AN ANALYSIS OF THE VEGETATION-MICROENVIRONMENTAL
COMPLEX ON PRAIRIE SLOPES
IN SASKATCHEWAN

A Thesis

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for the Degree of
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by

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INTRODUCTION

One of the basic questions of plant ecology is "why do plants grow where they grow?". Elucidation of any of the complex interrelationships between plant growth, plant distribution, and the physical environment is at least a contribution towards an appreciation of this question. Studies on the interrelations between slope-induced variations in microenvironment and vegetational composition appear to offer a particularly promising approach to the subject.

Studies on forest vegetation in North America have given considerable attention to the interrelations between plant distribution and environmental factors (Cantlon 1953, Cooper 1961, Loucks 1962). In contrast, grassland studies dealing with the environment-plant complex are few and not comprehensive in nature. This study was therefore initiated to fill this void.

The present study attempts to add to our comprehension of the complex interrelations between the microenvironment and vegetational patterns in grasslands, particularly as these are influenced by slopes within local areas. The main objectives of this investigation are: (a) to study the variations in the composition of grassland vegetation as they are correlated with slope aspect and position, (b) to analyse the variations in the environmental factors which may be responsible for species distribution, (c) to evaluate the degree of correlation

between environmental factors, species behavior, and vegetation pattern, and (d) to ascertain the degree of abruptness of vegetational variations which if great, would permit the recognition of separable units.

The rolling moraine topography of portions of central Saskatchewan provides, on a local scale, a variety of slopes which display a varied habitat spectrum. The study was carried out in an area about 25 miles east of Saskatoon. The field work was conducted during the summers of 1960, 1961 and 1962.

THE STUDY AREA

Location

Four sites, all 25 to 31 miles east of Saskatoon, were selected for this study. Two (sites 1 & 2) are about 1 mile south of St. Denis at SW 33-36-1-W3rd while the other two (sites 3 & 4) are along Saskatchewan Highway No. 5 at SE 5-37-28-W2nd. The first two sites are less than a quarter of a mile apart, and the second two represent adjacent knolls. The maximum distance between any two sites of the study is approximately 6 miles.

Geology and Soils

The landscape of the study area is characterized by a moderate to strongly rolling topography, consisting of a succession of knolls, intermediate slopes, and depressions. It exists on glacial till where glacial stones and boulders are prominent features.

All of the study sites are located within the Weyburn soil association in the dark brown soil zone (Mitchell et al. 1944). This association consists chiefly of hard columnar profiles which are predominantly loam in texture and dark brown in colour.

Regional Climate

The study area belongs to the "dry and sub-humid moisture region" of western Canada defined by Sanderson (1948). Kendrew and Currie (1955) recognized six climatic regions in central Canada and the sites of the present study are located in the southern part of region 4, which is essentially the parkland and the southern edge of the northern forest.

Annual precipitation at Saskatoon varies from 8.8 to 21.0 in., with a mean of 13.7 in. (Currie 1953a). Snow, which usually remains on the ground from November to March, constitutes 30 percent of the total annual precipitation.

The mean monthly temperature varies from 0°F. in January to 65°F. in July. Wide variations in diurnal and seasonal air temperature occur in the area. Summer temperatures above 100°F., and winter temperatures below -40°F. have been recorded in Saskatoon. The mean duration of frost-free season is 106 days, from May 26 to September 9 (Kendrew and Currie 1955).

The mean cloud-cover is about 5 tenths, varying little through the year from slightly more in June and November, to less in February and August. Small amounts of cloud are frequent in the early morning, but large amounts are frequent in the afternoon.

Winds from the northwest and southeast quadrants dominate throughout the year. The NW winds usually have their maximum frequency during winter months, while those from the SE are more common in summer. Warm SW winds may occur during the summer which have a destructive effect to vegetation, especially during prolonged dry periods. Monthly average wind speed at Saskatoon varies from 9 miles per hour in February to 13 miles per hour in April and May (Kendrew & Currie 1955).

Sanderson (1948) states that the southern parts of Saskatchewan are exposed to warm air masses from the southern United States and have higher water needs than corresponding latitudes in Ontario and Quebec, which are overlain by cooler polar air. In the dark brown soil zone, in which the study area is located, water deficiency ranges from 6 to 8 in. per year.

Vegetation

The study area lies in the transition region between the Mixed Prairie (Stipa-Bouteloua association) to the south and the Fescue Prairie (Festuca scabrella association) to the north. Clumps of Populus tremuloides in depressions and sheltered places are common.

Coupland (1961) recognized the following five climax communities in the Stipa-Bouteloua association in Saskatchewan:-

1. Stipa-Agropyron faciation of medium-textured soils in dark brown and moist parts of the brown soil zones.
2. Stipa-Bouteloua-Agropyron faciation of medium-textured soils in the arid portions of the brown soil zone.
3. Stipa-Bouteloua faciation, an edaphic climax community of well stabilized sandy soils.
4. Bouteloua-Agropyron faciation, an edaphic climax on clay loam solonetzic soils in the more arid areas.
5. Agropyron-Koeleria faciation, an edaphic climax on fine-textured lacustrine soils.

The Festuca scabrella association (Coupland & Brayshaw 1953) occupies portions of the black soil zone in Saskatchewan.

Coupland (1950) suggests the following distribution of species on rolling land in the moist parts of the dark brown soil zone adjacent to the black soil zone: Bouteloua gracilis and Stipa comata on the tops of knolls, Stipa spartea var. curtiseta and Agropyron dasystachyum on the intermediate slopes, with Festuca scabrella at lower levels.

REVIEW OF LITERATURE

The importance of slope effect on vegetation has been recognized for many years. Sendtner (1854), as quoted by Braun-Blanquet (1932), determined the altitudinal limits of plants on various exposures in southern Bavaria. Here the highest altitudinal limits of species almost constantly occurs on the southwest, and the lowest on north and northeast slopes. The maximum difference was 213 meters for Picea excelsa.

Warming (1925) was among the early workers to recognize the influence of slope degree and exposure on radiation and runoff, and consequently on vegetation. Similarly, Turesson (1914) found that the distribution of Douglas fir, in the arid parts of Arizona, was controlled by slope exposure, while Shaw (1916) described the differences in the vegetation on different slopes of the Selkirk Mountains in British Columbia. He suggested that winter differences in climate are the major causes for compositional differences in this vegetation.

Studies done by Shreve (1922-1927), in the western United States, indicated that the distribution of the vegetation is strongly influenced, through changes in soil temperature, soil moisture, and air temperature, by slope and exposure. He came to the conclusion that the differences between vegetation on north and south slopes are due to a group of conditions initiated by differences in insolation and soil temperature.

More recent studies are concerned with the quantitative evaluation of factors modified by slope aspect and position, and their

influence on vegetation composition. Cottle (1932), in his study of vegetation on the mountains of the Big Bend Country of southwestern Texas, indicated that environmental conditions on south slopes are much less favourable to plant growth than on north slopes. He found that water content in the soil was 5 to 16 percent lower, evaporation 24 to 44 percent higher, and soil temperatures were 10° to 20°F. higher at 2 inches above the surface on south slopes as compared to north slopes. The vegetation cover on south slopes was found to be less than one-half as much and the production of dry matter only about one-twentieth of that produced on north slopes. He came to the conclusion that several factors interact to produce these conditions, water relations being the controlling one.

In Indiana, a study by Potzger (1939) on a ridge which had a characteristically beech-maple forest on north slopes and oak-hickory on south slopes indicated that soil moisture-content is the factor which determined this difference. He reported that surface soil had 30 percent, and soil at six inches depth 28 percent more moisture on the north than on the south slope.

Aikman and his colleagues (Aikman & Smelser 1938, Aikman 1941, Aikman & Brackett 1944) studied the effect of slope exposure on natural vegetation and cultivated plants in Iowa. They attributed the differences in the structure of the forest communities to slope differences and to varying microclimate. They found the west slope to be the most xeric, with the highest average air and soil temperature, the highest maximum soil temperature at 2 inches, the longest frost-free season, the highest evaporation, and the greatest wind velocity. Other slopes were found to be less xeric than the west

in the following order: south, east, and north.

Shanks and Norris (1950), in Tennessee, studied an area occupied by ungrazed natural vegetation which had contrasting association-segregates on the opposing north-and south-facing slopes. They found that the mean air temperature at the 1 foot level was 3°F. higher on southern than on northern slopes, while the maximum temperatures were 11°F. higher. They reported that the particular species were more or less restricted in their distribution to different slope aspects.

Parker (1952) in Northern Idaho, found that Abies grandis and Thuja plicata are common on north slopes, and Pinus ponderosa and Pseudotsuga taxifolia are common on south-facing slopes. Their data indicated that wind velocity is higher and soil moisture is lost more rapidly on south than on north slopes. Physical characters of the soil are also different. South slopes had soils which are generally more coarse-textured and hold less moisture as compared to north slopes.

An extensive study of the effect of variations in the microclimate on the structure of the vegetation and life form spectra on Cussetunk Mountain in New Jersey was made by Cantlon (1953). He found the structure and composition of the vegetation on north and south slopes to be quantitatively different. The greatest differences in vegetation were found in the terrestrial bryophyte layer, where the magnitude of differences in the microclimate was also at a maximum. He found that the greatest differences between the slopes, in relation to some environmental factors, did not occur at the same season as did the greatest differences in periodicity of the vegetation. Environmental differences reached a maximum in the fall, while periodicity differences were greatest in spring.

One of the few studies which considered both slope aspect and position is that done by Cooper (1961) in southern Michigan. In considering the relationship between Raunkiaerian plant life-forms and microclimates, he concluded that the microclimates varied from a cool, moist (mesic) extreme of the bottom of north slopes to a warm, dry (xeric) extreme at the top of south slopes. By correlating a microenvironmental index with vegetational data, he found relative cover of hemicryptophytes to be greatest in xeric and the geophytes to be greatest in mesic microenvironments.

MacHattie and McCormack (1961), evaluated the effect of topography on surface climate and consequently on botanical processes in Ontario. They made microclimatic observations along a transect across a ridge from the north slope to a south slope. Maximum air temperatures were found to be higher on the north slope, while soil temperature at 4 inches, minimum air temperature, and evaporation were lower. They reported that the earliest flowering occurred on the ridge-top and latest on the north slope, that of the south slope being intermediate.

