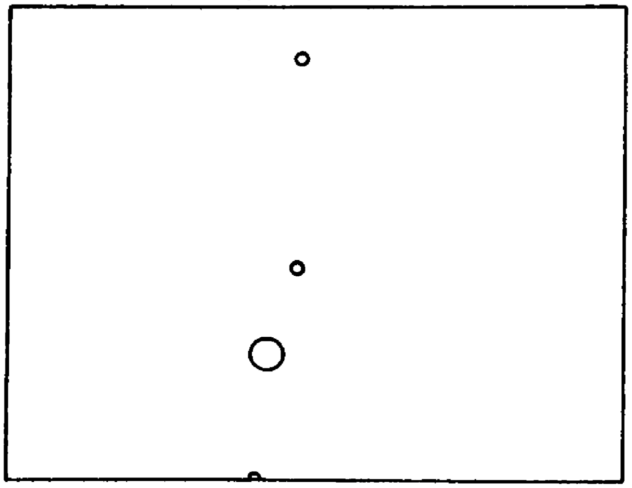
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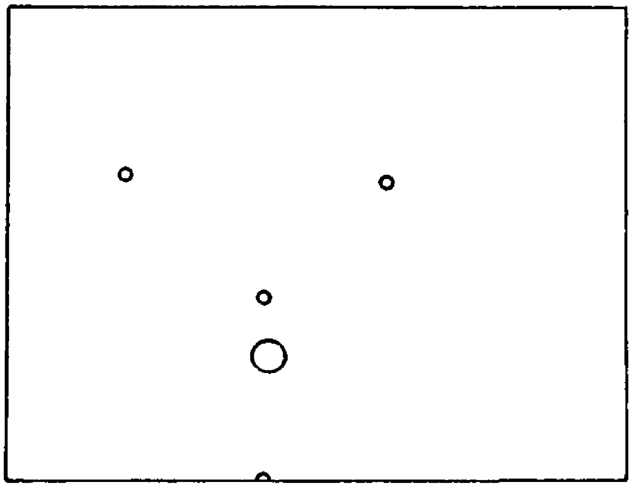
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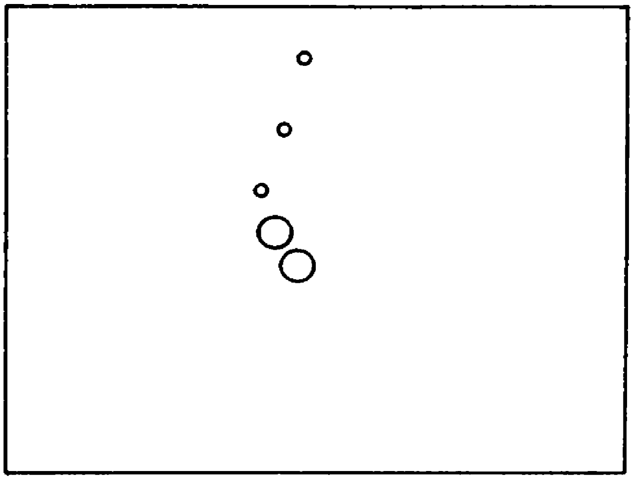
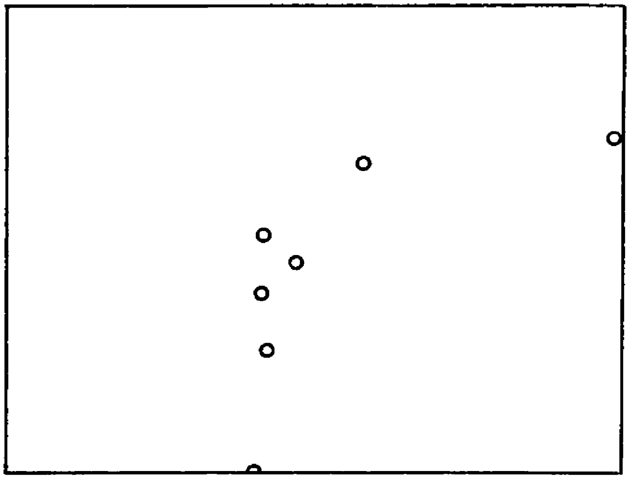
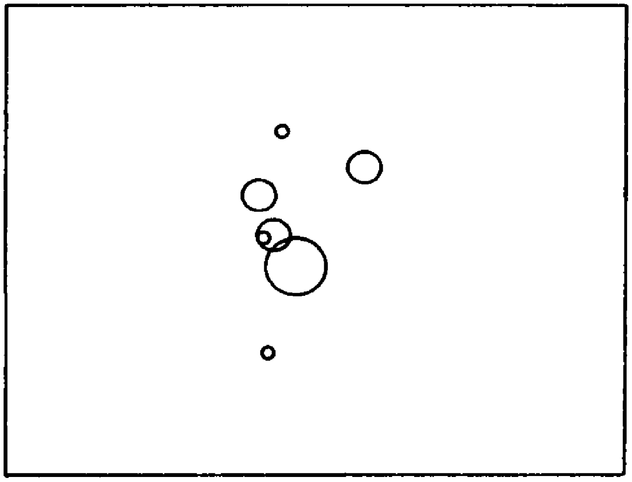
Danthonia intermedia



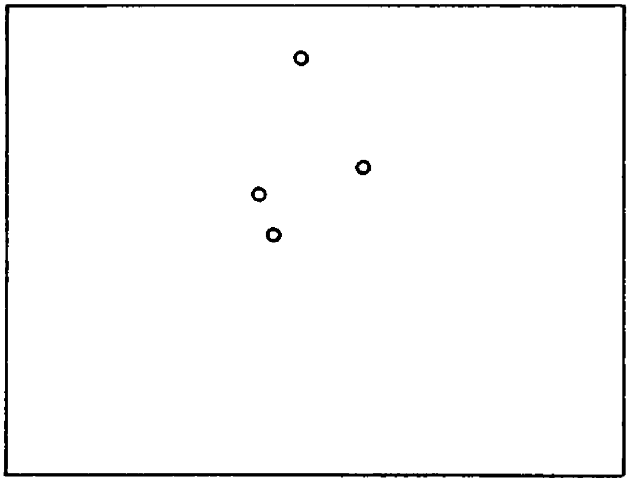
Spiraea betulifolia



Eriogonum flavum



Juncus parryi



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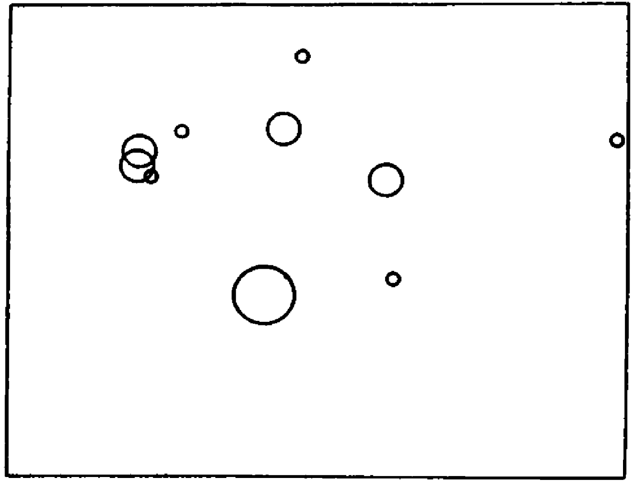
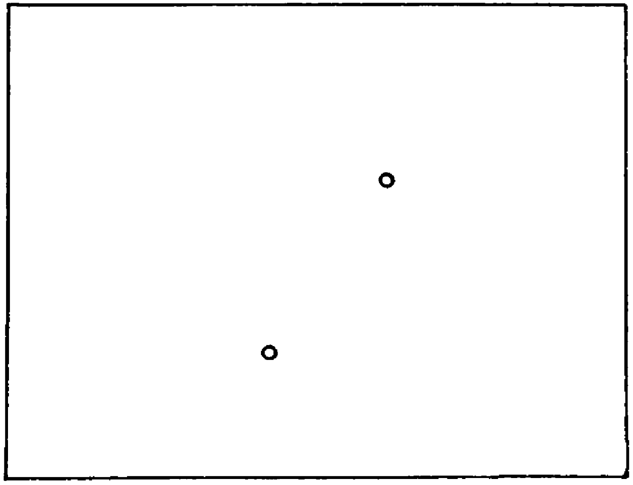
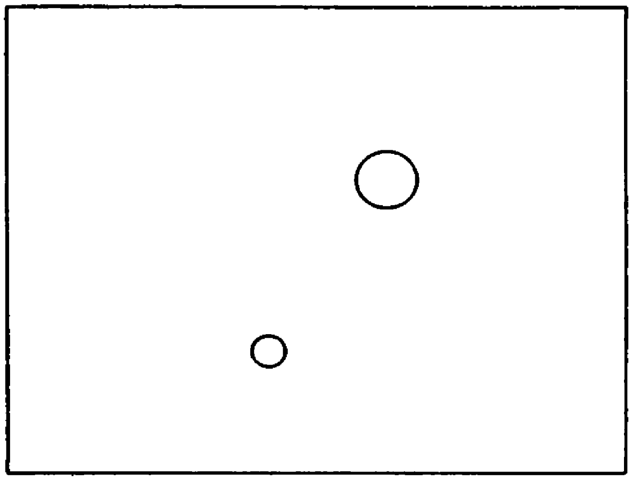


