Technical Report No. 101

# SPATIAL DISTRIBUTION AND SUCCESSIONAL STATE OF GRASSLAND VEGETATION RELATED TO GRAZING INTENSITY TREATMENTS

Glen C. Mitchell

Plant Science Division

University of Wyoming

Laramie, Wyoming

GRASSLAND BIOME

U. S. International Biological Program

May 1971

## ABSTRACT

Mitchell, Glen C., Spatial Distribution and Successional State of Grassland Vegetation Related to Grazing Intensity Treatments. M. S., Range Management, June 1971.

A study was conducted on the International Biological Program's (Grassland Biome) Pawnee Site to measure the pattern of several plant species in relation to grazing intensity. Five study sites were selected: a light grazed, a medium grazed, a heavy grazed, a 10-year exclosure and a 30-year exclosure. An analysis of variance procedure was used to determine the pattern scale and intensity of *Bouteloua gracilis*, *Carex eleocharis*, *Opuntia polyacantha*, and *Sphaeralcea coccinea*.

The five areas sampled were each determined to be in differing stages of secondary succession due to grazing pressure or lack of it. The four species selected for the pattern analysis were determined to be nonrandomly distributed. Small scale patterns which could be contributed to morphology and seed dispersal characteristics were exhibited by *O. polyacantha* and *S. coccinea*. At the medium scales the reciprocal pattern forced upon neighboring species by *O. polyacantha* seems to be dominant. Larger scale pattern was found but could not be attributed to grazing influences. The pattern intensity of all rhizomatous species decreased as the site approached a climax condition.

## ACKNOWLEDGEMENTS

The author wishes to express his sincere appreciation to Dr. Herbert G. Fisser, director of this thesis, for his advice and suggestions concerning this study. Gratitude is also expressed to Dr. Paul C. Singleton and Dr. Laurence Weinberg for their helpful suggestions and constructive criticism of the manuscript.

Thanks are also given to James Lester for assistance in collection of the field data, to Robert P. Gibbens and Gary Whysong for assistance with the data analysis, and to the Directors of the Pawnee Site for their cooperation during this study.

A special thanks goes to Mrs. Elizabeth Smith for typing the final manuscript.

My deepest gratitude goes to my wife, Jill, for needed moral support and encouragement.

The research on which this thesis is based was financed, in part, with funds provided by the Office of Water Resources Research of the U. S. Department of the Interior through the Wyoming Water Resources Research Institute under the Water Resources Research act of 1964, Public Law 88-379.

TABLE OF CONTENTS

PAGE

LIST OF TABLES

# LIST OF FIGURES

# INTRODUCTION

The spatial distribution of plants are an important part of the structure of a plant community. The form of these patterns are the result of many interacting factors. These influences are both physical and biological in nature.

The physical effects of the environment generally create patterns on a large scale, such as vegetation zones. Biological effects are primarily responsible for the spatial relations among plant individuals. The effect of grazing by domestic livestock is a composite of both physical and biological factors.

The patterns or "units of repeatability" exhibited by plants are a function of the intensity, range and interactions of these elements. The spatial distribution of many plants is of sufficient intensity that it may be described without the use of quantitative methods. Many other species, however, do not show patterns that are discernable by casual observation. In order that these patterns may be described quantitative methods must be used.

The successional stage of a grassland is regulated by time and the physical and biological effects mentioned previously. The pattern of many of the plant species change with the successional state of the area. How the spatial distribution of these plants change with respect to successional state is the objective of this study.

The Central Plains Experimental Station provided a unique opportunity to study pattern changes due to grazing by domestic livestock.

Since 1939 grazing had been regulated at varying intensities, light, medium, and heavy, and also several areas had been protected from grazing. This provided areas well suited to the study of pattern differences due to the successional state of the community.

## LITERATURE REVIEW

The subject of vegetation pattern has been an object of study and speculation since ecologists first recognized its existence in plant communities. Gleason (1920) and Svedberg (1922) demonstrated that individuals of a species exhibit a patchy distribution within an otherwise apparently homogeneous area. Since this initial observation, many ecologists have worked to develop methods for the detection and explanation of vegetation patterns.

Plant pattern is best defined as departure from randomness of distribution (Greig-Smith, 1957). This departure may take the form of a mosaic of vegetation differing in composition, or one of similar vegetation differing only in abundance between the different phases. Obvious cases where there are gross changes between phases do not require elaborate methods to describe. Careful quantitative evaluation is required where the pattern is expressed only as slight differences in abundance of the same species.

In cases where gross differences in vegetation are obvious, it is likely that variations in environment or history will be the causative factor (Kershaw, 1963). The environmental factors which cause obvious vegetation changes are likely to be made up of many interrelated factors. These factors cannot be segregated as to their effect on any one species (Greig-Smith, 1961a). Areas that are characterized by apparently homogeneous vegetation do not exhibit large variations in environmental factors (Greig-Smith, 1961a). Therefore the tolerance ranges of the species present are not often exceeded, and patterns are manifested by differences in abundance rather than by presence or absence. The correlation of environmental factors with patterns exhibited by individual species allow explanation of plant responses on the basis of these environmental differences. The significance of pattern is based on the premise that plant spatial distributions are a result of both environmental factors and inherent characteristics of the plant. Greig-Smith (1964) states that the analysis of pattern is the starting point for determining the factors responsible for plant distributions.

## Scales of Pattern

Plant patterns exist on many scales. On a large scale patterns are recognized as vegetation zones and are of primary interest to plant geographers (Greig-Smith, 1964). The smaller scales are of interest to ecologists and include the patterns of individual plants. Greig-Smith and Kershaw (1958) and Kershaw (1963) enumerated three scales of pattern that are of interest to ecologists: (1) morphological, (2) sociological, and (3) environmental. Patterns on the smallest scale usually result from the morphology or the reproductive traits of the species. Slightly larger scales of heterogeneity result from competition between individual plants and plant species. On the larger scales environmental factors predominate and over large areas these usually vary sufficiently so that the ability of each species to occupy all parts of the area is exceeded.

Morphological Patterns

Morphological patterns are the smallest scale of pattern present in a population (Kershaw, 1963). The scale of this pattern is related to the size and shape of the plant and will impose a reciprocal pattern on the other species present in the community. This is due to the fact that no two plants may occupy the same point at the same time (Ashby, 1948). Several other factors affecting morphological pattern are seed dispersal (Ashby, 1948), vegetative propagation (Phillips, 1953), and environment (Phillips, 1953).

Numerous scales of pattern may result from morphological causes, especially where the species in question has an extensive rhizome system. Phillips (1953) found three scales of pattern in *Eriophorum angustifolium* which he attributed to morphology. Kershaw (1959) also found three scales of pattern in *Trifolium repens* attributable to the rhizome system of the plant. The work of several investigators has revealed morphology to be responsible for most small scale pattern (Kershaw, 1958, 1959, 1960a, 1962a; Greig-Smith, 1961b; Anderson, 1961a).

The effect of time is important in relation to the pattern exhibited by plants. Anderson (1961b) describes the shortening of the rhizomes of *Pteridium* with increase in age of the stand. *Ammophila arenaria* is shown by Greig-Smith (1961b) to consistently demonstrate two scales of pattern. A small scale results from the production of tillers at the tips of vertical rhizomes, and a larger scale results from environmental control of seedling establishment and stimulation of buds on adjacent nodes of horizontal rhizomes at the earliest stages of colonization. Once this pattern has become established during the early stages of succession upright growth of the vertical rhizomes maintain this pattern. This results in a change in the primary cause of the pattern. Having originally been established by environmental control, it is now maintained as a morphological feature. Barnes and Stanbury (1951) found that grasses and rushes colonizing china clay residues exhibited a highly clumped distribution. They hypothesized that this clumping was due to reproductive spread from randomly estab-lished plants which were the original colonizers. As succession pro-gressed, the pattern changed from random to highly clumped. Chadwick (1960) reported two scales of pattern of *Nardus stricta*, one of which was primarily determined by grazing management. A small scale was detected at approximately 10-20 cm and a larger scale at 160 cm. The smaller scale pattern was a result of morphology. The larger scale was the result of a change in the type of sheep grazed, from wethers to breeding ewes. The ewes would not graze *Nardus* and thus allowed it to spread, accounting for the large scale pattern.

## Sociological Pattern

Sociological patterns are the result of interactions between or among species. These interactions cause changes in the microenviron-ment thereby affecting the ability of a species to compete for space and nutrients. Sociological pattern is usually on an intermediate scale up to approximately 80 cm in grasslands (Kershaw, 1963).

Scurfield (1956) emphasizes competition between species as the force which determines the direction of successional change and thereby pattern. Greig-Smith and Kershaw (1958) object to placing so much emphasis on the concept of competition. They point out that when large areas are considered, patterns are evident that have no relation to competition between species.