The effect of altitude and slope exposure on different community types on the Crested Butte area in Colorado were studied by Langenheim (1962). She correlated the vegetation pattern with a coincidence index of climatic factors. For the upland herb community type, east and, to a lesser extent, north slopes were found to be most favourable in all altitudinal ranges. The alpine communities reached optimum development from 12,500 to 13,500 ft. on north slopes and to a lower elevation on east and south slopes. The fescue grassland had its optimum importance from 9,500 to 10,500 ft. on south exposure.

In addition to the observations made by Moss (1944) and Moss and Campbell (1947) in Alberta and Coupland (1950) in Saskatchewan, only one quantitative study has evaluated the effect of slope exposure and position on vegetation and microenvironment in the Canadian prairies. Hird (1957) carried out a study on the vegetation and microclimatic patterns in the grassland of Saskatchewan. She found that the vegetation of north- and south-facing slopes was distinguished by the occurrence of characteristic communities. The former was dominated by Festuca scabrella and the latter by Bouteloua gracilis. Koeleria cristata and Agropyron dasystachyum were important on north slopes while Stipa comata, Stipa spartea var. curtiseta, and Muhlenbergia cuspidata were important on south slopes. Definite zonation was found to correlate with slope position. She suggested that variation in temperature factors may be of primary importance since the soil-moisture content did not show significant differences between south and north slopes.

In North Dakota, Dix (1958) studied the roles of slope and exposure in determining the species composition of some grassland types. An ordination of stands correlated with the soil moisture factor. Bouteloua gracilis and Agropyron smithii of the relatively xeric Great Plains were found to be more important at one end of the gradient, while Andropogon scoparius, Bouteloua curtipendula, and Muhlenbergia cuspidata, of the relatively mesic Midwestern prairies, were more important at the opposite end.

METHODS

Selection of Stands

In order to carry out the objectives of this study the following criteria were established for site and stand selection:

1. Evaluations of the slope-induced variations in vegetational and environmental factors are valid only if the regional climate and zonal soils are uniform from one site to the other. Therefore, only the sites located not more than 10 miles apart were considered.
2. Some climatic elements, such as air temperature and humidity, may fluctuate greatly within a brief time period and, to compare the magnitude of these on different slope aspects, measurements had to be taken very rapidly. To accomplish this, only knolls having at least 5 slope exposures were considered as adequate sites.
3. Since this study is mainly concerned with the effect of slope aspect and position, variations of slope steepness were permitted only within a range of 5 degrees. The range chosen was between 13 - 18°, since it is the most common in the study area.
4. Grazing in this area has been shown to cause noticeable changes in vegetational composition (Coupland et al. 1960); therefore, sites were considered only if they appeared to be free from recent grazing.

Four sites, the locations of which are described in "THE STUDY AREA", were found to meet the above requirements. Each of these sites had six slopes with differing exposures. Data from Hird (1957) and the preliminary work of the present study suggested that variations in vegetation and environment occurred on different

positions along the same slope. Accordingly, each of the 24 slopes was divided into three positions: upper, middle and lower. Care was taken that each position have the same degree of steepness and exposure. A total of 72 stands were thereby selected for study (Fig. 1).

Field Vegetational Measurements

The 72 stands of this study were sampled by the point-centered method. This method was developed by Cottam and Curtis (1956) for the study of forest vegetation, and adapted for use in grasslands by Dix (1961). Preliminary phytosociological sampling indicated that several species with low stature (e.g., Selaginella densa) have such high densities that the importance of larger, but less dense species, are obscured. It was decided therefore to sample the vegetation in two phases (Dix 1961). In the first phase, a lower synusium (i.e., Carex obtusata, Carex eleocharis, Carex filifolia, Phlox hoodii, and Selaginella densa) was considered. The second phase included all other vascular species. At least 40 points per stand were used in each sampling phase. From the data made available by this method, relative density and relative frequency were calculated for every species and these values were then summed to give an importance value.

Taxonomic nomenclature is according to Moss (1959). A list of the common names for the plants of the study is given in Appendix A.

Fig. 1. Location of stands in relation to slope aspect and position. The innermost circle indicates the lower positions of slopes.

Environmental and Physiographic Records

Slope measurements:

The exposure of slopes was determined by a hand compass, and the readings were corrected for magnetic declination. The percent slope for each stand was measured with an Abney level.

Microclimatic records:

Soil temperatures were measured by copper-constantan thermocouples and a temperature-calibrated portable potentiometer (model Rubicon, 2736) was used to make field readings. All thermocouples were calibrated in a water bath at five points from 0 - 100°C against a mercury in-glass thermometer. Actual data were derived from graphs which showed potentiometer readings plotted against thermometer readings.

Soil surface temperature was taken by inserting the head of the thermocouple into the first millimeter of the soil at the base of a grass shoot. As it was known that soil surface temperature is highly variable, preliminary tests were carried out to arrive at an adequate number of readings and on the basis of these tests, at least six readings were taken and their mean calculated. Other thermocouples were installed at depths of 6 and 12 in. and left throughout the period of the study. The temperature at these depths was less variable than at the soil surface, and here three readings were taken.

Air temperatures and vapor pressure deficit readings were obtained by the use of a battery-driven, aspirated psychrometer, (Gemware portable motorized #16W-925T). Readings of both the dry and

wet bulb thermometers were taken after leaving the instrument in position for 1 minute with the fan in operation, at 3, 6 and 12 in. above the soil.

Air temperatures were recorded from the dry bulb thermometer. Vapor pressure deficit values were derived from the nomograms made by Gordon (1940), using both the wet and dry bulb thermometer readings.

Geiger (1957) has suggested that the maximum differences in microclimatic elements between slopes can be expected to occur in the afternoon. This was confirmed by preliminary data of the present study (Table 1), which indicated that the maximum differences in air temperature, vapor pressure deficit, and soil temperature occurred, in most cases, between 2 and 5 p.m. Since this investigation was mainly concerned with variations that may affect the vegetation distribution on slopes, rather than in describing the microclimate itself, emphasis was laid on evaluating the magnitude of maximum differences that may occur. Thus all readings were taken between 2 and 5 p.m. Since the differences in microclimatic elements between slope exposures may be obscured by cloudy and overcast skies, only clear days were chosen for recording.

When the immediate objective was to evaluate differences between aspects, readings of the microclimatic elements were recorded on all aspects of a given position within as short a time span as possible, never more than 20 minutes. At sites 1 and 3, slope aspects were thus compared for soil temperature, air temperature, and vapor pressure deficit, at the levels already indicated, eight times during 1961 growing season. In comparing the above microclimatic elements on different slope positions, readings were always recorded on the

Table 1. Differences in climatic elements between NE and SW slopes, at different times of the day. Data presented are averages of readings taken at three different dates during 1961 growing season. Readings were taken at three depths and at three heights above the soil surface.

Climatic element Time of the day	Soil temperature (°C.)			Air temperature (°C.)			Vapor pressure deficit (%)		
	NE	SW	Difference	NE	SW	Difference	NE	SW	Difference
5 a.m.	16.6	17.2	0.6	12.9	11.9	1.0	8.3	8.3	0.0
8	19.7	19.3	0.4	24.6	23.6	1.0	13.3	12.5	0.8
11	22.9	24.5	1.6	30.0	30.5	0.5	24.4	25.5	1.1
2 p.m.	24.2	27.4	3.2	32.1	33.4	1.3	29.1	32.6	3.5
5	22.2	26.2	4.0	30.2	31.5	1.3	25.9	27.9	2.0
8	20.8	23.2	2.4	23.1	23.2	0.1	14.1	14.1	0.0
11	18.8	21.8	3.0	17.9	18.3	0.4	8.9	9.1	0.2
2 a.m.	10.9	11.2	0.3	9.2	9.4	0.2	6.3	6.8	0.5

three positions of a given slope within 15 minutes. These readings were made five times on a north and five times on a south slope.

The role of vegetation in modifying the microclimate was also investigated. On each of two slopes, one north and one south, three 9 ft.² areas were clipped as close to the ground as possible, and the vegetation and mulch were removed. Readings of the microclimatic elements, as described above, were recorded at different depths and heights from the soil surface and comparable readings were recorded at the same time in the nearby undisturbed areas.

Data from the 1961 growing season were used to test the statistical significance of differences in microclimatic elements between slope aspects and positions. The next step was to correlate those differences with the vegetation pattern and for this purpose, readings were made in the 1962 growing season. Two sites (36 stands) were chosen to record the microclimatic elements, and all readings were made within one hour around 3:00 p.m. Due to the large number of readings needed, only soil temperature at the surface, and air temperature and vapor pressure deficit at 3 in. above the soil were recorded. These measurements were selected because preliminary study had suggested that variations in the microclimate were greatest at the layers closest to the soil surface (Table 2).

Solar radiation, as modified by slope and aspect, is of major importance to the present investigation. Since no instrument was available to measure the actual amounts of radiation received by the various slopes, this factor was calculated from the following formula, as used by Jordon & Threlkeld (1953):

$$I_{st} = \frac{I_h}{\sin \beta} \cdot \cos (\beta - \phi) \cdot \cos \alpha, \text{ where}$$

Table 2. Differences in climatic elements between NE and SW slopes, at different depths and heights from the soil surface. Data presented are averages of readings taken on four different dates during the 1961 growing season. Readings were taken at three different positions on each of the two slopes.

Climatic element Depth or height from soil surface (in.)	Soil temperature (°C.)			Air temperature (°C.)			Vapor pressure deficit (%)		
	NE	SW	Difference	NE	SW	Difference	NE	SW	Difference
0	30.6	38.6	8.0	-	-	-	-	-	-
3	20.7	25.3	4.6	32.6	34.2	1.6	29.4	32.4	3.0
6	13.5	16.8	3.3	32.3	32.9	0.6	28.8	30.0	1.2
12	13.0	16.1	3.1	31.7	32.0	0.3	27.7	28.5	0.8
18	-	-	-	30.6	31.5	0.9	26.2	27.6	1.4
24	12.1	15.5	3.3	30.2	30.7	0.5	25.6	26.7	1.1
36	10.7	14.2	3.5	-	-	-	-	-	-

I_{st} = solar radiation on a tilted surface (steepness and aspect of stand under consideration)

$\frac{I_h}{\beta}$ = solar radiation at normal incidence (horizontal)

β = solar altitude

ϕ = angular tilt from vertical position, (e.g., 20° slope has $\phi = 70$)

α = the difference between direction of slope and solar azimuth, (for a south-facing slope $\alpha = 180$ - the solar azimuth).