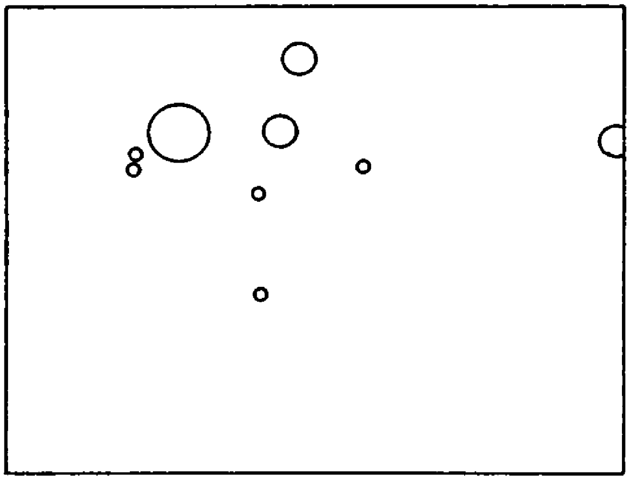
Berberis repens



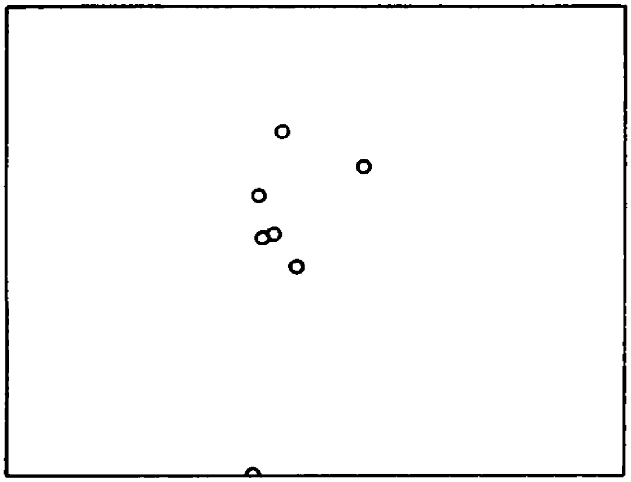
Senecio integerrimus



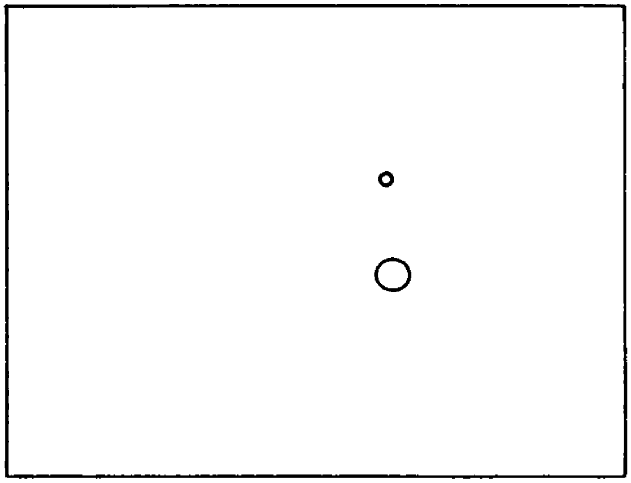
Bromus polyanthus



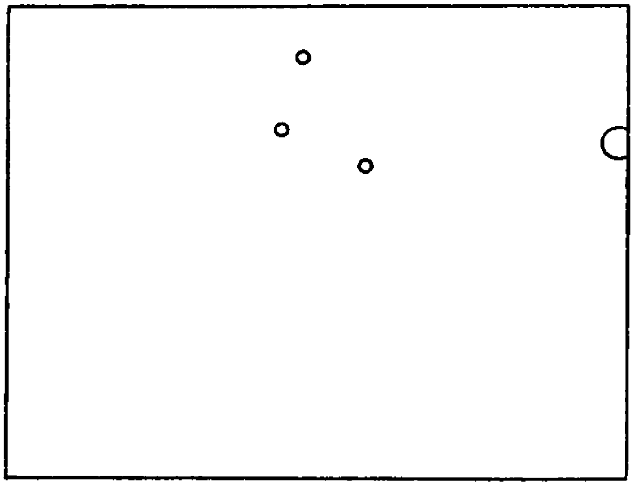
Calochortus elegans



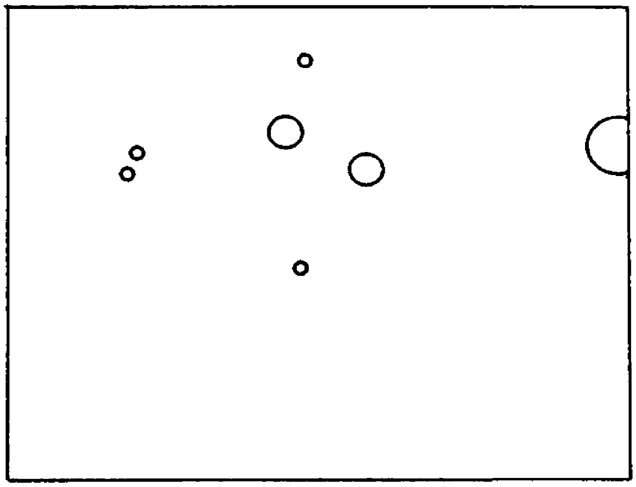
Amelanchier alnifolia

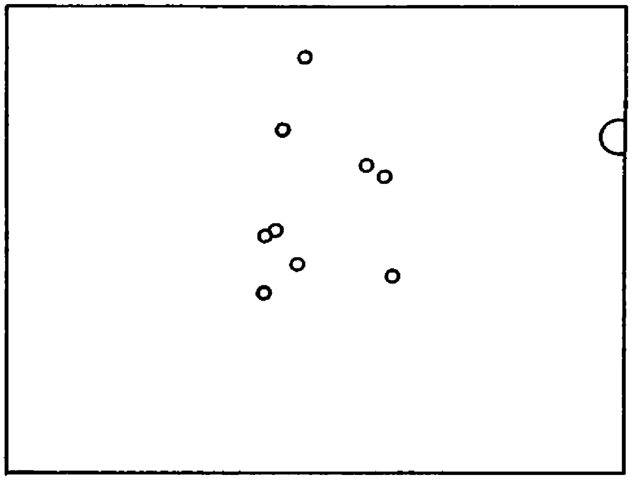


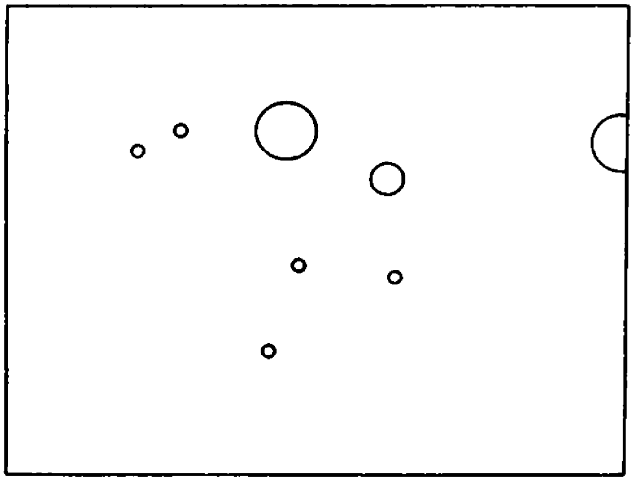
Elymus glaucus

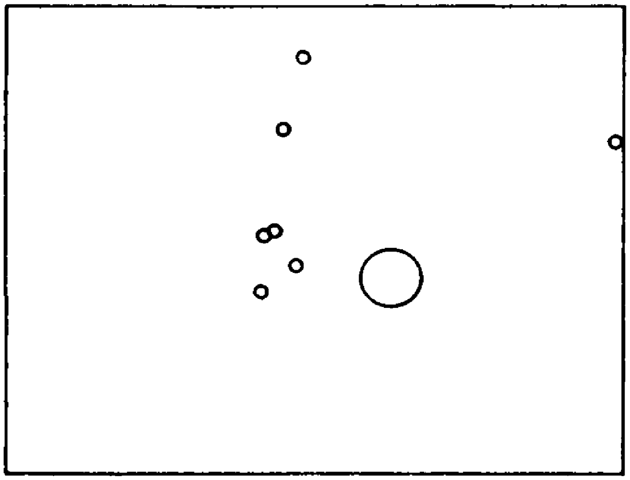


Polygonum douglasii




Polygonum phytolaccaefolium


Carex paschystachya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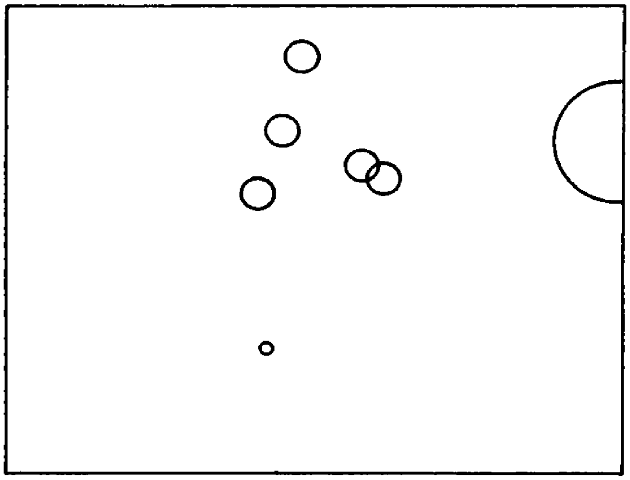