Watt (1947a) suggested that cyclic phases were present in vegetation which accounted for vegetation pattern. These phases were of varying size and age. Cooper (1960, 1961) found a cyclic development in ponderosa pine forests. This cycle was maintained by fire which prevented young trees from invading even aged stands. An established even aged stand remained as a unit until the degeneration stage was reached. The size of these even aged stands was about 1/5 acre.

Environmental Pattern

Kershaw (1963) states that major discontinuities of the environment create patterns in the true sense of the word. These patterns are often on large scales and are characterized by changes in floristic composition. These changes are well marked and are not usually described by quantitative methods. Further study has found that environmental factors are responsible for some small scale patterns.

Owen and Harberd (1970) found that 8 out of 13 species tested in a grassland exhibited positive correlation with microtopography. They suggest that topography may be an important ecological factor affecting plant distributions. Kershaw (1962c) demonstrated that the pattern of *Carex bigelowii* and *Festuca rubra* in Iceland were positively correlated with microtopography.

Kershaw (1958) investigated the patterns exhibited by *Agrostis tenuis*. He found *A. tenuis* showed the same scale of pattern as the associated species of *Dactylis*, *Lolium*, and *Trifolium*. This pattern was found in fact to be an inverse pattern, *Agrostis* occupying the shallow soil and the associated species present on areas of deeper soils. The pattern of *Agrostis* also varied with the successional state of the area. *Agrostis* first exhibited an intense pattern which later disappeared as the area stabilized.

Anderson (1961a, b) found that there was a close correlation between the pattern of *Pteridum* and *Vaccinum* and the pattern of oxygen diffusion rates in the soil. Owen and Harberd (1970) proposed pH as a cause of pattern in grassland vegetation. Microtopography, in fact, may not actually be a causal factor, but may affect such other factors as drainage, leaching, water availability, pH, and nutrient supply (Kershaw, 1963).

## Quantitative Methods

Most of the methods developed to date are based on the measurement of departure from randomness of quadrat data. The coefficient of dispersion (Blackman, 1942), and the relative variance tests (Clapham, 1936), take advantage of the fact that the variance and the mean of the Poisson distribution are equal. Blackman (1935) used a Chi-square test for goodness of fit between the number of observed and expected plants per quadrat based on a Poisson distribution. There are many variations of these tests, such as David and Moore's (1954) Index of Clumping, Moore's (1953) $\phi$ Test, McGinnie's (1934) Observed Density:Calculated Density ratio, and Whitford's (1949) Abundance:Frequency ratio to mention but a few of the methods devised. These methods all have the distinct disadvantage of measuring only the presence of non-randomness in data.

In the majority of cases where the spatial distribution of vegetation has been investigated, evidence of some type of non-randomness has been found. In most cases the plant individuals exhibit aggregation rather than a random or regular dispersion. Several investigations have been concerned primarily with the smaller scales of pattern. Blackman (1942) demonstrated evidence of clumping in vegetation in plots as small as 18 x 15 ft. Since then evidence of clumping has been shown to exist on an even smaller scale (Greig-Smith, 1961b; Kershaw, 1958, 1959; Kershaw and Tallis, 1958). Watt (1947b) found that phases of 1 sq. ft. could be assigned to vegetation.

The measurement of non-randomness led to the development of a method by Greig-Smith (1952) for determining the mean area of a scale of pattern. This method took advantage of the fact that the size of quadrat used in sampling determines whether abundance data will show randomness, aggregation, or a regular distribution. Consider an area of vegetation with a mosaic of high and low density patches. If a quadrat is small in proportion to the size of the plant or the scale of pattern of the vegetation, many of the quadrats will include no individuals. Therefore, since so many of the quadrats contain few or no plants the variance between samples will not be large. As the quadrat size is increased to the area that corresponds to the scale of heterogeneity of the vegetation, the variance will consequently rise, peaking when the area of the quadrat equals the area of heterogeneity. With a further increase in quadrat size, each quadrat will tend to have an equal abundance of plants since each quadrat now includes an area of high density plus part of the surrounding area of a lower density. This causes the variance to decrease until it reaches a minimum when the quadrat size equals the area of both high and low density.

Frequency data is affected by the pattern of the vegetation being sampled (Greig-Smith, 1964). When only one size quadrat is used comparisons among sites must take into consideration pattern scale and intensity differences. Frequency values will tend to be low where highly clumped vegetation occurs and increase where the vegetation exists in a dispersed form. Greig-Smith (1952) utilized a grid of contiguous quadrats within which density of vegetation was determined. Then these individual quadrats were blocked together into groups, the size doubling with each blocking, such as groups of 2, 4, 8, and 16 quadrats. The density data from each basic unit of 1 quadrat was combined to give the density of each succeedingly larger block size. By this method a series of samples was created, each larger than the preceding one by a factor of two. The data was then analyzed by an analysis of variance, such that the total variance was partitioned among the different sizes of blocks. This results in a description of the vegetation similar to that obtained by sampling with various quadrat sizes. The result is usually shown as a graph with mean square plotted against block size, the peaks on the graph representing areas of heterogeneity. The advantage lies in the fact that the larger quadrat sizes are built up from smaller basic units, which are not difficult to sample.

Kershaw (1958) modified this method by orienting the basic units along a line transect instead of a grid. The basic units were then blocked in a linear fashion in order to obtain the larger block sizes. The peaks of the mean squares in the analysis of variance represent the linear dimensions of the scales of pattern rather than the area, as was obtained when a grid of quadrats were used. The proper size of the basic unit has presented some problems, but Kershaw (1957) recommended the use of a basic unit not more than one half as large as the smallest scale of pattern suspected.

The type of data best suited to this method is debatable. Various authors have used density data (Greig-Smith, 1952, 1961b; Cooper, 1960; Kershaw, 1960b). Kershaw (1957) used cover measurements in a grassland vegetation. This eliminated the need to delimit individual plants. Frequency data was also used by Kershaw (1957) and showed results similar to cover data. Greig-Smith (1961a) stated that frequency, either rooted or shoot, could be used satisfactorily. The type of measurement used depends on the ease of which it can be applied in a particular vegetation type. Greig-Smith (1964) recommends that cover data may be used where cover values down to 10 percent are found. Below this amount of cover, frequency data must be used.

The assessment of the peaks produced when mean square is plotted against block size has presented problems when this method is used. Greig-Smith (1952) used a standard F test to determine if the mean squares departed significantly from randomness. Thompson (1955, 1958) showed that once non-randomness has been established, the F test no longer applies. Thompson (1955, 1958) then proposed that significance bands could be constructed if a mathematical model could be formulated to describe the pattern. This approach has not been proven to be useful due to the high variance found in natural vegetation. It was summarily concluded by Thompson (1955, 1958) that the best method of assessment of the peaks was subjective. This conclusion was also reached by others who have used the method (Kershaw, 1957; Greig-Smith, 1961a).

Various authors (Pielou, 1969; Goodall, 1961, 1963) have pointed out several limitations of the mean square - block size method. Goodall's (1961, 1963) criticism dealt mainly with the assessment of the increase in variance at the larger block sizes. He pointed out that the variance observed between any two vegetation samples increased as their distance apart increased. Greig-Smith et al. (1963) argued that this increase in variance was due mainly to a trend in abundance along the transect. Pielou (1969) listed five difficulties encountered with this method: (1) Because each block is a combination of basic units, the mean squares are not independent and cannot be tested by a variance ratio test to determine significance. Therefore, subjective assessment of the mean squares seems to be the only analysis. (2) The whole area to be sampled must be included in the grid. (This applied only to Greig-Smith's (1952) early method and not to Kershaw's (1958) improvement). (3) The graph of mean squares against block size has a sawtooth shape because the oblong blocks consistently give smaller mean squares than the square blocks. This criticism also applied to the grid method and not Kershaw's (1958) line transect improvement. (4) Block size is doubled at each step; therefore, the analysis becomes crude at the larger steps. (5) The graphs for clumps that are regularly dispersed and for the intermediate areas, look the same. Therefore, it is difficult to determine whether the clumps or the intermediate areas are being measured. Despite these arguments, the method seems to produce much information concerning the form of vegetation pattern.

The two arguments most difficult to overcome are the necessity of a subjective assessment of the graphs and the roughness at the larger block sizes. The subjective assessment is overcome by repeated sampling and clumping of the data from individual transects, (Kershaw, 1964). The roughness of data at the larger block sizes is a very real problem. For instance, a peak at block size 16 can only be interpreted as a scale of pattern somewhere between block size 8 and block size 32. Although this data is relatively inaccurate, it appears that the natural variation in vegetation makes exact measures of pattern inappropriate.