The solar azimuth and altitude were obtained from the U.S. Hydrographic office (1958). In order to obtain the solar azimuth and altitude the declination of the sun relative to the Earth at a given time must be determined. This figure is given by the U.S. Naval Observatory (1961).

The solar radiation at normal incidence ($\frac{I_h}{\beta}$) is calculated from the solar constant. Determinations fix the solar constant at 1.896 cal/cm² x min which is the radiation intensity outside the atmosphere. This figure was multiplied by factors presented by Jordon & Threlkeld (1953) to give normal incidence radiation outside the atmosphere for each day of the year. Calculations of $\frac{I_h}{\beta}$ were thus carried out for the 15th of every month from April to September inclusive. An average for these months, for each of the 72 stands, was then calculated.

The importance of the amount of albedo of surface vegetation was recognized, but it was assumed that the differences between various grassland stands would be negligible and this factor was ignored. Cloudiness is also important in this connection, but it too was considered uniform over the study area and therefore not a variable.

Soil factors:

Soil samples, for moisture-content determination, were taken from two different locations and at two different depths (0-6 in. and 6-12 in.) in each stand, placed in air tight plastic bags and brought to the laboratory within 4 hours after collection. Fifteen to 20 g. from each sample was weighed twice, dried at 110°C. for at least 48 hours, cooled in a desiccator, and weighed again. The decrease in weight due to moisture loss was expressed as a percentage of oven-dry weight. The sampling was repeated seven times during the growing season of 1961. During the 1962 growing season, sampling was repeated five times. Each time, a complete set of soil samples was taken in the same day with the aim of correlating the soil-moisture content with the vegetation pattern. Following rains, samples were not taken for four days.

The physical and chemical characters of Northern Great Plains grassland soils, as affected by slope aspect and position, have been dealt with in detail by J. H. Ellis (1938) in Alberta and J. G. Ellis (1957) in Saskatchewan. In the present study, therefore, this work was not repeated in detail. However, to correlate some of the physical and chemical properties of the soil with vegetation pattern, two samples were collected from each stand at 0-6 in. and 6-12 in. depths. Samples were pooled, spread over sheets of paper, air-dried, mixed and passed through a 2 mm. sieve to remove debris. The methods followed in analyzing the samples except for water retaining capacity are outlined by Wilde & Voigt (1955). Soil texture was determined by the Bouyoucos hydrometer method and percent sand, silt, and clay were calculated. The organic matter

content was determined by the loss on ignition method. Determination of the soil reaction was done by the use of a glass electrode pH meter. The water retaining capacity (WRC) was determined by the use of "Hilgard cups" (Piper 1944).

Treatment of Data

Vegetation:

The structure of vegetation is determined by the differing responses of species to the existing environment. The greater the similarity between the amplitudes of tolerance of two species, the more likely they will be found together and therefore, similar habitats are likely to support similar groups of plants. If the degree of dissimilarity in vegetational composition of two stands is assessed, this can be expected to reflect the differences in the environmental complex in the two stands. All stands in the study can then be compared with each other as to the degrees of similarity or dissimilarity between them. The matrix resulting from these comparisons will give an initial indication of the relationship between the vegetation and its environment, beside evaluating, with a degree of quantitative exactness, the compositional structure. From this matrix, stands can be arranged on a linear scale according to the degrees of similarity between them. Goodall (1954) proposes the term "ordination" for such an arrangement. Many attempts have been made to use the ordination techniques in the study of vegetation. Of these, the ordination was in either a single dimension (Curtis & McIntosh 1951, Clausen 1957, Dix 1958, Dix & Butler 1960), in two dimensions (Hulett 1962), in three dimensions (Bray & Curtis 1957, Maycock &

Curtis 1960, Loucks 1962), or in more than three dimensions (Goodall 1954).

The ordination technique described by Maycock & Curtis (1960), which provides a spatial ordering in three dimensions, was used in the present study. The first step of this technique was to express the importance value (relative frequency + relative density) of each species in each stand as a percentage of the maximum it attained in any single stand. The percentages thus obtained were called actual scores. The actual scores for all species in each stand were then summed and each expressed as a relative value of that total. These values are called the final scores (relative actual scores for each species in each stand). The 72 stands were compared, each one with each of the others separately. In comparing one stand with the other, lower final **scores** for species in common (or the same score for species with identical values) were recorded and totalled. This total represents the similarity between the two stands. Similar comparisons were made between each two stands of the study and all these comparisons were entered into a matrix. The matrix values for each stand were then summed to give a stand total. The lowest of these stand totals represented the stand most dissimilar to all other stands and it was considered to be one end of a primary (X) axis. The matrix values of this first end-stand were again examined and the lowest value was interpreted as belonging to the stand with the least in common to the first end-stand. The latter became the second end-stand of the axis.

The next step was to arrange the remaining stands between the two end-stands. To accomplish this, all matrix values for the

two end-stands were examined and the single highest value was selected. All matrix values of the stand chosen as the second end of the axis were subtracted from this highest value. The values so obtained were added to the matrix values of the stand chosen as the first end, and divided by two. The average values resulting from this represented the position of each stand on the primary (X) axis.

The secondary (Y) axis ordination was accomplished by first determining the mid-point of the primary axis, and selecting the 20 stands closest to it. A partial matrix was made up for these stands in exactly the same procedure followed for the primary axis matrix. Then, the two end stands were selected and all other stands were subsequently arranged in the same way as before. Finally the tertiary (Z) axis was built by selecting 15 stands around the intersection of the mid-points of the primary and secondary axes, and then repeating the same procedure employed for the first two axes.

Position of stands resulting from this three-dimensional ordination were plotted on three separate sheets. One for primary (X) and secondary (Y), the second for primary (X) and tertiary (Z), and the third for secondary (Y) and tertiary (Z) axes. Actual values for any of the quantities of vegetation or environment were then plotted for each stand to indicate their different patterns.

Environment:

Among the aims of this study is an evaluation of the magnitude of differences in some environmental factors between various slope aspects and positions, and between vegetated and clipped areas. These values were tested for statistical significance. An analysis of

variance (F test) was used to estimate the level of significance of the overall variations in each of the environmental factors studied. To ascertain whether the significance of the overall variation is due to one or more differences and to which difference in particular, a Duncan multiple range test or least significant range (LSR), was used. The least significant difference (LSD) was used in testing the significance of the differences between vegetated and denuded areas. This test helps to show how far the difference is from the lowest level of significance, because some of the differences indicated as significant by the F test may be very close to the LSD, which means that they have a very low degree of significance. The procedures followed in F, LSR, and LSD tests are according to Snedecor (1957).

To examine the degree of correlation between the physical environment data and the compositional gradients of the three-dimensional ordination, correlation coefficients (r) were calculated between each single factor and each of the gradients. A test of significance (t) was carried out for each correlation coefficient, to indicate the level of its significance. To find out if any single factor is significantly correlated with any of the axes, when another factor is held constant, a partial correlation coefficient was calculated and a "t test" employed. This was used only for the factors which have had highly significant simple correlations with any of the axes (Ezekiel & Fox 1959 & Cook 1960).

RESULTS

Variations in Vegetational Composition with Slope Aspect and Position Gradients

This section attempts to analyse variations in vegetational composition along a multiplicity of gradients which are seemingly under the control of two physiographic factors - slope aspect and position. Similar approaches have been used by Whittaker (1960), Hulett (1962) and others.

The physiographic position of each of the 72 stands of this study is plotted in Fig. 1. The slopes were then grouped into seven categories according to their degree of exposure from true north: exposures 340 to 360 and 0 to 20 represent N, exposures 25 to 65 represent NE, exposures 70 to 110 represent E, exposures 160 to 200 represent S, exposures 205 to 245 represent SW, exposures 250 to 290 represent W, and exposures 295 to 335 represent NW. No slopes were available to represent SE. Each of these seven categories was further subdivided into three slope positions: upper, middle, and lower. This resulted in 21 physiographic units. The importance values of each of the 17 most important species were averaged for all the stands which occurred in a particular physiographic unit (Table 3). These species included all those which have an importance value of 5% or more in at least one stand.

The data indicate that the behavior of all but one species varies in relation to slope aspect gradient. Some species have narrow ranges of distribution, being more or less restricted to one or two aspects. Thus, Bouteloua gracilis is identified with E and S

Table 3. Mean importance values of the major species in relation to slope aspect and position.

I. Species of the lower synusium	Slope position	Slope aspect						
		N	NE	E	S	SW	W	NW
<i>Carex eleocharis</i>	Upper	147.3	173.1	88.5	57.3	120.0	138.4	111.1
	Middle	56.6	124.3	42.2	22.4	123.5	85.5	83.8
	Lower	31.6	66.1	30.1	72.0	140.5	67.1	69.5
<i>Carex filifolia</i>	Upper	20.2	2.3	7.5	41.4	31.4	25.3	16.7
	Middle	24.5	1.7	1.1	38.2	39.1	16.8	-
	Lower	-	36.7	-	17.7	19.8	17.8	-
<i>Carex obtusata</i>	Upper	27.3	9.9	-	0.7	-	5.4	26.2
	Middle	108.5	42.4	15.2	-	5.1	68.6	89.4
	Lower	166.1	82.1	135.0	0.6	3.8	99.7	125.8
<i>Phlox hoodii</i>	Upper	2.9	13.1	102.5	101.0	26.3	30.9	46.0
	Middle	5.4	30.5	57.5	137.7	32.3	29.1	23.8
	Lower	2.3	10.9	2.7	96.0	28.0	9.0	2.7
<i>Selaginella densa</i>	Upper	2.4	1.6	1.5	0.6	22.3	-	-
	Middle	5.0	1.4	84.1	1.8	-	-	-
	Lower	-	4.2	32.1	13.7	7.9	6.4	1.9

Table 3 (Cont.). Mean importance values of the major species in relation to slope aspect and position.