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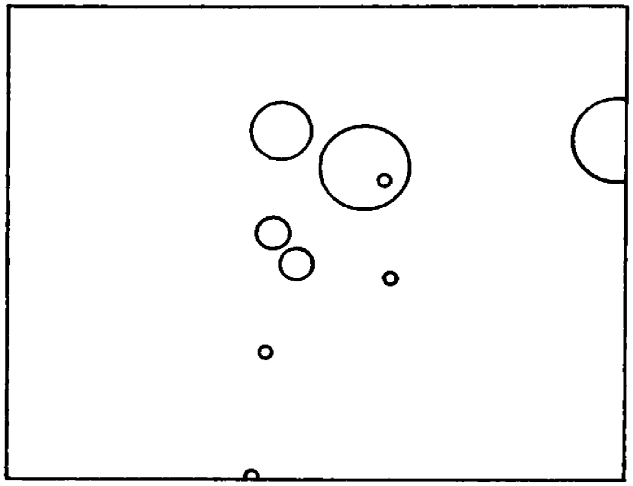
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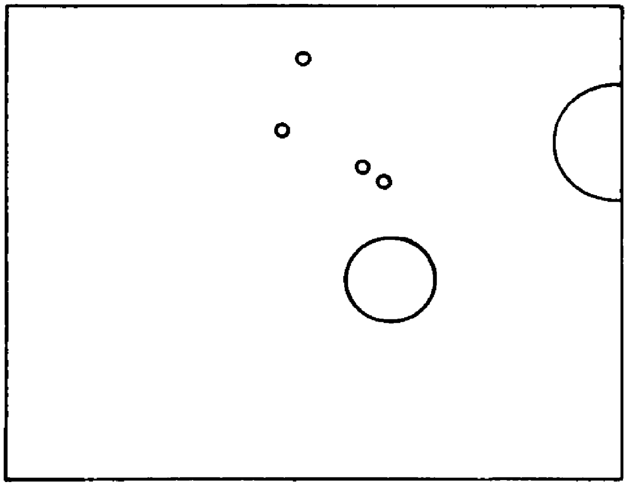
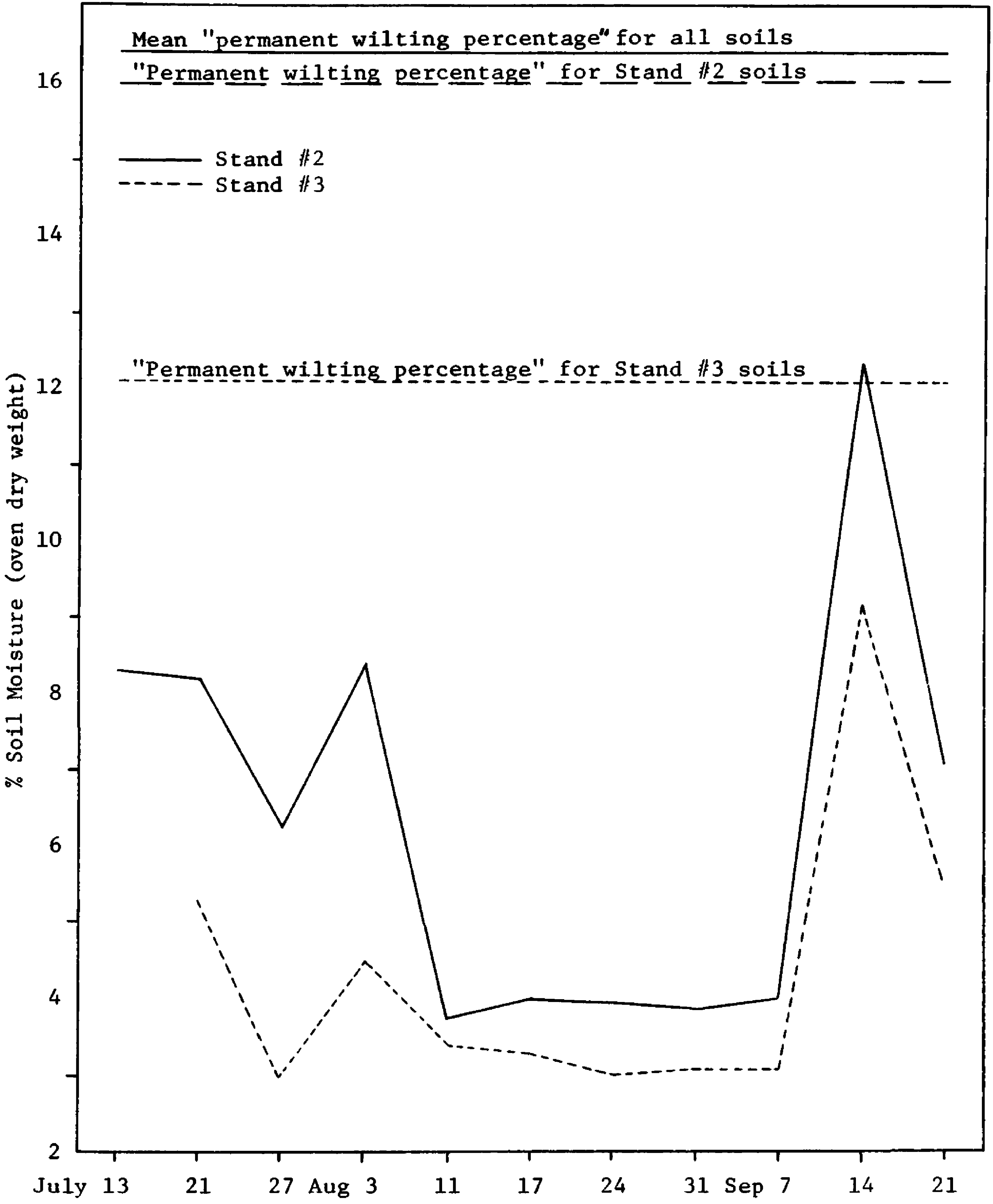

Calamagrostis canadensis

Figure 3. Weekly Soil Moisture Readings.



The soil moisture level between August 11 and September 7 for both curves is based on 55 readings which have a standard deviation of ±.09 and a standard error of ±.12.

Figure 4. Weekly Temperature Readings.

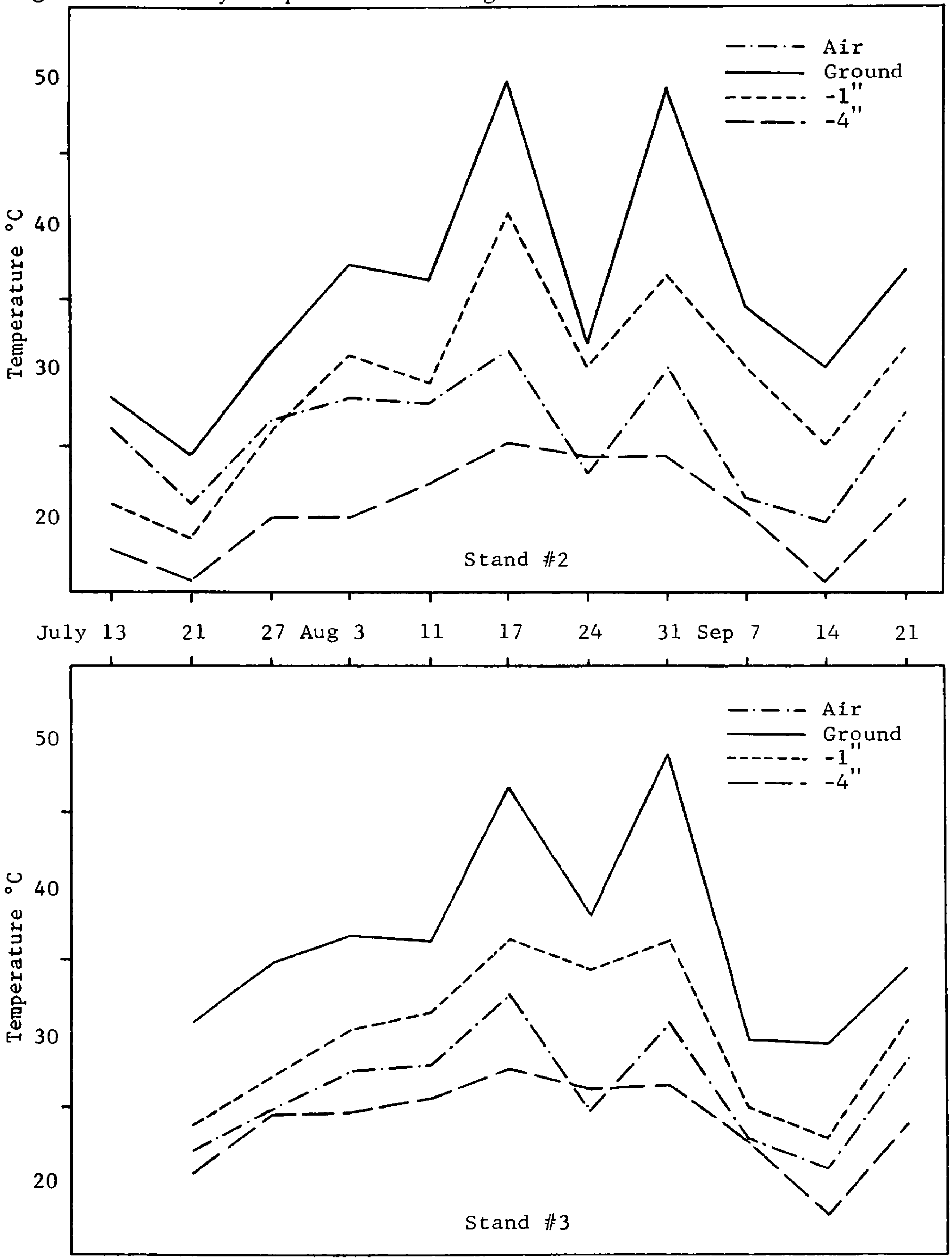
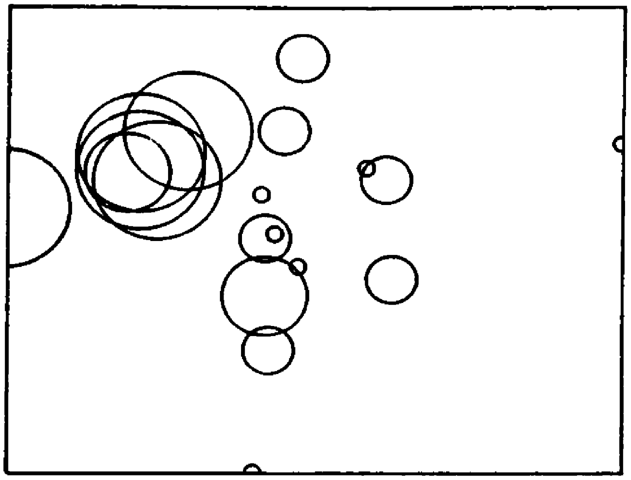