# DESCRIPTION OF THE AREA

## Location

The site of this study was the International Biological Program's (Grassland Biome) Pawnee Site, approximately 25 miles south of Cheyenne, Wyoming and 12 miles northeast of Nunn, Colorado. The Pawnee Site is made up of two areas, the Pawnee National Grassland, encompassing approximately 105,000 acres, is used for studies which require a large area of land. The Central Plains Experimental Range, consisting of approximately 15,000 acres, is available for International Biological Program studies requiring strict control. Certain pastures within the Central Plains Experimental Range have been designated as intensive study areas (Fig. 1). This study was conducted in three of these pastures: 15E, 23W, and 23E.

The Central Plains Experimental Range was established in 1939. At that time four repetitions of three grazing treatments were installed. The three pastures (15E, 23W, and 23E) represent one repetition of these grazing treatments, light, medium, and heavy, respectively. Exclosures of one to two acres in size were also located within each of these grazing treatment pastures.

## Vegetation

The vegetation in this region is dominated by blue grama (*Bouteloua gracilis* (H.B.K.) Lag.) and buffalo grass (*Buchloe dactyloides* (Nutt.) Engelm.) (Klipple and Costello, 1960). Numerous other species

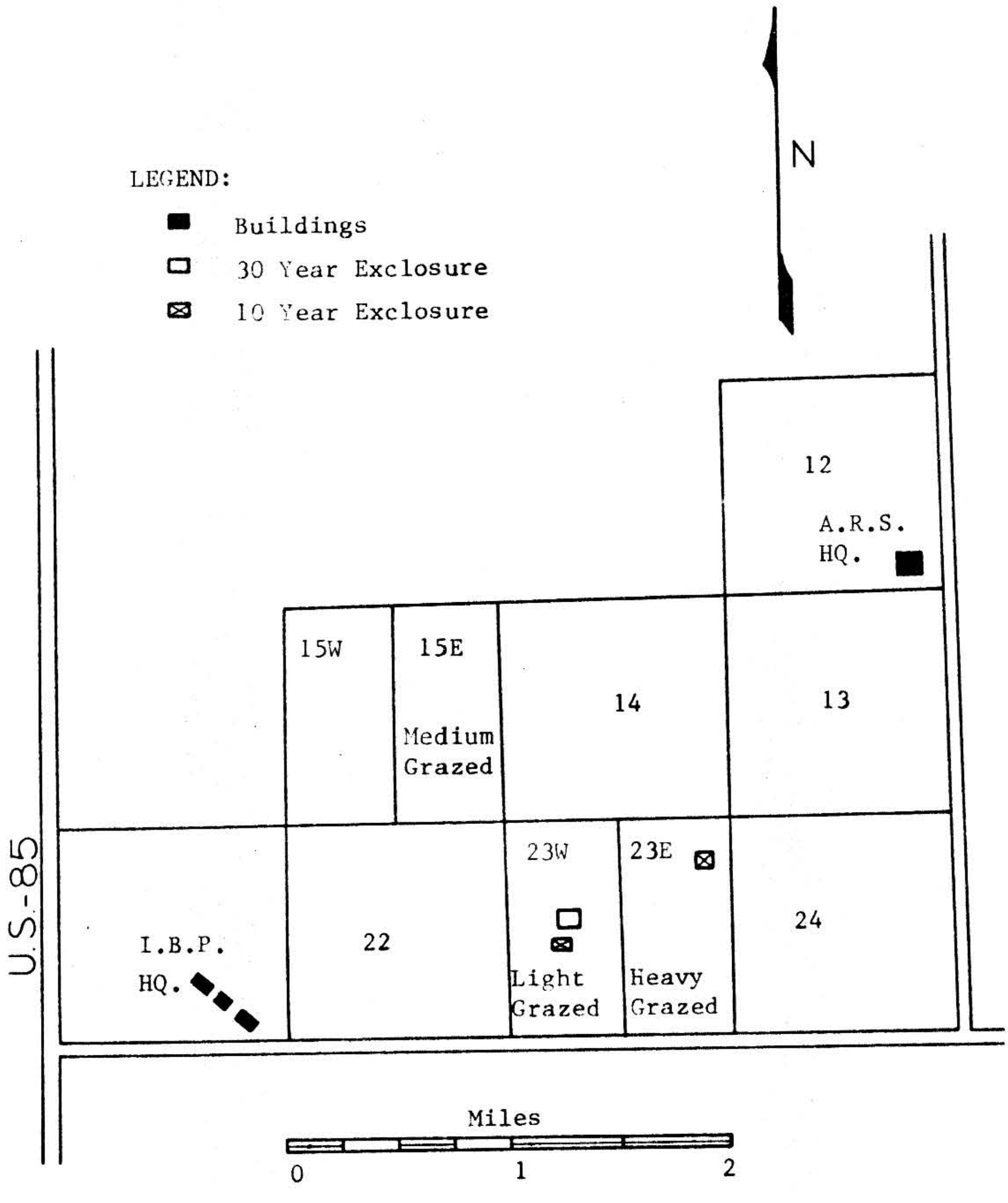



Figure 1. Experimental Pastures Used in the Pattern Study at the Central Plains Experimental Range.

of midgrasses grow in association with these dominant species. Western wheatgrass (Agropyron smithii Rydb.), needle-and-thread (Stipa comata Trin. and Rupr.), red threeawn (Aristida longiseta Steud.) and sand dropseed (Sporobolus cryptandrus (Torr.) A. Gray) are quite common and are a conspicuous element of the vegetation during wet years or on areas that are lightly grazed. Needleleaf sedge (Carex eleocharis) is also common, although not a conspicuous part of the vegetation.

Several perennial forbs are commonly found on the upland sites. These include scarlet globemallow (Sphaeralcea coccinea (Pursh.) Rydb.), slim flower scurfpea (Psoralea tenuiflora Pursh.), slender bush eriogonum (Eriogonum effusum Nutt.), and scarlet gaura (Gaura coccinea Nutt. ex Pursh.). Annual forbs such as lambsquarter (Chenopodium species), Russian thistle (Salsola kali tenuiflora Tausch.), cryptantha (Cryptantha species), and bee flower (Cleome serrulata Pursh.) are present in most areas. These forbs vary in abundance with the amount of precipitation received during the year.

## Grazing

Since 1939 the pastures selected for sampling have been subjected to summer grazing, regulated so that 60 per cent of the current herbage growth of the dominant forage grasses (blue grama and buffalo grass) has been utilized by the end of the grazing season on the heavy use pastures, 40 per cent on the medium use pastures, and 20 per cent on the light use pastures. During years of above average rainfall production increases and 60 per cent utilization is difficult to obtain. During the first 13 years of this experiment heavy use was obtained only 8 years on some pastures. Light and moderate use were easier to regulate even in dry years since the cattle could be removed when the proper grazing use was obtained (Klipple and Costello, 1960).

## Climate

The Pawnee Site is located in an area which receives 10 to 15 inches of precipitation per year. The 15 year average, 1939 to 1953, recorded at the Central Plains Experimental Range headquarters was 11.96 inches (Klipple and Costello, 1960). During this same 15 year period, the amount of precipitation recorded during the growing season, May 1 to September 30, was approximately 70 per cent of the total. The amount of precipitation received both during the growing season and annually show large variations. Large variations were also found between pastures located only short distances from one another. This variation was attributed to severe summer storms which affect only portions of the area.

The growing season at the Pawnee Site averages about 135 days, but frost has occured in all months except July and August. During the growing season, high daily temperatures average 80 degrees F but are characterized by large variations. Winters are typically dry and cold, with snow seldom covering the vegetation for extended periods.

Wind movement is generally great throughout the winter months. During the months of June, July, and August, however, calm to slightly windy days are the rule.

## Soils

The soil groups represented in this area are the brown and dark brown soils of the semiarid Great Plains. The major soil series on the upland sites of the Pawnee Site are Ascalon, Vona, Renohill, and Shingle. The soils of the Vona and Ascalon series are derived from fluvial outwash materials. The Vona series has been formed from the coarser of these materials. The Ascalon series has a calcareous layer 24-30 in. below the surface which is absent in the Vona soil series (Hyder et al., 1966).

The three pastures include areas of both upland and lowland sites; Hyder et al. (1966) differentiated seven range sites in this area on the basis of interpretive soil groups. Four of these sites were in upland areas and three were lowland sites. All of the sampling conducted for this experiment was confined to the upland sites on Vona sandy loam and Ascalon sandy loam soils as described by Hyder et al., (1966).