II. Species of the upper synusium	Slope position	Slope aspect						
		N	NE	E	S	SW	W	NW
<i>Agropyron dasystachyum</i>	Upper	74.4	106.2	107.5	86.2	138.5	39.1	47.3
	Middle	17.5	33.0	57.5	38.7	119.6	54.5	34.6
	Lower	19.8	10.6	9.2	20.6	110.6	41.8	35.2
<i>Artemisia frigida</i>	Upper	0.9	6.9	13.5	15.1	12.8	13.5	2.8
	Middle	-	-	4.1	27.5	8.8	5.9	-
	Lower	1.8	2.8	-	11.5	6.1	1.7	-
<i>Bouteloua gracilis</i>	Upper	-	-	1.6	-	-	-	-
	Middle	-	-	18.0	19.2	-	-	-
	Lower	-	-	25.4	68.1	-	-	-
<i>Erigeron caespetosus</i>	Upper	1.5	-	-	-	2.2	3.3	12.3
	Middle	3.7	1.8	-	-	4.4	3.5	10.4
	Lower	-	4.1	-	1.8	3.6	2.6	4.0
<i>Festuca scabrella</i>	Upper	83.2	41.7	-	-	1.5	55.3	116.1
	Middle	121.5	98.2	7.1	-	3.5	72.6	99.5
	Lower	126.8	107.4	62.0	0.7	10.6	87.6	111.2
<i>Galium boreale</i>	Upper	-	-	-	-	-	1.6	0.9
	Middle	1.6	3.0	-	-	-	6.2	11.3
	Lower	5.8	7.8	20.9	-	-	20.5	20.1

Table 3 (Cont.). Mean importance values of the major species in relation to slope aspect and position.

II. Species of the upper synusium (cont.)	Slope position	Slope aspect						
		N	NE	E	S	SW	W	NW
<i>Gaillardia aristata</i>	Upper	0.7	-	-	-	-	-	-
	Middle	14.2	-	-	-	-	-	-
	Lower	3.7	4.6	-	-	-	-	-
<i>Koeleria cristata</i>	Upper	6.4	27.5	48.6	59.6	12.3	10.3	6.1
	Middle	3.0	20.9	40.9	34.1	18.2	19.3	5.1
	Lower	1.4	7.2	18.5	47.8	15.3	4.4	2.8
<i>Muhlenbergia cuspidata</i>	Upper	-	-	-	-	-	-	-
	Middle	-	-	1.7	13.4	17.2	-	-
	Lower	-	-	-	15.7	14.9	-	-
<i>Poa cusickii</i>	Upper	8.4	5.8	-	-	4.3	3.3	11.1
	Middle	12.5	6.9	-	0.5	1.5	7.5	19.5
	Lower	7.5	14.4	4.5	1.2	1.6	1.9	10.0
<i>Stipa comata</i>	Upper	-	-	-	25.9	1.9	1.1	
	Middle	-	-	2.1	34.2	-	2.3	
	Lower	-	-	-	16.4	-	-	
<i>Stipa spartea</i> var. <i>curtiseta</i>	Upper	6.8	7.1	16.3	10.1	19.3	9.0	7.1
	Middle	5.3	21.9	66.0	-	22.5	4.5	3.0
	Lower	1.6	16.8	35.4	8.8	28.4	10.9	1.7

exposures, Muhlenbergia cuspidata with S and SW, Stipa comata with S, and Gaillardia aristata with N and NE slopes. Most of the species, however, have wide ranges of distribution in relation to aspect with a gradual increase in importance values towards a maximum on one or two orientations. Carex obtusata and Festuca scabrella increase in importance value towards a maximum on N-facing slopes, Carex filifolia, Koeleria cristata and Artemisia frigida towards the S exposures, Poa cusickii and Erigeron caespitosus towards the NW, Galium boreale to the W and NW slopes, Selaginella densa to the E, Agropyron dasystachyum to the SW, Phlox hoodii to the E and S, and Stipa spartea var. curtiseta towards the E aspects. Carex eleocharis is the only species which acted indifferently without a recognizable pattern.

In relation to behavior along the slope position gradient, some species show a gradual increase in importance value towards one maximum at one position. Thus, Carex eleocharis and Agropyron dasystachyum increase in importance value towards the upper level, and Carex obtusata, Festuca scabrella and Galium boreale towards the lower position. Some other species show no gradual change towards one position, but rather are more important in two adjacent positions. Bouteloua gracilis and Muhlenbergia cuspidata are more important on lower and middle positions, and Carex filifolia, Phlox hoodii, Artemisia frigida, Koeleria cristata and Stipa comata on upper and middle ones. Species which show no preference for any particular slope position are Selaginella densa, Erigeron caespitosus, Poa cusickii and Stipa spartea var. curtiseta.

The behavior of the eight most abundant species along aspect

and position gradients, as expressed by their relative densities, is shown in Fig. 2. The highest one or two quartiles of relative density attained by some of the major species were plotted on "targets" of slope aspect and position. Again it can be seen that some species act indifferently, and some others exhibit special distribution patterns. These patterns are more or less similar to those obtained above from analysis of importance values. It is worth noting that the greatest relative densities of most species occupy ranges of several slope aspects and positions.

Phytosociological Ordination of Stands

A phytosociological ordination was used in this study to sort out the behavioral patterns of species with respect to each other and to illustrate the interrelations between changes in the vegetation and the physical environment.

The distance of each stand from the zero point on each of the three axes is given in Appendix B and the positions of the stands are plotted on three dimensional ordination in Fig. 3. Primary and secondary, primary and tertiary, and secondary and tertiary axes were included on separate graphs. The density values of each of the nine most important species are superimposed on these positions.

At a glance, it becomes clear whether or not a species has a special pattern among the different ordinations. Festuca scabrella and Carex obtusata occupy more or less low positions on the primary, and high positions on the secondary axis. Bouteloua gracilis and Phlox hoodii have more or less the reverse position. Some species, however, have intermediate positions on one of the axes. Agropyron

Fig. 2. The distribution of the upper one or two quartiles of relative density attained by eight of the major species in relation to slope aspect and position. The largest circle size represents densities of 75% or more, the second largest between 50-74% and the smallest for densities between 25-49%. The lower positions of slopes are the closest to the center.

Antropus densiflorum *Bouteloua gracilis* *Carex elaeocharis* *Carex obtusata* *Festuca scabrella* *Koeleria cristata* *Phlox hoodii* *Stipa spicata* var. *curiseta*

Fig. 3. The pattern of distribution as expressed by relative density values of the most important lower synusium species in relation to the three ordinations viewed in two-dimensional planes. The largest circle size represents densities of 75% or more, the second largest between 50-74%, the third 25-49%, and the smallest for densities less than 25%. The dots represent the position of stands in which the species was absent.

Carex eleocharis Carex obtusata

Fig. 3 (cont.). The pattern of distribution as expressed by relative density values of the most important lower synusium species in relation to the three ordinations viewed in two-dimensional planes. The largest circle size represents densities of 75% or more, the second largest between 50-74%, the third 25-49%, and the smallest for densities less than 25%. The dots represent the position of stands in which the species was absent.

Phlox hoodii

Fig. 3a. The pattern of distribution as expressed by relative density values of the most important upper synusium species (grasses) in relation to the three ordinations viewed in two-dimensional planes. The largest circle size represents densities of 75% or more, the second largest between 50-74%, the third 25-49%, and the smallest for densities less than 25%. The dots represent the position of stands in which the species was absent.

Agropyron dasystachyum Bouteloua gracilis

Fig. 3a (cont.). The pattern of distribution as expressed by relative density values of the most important upper synusium species (grasses) in relation to the three ordinations viewed in two-dimensional planes. The largest circle size represents densities of 75% or more, the second largest between 50-74%, the third 25-49%, and the smallest for densities less than 25%. The dots represent the position of stands in which the species was absent.

Festuca scabrella Koeleria cristata

Fig. 3a (cont.). The pattern of distribution as expressed by relative density values of the most important upper synusium species (grasses) in relation to the three ordinations viewed in two-dimensional planes. The largest circle size represents densities of 75% or more, the second largest between 50-74%, the third 25-49%, and the smallest for densities less than 25%. The dots represent the position of stands in which the species was absent.

Stipa spartea var. curtiseta

Fig. 3b. The pattern of distribution as expressed by relative density values of the most important upper synusium species (Artemisia frigida) in relation to the three ordinations viewed in two-dimensional planes. The large circle size represents densities between 25-49%, and the small one for densities less than 25%. The dots represent the position of stands in which the species was absent.

Artemisia frigida

dasystachyum and Stipa spartea var. curtiseta occur towards the middle of the primary and Koeleria cristata the tertiary axes. Two species that do not have a clear pattern are Carex eleocharis and Artemisia frigida.

The spatial ordination of 21 of the important species is further illustrated in Fig. 4, where the central points of behavior of a majority of species, as expressed by relative density values, are presented in a three-dimensional aspect. The central point of any species on each axis was determined by averaging the distances from the zero point of the stands that have the highest quartile values of relative density of that species. The size of circle represents the magnitude of the highest quartile of relative density for each species. The smaller the distance between the central points of any two species, the more likely they are to be found together in nature. It is important to note that the species are distributed over a wide range in relation to the primary and secondary axes, while on the tertiary axis there is no wide separation.

Effect of Slope Aspect, Slope Position, and Vegetative Cover on the Environment

Slope aspect

The fact that slope aspect induces variations in the micro-environment is clearly established. The results presented here are intended to show the magnitude and the significance of the differences between aspects as they occur in the study area. The effect of the degree of slope was eliminated by selection of slopes of approximately the same steepness (13 - 18°). The means of temperature and moisture readings at various depths below the soil surface, and of air temperature

Fig. 4. The three-dimensional aspect of the location of central points of the behavior of a majority of species as expressed by their relative densities. The largest circle size represents relative densities of 75% or more, the second largest between 50-74%, and the smallest for densities less than 25%.