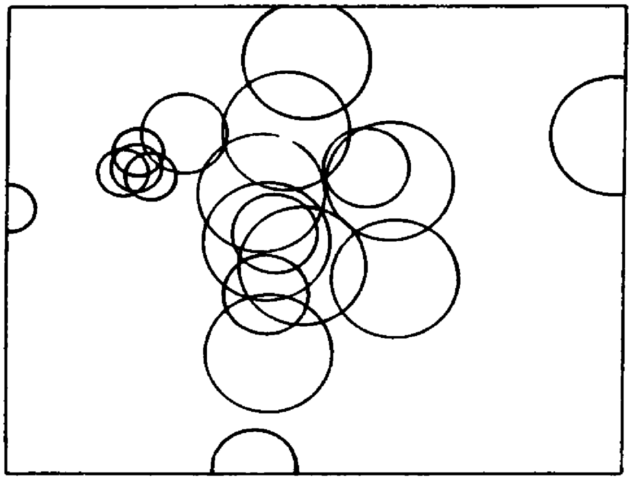
Figure 5. The ordination for the soils data. The four quartiles are represented by four different sized circles as follows:

	Calcium lbs/A	pH	OM tons/A	Phosphorus lbs/A	Potassium lbs/A	Magnesium lbs/A
∘	1-500	4.80-5.35	1.0-22.5	1.0-62.5	1-125	1-175
○	501-1000	5.36-5.90	22.6-45.0	62.6-125.0	126-250	176-350
◯	1001-1500	5.91-6.45	45.1-67.5	125.1-187.5	251-375	351-525
〇	1501-2000	6.46-7.00	67.6-90.0	187.6-250.0	376-500	526-700

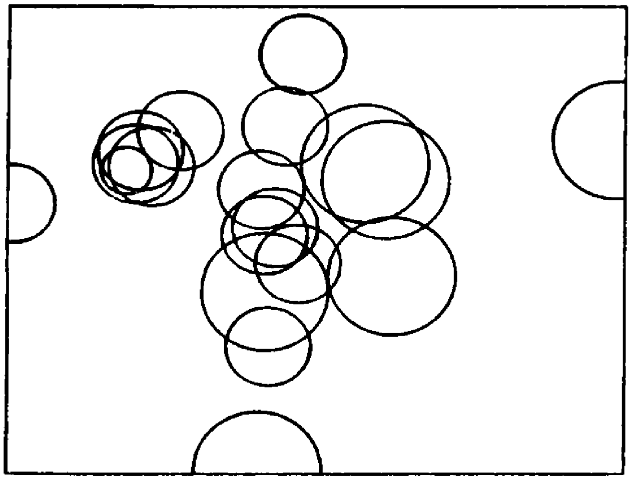
Calcium



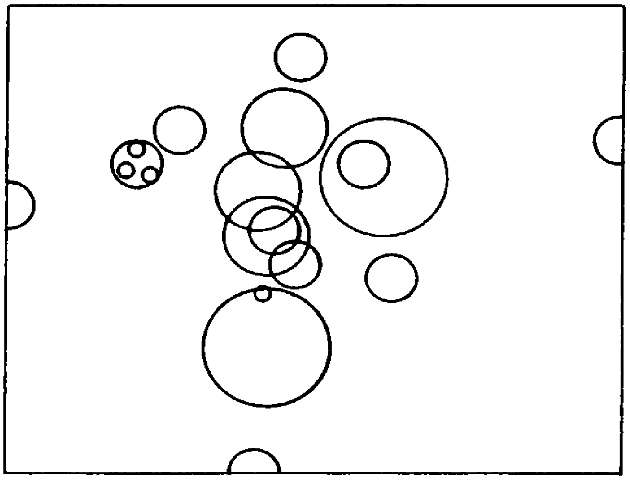
pH



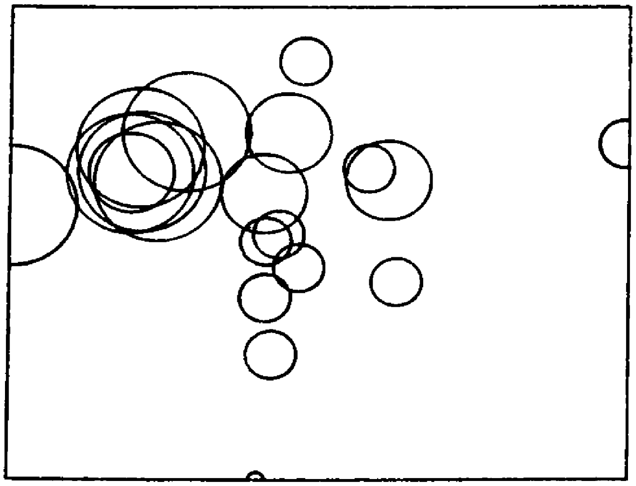
Organic matter



Phosphorus



Potassium



Magnesium

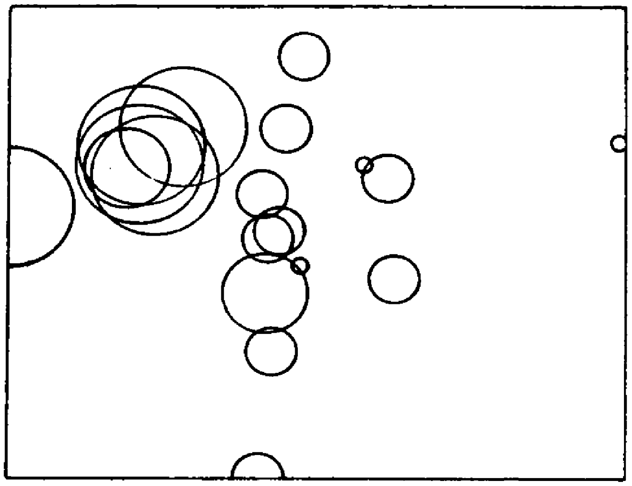
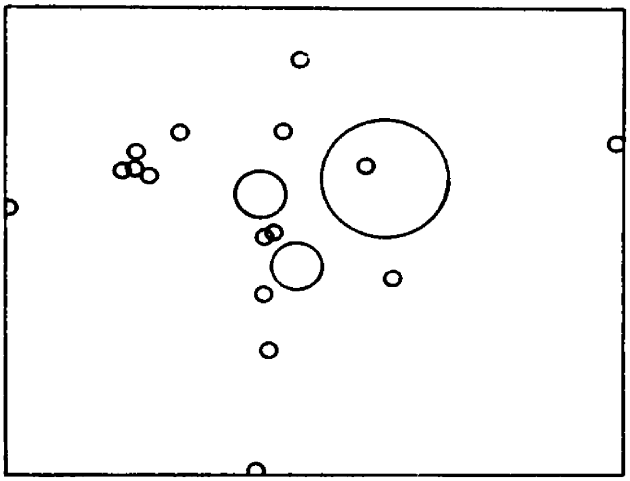
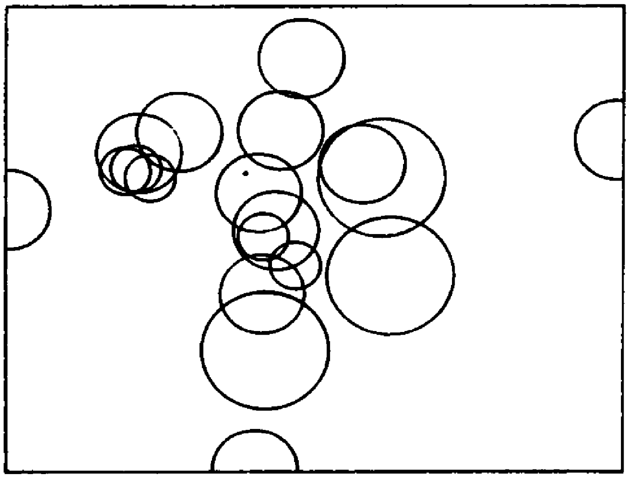