## METHODS

The mean square-block size method of pattern analysis developed by Greig-Smith (1952) and later modified by Kershaw (1958) was used in this study. This method is well suited for use in grassland vegetation, and allows detection of nonrandomness, as well as measurement of pattern scale. The statistic $\sum_{n} \left| X_{2n-1} - X_{2n} \right|$ n. Ns (where x = individual values of the data matrix at any one block size (Ns), n= the number of comparisons at any one block size) was used to compare pattern intensity among pastures (Kershaw, 1970). This statistic allows comparisons of pattern intensity regardless of plant abundance differences between areas.

## PROCEDURES

The areas chosen for sampling were within the three summer grazed pastures: 23E, 23W, and 15E. These pastures contain a variety of range sites, each producing a distinctive vegetation, differing in composition, abundance, and spatial distribution. The grazing patterns in these pastures are also unique. These variations made it necessary to subjectively locate areas which were uniformly representative of each of the three grazing treatments. In each of the three pastures, two upland sites were selected for intensive sampling. In addition, two ten-year old exclosures, one located in pasture 23E and the other in pasture 23W, and a 30 year old exclosure located in pasture 23W were sampled. The three exclosures were small enough so that the area contained within could be considered homogeneous. The sites selected in the pastures varied in size from two to five acres, and were selected to obtain an area of uniform vegetation. Figures 2, 3 and 4 show the approximate areas where the sites in the grazing treatment pastures were located.

In the old exclosure, eight transects were sampled. Four transects were sampled at each of the other sites. This gave two repetitions of each of the grazing treatment sites and the ten year old exclosures. The number of transects needed for an adequate sample is difficult to determine. Greig-Smith (1961a) recommended that sample size be determined by density of vegetation and intensity of pattern. Kershaw (1958) used eight transects in grassland vegetation with good results, indicating that eight transects are an adequate sample in this type of vegetation.

The transects were located within the study site on a restricted randomized basis, i.e., the starting points of the transects were randomly located within the sites but their directions were selected so that half were north-south and half were east-west oriented. The randomization of the starting points was accomplished by establishing a coordinate grid on the selected site. Then grid coordinates were picked from a random numbers table.

The transects were each 25.6 meters long and one decimeter wide. They consisted of 256 contiguous units one decimeter square in size which were subdivided into one sixteenth decimeter square subunits. The frequency of all plant species occuring within these subunits was recorded. Rooted frequency was used in all cases except Opuntia

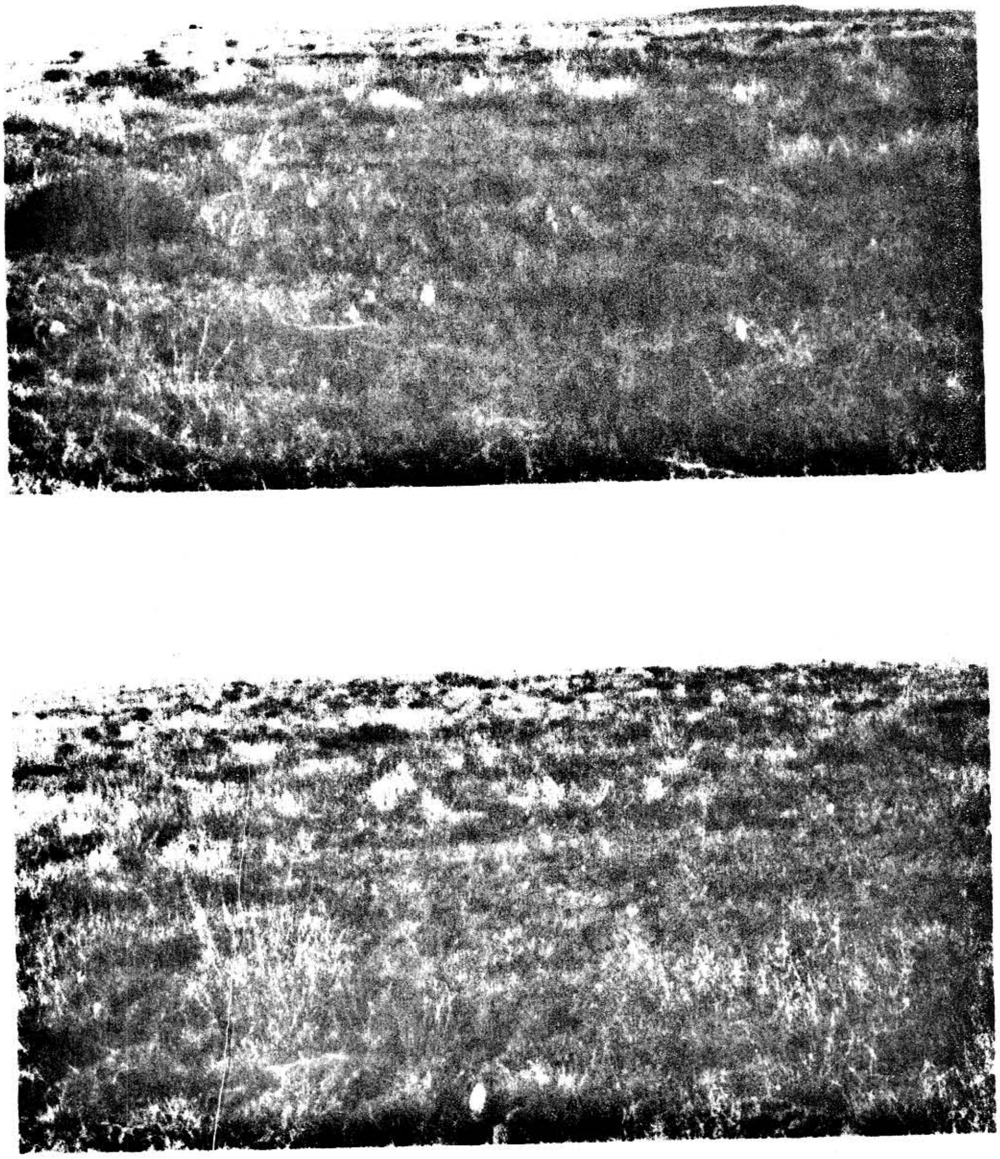


Figure 2. Light grazed pasture. Upper view shows upright growth form of blue grama, and presence of perennial shrubs such as fringed sagewort and broom snakeweed. Note abundance of fringed sagewort in lower view.