A. da. = *Agropyron dasystachyum*; A. tr. = *Agropyron trachycaulum*; An. pa. = *Anemone patens*;
Ar. fr. = *Artemisia frigida*; B. gr. = *Bouteloua gracilis*; C. el. = *Carex eleocharis*;
C. fi. = *Carex filifolia*; C. ob. = *Carex obtusata*;
E. ca. = *Erigeron caespitosus*; F. sc. = *Festuca scabrella*; G. bo. = *Galium boreale*;
Gu. di. = *Gutierrezia diversifolia*; K. cr. = *Koeleria cristata*; L. pu. = *Liatris punctata*; P. cu. = *Poa cusickii*; Ph. ho. = *Phlox hoodii*; S. co. = *Stipa comata*; S. sp. cu. = *Stipa spartea* var. *curtiseta*;
Se. de. = *Selaginella densa*; So. mi. = *Solidago missouriensis*.

and vapor pressure deficit at three heights above the soil surface, on each slope at two sites, are presented in Tables 4, 5, 6, and 7, for several dates during the growing season of 1961.

Variation in soil temperature between slopes was found to be highly significant on all dates at both sites (Table 4). The differences between the members of the majority of slope pairs proved to be significant according to the LSR test. At site 1, the average soil temperature value for slopes which are predominantly north-facing was $24.4^{\circ}\text{C}.$, compared to $26.3^{\circ}\text{C}.$ for south-facing ones. At site 3, the average values were $22.4^{\circ}\text{C}.$ for N and $26.0^{\circ}\text{C}.$ for S. This means that on the average N slopes were $1.9^{\circ}\text{C}.$ cooler than S slopes at one site, and $3.6^{\circ}\text{C}.$ at the other.

The means of air temperature readings on six slope aspects are compared in Table 5. The overall variation was highly significant on most dates. On two occasions, the variation was significant due to differences between members of only a few pairs of means. The average air temperature for all the predominantly N slopes at site 1 was $32.2^{\circ}\text{C}.$ and for S slopes it was $33.0^{\circ}\text{C}.$ At site 3 the averages were 32.3 for N and 33.2 for S. This shows that, on the basis of the whole season average, air temperature was only $0.8^{\circ}\text{C}.$ higher on south-facing slopes than on north-facing ones at one site and $0.9^{\circ}\text{C}.$ at the other.

Variations in vapor pressure deficit with slope aspect are either significant or highly significant on most dates (Table 6). It is clear however, that this significance is due to high differences between the members of only a few pairs of means. In almost all cases, high vapor pressure deficit values are found on S slopes and low ones

Table 4. Means of soil temperature readings on slope aspects on different dates of 1961 growing season. F value indicates the degree of significance of overall variations. Pairs of means with common letters have an insignificant difference according to the LSR test.

Site 1

Date Slope aspect	June 12	July 9	July 20	August 19
ENE	18.7	24.9 b	23.9	24.1 a
ESE	19.9 a	27.7	25.1 b	25.8 b
SSE	20.9	29.4 c	27.7	28.0 c
SSW	21.4	29.1 c	26.3 b	27.2 b c
NNW	19.5 a	23.4 a	21.4 a	22.7 a
NNE	19.6 a	23.8 a b	21.6 a	22.8 a
F Value	20.7**	54.4**	50.6**	31.6**

Site 3

Date Slope aspect	June 29	August 12	August 22	September 14
N	25.1 b	24.6	25.4 b	15.2
NNW	22.1 a	22.6	24.8 a	14.2
WNW	21.4 a	23.4	25.3 a b	15.7
WSW	24.1 b	25.2	27.3	16.7 a
SSW	27.3	27.2	30.6 c	18.9
NNE	25.3 b	25.7	26.8 c	16.4 a
F Value	24.7**	54.3**	77.9**	56.8**

* F is significant at the 5% level.

**F is significant at the 1% level.

Table 5. Means of air temperature readings on slope aspects on different dates of 1961 growing season. F value indicates the degree of significance of overall variations. Pairs of means with common letters have an insignificant difference according to the LSR test.

Site 1

Date Slope aspect	June 12	July 9	July 20	August 19
ENE	31.9	37.3 b	30.9	34.2
ESE	32.5	36.2	29.9 a	32.1 a b
SSE	33.7	35.7 a	29.9 a	31.9 a
SSW	34.9	35.4 a	29.4 a	32.5 c
NNW	31.2 a	37.2 b	27.8 b	32.3 b c
NNE	31.1 a	38.4	27.3 b	32.5 c
F Value	63.5**	27.5**	23.3**	18.6**

Site 3

Date Slope aspect	June 29	August 12	August 22	September 14
N	33.3 a b	36.1 a	36.0 a	23.6 a b
NNW	33.9 b c	35.9 a	35.9 a	23.1 a
WNW	33.4 b	35.8 a	36.7	23.1 a
WSW	34.8	37.2	38.2 b	23.5 a b
SSW	34.1 c	36.2 a	38.4 b	23.7 b c
NNE	32.9 a	36.1 a	36.3	24.2 c
F Value	8.6**	3.4*	46.3**	3.0*

* F is significant at the 5% level.

**F is significant at the 1% level.

Table 6. Means of vapor pressure deficit readings on slope aspects on different dates of 1961 growing season. F value indicates the degree of significance of overall variations. Pairs of means with common letters have an insignificant difference according to the LSR test.

Site 1

Date Slope aspect	June 12	July 9	July 20	August 19
ENE	24.1 a b	37.8 a b	24.5 c	28.4 b
ESE	25.7 b	39.1 a b	24.0 c	27.1 a b
SSE	29.3	37.3 a b	25.9 c	27.0 a
SSW	31.3	36.4 a	23.7 b c	27.5 a b
NNW	23.2 a	39.8 b	19.7 a b	28.2 a b
NNE	23.4 a	43.2	18.5 a	28.3 a b
F Value	55.7**	19.5**	19.2**	2.7

Site 3

Date Slope aspect	June 29	August 12	August 22	September 14
N	30.7 a b	39.4 a b	36.5 a	17.8 b c
NNW	32.3 a b	38.3 a b	36.6 a	17.0 a b
WNW	31.5 a b	37.4 a	39.6 b	16.6 a
WSW	34.8 b	40.9 b	43.3 c	17.1 a b
SSW	33.9 a b	39.2 a b	43.8 c	17.3 a b c
NNE	29.5 a	39.3 a b	37.5 a b	18.5 c
F Value	8.4**	3.4*	41.8**	2.9*

* F is significant at the 5% level.

**F is significant at the 1% level.

Table 7. Means of soil-moisture content readings on slope aspects on different dates of 1961 growing season. F value indicates the degree of significance of overall variations. Pairs of means with common letters have an insignificant difference according to the LSR test.

Site 1

Date Slope aspect	May 19	July 7	August 4	September 4
ENE	23.2 c	9.4 b	11.5	8.1
ESE	21.2 b	9.2 b	10.9 b	7.6 a
SSE	18.6 a	8.0 a	8.5 a	6.2
SSW	19.0 a	7.0	8.5 a	5.7
NNW	21.5 b	8.1 a	9.4	7.0
NNE	24.4 c	9.3 b	10.6 b	7.6 a
F Value	41.4**	15.4**	42.9**	46.3**

Site 3

Date Slope aspect	June 20	July 28	September 10
N	10.7 b c	7.5 a	8.8 b
NNW	12.8	9.1 b	8.7 b
WNW	13.7	9.0 b	9.8
WSW	10.1 a b	7.9 a	6.5 a
SSW	10.0 a	6.5	6.9 a
NNE	11.3 c	7.5 a	8.6 b
F Value	35.8**	17.4**	23.1**

* F is significant at the 5% level.

**F is significant at the 1% level.

on N slopes

Soil-moisture content varies significantly at the 1% level with changes in slope aspect on all dates (Table 7). The average value for predominantly N slopes, at site 1, is 12.3%, and for S slopes 10.2%. At site 3, the average values are 9.5% for N and 7.8% for S. This means that N slopes are on the average 2.1% higher in soil-moisture content than S slopes at one site and 1.7% at the other.

Slope position

The microclimate at different elevations on the same slope may differ for various reasons. One may be due to varying amounts of runoff water; the greater amounts being received by the lower positions may cause higher soil-moisture content. Upper positions of slopes may be exposed to greater wind velocities than lower ones, resulting in higher evaporation rate. Differences in density of vegetative cover at various slope elevations may have an effect on the heat and moisture balance near the soil surface.

Variations in soil temperature with slope position measured during this study are presented in Table 8. These variations are either significant or highly significant on most dates. Upper and middle slopes seem to be warmer than lower ones. The average values for all dates are 21.8°C. on upper, 21.0°C. on middle and 19.2°C. on lower positions of the N slope. On the S slope the respective average values are 5 to 6 degrees higher (27.2°, 27.0° and 24.9°C.). This also indicates that the differences are, on the average, much smaller between upper and middle slopes (0.8 and 0.2°C.) than between middle and lower ones (1.8 and 2.1°C.).

Table 8. Means of soil temperature readings on slope positions on different dates of 1961 growing season. F value indicates the degree of significance of overall variations. Pairs of means with common letters have an insignificant difference according to the LSR test.

A. North Slope

Date Slope level	May 18	June 16	July 31	August 21	September 17
Upper	9.0	20.8	17.4 a	24.1 b	16.0 b
Middle	5.5 a	21.3	18.3 a	23.1 a b	13.9 a b
Lower	3.9 a	20.2	17.2 a	22.2 a	13.2 a
F Value	17.7**	11.9**	3.9	6.8*	5.1

B. South Slope

Date Slope level	May 18	June 16	July 31	August 21	September 17
Upper	13.2	24.3 a b	20.7	29.8 a b	20.8
Middle	9.3	25.0 b	21.7	31.8 b	20.2
Lower	7.2	23.3 a	19.8	29.7 a	19.8
F Value	38.5**	5.2*	15.8**	4.4	18.4**

* F is significant at the 5% level.

**F is significant at the 1% level.

Air temperature and vapor pressure deficit do not vary significantly from one position on the slope to another (Tables 9 & 10). On only four of ten occasions did the air temperature and vapor pressure deficit vary significantly. The data also indicate that higher air temperature and vapor pressure deficit values are more likely to be found on middle and lower positions than on upper ones.

Variations in soil-moisture content with slope position proved to be either significant or highly significant on all occasions but one (Table 11). There is a gradual but clear change from low values at upper positions towards higher values at lower ones. The average soil-moisture content for all dates on the N slope is 11% for the lower position, 10.2% for the middle, and 9.3% for the upper, while the respective values for the S slope are 8.3%, 7.9% and 5.3%.