Figure 5 (continued). The ordination for the soils data. The four quartiles are represented by four different sized circles as follows:

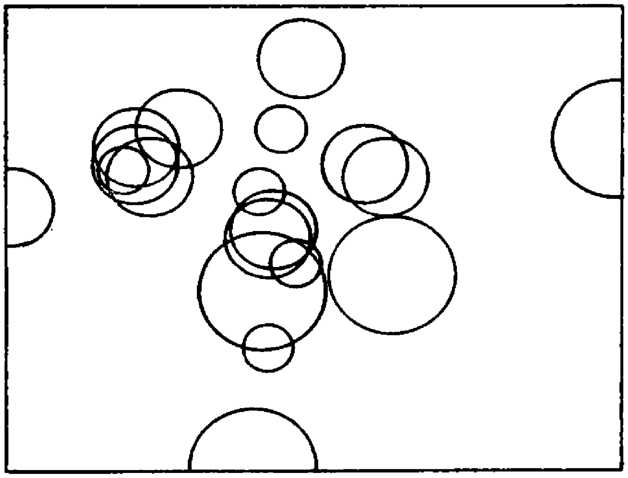
	NO_3^- lbs/A	NH_4^+ lbs/A	WHC
∘	1-2.5	1-10	1.00-16.25
○	2.6-5.0	11-20	16.26-32.50
◯	5.1-7.5	21-30	32.51-48.75
◯	7.6-10.0	31-40	48.75-65.00



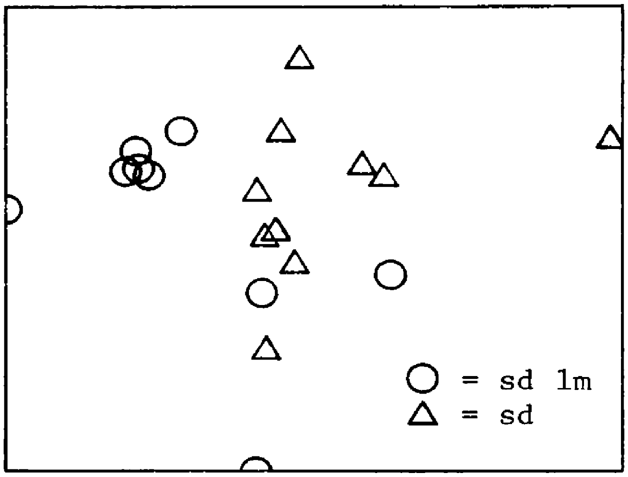
NO_3^-



NH_4^+



Water Holding Capacity



Soil type

CHEMICAL DATA

Stand No.*	Calcium	Phosphorus	Potassium	Magnesium	NO_3^-	NH_4^+	Organic matter	pH
1	656 lb/A	102 lb/A	135 lb/A	300 lb/A	2 lb/A	40 lb/A	88 tons/A	5.2
2	550	250	285	250	10	35	74	5.0
3	600	190	250	300	2	30	60	5.3
4	1,900	82	500	700	2	25	65	5.9
5	1,600	67	500	690	2	20	48	6.0
6	1,500	44	350	500	1	15	39	6.1
7	1,850	48	450	700	1	20	59	6.4
8	2,000	98	500	700	2	25	65	6.1
9	1,800	62	450	600	1	25	60	6.1
10	400	100	85	220	1	30	90	5.8
11	1,350	44	135	410	2	30	85	5.9
12	650	116	225	260	2	30	62	5.1
13	700	155	275	200	2	25	55	5.1
14	450	120	165	110	1	25	70	5.5
15	500	112	175	200	2	25	67	5.4
16	400	116	150	100	3	20	67	4.8
17	300	109	200	110	1	25	90	5.2
18	500	148	325	310	3	25	61	5.0
19	600	130	230	200	2	20	64	5.3

* The geological location of the stands are identified opposite page 30. The results of the chemical and soils data have been plotted on the ordination on pages 42 and 43.

SOIL AND STAND DATA

Stand No.	Elevation	Exposure	Slope	Sand	Silt	Clay	Water Holding Capacity	Permanent Wilting Percentage	Available Soil Moisture
1	6,400 ft.	SE	25°	79.2%	18.6%	2.2%	65.0%	26.0%	39.0%
2	6,400	E	33°-39°	84.2	12.5	3.3	46.7	16.4	30.3
3	6,650	E	35°-40°	84.3	13.6	2.1	31.9	12.1	19.8
4	6,075	S	20°	75.1	21.8	3.1	35.9	16.1	19.8
5	5,900	S	5°-10°	79.4	18.6	2.0	34.4	25.6	8.8
6	6,000	SE	10°-15°	78.6	15.5	5.9	29.5	9.3	20.2
7	6,000	SE	10°-20°	79.6	16.6	3.8	33.2	14.0	19.2
8	5,800	S	5°	76.4	20.4	3.2	45.0	17.9	27.1
9	6,000	S	10°-15°	78.4	18.2	3.4	35.2	14.4	20.8
10	5,950	E-NE	28°-35°	67.5	29.4	3.1	54.0	17.6	36.4
11	6,100	S	26°	72.2	23.3	4.5	61.6	23.0	38.6
12	6,600	S	14°	85.7	13.3	1.0	34.8	11.7	23.1
13	6,450	S	17°	85.7	13.3	1.0	29.6	10.7	18.9
14	6,525	S	5°	83.3	15.1	1.6	41.5	14.2	27.3
15	6,850	S	8°-18°	82.5	16.5	1.0	36.0	12.0	24.0
16	6,500	S	15°	80.0	18.8	2.2	29.4	13.1	16.3
17	6,600	S	12°-15°	82.9	15.0	2.1	55.0	23.0	32.0
18	6,700	S	13°-17°	84.4	12.1	3.5	27.6	12.9	14.7
19	6,850	SE	24°-28°	82.1	16.9	1.0	43.1	14.6	23.5

The Water Holding Capacity was determined by the pressure membrane technique at 1/3 atmospheres of pressure; the Permanent Wilting Percentage was determined at 15 atmospheres. The Available Soil Moisture was calculated by subtracting the Permanent Wilting Percentage from the Water Holding Capacity. The soil moisture data (page 40) indicate that during the growing season of July through mid-September the soil moisture never came up to the Permanent Wilting Percentage.

DISCUSSION

The question of bald origin and stability has been the object of numerous studies. These investigations have been conducted mostly in the Appalachian Mountains where the vegetation has often been disturbed by man and domestic animals. Such disturbed sites are not easily analyzed and to date there is still no commonly accepted explanation for their occurrence.

The Rocky Mountain subalpine balds, on the other hand, are believed to be relatively undisturbed. Moreover, there has been no published study documenting the distribution of communities within the Rocky Mountain balds, nor has any study provided a satisfactory explanation for their existence. Therefore, the primary purpose of this study has been to establish vegetational distribution patterns for these balds, and to correlate these patterns with environmental factors present.

An ordination was used to discover the patterns of distribution of the important species growing within the bald communities. The categorizing of species as ubiquitous and restricted, and as those found in a majority of stands or those which were exceptions, has aided in defining grassland communities. Transition zones, alder swales, and forest invasion of the balds were also part of the vegetation distribution pattern. The vegetation within plant communities forms such patterns according to specific environmental factors. These environmental features include slope, exposure, climate, geology, soils, and human influences.

One of the distinguishing characteristics of the balds in this study was the relative absence of man's influence. For example, Wells (1936) believes that Indians destroyed Appalachian forests in order to attract to the resulting grasslands grazing animals which could then be hunted more easily. Although Wells' hypothesis has been rejected by Mark (1958) and others as being without scientific support, his theory has never been scientifically disproven. In western Montana also, Indians relied heavily upon grazing animals for their livelihood. But in this area there were many naturally occurring prairies in the valleys. Thus, it seems very unlikely that these Indians would have needed to establish and maintain grasslands over 3,000 feet in altitude above their villages, especially since historical records indicate that there was abundant game on the prairies during the summer months.

Grazing has been another important domestic disturbance on the Appalachian balds. Domestic animals use these grasslands during the summer months, and although it is improbable that they were responsible for the creation of the balds, it is clear that they inhibit the establishment of tree seedlings (Brown, 1953).

A careful selection of the Rocky Mountain balds studied has eliminated the complexity of prior disturbance by man or his domestic animals. Most of the balds were inaccessible to cattle, and there was little evidence that these grassy areas were even used much by native grazing animals.