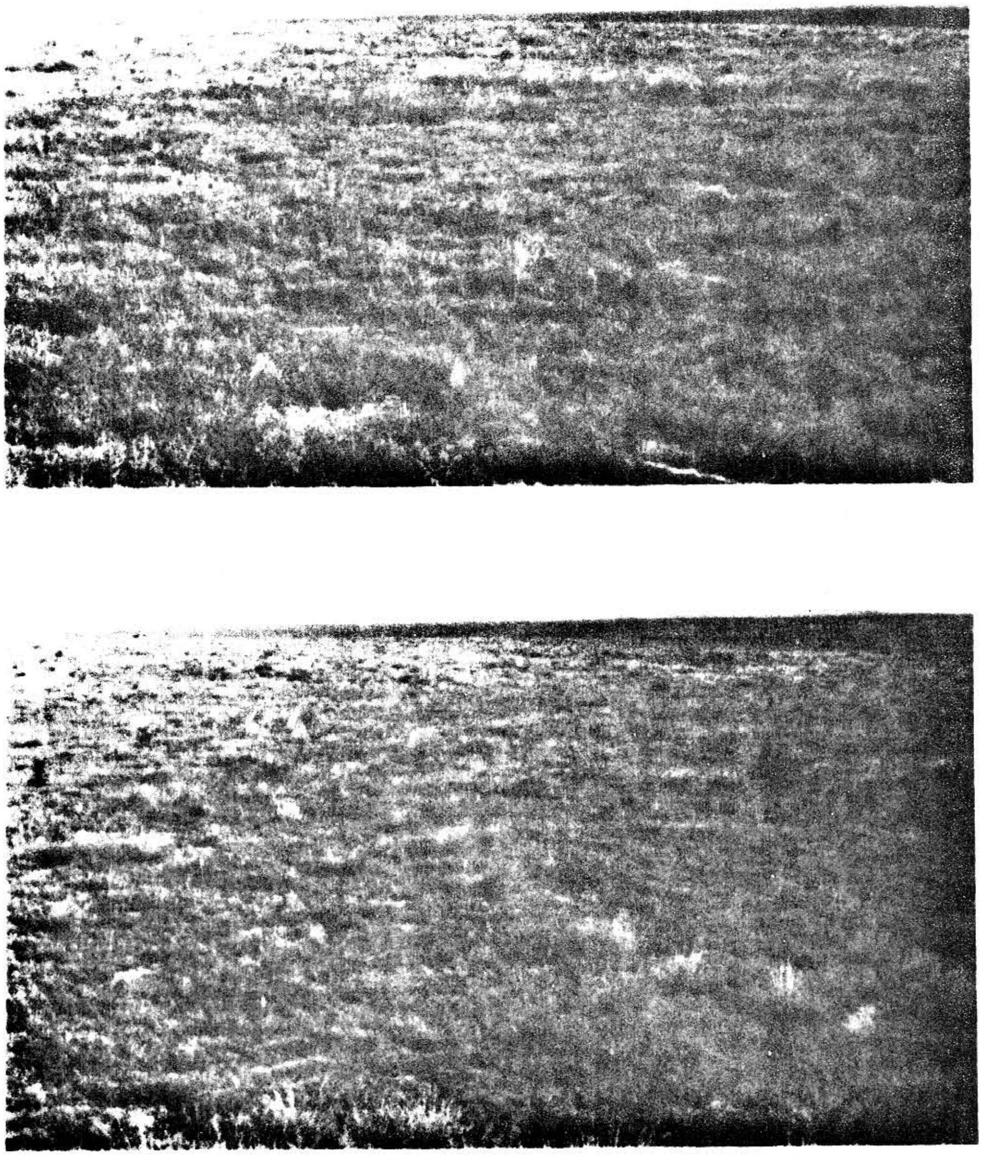
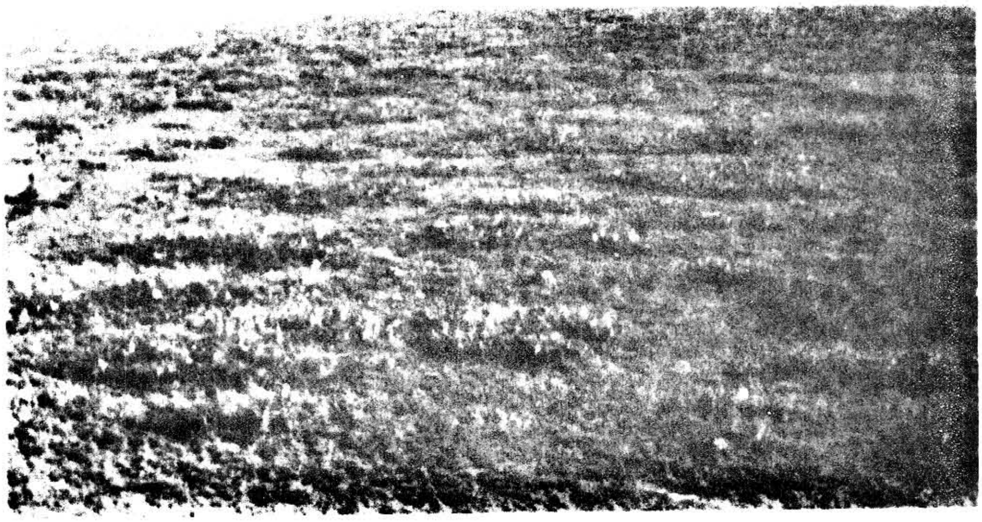


Figure 3. Medium grazed pasture. In upper view red threeawn is conspicuous but tall shrubs are largely absent. In lower view note dispersed growth form of plains pricklypear.



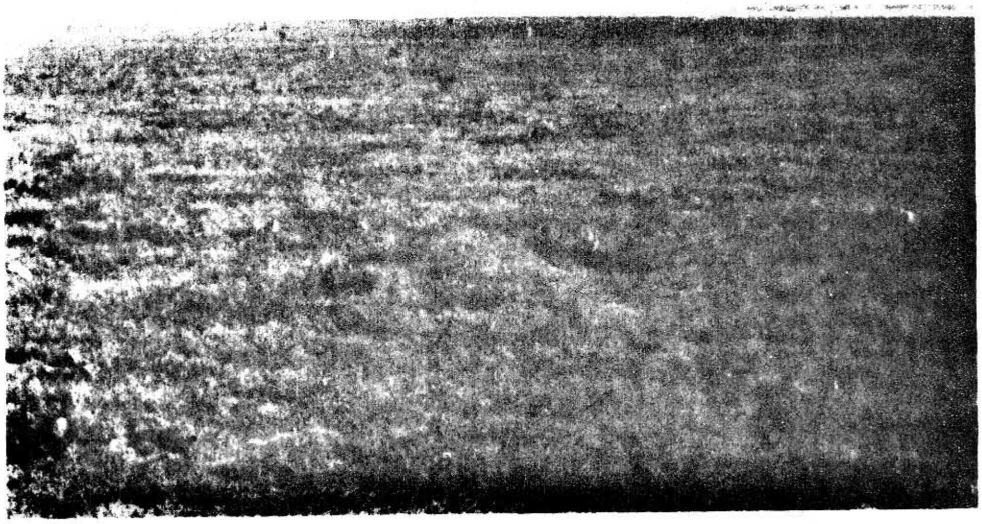


Figure 4. Heavy grazed pastures. Upper view showing extreme clumping of plains pricklypear, and mat growth form of blue grama. Lower view shows a less severly grazed portion of heavy grazed pasture, but even here, there are few mid-grasses and upright shrubs present.

*polyacantha* in which case shoot (pad) frequency was recorded. This procedure was necessary because individuals of *O. polyacantha* are not easily distinguishable. The data were recorded in such a manner that basic units of both one $dm^2$ and 1 dm x 1/2 dm could be used in the analysis. The selection of the size of the basic units followed Kershaw's (1957) recommendation that the basic unit be not larger than half the dimension of the smallest scale of pattern to be detected. Most of the workers in grasslands have used a basic unit of 5 $cm^2$ and 1 $dm^2$ size (Kershaw, 1958, 1959; Owen and Harberd, 1970).

The individual transects were first analyzed separately. Then the data from the lines running in parallel directions in each area were added and analyzed collectively.

An example of the analysis is given in Table I. The procedure is analogous to a heirarchial analysis of variance. The individual observations are first squared and added. This gives the value $S(X^2)$. This value is then divided by the appropriate block size (N). The block size is doubled by adding the frequency data and the process is repeated until the block size equals 128. The sum of squares for block size N is obtained by subtracting $\frac{S(X^2)}{N}$ for block size N·2 from $\frac{S(X^2)}{N}$ for block size N. The D. F. (degrees of freedom) equal one half the number of quadrats in the transect, divided by the block size in question. The M. S. (mean squares) equal the sum of squares divided by the D. F.

# RESULTS

## Vegetation Composition

Numerous changes in the vegetational composition of these pastures have occured as a result of grazing regulation. Table II and Appendix B illustrate some of these changes. The frequencies for these tables were obtained from the transects used in the pattern analysis. The size of the basic unit used to obtain these frequency values was 1 dm square. Significance in Table II was determined by use of Duncans (1955) "new multiple-range test".

Blue grama was the dominant grass on all sites sampled. Its frequency values ranged from 86.08 to 98.10 (Table II). Blue grama has increased under heavy use as compared to light use or no use. The only exception to this is in the 10-year old exclosure where blue grama frequency remained high.

Red threeawn rarely occured in the heavy grazed pastures. Under the light and medium grazed treatments this species increased significantly. The 7.22 per cent frequency of red threeawn found in the old exclosure did not differ significantly from the 4 per cent and 6.78 per cent found in the light and medium grazed pastures (Table II). Sand dropseed also was practically absent from the heavy grazed pasture, but was more abundant under less severe grazing conditions. Needleleaf sedge did not differ significantly in frequency among the three grazing treatments. The frequency within the exclosures was significantly lower. The 30-year exclosure being even lower than the 10-year exclosures. Six-weeks fescue also showed a similar increase

TABLE II. PER CENT FREQUENCY OF SPECIES COMMON TO ALL 5 STUDY SITES.

| Species | 10-year Exclosure | 30-year Exclosure | Light Grazed | Medium Grazed | Heavy Grazed |
|---|---|---|---|---|---|
| Grasses and Grasslike Species | | | | | |
| Bogr[1] | 95.41 ab[2] | 86.08c | 93.07b | 94.34ab | 98.10a |
| Cael | 16.21c | 11.23b | 29.44a | 29.10a | 25.68a |
| Vuoc | 11.43a | 1.76b | 7.03a | 8.98a | 8.25a |
| Arlo | 2.59b | 7.22a | 4.00a | 6.78a | 1.37b |
| Spcr | 1.27ab | 3.75ab | 4.54a | 1.95ab | 0.15b |
| Forbs and Shrubs | | | | | |
| Spco | 13.13a | 18.07a | 16.50a | 4.00b | 7.18b |
| Oppo | 11.13a | 17.97b | 11.62a | 4.98c | 6.20c |
| Lede | 6.44a | 1.56b | 3.23b | 1.46b | 2.56b |
| Plpu | 1.27a | 0.44a | 1.56a | 4.25b | 3.63b |
| Lare | 0.24a | 0.19a | 0.63a | 0.10a | 0.39a |
| Saka | 1.07a | 0.78a | 1.76a | 0.34a | 1.22a |
| Gaco | 0.39a | 0.24a | 1.22a | 0.29a | 1.07a |
| Gusa | 0.73a | 0.62a | 0.88a | 0.10a | 0.05a |

[1]Four letter abbreviations are combinations of the first two letters of the genus and species. A complete explanation is given in Appendix A.