Effect of vegetative cover

The role of vegetation in modifying the microclimate is well established and an attempt is made in the present study to examine the magnitude of changes in some microclimatic elements caused by vegetation. Data from two slopes are presented in Table 12. The data show that the vegetation has either a significant or highly significant effect in modifying soil and air temperature in most cases. It is also clear that soil temperature was lower in vegetated areas on all dates of sampling while air temperature was higher than in unvegetated areas. It is interesting that the differences in soil temperature between vegetated and unvegetated areas on the N slope were greater (6.3°C.) than those on the S slope (2.6°C.). This is probably due to the greater insulation

Table 9. Means of air temperature readings on slope positions on different dates of 1961 growing season. F value indicates the degree of significance of overall variations. Pairs of means with common letters have an insignificant difference according to the LSR test.

A. North Slope

Date Slope level	May 18	June 16	July 31	August 21	September 17
Upper	23.9 a	34.8 a	32.3	33.5 a	27.3
Middle	22.2 a	35.1 a	33.3	33.5 a	28.4 a
Lower	22.6 a	35.3 a	32.7	34.7	28.1 a
F Value	4.2	1.2	6.2*	8.5**	5.2*

B. South Slope

Date Slope level	May 18	June 16	July 31	August 21	September 17
Upper	25.8 a	35.5 a	32.8 a	35.8	27.8 a
Middle	26.8 a	35.8 a	33.8 a	36.8 a	27.8 a
Lower	27.8 a	36.1 a	33.2 a	36.8 a	28.3 a
F Value	4.0	1.5	2.5	42.3**	0.8

* F is significant at the 5% level.

**F is significant at the 1% level.

Table 10. Means of vapor pressure deficit readings on slope positions on different dates of 1961 growing season. F value indicates the degree of significance of overall variations. Pairs of means with common letters have an insignificant difference according to the LSR test.

A. North Slope

Date Slope level	May 18	June 16	July 31	August 21	September 17
Upper	16.9 b	30.2 a	27.1 a	30.3 a b	23.1 a
Middle	14.7 a b	30.0 a	28.4 a	29.8 a	25.4 b
Lower	13.5 a	33.3 a	27.0 a	31.7 b	24.3 a b
F Value	8.1**	4.2	1.6	4.4*	5.4*

B. South Slope

Date Slope level	May 18	June 16	July 31	August 21	September 17
Upper	18.3 a	32.9 a	26.4 a	33.5	24.8 a
Middle	20.2 a	34.1 a	28.9 a	38.5 a	24.0 a
Lower	21.0 a	33.3 a	27.3 a	38.5 a	24.6 a
F Value	3.0	0.8	2.7	40.0**	0.5

* F is significant at the 5% level.

**F is significant at the 1% level.

Table 11. Means of soil-moisture content readings on slope positions on different dates of 1961 growing season. F value indicates the degree of significance of overall variations. Pairs of means with common letters have an insignificant difference according to the LSR test.

A. North Slope

Date Slope level	June 23	July 14	August 17	September 15
Upper	10.9 a	9.3 a	9.0	8.1 a
Middle	11.9 a	9.9 a b	9.6	9.3 a b
Lower	13.2	10.5 b	10.3	9.9 b
F Value	10.6**	3.3	9.0**	4.9*

B. South Slope

Date Slope level	June 23	July 14	August 17	September 15
Upper	6.5	4.8	6.0 a	3.8
Middle	9.5 a	8.2 a	7.3 a b	6.7
Lower	9.6 a	8.2 a	8.3 b	7.2
F Value	66.5**	39.7**	6.1**	53.0**

* F is significant at the 5% level.

**F is significant at the 1% level.

Table 12. Means of soil temperature, air temperature and vapor pressure deficit readings in vegetated and unvegetated areas on north- and south-facing slopes, on different dates of 1961 growing season. F value indicates the degree of significance of each difference. LSD values are the least significant differences.

A. Soil Temp.

Date Area	North slope			South slope		
	July 31	August 21	September	July 31	August 21	September
Veg.	18.0	23.9	14.9	20.8	30.7	21.1
Non Veg.	23.2	26.9	25.0	24.5	32.7	23.1
F Value	254.4**	6.8*	76.0**	5.4	37.6**	228.0**
LSD	0.84	2.99	1.12	-	0.89	0.43

B. Air Temp.

Date Area	North slope			South slope		
	July 31	August 21	September	July 31	August 21	September
Veg.	32.4	34.0	28.2	32.8	35.9	27.5
Non Veg.	31.7	33.1	27.2	32.8	35.0	28.8
F Value	20.8*	24.1**	21.4**	0.0	67.0**	6.3
LSD	0.43	0.36	0.51	-	0.25	-

C. V.P.D.

Date Area	North slope			South slope		
	July 31	August 21	September	July 31	August 21	September
Veg.	26.2	30.7	24.7	26.9	36.1	23.7
Non Veg.	25.8	29.1	22.9	27.8	34.3	23.9
F Value	2.3	1.1	12.1*	3.8	10.8*	0.88
LSD	-	-	1.17	-	1.17	-

* F is significant at the 5% level.

**F is significant at the 1% level.

Fig. 5. The relation between slope aspect and phytosociological ordinations in two-dimensional graphs. Stands of predominantly N, E, W or S were connected to form an area representing each of these exposures.

Upper position

Middle position

Fig. 5 (cont). The relation between slope aspect and phytosociological ordinations in two-dimensional graphs. Stands of predominantly N, E, W or S were connected to form an area representing each of these exposures.

Lower position

or less centered towards the right end. East and W slopes occupy intermediate positions. There is no clear separation between slope aspects on the secondary (Y) and tertiary (Z) axes. It is to be noted that the separation of slope aspects on the primary axis is greater on middle and lower positions than on upper ones, which presumably means that the effect of slope aspect is more manifested on middle and lower positions.

The relationship between phytosociological ordinations represented by the primary and secondary axes and slope positions, is summarized in Fig. 6. A median line was drawn through each slope aspect area on the primary-secondary axes dimension shown in Fig. 5. To accomplish this the midpoint between the two stands to the extreme left and the midpoint between the two stands to the extreme right of each aspect area were located. These two midpoints were then connected with a line. All lines thus obtained were placed on a single graph, where each slope exposure was represented by three lines, one each for the upper, middle and lower positions (Fig. 6). It is clear that all exposures except S have the upper position at a greater distance from the zero point of the secondary axis than the lower position. The middle position is intermediate between upper and lower. This indicates that the slope position gradient is more or less related to the secondary (Y) axis.

Correlations between microenvironmental factors and phytosociological ordinations

Correlation coefficients between the ordination of stands on the three axes and the factors of the microenvironment may help in understanding the nature of these ordinations. A list of

Fig. 6. The relation of slope position to the phytosociological ordination as viewed in the two-dimensional plane of primary and secondary axes. Each of the slope exposures, N, E, W and S is represented by three lines, one each for the upper, middle and lower positions. The determination of the location of each line is presented in the text (Page 51).

microenvironmental factors dealt with and their correlation coefficients with each of the three axes is shown in Table 13. Primary and secondary axes have highly significant correlations with mean and April radiation, soil surface temperature, soil-moisture content, pH, organic matter, and maximum water retaining capacity. The tertiary axis has significant correlations with soil surface temperature and pH only.

Partial correlation coefficients were calculated to estimate the degree of correlation between either the primary or the secondary axis and either the soil surface temperature or the soil-moisture content, when one of these factors is constant. Significant partial correlations of -0.61 for soil-moisture content, and 0.39 for soil temperature indicate that the primary axis is partly expressing a moisture factor and partly a temperature factor. On the same basis, the secondary axis seems to be essentially one of moisture, because, while it has a significant partial correlation of 0.37 with soil-moisture content, its correlation with soil surface temperature (-0.21) is not significant.

The nature of the tertiary axis is not clear since its partial correlations with soil surface temperature and pH are insignificant (being 0.27 and 0.09 , respectively).

The ranges of variation in soil-moisture content and soil surface temperature were divided into five equal segments. Numbers from I to V were assigned to the stands and these were plotted on the primary-secondary plane of the ordination. It was possible, with few or no discrepancies, to separate the moisture or temperature segments in space (Figs. 7 & 8). It can be seen that the moisture

Fig. 7. Distribution of soil moisture segments (I - V) in relation to phytosociological ordinations, viewed in the primary-secondary axes dimension. With few exceptions, the lines separate groups of adjacent stands having the same soil moisture segment.

Fig. 8. Distribution of soil temperature segments (I - V) in relation to phytosociological ordinations viewed in the primary-secondary axes dimension. With few exceptions, the lines separate groups of adjacent stands, having the same soil temperature segment.

Table 13. Correlation coefficients of environmental factors with ordination axes.

Axes	Radiation a. mean b. April	Soil surface temp.	Air temp. (at 3")	Vapor pressure deficit (at 3")	Soil- moisture content (1st ft.)	pH value (1st ft.)	Organic matter (1st 6")	Sand % (6-12")	Water retaining capacity (1st ft.)
X	a. 0.68** b. 0.73**	0.67**	0.27	0.13	-0.77**	0.57**	-0.73**	-0.046	-0.73**
Y	a.-0.51** b.-0.49**	-0.47**	0.18	0.15	0.54**	-0.58**	0.57**	-0.045	0.49**
Z	a. 0.13 b. 0.13	0.41*	0.14	0.12	0.02	0.33*	0.22	-0.06	0.14

* Indicates a significant correlation coefficient (at the probability level of .05).

**Indicates a highly significant correlation coefficient (at the probability level of .01).

segments form a distinct pattern in relation to the primary axis, the highest values being to the extreme left and the lowest to the extreme right. In relation to the secondary axis, the moisture segments form a less distinct pattern, with the highest at a greater distance from the zero point. The temperature segments form a more or less clear pattern, in relation to the primary axis, where the high segments are to the right and the low ones to the left, while there is no obvious pattern in relation to the secondary axis. This may suggest that the primary axis is expressing partly a moisture factor and partly a temperature factor, while the secondary axis may be predominantly one of moisture.

Behavior of individual species

If sufficient phytosociological data are obtained for any species over its entire amplitude and plotted against any of the prevalent factors of the environment, that species tends to have a normal distribution curve with an optimum at a certain level of that factor. If several species have similar optima with regard to a certain factor their presence in the field together may be indicative of the approximate magnitude of that factor.