Fire can also be an environmental influence; especially in western Montana it is a frequent and often natural phenomenon. One of the stands studied (#3) had evidence of a recent burn up to one of its borders, and it is probable that the bald was also burned although no positive evidence was obtained. The burning of an entire area, however, cannot explain the isolated distribution of the balds within the forest. For example, in the Missoula area the NE slope of Mt. Sentinel has been repeatedly burned (naturally, and because of human influences such as woodburning railroad locomotives) in the past, preventing the invasion of the forest on the western slope. Recently, however, the forest has been invading the western slope as an indirect result of man's fire prevention, only to have its outer borders oscillate yearly with the available soil moisture.

Slope and exposure are still other environmental features which may influence the distribution of vegetational communities and of balds within the forest. Slope was not a consistent factor among the different balds. However, the slopes of any one bald and the adjoining forest were usually more or less identical, and therefore one would expect water runoff to be very similar also. Thus, water availability as correlated with slope appears to be an inadequate explanation for the occurrence of the balds within the forest.

This study made no direct attempt to correlate slope with species distribution within the balds. Blinn (1967) found that slope played an important role in the variations of grassland community composition. This he attributed to the fact that water received on higher portions of the slope was lost through runoff, consequently creating more mesic environments at the lower positions.

Slope is also important through its connection with exposure. Early in the year, when the direction of incident solar radiation is southerly, the degree of slope influences the amount of radiant energy received by the ground. South-facing slopes receive more energy earlier in the growing season, becoming more xerothermic than other slopes. Figures 6 and 7 represent typical balds.

Balds in the Appalachian Mountains are situated either on the crest of a mountain or in a southwest exposure. Mark (1958) has shown the southwest slope in this area to be the hottest and driest. In the Upper Blackfoot Valley northeast of Missoula, Blinn (1967) found the southeast slope to be the hottest and driest. The average exposure of the balds in my study was south-southeast. Although it has been established that the southeast exposures in western Montana are hot and dry, this fact alone cannot explain the occurrence of the balds. It must be remembered that the typical subalpine spruce-fir communities surround the balds on the same exposure. However, this regular occurrence of balds on the hottest and driest exposures does suggest that temperature and moisture may be critical at certain times during the growing season.

The effects of soil temperature and soil drought are difficult to

Figure 6 (above) and 7 (below).

A Skookum Butte bald in August

Rocks on Stand #3

separate, because it is hard to demonstrate the effects of high soil temperature without creating drought conditions. Daubenmire (1943) has shown that soils do not become dangerously hot while they contain abundant moisture, because as the moisture evaporates it cools the soil. It had previously been supposed that the cooling effect of transpiration was responsible for keeping plants from becoming overheated, but this has not proven to be the case. It has been shown by Ansari and Loomis (1959) that internal water balance is more important than transpiration. They found that when the internal water balance of a plant is maintained, mechanical injury by heat occurs only at extremely high temperatures.

The data show that the soil moisture decreases as the temperature increases. The minimum soil moisture was reached at the two weekly sampling stations on August 11, approximately one week before the highest temperatures were reached on August 17. Thus it would appear that temperature extremes were not responsible for the minimum soil moisture readings. It is believed that, regardless of hot years or cool years, the soils on these balds are incapable of holding higher levels of moisture.

Day (1964) attributes the lack of rapid establishment of spruce (<u>Picea engelmannii</u>) and fir (<u>Abies lasiocarpa</u>) seedlings mainly to drought and to high surface temperatures. He states that after logging, the majority of seedlings do not become established in the open. Instead, they develop best in the shade of "such semi-permanent features... as humps, stumps, logs, slash, and residual trees." These seedlings are not drought resistant: for spruce and fir the average root development during the first year is about one inch. Day's work has shown that even within the forest, drought is often responsible for the death of seedlings. Daubenmire (1943) has shown that tree seedlings can withstand dry air, provided there is adequate soil moisture. In his experiments the seedlings died after relatively short periods when soil moisture was reduced to the "permanent wilting percentage." McMinn (1952) states that "the results show that in the region of the northern Rocky Mountains, where precipitation is mostly in the winter and summer drought is normal, different plant associations are correlated with different extents of soil drought." Thus, soil moisture is often the limiting factor for the successful establishment of spruce and fir seedlings, and must be considered one of the major environmental factors in the maintenance of subalpine grassy balds. Moreover, it is believed that at present these balds are too dry to permit the establishment of any subalpine tree species.

The Mormon Peak stands receive the least amount of moisture: approximately 20 inches of annual precipitation (U.S. Weather Bureau, 1963), most of which occurs in winter. It is only here, therefore, that certain restricted species typical of very dry habitats (such as Lewisia rediviva and Artemisia ludoviciana) are found. The lack of forest invasion on the southern slope of Mormon Peak is primarily a result of exposure, coarse soil and the low annual precipitation.

The capacity of a soil to hold water is mostly dependent upon the particulate size of the inorganic material, and upon the amount of organic matter incorporated in the soil. The soils found in the balds were classified as sand or sandy loam, and thus particle size was of limited help in retaining water. The soils, however, contained much organic matter, which probably accounts for the high field moisture capacity recorded.

Day (1963) found, in his experiments on the success of spruce seedling establishment on different soil types, that mineral soils did not hold adequate soil moisture for the successful development of most seedlings. He found decayed wood to be the best because it could retain great amounts of water. It is apparent that the soils found in the balds are poor seedbed material in which to establish spruce and fir seedlings. The distributional patterns of the various inorganic minerals analyzed do not indicate that these play a major role in the distribution of the vegetation within the balds.

In the ordination, the Mormon Peak stands separate themselves from the Stateline stands along a soil moisture gradient. The large number of species restricted to Mormon Peak and, conversely, the large number restricted to the Stateline stands, shows the difference in annual precipitation between the two locations. The Stateline stands (with the exception of stand #17) show little variation along this moisture gradient. There is a good spatial separation of these Stateline stands along the Y-axis, but no single environmental factor is discernably correlated with this axis. This axis probably represents a complex of factors, together producing the patterns of distribution. *Carex geyeri*, for example, stretches itself along the Y-axis of the ordination in apparent response to this complex of factors.

Of the species found to have a ubiquitous distributional pattern, *Festuca idahoensis* was the most restricted, while *Achillea millefolium* and *Agropyron spicatum* had the widest distribution. *Hieracium albertinum*, which was fairly widespread, did not occur very frequently within any particular stand. *Agropyron spicatum* and *Festuca idahoensis* were the dominant grasses in the balds. These species are the same two which form the association commonly found on the prairies of Montana, Idaho and Washington.

The sharp transition zones, almost completely devoid of young spruce and fir, provide another pattern of vegetational distribution characteristic of these grassy balds. The invasion of the transition species *Xerophyllum tenax* into the Stateline balds shows that there are some microhabitats within the balds which can support *Xerophyllum* (see Figure 9). At the end of the severe drought in western Montana in 1967 it was observed that many individual beargrass clumps extending into the balds had apparently been killed as a result of the drought.

The occurrence of grassy balds in the Rocky Mountains is believed to be natural. Soil moisture is the primary limiting environmental factor, and the low amount of moisture in the soil is influenced by many climatic and microenvironmental features of the area. Under existing climatic and microenvironmental conditions these balds are thought to be stable. None of the above discussion, however, explains completely why the balds are not invaded along their periphery and

Figure 8 (above) and 9 (below).

Alders in the grassy balds

Sharp zonation

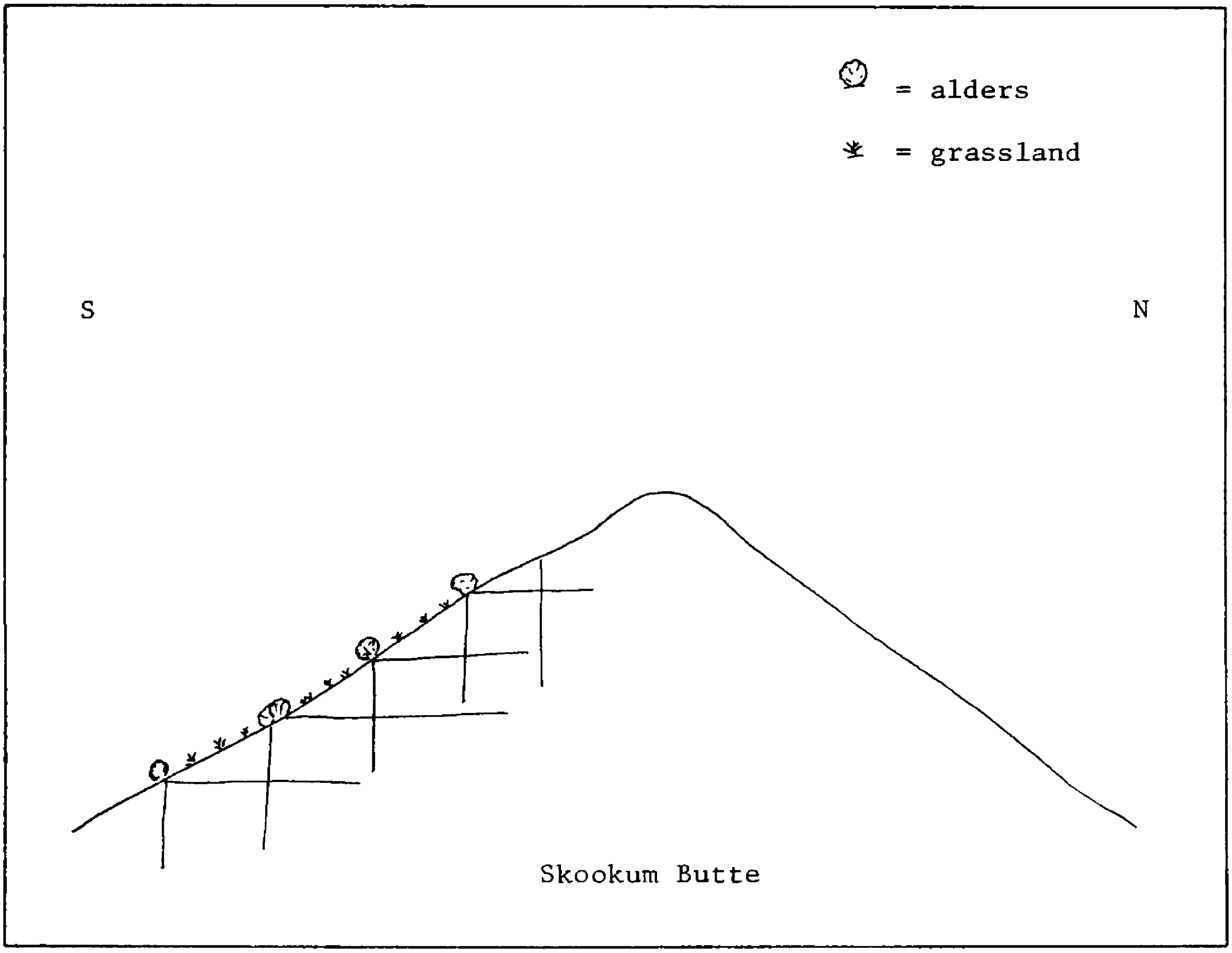
eventually forested. There is good reason to suspect drainage to be the answer.