[2]Row means followed by the same small letter are not significantly different ($p < .05$).

on areas where grazing occured, with the exception of the 10-year exclosures where the highest frequency value occured. Two good forage species, western wheatgrass and needle-and-thread are present in the old exclosure, 4.07 per cent and 11.23 per cent respectively, but are practically absent on the grazed sites. Buffalo grass was abundant on all the grazed sites and the 10-year exclosures, but was absent in the 30-year exclosure.

The predominant shrub on the Pawnee Site was plains pricklypear. The frequency of this shrub varied from 17.96 per cent on the 30-year exclosure to 4.98 per cent on the medium grazed pasture. The increased frequency under light or non-grazed conditions compares favorably with data from Klipple and Costello (1960). Plains pricklypear is generally thought to increase under grazing pressure, but from these data it is apparent that heavy grazing creates conditions unfavorable for its spread. This results in an extremely clumped pattern in the heavy grazed pastures, which contrasts with a dispersed form in the other grazing treatments. Since frequency measurements are dependent upon dispersion characteristics (Greig-Smith, 1964), the frequency differences among the grazing treatments may be exaggerated due to the observed pattern differences. The other shrub species encountered in this sampling, such as broom snakeweed, (*Gutierrezia sarothrae*); fringed sagewort, (*Artemisia frigida*); and rubber rabbitbush, (*Chrysothamnus nauseosus*), (Table II and Appendix B) were generally most frequent on the areas of light use or no grazing.

Only two perennial forbs were common to all five areas. These were scarlet globemallow and scarlet gaura (Table II). Scarlet gaura occured in low frequency and showed no significant changes among treatments. Scarlet globemailow, however, occured in the highest frequency of all forbs encountered, and showed a significant increase under light grazing, as compared to medium and heavy grazing. Protection from grazing did not result in a significant increase in frequency of this species as opposed to light grazing. This indicates that when scarlet globemallow is present at the frequency found in the light grazed pasture competition rather than grazing may regulate abundance.

The frequency of annual forbs varies widely with annual and seasonal growing conditions. The summer of 1970 proved to be a poor year for annual forb growth due to sparse rainfall. The frequency range of these plants was erratic, but generally significant increases were found on the more heavily grazed pastures. The predominance of blue grama in the heavy grazed pasture may create favorable competititive conditions for annual plants. Blue grama is a warm season grass which does not start vigorous growth until midsummer. This allows annual plants to initiate growth with little competition from other species.

## Pattern Scale Analysis

Analysis of the pattern data revealed only four species which were present in sufficient frequency, 5 percent - 10 percent, to make a pattern analysis feasible. The four species were blue grama, needleleaf sedge, plains pricklypear, and scarlet globemallow. No significant differences in pattern due to direction of the transects could be determined. Analysis using a 1/2 dm x 1 dm block size did not reveal significant small scale patterns. Therefore, the basic unit used in the pattern analysis was 1 $dm^2$.

Blue grama

The pattern exhibited by blue grama is surprising since small scale pattern was largely absent. Even when the analysis was performed using a basic unit of 1/2 x 1 dm, no small scale pattern, which could be attributed to morphology, was detected. Since this plant propogates by means of rhizomes, some small scale pattern could be expected. Even at the larger block sizes, only the heavy grazed pastures exhibited a significant scale of pattern. This was at block size 16 (16 dm). The graph for the ten-year exclosures (Fig. 5) showed a peak at block size 64 (64 dm), but from examination of the data using the 1/2 x d dm basic unit, it appears that this peak is due to a density difference between alternate fourths of the data. Peaks at the largest block sizes, such as are exhibited by all analyses of blue grama, have been shown by Greig-Smith (1964) to be caused by density differences between halves of the transects. Because of the high frequency of blue grama, even small differences will create large variances at the larger block sizes.

The totaled pattern intensities from Table III show a decrease in pattern intensity with a decrease in grazing intensity, with the exception of the ten-year exclosures.

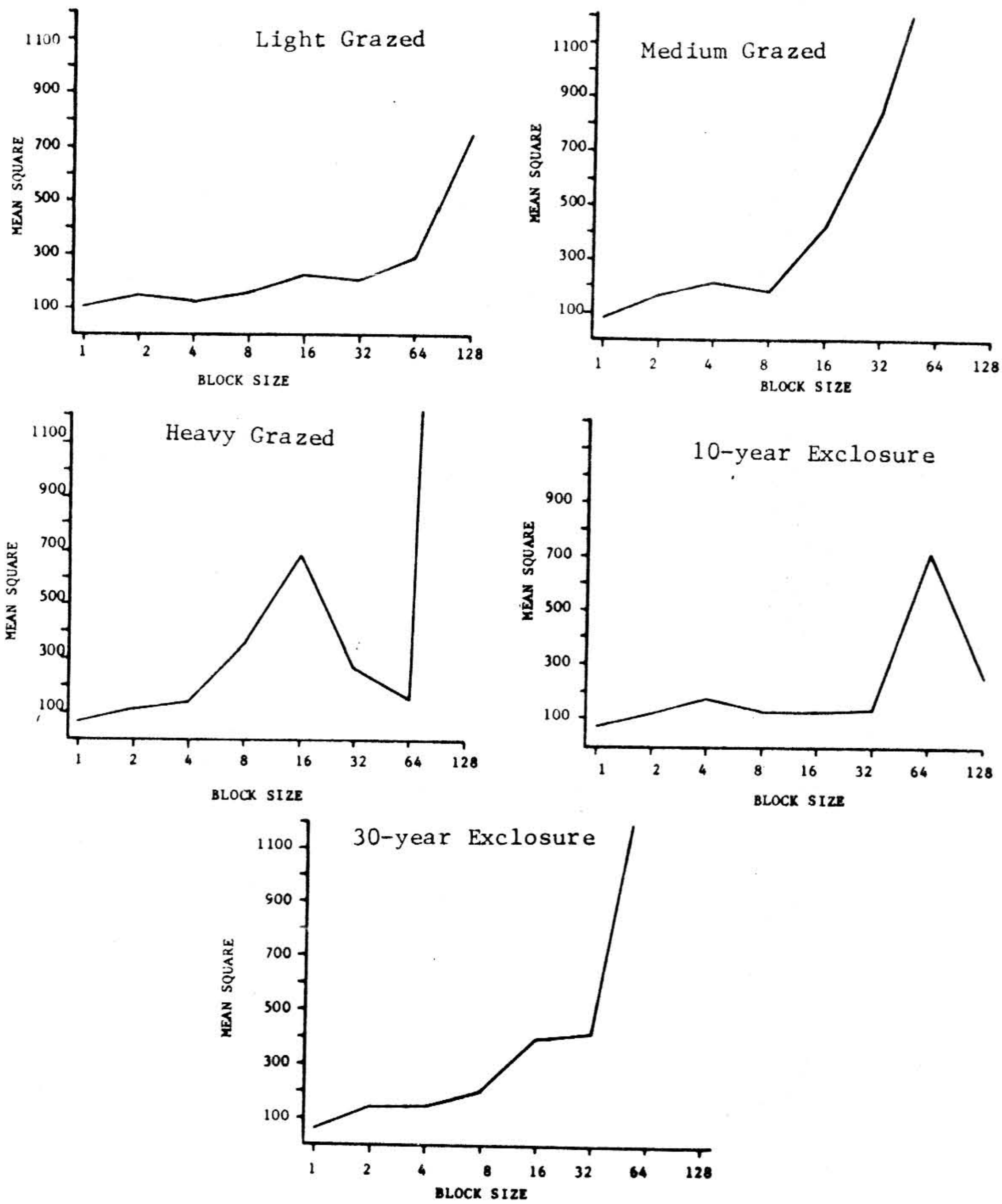



Figure 5. Mean square/block size analysis for blue grama using a basic unit of 1 dm square. Graphs are a composite of all 8 transects in each area.