Behavior of twelve of the major species as expressed by their relative density values along a five-segmented temperature gradient are shown in Fig. 9. Carex obtusata, Festuca scabrella, and Galium boreale peak at the lowest temperature segment, while Phlox hoodii, Koeleria cristata, Stipa comata, Bouteloua gracilis, and Artemisia frigida have their optimum densities towards the highest temperature segment. Carex eleocharis, Agropyron dasystachyum, and Stipa spartea var. curtiseta have their optima at intermediate positions.

Fig. 9. The distribution of average relative density of some major species along a five-segmented temperature gradient.

Curves of species behavior along a certain factor are not always of the monomodal type, with one optimum at a certain value of that factor. Some species have bimodal or multimodal curves of behavior. The bimodal type is represented in the present study by the behavior of Anemone patens along the temperature gradient.

It is clear from Fig. 10 that the same species which peak at low temperatures have their optima of relative density at high moisture segments, and vice versa. It is to be noted that Stipa comata and Galium boreale seem to have narrower amplitudes of tolerance than most other species being absent from some temperature and moisture segments.

Fig. 10. The distribution of average relative density of some major species along a five-segmented moisture gradient.

DISCUSSION

The variation in vegetational composition in relation to slope aspect and position has been emphasized in the present study. Individual species variations with slope aspect are more or less in agreement with those obtained by Hird (1957), except for Koeleria cristata and Agropyron dasystachyum. The first species attains its maximum importance on S and E slopes of the present study, and the second on SW slopes, while Hird reported greatest abundance on N and NE slopes respectively. This difference in behavior is not surprising with respect to Koeleria cristata, which is recognized as having a wide ecological amplitude (Coupland 1961). In respect to Agropyron dasystachyum, this difference in results may be due to the fact that the sites in the two studies are different in their location and time of sampling. Those of the present study are closer to the Fescue Prairie (Coupland & Brayshaw 1953, & Coupland 1961). This difference in the locations of the sites in the two studies may result in enough changes in the environment to cause differences in vegetation composition.

Previous workers have emphasized the importance of the effect of slope aspect alone on vegetation. Thus, Perring (1959) concluded that the vegetation distribution due to topographical gradients of chalk grassland in England is mainly along an axis from NE to SW. Sato and Tatum (1960) arrived at the same conclusion in dealing with plant production on slopes. Although it is true that radiation changes, in the northern hemisphere, induce the lowest moisture conditions on SW slopes, as compared to the highest on NE, the runoff effect in relation to slope position may alter the effect of radiation.

Striking differences in species composition between different slope positions support this idea. For example, Festuca scabrella, which has its optimum abundance on N and NE slopes, attains a higher mean importance value (87.6) on the lower position of W slopes than on the upper position of NE slopes (41.7). Again, Carex eleocharis has comparable values of 147.3 and 140.5 on the upper position of N slopes and the lower position of SW slopes. This indicates that emphasizing the importance of slope aspect alone is not valid unless we are dealing with a particular position on the slope. If there is any axis of variation, it is more logical to be from the lower position of the NE slope to the upper level of the SW slope.

The magnitudes of difference in importance values with slope aspect and position, in the present study, differ with different species depending on their amplitudes of tolerance towards a complexity of environmental factors. "Every plant species is distributed according to its own genetically determined tolerance limits providing time has been sufficient to allow it to occupy the whole potential environment open to it." (Billings 1952). Those species which show large variations in distribution with only small changes in slope aspect and position may be considered to provide good quantitative measurements of environment. One example of this principle is Phlox hoodii, which changes in importance value from 13.1 to 102.5 from NE to E slopes on the upper position and again from 26.3 on SW slopes to 101.0 on S slopes. Another example of Agropyron dasystachyum which has an importance value of 20.0 on lower S slopes and 110.6 on lower SW ones. Boyko (1947) stresses the importance of the limits of microdistribution to the deduction from vegetation studies

of quantitative, as well as qualitative, values of ecological amplitudes. Goodall (1954) states, "There is much to be said for the view that the complexes of environmental factors determining plant distribution can be indicated and measured better indirectly, through the plants themselves, than by direct physical measurements".

The arrangement of stands along compositional gradients proved useful in several ways. Central points of the optimum densities of species are widely separated on the primary and the secondary axes, while on the tertiary there is only very narrow separation (Fig. 4). This suggests that the vegetation composition on slopes is largely controlled by two main factors or groups of related factors. Furthermore, this indicates that there is no need to separate the stands along any more gradients.

This study has emphasized that each species has its own distributional pattern (Fig. 3). Certain species may have similar patterns, but there are no two identical. Moreover, the clumping of the points of maximum density in the three dimensional ordination (Fig. 4) emphasizes that the variations in vegetation composition on the slopes studied are continuous rather than abrupt. In Goodall's opinion (1954), however, the division of vegetation into arbitrary units or classes may be justified for purposes of practical convenience, provided that its arbitrariness is recognized and that it is not claimed to represent an objective state of things. This study has shown that the highest densities among the low stratum species are attained by Carex obtusata at one extreme end, Phlox hoodii at the other end, and Carex eleocharis in the middle. In the upper stratum, the highest densities are obtained by Festuca scabrella at one end,

Stipa spartea var. curtiseta, Agropyron dasystachyum and Koeleria cristata in the middle, and with no species having particularly high densities at the other end. Festuca scabrella was classified by Coupland (1961) as a dominant of the Fescue Prairie, which is the most mesic of the Canadian grassland. He also classified Stipa spartea var. curtiseta, Agropyron dasystachyum and Koeleria cristata as dominants in the Mixed Prairie which is less mesic than the former.

The results of the present study show that both the slope position- and slope exposure-induced variations in the microenvironment are highly significant in the case of soil temperature and soil-moisture content. Equations of the heat and moisture balance at the earth's surface have been developed (Thornthwaite 1948, Thornthwaite & Mather 1955, Pennman 1948-1956, Houghton 1954, Budyko 1956, and London 1957). From these and other studies it became evident that the components of the heat balance equation depend primarily on the radiation exchange between the earth and the atmosphere. Since the amount of radiation varies with slope aspect and degree it is to be expected that such differences in the microclimate will occur as shown in the results of this treatise. The moisture balance, on the other hand, is controlled partly by the amount of precipitation received and partly by the main processes of solar energy transformation on the earth's surface. On different positions of a slope and with variations in the degree of steepness, the amount of precipitation received will be modified. Another factor that may have an influence to a certain extent on the moisture balance of the soil on different positions of the slope is the vegetative cover. Mitchell and Closs (1958) report a greater loss of moisture, under high intensity radiation, under short grass

pastures than under "long" grass pastures. Lower positions of slopes having a denser vegetative cover may be expected to lose less moisture from upper layers of the soil.

The effect of slope position on inducing variations in soil temperature can be thought of partly in terms of the effect of vegetation and the conditions of the soil surface, and partly in terms of changes in degree of slope from one position to the other. The measurement of soil temperature reported above (Table 8) indicates that in all cases the lower positions are cooler than the middle and upper one and that the middle positions in most cases are still cooler than the upper slopes. This regular pattern excludes the possibility that these changes in soil temperature can be caused by irregularities in the degree of slope from one position to the other within the narrow range of variation dealt with in this study. Consequently, the results can better be explained by changes in vegetation density and moisture conditions of the soil surface. It has been shown that the vegetated areas have much lower soil temperature than the barren ones (Table 12). Since the vegetation is denser on lower slopes, it may follow that the soil temperature becomes cooler. Moreover, the higher soil-moisture content on the lower slopes caused by the runoff, may cause a reduction in the soil temperature. Geiger (1957), cited Wollny, Ramdas, and Fuchs, among others who have demonstrated the cooling effect of soil moisture.

Air temperature and vapor pressure deficit data show low or insignificant variations in response to changes in slope aspect and position (Tables 5, 6, 9 & 10). This may be attributed to the mixing effect of the wind. Air temperature (Table 12) was significantly

higher in vegetated areas than in barren ones in most cases, especially on the N slope. It is well known that the temperature of a plant may differ from that of the surrounding air, because it is being heated or cooled by radiation and evapotranspiration. While evapotranspiration uses heat and consequently cools the adjacent air, radiation warms the plant and air during the day. Therefore, during the day, the air will be heated by the vegetation if the radiation warms the plant more than evapotranspiration cools it. This offers a possible explanation for the situation encountered in this study. Similar results were obtained by Geiger (1957), while the reverse was shown by Jarman (1959). Jarman noted that in temperate lands with moderate humidities, the low evapotranspiration rates often cause only a limited cooling and that extensive heating by daytime solar radiation more than compensates for this, so that the plant surface temperature is raised above the air temperature. This causes the air temperature between plants to rise above that over bare soil. The differences in vegetative cover seem to have too small an effect to cause significant differences in vapor pressure deficit. In the two instances in the present study where the differences in vapor pressure deficit between barren and vegetated areas were significant, the latter was drier. This may be attributed to the desiccating effect of higher air temperature between plants.

The greatest differences in microclimatic elements, in the present study, are often found to be between NNE and SSW slopes. This coincides with the results of microclimatic studies discussed by Geiger (1957). The reason why the greatest differences are not found between directly N- and S-facing slopes is explained by him as follows.

The morning sun finds a moist soil and vegetation and a great part of the solar energy radiated during the forenoon is therefore used up in evaporation, with mostly a drying out effect. But when the afternoon sun is most direct on the SW slopes, the soil is already comparatively dry, and heat is applied largely towards raising the temperature. The variations in the microclimatic elements in intermediate slopes, between NNE and SSW are often so gradual that the differences between adjacent slopes are sometimes insignificant.

In so far as vegetational differences are determined by environmental differences, they may be expected to correlate with them (Greig-Smith 1957). The high degree of correlation of the environmental elements, considered in this study, with the arrangement of stands on the three compositional gradients, suggests that distribution of species is primarily governed by two main factors.

The first factor is the moisture regime, which is determined partly by slope position, through runoff, and partly by slope aspect, through radiation. Fig. 6 indicates that the slope position is associated with the secondary axis ordination. This means that the nature of this axis is mainly one of moisture. The significant partial correlation of the secondary axis with soil-moisture content varifies this contention. Again, the pattern of moisture segments on the two-axis plane of the primary and the secondary ordinations (Fig. 7), suggests that the moisture factor is associated with the primary as well as the secondary axis. The secondary axis may then be considered as an expression of a moisture regime. Although there is a highly significant correlation between the secondary axis and soil temperature, this significance does not hold in case of partial correlation. Soil

pH, water retaining capacity and organic matter which either affect or are affected by soil-moisture content, all have highly significant correlations with the secondary axis.