Alder swales, it has been pointed out, grow where running water is available. These swales were found wherever balds were found, and in several places swales were above or below the balds (see Figure 8), indicating the availability of water.

J. L. Nold (personal communication), a geologist familiar with the geology of Skookum Butte, stated that the granitic intrusive formations which are found on the south-facing slope of Skookum Butte are jointed horizontally and vertically. Pevear (1964) shows the jointing pattern exhibited by the granitic intrusive formations on Skookum Butte. This jointing, according to Nold, is stair-like under the ground surface (see Figure 10), and the drainage of the slope follows this mosaic of joints. This drainage pattern seems to coincide with the swale pattern on Skookum Butte (see Figure 8). (Alder swales also occur on slopes which are not southern, and it is believed that even though similar drainage patterns may exist here, the soil does not become so dry because of the cooler and moister environments that are found on non-southern slopes.) Although Nold was less familiar with the Hoodoo Pass area, it is his belief that the bald there is possibly underlain by sedimetric strata which cause a similar drainage effect.

It is thought probable that the balds are underlain by rock strata or joints which divert water from the bald soil. These joints and strata are probably the reason for the sharpness of the ecotone which

Figure 10. Joint Patterns on Skookum Butte.



is found between the grasslands and the forest. Since the surface moisture which evaporates is not replaced by water from below the surface, the balds become very dry and will not support trees. The grassland species, however, complete their life cycles before or aestivate during the annual August dry spell, and thus are spared (Daubenmire, 1943). The ability of the prairie species to endure the xerothermic bald environment created by the underlying rock formations enables them to form a climax grassland vegetation in these areas.

SUMMARY

An ecological study of the subalpine grassy balds in the Rocky Mountains was conducted during the summer of 1967. The purpose of the study was to document and analyze the bald communities and to establish their stability.

The balds were located in two climatically different areas: at Mormon Peak where the annual precipitation is about 20 inches and along the Bitterroot Range divide where the annual precipitation is about 60 inches. Balds occurred on the south-facing slopes and generally were surrounded by the spruce-fir forest.

The frequency percentages of 60 representative species were used to construct an ordination. The frequency of each species for each stand was then plotted on the ordination to establish vegetational patterns among the stands. Weekly soil and surface temperatures and soil moisture readings were recorded. Soil samples were taken for further analysis in the laboratory.

Most of the balds were characteristically dominated by *Agropyron spicatum* and *Festuca idahoensis* and along the Bitterroot Range divide by *Carex geyeri* as well. The vegetation responds primarily to a soil moisture gradient between the stands and apparently to a complex of other environmental factors.

The results indicate that the balds are extremely dry during the latter half of the summer. The Mormon Peak stands do not receive enough precipitation during the year to support trees. The Stateline stands, on the other hand, do receive adequate precipitation, yet the balds form "islands" within the forest on the south-facing slopes. It is clear from the data that the dryness of the soils on the balds is not merely a result of exposure. The occurrence of alder swales and thus available water was noticed wherever balds were found. There is no significant difference between the forest and bald soils that would suggest mineral deficiency or toxicity; hence the chemical composition of the soil does not explain the occurrence of the balds.

The geology of Skookum Butte shows that there are numerous horizontal and vertical joints in the bedrock. A geologist familiar with this area believed the drainage pattern follows the mosaic pattern of the joints. It is also believed that in areas where strata occur the balds are underlain by the strata, which thereby prevents the upward movement of water to the bald as it dries out. Thus, drought is the primary environmental factor which prevents the establishment of trees on the balds and this mosaic of drought among the Stateline stands is determined by the underlying rock formations.

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APPENDIX

LIST OF PLANTS FOUND IN SUBALPINE GRASSY BALDS

Apocynaceae
- Apocynum androsaemifolium L.

Berberidaceae
- Berberis repens Lindl.

Betulaceae
- Alnus sinuata (Regel) Rydb.

Boraginaceae
- Cryptantha affinis (Gray) Greene.
- Cryptantha torreyana (Gray) Greene.
- Luppula redowskii (Hornem.) Greene.
- Lithospermum ruderale Dougl.
- Mertensia oblongifolia (Nutt.) G. Don.
- Mertensia paniculata (Ait.) G. Don.

Campanulaceae
- Campanula rotundifolia L.

Caprifoliaceae
- Lonicera utahensis Wats.

Caryophyllaceae
- Arenaria congesta Nutt.
- Cerastium arvense L.
- Silene douglasia Hook.

Compositae
- Achillea millefolium L.
- Agoseris aurantiaca (Hook.) Greene.
- Agoseris glauca (Pursh) D. Dietr.
- Anaphalis margaritacea (L) Benth. & Hook.
- Antennaria rosea (Eat.) Greene.
- Antennaria umbrinella Rydb.
- Arnica cordifolia Hook.
- Arnica fulgens Pursh.
- Artemisia dracunculus L.
- Artemisia frigida Willd.
- Artemisia ludoviciana Nutt.
- Aster intergrifolius Nutt.
- Balsamorrhiza sagittata (Pursh.) Nutt.
- Erigeron compositus Pursh.
- Erigeron corymbosus Nutt.

Erigeron peregrinus (Pursh.) Greene.
Erigeron speciosus (Lindl.) DC.
Hieracium albertinum Farr.
Lactuca serriola L.
Microseris nutans (Geyer) Sch.
Senecio canus Hook.
Senecio sphaerocephalus Greene.
Taraxicum laevigatum (Willd.) DC.
Tragopogon dubius Scop.

Crassulaceae
Sedum stenopetalum Pursh.

Cruciferae
Arabis holboellii Horn.
Camelina microcarpa Andrz.
Sisymbrium altissimum (L) Britt.
Thlaspi fendleri Gray.

Cyperaceae
Carex filifolia Nutt.
Carex geyeri Boott.
Carex paschystachya Cham.
Carex rossii Boott.

Ericaceae
Menziesia ferruginea Smith.
Vaccinium caespitosum Michx.
Vaccinium globulare Rydb.
Vaccinium membranaceum Dougl.

Gramineae
Agropyron spicatum (Pursh)Scribn. & Smith
Agrostis diegoensis Vasey.
Agrostis scabra Willd.
Bromus polyanthus Scribn.
Bromus tectorum L.
Calamagrostis canadensis (Michx.) Beauv.
Calamagrostis rubescens Buckl.
Danthonia intermedia Vasey.
Danthonia unispicata (Thurb.) Munro ex Macoun.
Elymus glaucus Buckl.
Festuca idahoensis Elmer.
Festuca viridula Vasey.
Koeleria cristata (L.) Pers.
Melica spectabilis Scribn.
Oryzopsis exigua Thurb.
Poa gracillima Vasey.
Poa pratensis L.
Poa secunda Presl.
Stipa williamsii Scribn.

Grossulariaceae
    Ribes lacustre (Pers.) Poir.
    Ribes viscossissimum Pursh.

Hydrophyllaceae
    Nemophila breviflora Gray
    Phacelia linearis (Pursh.) Holz.

Juncaceae
    Juncus parryi Engelm.
    Luzula glabrata (Hoppe) Desf.

Labiatae
    Agastache urticifolia (Benth.) Rydb.

Leguminosae
    Astragalus miser Doubl.
    Lupinus spp.

Liliaceae
    Allium cernuum Roth.
    Calochortus elegans Pursh.
    Erythronium grandiflorum Pursh.
    Fritillaria pudica (Pursh) Spreng.
    Xerophyllum tenax (Pursh) Nutt.
    Zigadenus venenosus S. Wats.

Onagraceae
    Clarkia pulchella Pursh.
    Epilobium angustifolium L.
    Epilobium paniculatum Nutt.