TABLE III. OBSERVED PATTERN INTENSITIES TOTALED OVER ALL BLOCK SIZES. INTENSITIES WERE OBTAINED BY USE OF THE FORMULA RECOMMENDED BY KERSHAW (1970).

| AREAS | BLUE GRAMA | PLAINS PRICKLYPEAR | NEEDLELEAF SEDGE | SCARLET GLOBEMALLOW |
|---|---|---|---|---|
| Exclosure (30 yr.) | 75.56 | 24.31 | 16.37 | 33.81 |
| Light Grazed | 81.21 | 29.17 | 24.32 | 33.53 |
| Medium Grazed | 103.55 | 31.87 | 28.56 | 34.05 |
| Heavy Grazed | 115.69 | 32.41 | 34.04 | 33.87 |
| Exclosure (10 yr.) | 61.12 | 11.92 | 8.41 | 33.26 |

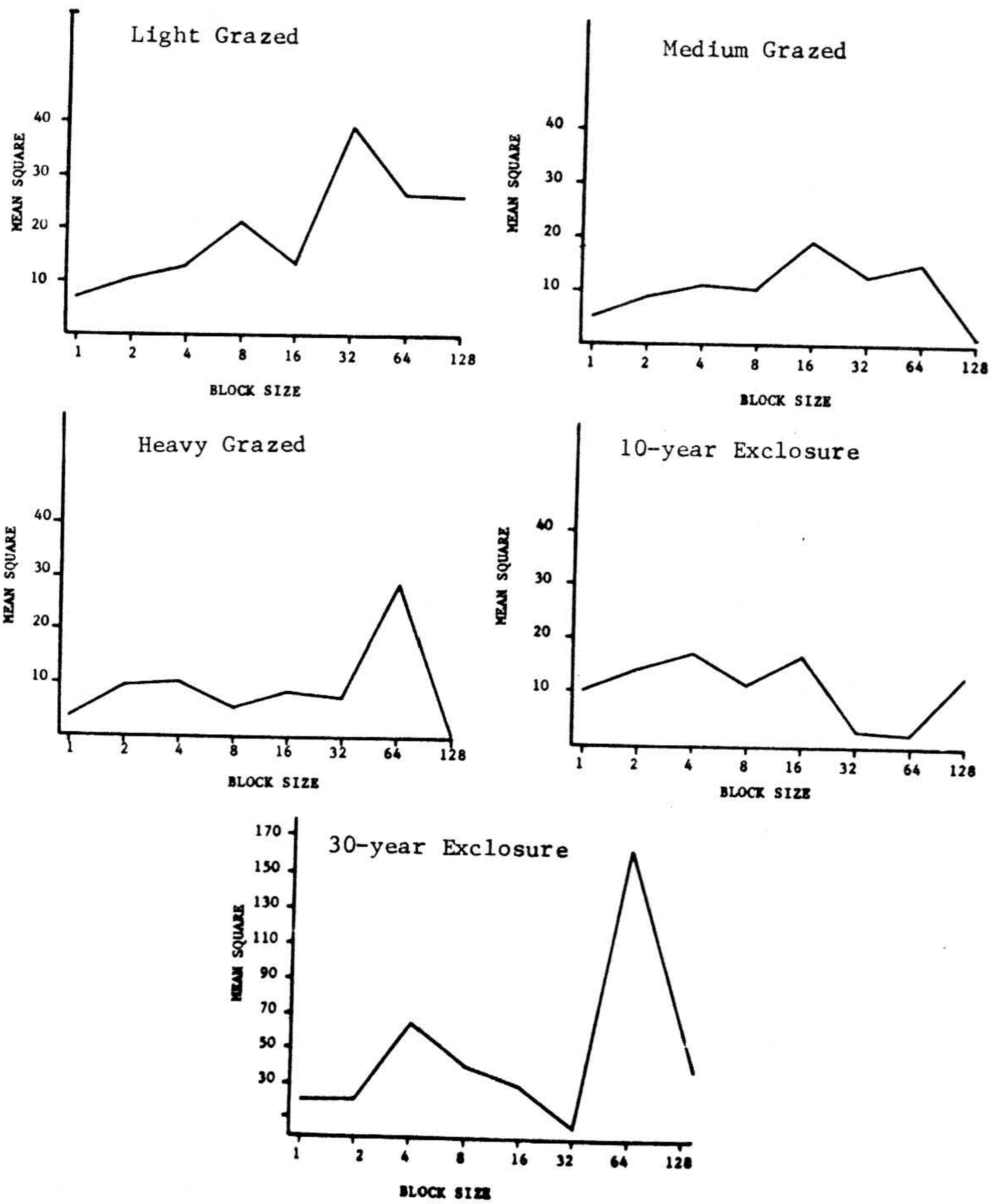



Figure 6. Mean square/block size analysis for Plains pricklypear using a basic unit of 1 dm square. Graphs are a composite of all 8 transects in each area.

Plains pricklypear

The highly clumped pattern exhibited by plains pricklypear on the heavier grazed pastures of the Pawnee Site is one of the most striking features of these grasslands. In comparison to the analysis of the three other species, the graphs of mean square - block size do not show the highly contagious distribution obvious in the field (Fig. 6). Both Greig-Smith (1964) and Kershaw (1964) observed that this method is not suitable or necessary where extremely clumped distributions are observable. Generally, two scales of pattern seem to be present, one at a small block size 2-8 (2-8 dm) units, and one varying from 16-64 (16-64 dm) units in size. The spread in the peak size may result from variability in the actual size of the clump (Kershaw, 1957).

The analysis of the pattern intensity, however, shows results similar to what would be expected from field observations (Table III). The heavy grazed pastures exhibited the highest intensity of pattern, while the pattern intensity decreased in direct relation with grazing intensity. This indicates that while the peaks on the 30-year exclosure graph appear to be more significant than those of the other areas, they are in reality a function of density rather than pattern (Kershaw, 1970).

Needleleaf sedge

Needleleaf sedge was ideally adapted to the standard method of pattern analysis. Its frequency values ranged from 10 to 30 per cent, and no apparent pattern was visible. In the pattern analysis

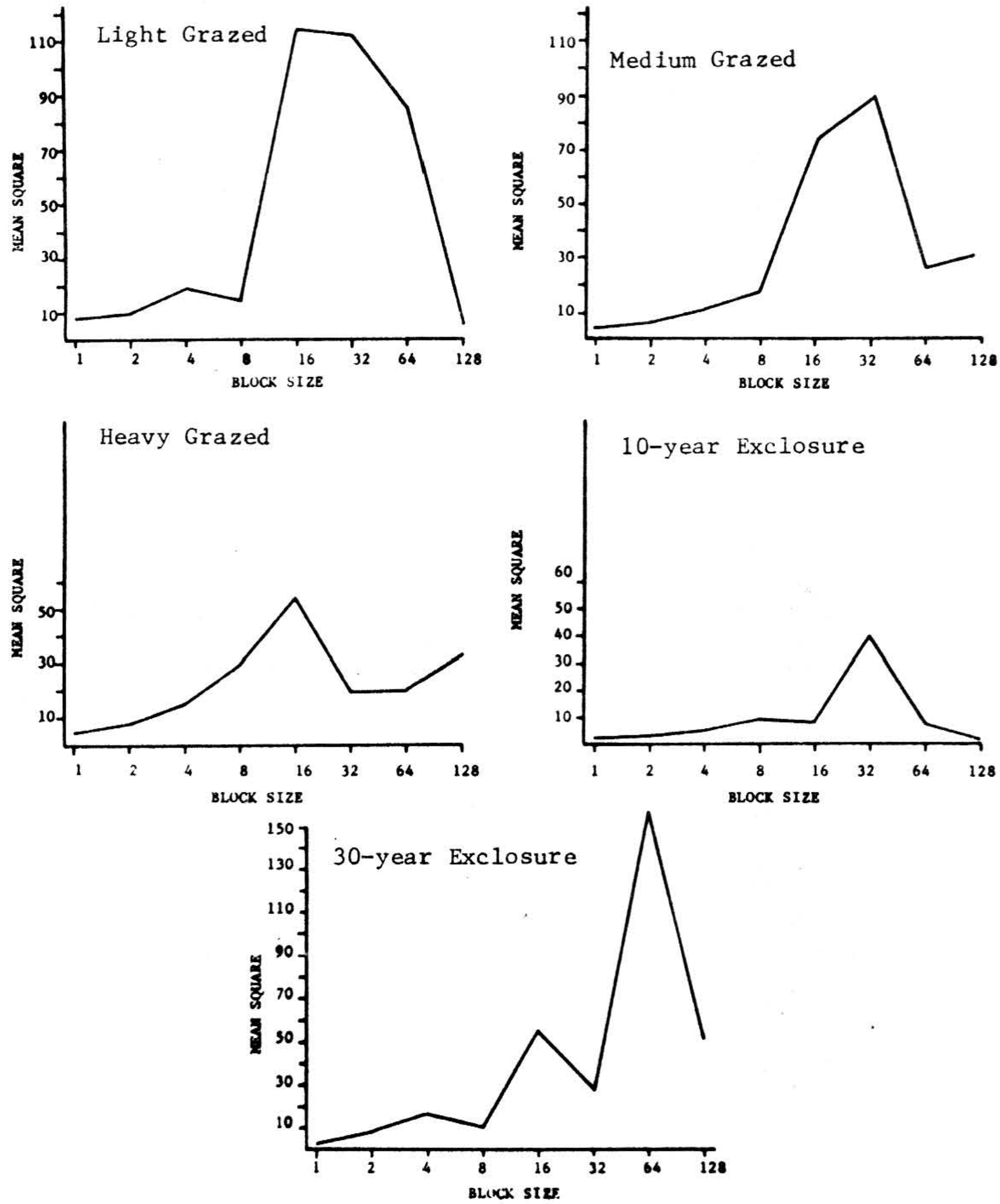



Figure 7. Mean square/block size analysis for needleleaf sedge using a basic unit of 1 dm square. Graphs are a composite of all 8 transects in each area.