The second main factor which influences the vegetation distribution on slopes, is the heat budget as controlled by the radiation balance. It is well established that radiation on slopes is mainly a function of aspect. The highly significant correlation coefficients of radiation and soil temperature with the primary axis, suggests that this axis is at least partly an expression of heat balance. On the other hand, the primary axis has a highly significant correlation with soil-moisture content. This significance still holds in the case of the partial correlation. This may be attributed to the effect of radiation and soil temperature on soil-moisture content. This effect was studied by Stearns and Carlson (1960) who obtained a correlation coefficient as high as 0.79 between soil moisture loss and soil temperature. Thornthwaite (1948) based his calculations of evapotranspiration from the soil and vegetation on radiation and temperature readings. Fig. 8 shows that temperature segments have a more or less regular pattern in relation to the primary axis and it was indicated before that the pattern of the moisture segments is partly related to this axis. The primary axis may, therefore, be considered to represent the effect of slope aspect partly on the heat balance and partly on the moisture balance.

The results obtained by Hird (1957) failed to show any significant variations in soil moisture content, and she came to the conclusion that the moisture does not play an important role in determining the differences in vegetation composition. On the other hand, Dix (1958)

working on slope-plant relationship in North Dakota showed an ordination of stands to express a moisture gradient. Dix and Butler (1960) arrived at the same conclusion in south central Wisconsin. Perring (1959), studying the topographical gradients of chalk grassland in England, found that moisture is the main factor controlling species distribution. From the foregoing discussion of the results obtained in this study, it becomes clear that both moisture and temperature have a major role in determining the variations in vegetation composition on prairie slopes.

It is interesting to note that the separation between different slope aspects on lower and middle positions is more obvious than on upper positions (Fig. 5). This may be due to the fact that on middle and lower slopes the moisture factor is not limiting because of the greater amounts of runoff water received, and the aspect-induced variations in radiation become more evident. Conversely on upper positions, the moisture factor may be limiting to a certain extent because it is at a minimum, and the effect of the differences in radiation will be less manifested.

The behavior patterns of individual species along soil moisture or soil temperature segments follow normal curves. Most of the species have monomodal curves, whereas few have bimodal ones. The normal distribution curve of any species behavior in relation to any single factor must be recognized as a solid curve in more than two dimensions, its shape being dependent on averages of high and low values in each segment. This is particularly true with bimodal and multimodal curves where the effect of one or more factors suppresses the presence of the species in a segment of another factor where it should be high.

The scope of this study was, by necessity, limited in space and time. Only slope aspect and position were considered and the sites were within a narrow range of 6 miles. All microclimatic measurements were limited to the early afternoon during the growing seasons. More comprehensive studies of this type, over a wider geographical range, on other varieties of topographical changes and in different hours of the day and different months of the year, would reveal more about the relation between plant growth, distribution, and the physical environment. An understanding of such relationships is fundamental to a comprehension of the composition of grassland vegetation and its variations on slopes. There is also a definite need for autecological studies concerning the amplitudes of tolerance of species both in the field and under controllable environments.

SUMMARY

The aim of the present study is to add to the comprehension of the complex interrelations between vegetational composition and microenvironment, particularly as they are influenced by slope position and exposure. Four sites, all within 6 miles of each other, and about 25 miles east of Saskatoon, were selected for study. The vegetation was sampled in 72 stands, representing various slope positions and aspects.

A three-dimensional phytosociological ordination, based on degrees of similarity between stands, was constructed to: (1) provide a model of the compositional structure of the vegetation, and (2) offer data which would help in interpreting the interrelationships between the vegetation and microenvironmental factors.

Four microenvironmental factors were thought particularly important in determining vegetational distribution. These were measured to ascertain the significance of their variations with slope position and aspect, and to test the degree of their correlation with variations in vegetational composition. Soil temperature and moisture content were shown to vary significantly with slope aspect and position. In relation to slope aspect variations in air temperature and vapor pressure deficit were, with few exceptions, significant. The data suggested that the vegetation performs a significant role in modifying air and soil temperature.

Collective information from the correlations between phytosociological gradients and environmental factors led to the conclusion that the distribution of species on the slopes is controlled by

moisture and heat regimes of the air and soil layers in contact with the vegetation. It is further suggested that the moisture regime is a function of both slope aspect and position, while the heat regime is a product of slope aspect only. Festuca scabrella, Carex obtusata and Galium boreale have their highest densities on the relatively moist cool lower positions of N slopes, whereas Phlox hoodii, Carex filifolia, Stipa comata and Artemisia frigida are among the species which attain their optimum densities at the dry warm upper positions of S slopes. Koeleria cristata, Carex eleocharis, Stipa spartea var. curtiseta and Agropyron dasystachyum occupy intermediate positions.

The data indicated that each species has its own characteristic behavioral pattern in relation to both environmental and phytosociological gradients. Variations in species composition, along those gradients, were so gradual that no vegetational units were recognizable.

The present investigation provides quantitative information about amplitudes of species tolerance in relation to the major environmental factors. This information may serve as a basis for autecological studies in the field and under controlled environments. It also emphasizes the importance of dealing with the vegetation and environment of grassland as one complex system, rather than with either separately.

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Appendix A. Scientific and common names for species sampled.

<u>Scientific name</u>	<u>Common name</u>
<i>Agropyron dasystachyum</i>	Northern wheat grass
<i>Agropyron smithii</i>	Western wheat grass
<i>Agropyron trachycaulum</i>	Slender wheat grass
<i>Anemone patens</i>	Pasque flower
<i>Artemisia frigida</i>	Prairie sagewort
<i>Artemisia ludoviciana</i>	Prairie sagewort
<i>Astragalus flexuosus</i>	Slender milk-vetch
<i>Bouteloua gracilis</i>	Blue grama
<i>Calamagrostis montanensis</i>	Plains reed grass
<i>Carex eleocharis</i>	Low sedge
<i>Carex filifolia</i>	Thread-leaved sedge
<i>Carex obtusata</i>	Bunt sedge
<i>Chrysopsis villosa</i>	Golden aster
<i>Comandra pallida</i>	Bastard toad-flax
<i>Erigeron caespitosus</i>	Tufted fleabane
<i>Festuca scabrella</i>	Rough fescue
<i>Fragaria glauca</i>	Smooth wild strawberry
<i>Gaillardia aristata</i>	Gaillardia
<i>Galium boreale</i>	Northern bedstraw
<i>Gutierrezia diversifolia</i>	Common broom-weed
<i>Hedysarum alpinum</i> var. <i>americanum</i>	American hedysarum
<i>Koeleria cristata</i>	June grass
<i>Liatris punctata</i>	Dotted blazing-star
<i>Linum lewisii</i>	Wild blue flax
<i>Muhlenbergia cuspidata</i>	Plains muhly
<i>Oxytropis deflexa</i>	Reflexed loco-weed
<i>Phlox hoodii</i>	Moss phlox
<i>Poa canbyi</i>	Canby bluegrass
<i>Poa cusickii</i>	Early bluegrass
<i>Poa secunda</i>	Sandberg bluegrass
<i>Rosa</i> sp.	Rose
<i>Selaginella densa</i>	Prairie selaginella
<i>Solidago missouriensis</i>	Low golden-rod
<i>Stipa comata</i>	Needle and thread spear grass
<i>Stipa spartea</i> var. <i>curtiseta</i>	Porcupine grass

Appendix B. Stand location in three dimensions.

Stand no.	Ordination axis			Stand no.	Ordination axis		
	X	Y	Z		X	Y	Z
1	23.5	63.4	26.4	37	40.2	25.1	7.7
2	10.3	53.2	26.4	38	24.3	47.1	21.0
3	18.4	58.0	21.6	39	29.5	47.4	6.3
4	19.5	57.6	29.7	40	52.1	8.2	28.6
5	20.9	62.8	18.6	41	46.8	11.7	16.9
6	83.4	31.2	24.9	42	51.6	16.7	24.5
7	72.1	25.5	29.8	43	45.5	16.3	25.5
8	62.2	29.9	30.3	44	56.2	7.7	21.6
9	80.6	32.5	23.7	45	45.8	10.8	23.4
10	66.4	31.6	31.3	46	22.9	27.3	15.3
11	0.6	51.7	37.8	47	32.7	34.6	-
12	-	55.5	31.2	48	47.3	18.4	52.7
13	33.5	39.9	10.5	49	52.2	20.8	33.4
14	24.7	47.8	11.1	50	29.5	35.8	29.6
15	16.2	52.8	23.3	51	31.5	40.5	13.4
16	47.4	68.0	22.8	52	34.4	32.0	28.1
17	19.7	45.0	34.4	53	33.6	39.1	3.7
18	21.7	50.9	21.3	54	18.3	41.3	30.2
19	18.6	46.5	30.0	55	28.7	50.2	19.1
20	23.2	47.3	14.7	56	31.4	37.7	16.2
21	69.7	21.8	22.9	57	26.0	42.5	9.4
22	59.9	17.6	16.6	58	39.8	16.5	34.9
23	68.7	34.3	20.7	59	38.6	21.2	26.2
24	55.1	18.5	23.9	60	44.6	18.0	28.2
25	52.9	21.3	30.2	61	47.7	22.5	20.0
26	62.4	31.8	20.4	62	29.4	51.6	16.1
27	51.5	24.9	24.7	63	49.9	21.3	28.8
28	53.7	33.9	35.5	64	55.3	20.4	39.9
29	55.8	29.8	29.7	65	61.1	19.8	14.0
30	66.7	24.2	26.0	66	60.6	23.8	19.0
31	39.0	34.4	58.9	67	27.9	33.0	13.3
32	46.7	-	22.7	68	36.6	13.4	33.3
33	40.9	10.5	7.3	69	48.1	11.9	6.7
34	43.6	15.2	9.6	70	57.1	18.6	8.4
35	25.2	37.3	26.5	71	49.0	16.7	17.2
36	38.9	25.1	26.6	72	32.6	23.8	11.1