Pinaceae
    Abies lasiocarpa (Hook.) Nutt.
    Pinus albicaulis Engelm.
    Pinus contorta Dougl.
    Picea engelmannii (Parry) Engelm.
    Pinus ponderosa Dougl.
    Pseudotsuga menziesii (Mirb.) Franco

Polemoniaceae
    Collomia linearis Nutt.
    Collomia tinctoria Kell.
    Linanthus septentrionalis Mason.
    Microsteris gracilis (Dougl.) Greene.
    Phlox pulvinata (Wherry) Cronq.
    Polemonium pulcherrimum Hook.

Polygonaceae
    Eriogonum flavum Greene.
    Eriogonum umbellatum Greene.

Polygonum douglasii Greene.
Polygonum phytolaccaefolium Meisn.

Portulacaceae
Lewisia rediviva Pursh.

Primulaceae
Dodecatheon conjugens Greene.

Ranunculaceae
Delphinium bicolor Nutt.
Delphinium nuttallianum Pritz.
Ranunculus glaberrimus Hook.
Thalictrum occidentale Gray.

Rhamnaceae
Ceanothus velutinus Dougl.

Rosaceae
Amelanchier alnifolia Nutt.
Geum triflorum Pursh.
Potentilla glandulosa Lindl.
Potentilla gracilis Dougl.
Potentilla recta L.
Rosa gymnocarpa Nutt.
Rubus parviflorus Nutt.
Sorbus scopulina Greene.
Spiraea betulifolia Pall.

Saxifragaceae
Lithophragma parviflora (Hook) Nutt.
Mitella stauropetala Piper.
Saxifraga occidentalis Wats.

Scrophulariaceae
Castilleja hispida Benth.
Castilleja linariaefolia Benth.
Castilleja rexifolia Rydb.
Collinsia parviflora Lindl.
Orthocarpus tenuifolius (Pursh.) Benth.
Pedicularis bracteosa Benth.
Penstemon albertinus Greene.
Penstemon rydbergii A. Nels.

Umbelliferae
Lomatium ambiguum (Nutt.) C & R.
Lomatium cous (Wats.) C & R.
Lomatium dissectum (Nutt.) M & C.
Lomatium triternatum (Pursh.) C & R.
Perideridia gairdneri (H & A) Mathias.

CANOPY-COVERAGE

	Stand									
Species	1	2	3	4	5	6	7	8	9	10
Achillea millefolium	5.3	2.2	6.3	9.8	7.3	3.7	2.4	12.9	5.4	.2
Agastache urticifolia	3.4	1.8		.1	15.8		.1		2.4	
Agoseris glauca				1.6	.5	.2	1.7			
Agropyron spicatum		6.6	.1	1.7	7.4	6.8	16.5	8.8	15.1	15.1
Allium cernuum					.8	.1	2.8			
Amelanchier alnifolia	4.7	1.0								
Antennaria umbrinella				.6	3.3	6.2	1.8	12.1	1.3	
Arabis holboellii					.1					
Arenaria congesta			3.4	14.6	11.1	1.9	5.6	5.0	3.4	
Arnica fulgens				.1	4.0	.2		2.0		
Artemisia dracunculus						1.0	9.2			
Artemisia ludoviciana					12.3	5.7	2.6		12.0	
Aster intergrifolius			.1							
Agrostis diegoensis										55.3
Balsamorrhiza sagittata				9.0	1.7	7.3	4.8		15.6	

CANOPY-COVERAGE

Species	11	12	13	14	15	16	17	18	19
Achillea millefolium	5.5	.7		1.8					2.1
Agastache urticifolia	8.7	.8	3.7				.1		
Agoseris glauca									
Agropyron spicatum	30.6	9.4	9.5	21.1	15.9	6.3		30.3	25.8
Allium cernuum									
Amelanchier alnifolia									
Antennaria umbrinella					.3				
Arabis holboellii									
Arenaria congesta				1.9	1.1	2.1	.1	2.8	
Arnica fulgens									
Artemisia dracunculus									
Artemisia ludoviciana									
Aster intergrifolius	1.9							6.2	13.4
Agrostis diegoensis									
Balsamorrhiza sagittata									

CANOPY-COVERAGE

Species	1	2	3	4	5	6	7	8	9	10
Berberis repens		.6	2.1							
Bromus polyanthus				9.3	2.2				.1	
Bromus tectorum				6.6	9.3	2.9	6.2	2.7		
Calamagrostis canadensis	16.0	6.6	31.3							
Calamagrostis rubescens	6.6									
Calochortus elegans										.1
Campanula rotundifolia				1.4					2.8	
Carex geyeri	2.8	14.2	21.5							21.8
Carex paschystachya	.6	6.6	.1	.6					3.3	
Castilleja spp.				.2	.5				.5	
Collomia linearis				3.8	1.8	1.9	2.3	.1	.8	
Danthonia intermedia										
Danthonia unispicata				.2	.5	13.4			.1	
Delphinium spp.					.8	2.2				
Elymus glaucus										

CANOPY-COVERAGE

Species	11	12	13	14	15	16	17	18	19
Berberis repens									
Bromus polyanthus	.1	2.0	3.2	1.0			4.5	.5	
Bromus tectorum									
Calamagrostis canadensis		.1	7.1	.6			70.9		.1
Calamagrostis rubescens				.1				.1	
Calochortus elegans			.1	.8	.1	.4		.1	.2
Campanula rotundifolia	4.3								
Carex geyeri	29.8	12.7	18.1	10.1	20.0	17.1		26.8	25.0
Carex paschystachya			4.3			1.3	7.4		
Castilleja spp.	.8	.1							
Collomia linearis									
Danthonia intermedia		1.5	.5		.6	3.2		1.2	
Danthonia unispicata									
Delphinium spp.			5.0	.7		.2			
Elymus glaucus		.8	.1	.1			.5	.2	

CANOPY-COVERAGE

Species	1	2	3	4	5	6	7	8	9	10
Erigeron peregrinus	4.0	1.0								.1
Erigeron speciosus				2.5	2.0	.3	2.3	7.1	2.2	.5
Eriogonum flavum			3.4							
Eriogonum umbellatum		3.3	9.8			1.3				3.3
Erythronium grandiflorum			.6							.3
Festuca idahoensis				19.6	35.3	16.8	27.3	1.3	9.8	
Hieracium albertinum	.6	.6	3.0	.3		.5	1.3		1.1	7.4
Juncus parryi										
Koeleria cristata				1.0	.1	1.3	.8	.1	.6	
Lomatium triternatum					.2	.2			.2	
Lupinus spp.				34.2	.5	15.9	28.8	.1	4.2	
Melica spectabilis		1.4	.6							
Microseris nutans			.2	.1	.1					
Orthocarpus tenuifolius				1.9	3.8	2.8	1.7		.6	
Penstemon albertinus			.2							

CANOPY-COVERAGE

Species	11	12	13	14	15	16	17	18	19
Erigeron peregrinus			6.8	9.6	9.6	1.9	15.1		
Erigeron speciosus		17.4							
Eriogonum flavum			4.0	4.9	7.3	5.9		9.1	.7
Eriogonum umbellatum	1.8								
Erythronium grandiflorum		.2				1.3			
Festuca idahoensis		19.6	3.8	16.1	14.2	7.8		18.4	15.3
Hieracium albertinum	1.8				1.6			.7	1.8
Juncus parryi		.1		.5	.1			.6	
Koeleria cristata									
Lomatium triternatum			.1	.4		.5			.1
Lupinus spp.		2.7		3.7	3.1			.3	.9
Melica spectabilis		1.1	.6	3.1			2.0	.6	
Microseris nutans									
Orthocarpus tenuifolius									
Penstemon albertinus	1.3								.1

CANOPY-COVERAGE

Species	1	2	3	4	5	6	7	8	9	10
Phacelia lineralis							.1	.6	.6	
Phlox caespitosa		.1	1.0		.1					
Poa secunda						2.6	.6	43.8		
Polygonum douglasii						.2			.1	
Polygonum phytolaccaefolium	2.1	2.9								
Potentilla glandulosa	.6		2.1	8.8	3.0		.1		4.8	
Senecio integerrimus			12.4							
Sisymbrium altissimum					.5	.2	.1			
Spiraea betulifolia			1.7							1.8
Stipa williamsii					6.3			1.6	.3	
Tragopogon dubius				1.3	1.3	1.3	5.3	.2	.8	
Vaccinium globulare	9.8									.5
Vaccinium membranaceum		1.3	2.4							
Xerophyllum tenax	17.7									

CANOPY-COVERAGE

Species	11	12	13	14	15	16	17	18	19
Phacelia lineralis									
Phlox caespitosa		.5	3.3	.3	10.6	29.6		10.8	3.2
Poa secunda									
Polygonum douglasii		.1	.6	.7		.4	1.0		
Polygonum phytolaccaefolium	.7	3.2	1.9	3.8	3.4	2.8	2.8		5.0
Potentilla glandulosa									
Senecio integerrimus									
Sisymbrium altissimum									
Spiraea betulifolia	1.4			.1		.2	.1		.7
Stipa williamsii									
Tragopogon dubius									
Vaccinium globulare									
Vaccinium membranaceum									
Xerophyllum tenax	2.1	2.5	2.4		2.8	4.0	.1		2.1