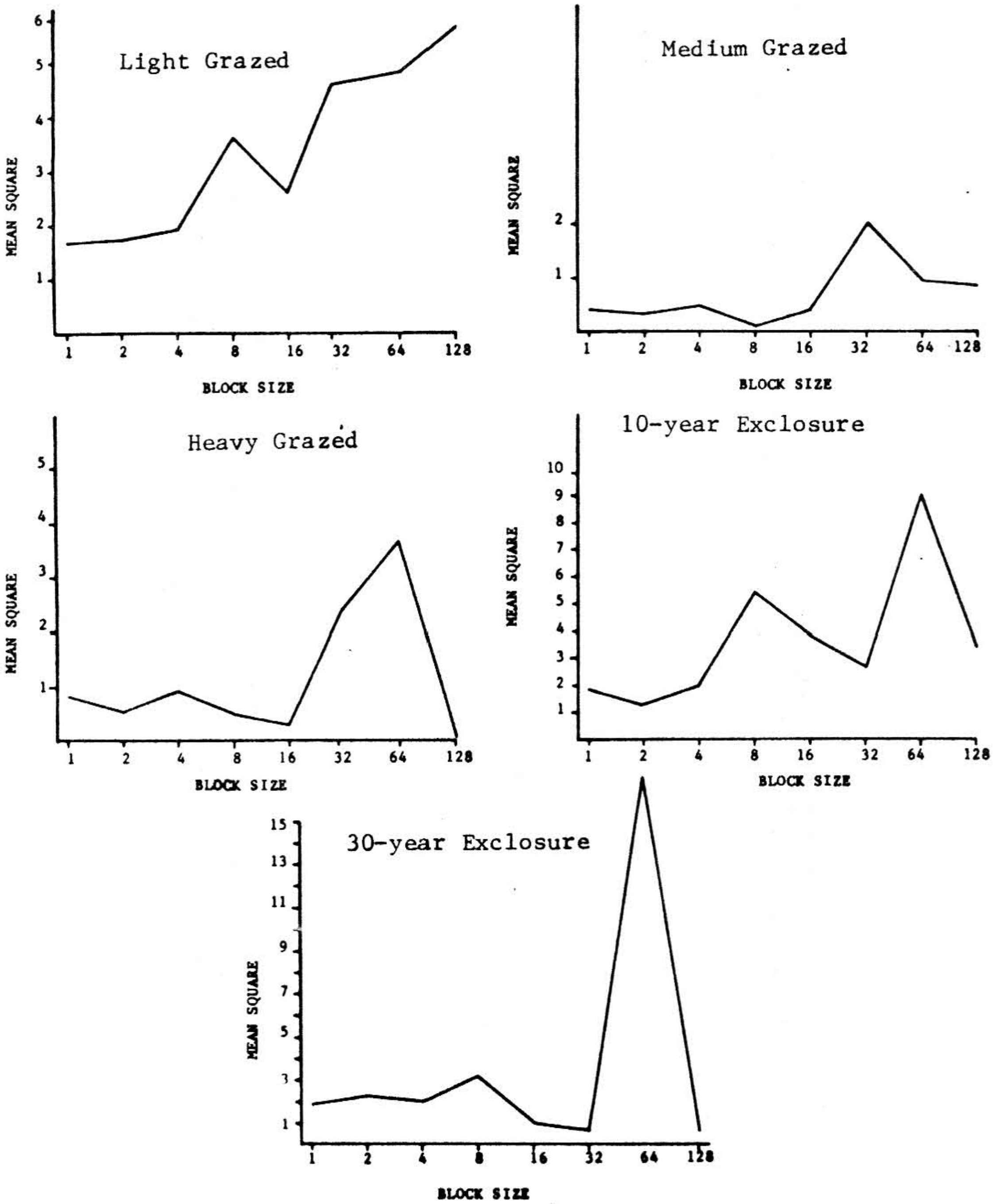



Figure 8. Mean square/block size analysis for scarlet globemallow using a basic unit of 1 dm square. Graphs are a composite of all 8 transects in each area.

no small scale pattern could be discerned, even when a basic unit 1/2 x 1 dm was used. In each of the areas a large scale of pattern was observed (Fig. 7). This scale varied from 16 (16 dm) to 32 (32 dm) units in length, and resulted in a sharp peak in the mean square - block size graph in all instances. The graph for the 30-year exclosure shows two distinct peaks, one at block size 16 (16 dm) and one at block size 64 (64 dm). As was stated before, the significance of peaks at the largest block size are questionable. The pattern intensity values illustrated that the pattern intensity of needleleaf sedge decreased as grazing intensity decreased.

Scarlet globemallow

Scarlet globemallow was the only forb present in sufficient frequency to warrant pattern analysis. The presence of two scales of pattern was noted in all instances, a small scale pattern at block size 4 (4 dm) to 8 (8 dm) and a large scale pattern at block size 32 (32 dm) to 64 (64 dm) (Fig. 8). Scarlet globemallow, like needleleaf sedge, is an ideal choice for pattern analysis due to adequate frequency and lack of observable pattern.

Little difference in the pattern intensity results could be found between pastures. Although frequency differences between treatments are observable, grazing did not seem to have any effect on the pattern intensity.

## DISCUSSION

### Successional stage

Determination of the successional stages of the five areas sampled was a necessary prerequisite to the pattern study. The basis of this study was the correlation of pattern trends with secondary successional state. Since information on pattern in this type grassland is sketchy, the results could not be anticipated. Therefore, it was necessary to establish a successional basis upon which the patterns could be evaluated. The frequency data obtained from the transects sampled for the pattern analysis proved useful for this purpose.

The dominant plant on the Pawnee Site, blue grama, is also the best indicator of successional stage. This grass is recognized as an increaser under grazing pressure. Only one site, the 10-year exclosures, fails to follow the trend of decreased frequency of blue grama with decreased grazing. This result is similar to reports by Klipple and Costello (1960) that after 13 years of grazing treatment, no change in blue grama frequency could be detected. In fact, the frequency values found by Klipple and Costello (1960) show blue grama

within the exclosures to be more frequent than within the grazing treatment pastures. This may be due to increased vigor of blue grama when protected from grazing, allowing it to actually spread during the first few years of protection. However, after protection for 30-years blue grama seems to have returned to a near climax state, its frequency being significantly lower than in the grazed treatments.

Although blue grama comprises a major portion of the vegetation in this area, numerous other species are indicative of the successional state of a site. The midgrasses such as western wheatgrass, red threeawn, needle-and-thread, and sand dropseed are sensitive to grazing pressure and become less frequent as grazing pressure increases. Perennial shrubs and forbs follow a similar trend, becoming less abundant as use increases, as is illustrated by scarlet globemallow (Table II). Frequency data for annual grasses and forbs show an expected increase on the grazed pastures, even though there seems to be less space available for establishment of seedlings due to the mat type growth form of blue grama. The annual plants observed on the heavy grazed area were numerous but were small in stature and showed signs of heavy use by cattle.

These results indicate that there is a definite successional gradient among the five areas sampled. These successional states are the result of different intensities of grazing by domestic livestock, but may not be attributed solely to the effect of the livestock eating certain plants. Many other effects accompany grazing which may alter the environment, thereby creating changes in the plant community. These changes are not restricted to composition and abundance, but may also affect distribution. Some of these effects will be discussed in relation to the pattern exhibited by several plant species.

## Pattern

Most plant species have been found to be nonrandomly distributed in their environment. In this study all the species examined were nonrandomly distributed. The mean square-block size analyses show significant peaks in each case. This result could be expected where the factors affecting the growth of these species are also nonrandom. The patterns of individual species are affected not only by environmental factors but also by the growth forms and patterns of neighboring species.

The intensity values of the patterns exhibited by the various species were determined by the degree to which they were aggregated and is not dependent upon the density of the species or the scale of the pattern. The formula given by Kershaw (1970) results in a density-independent measure of aggregation based on the difference between block sizes.

### Blue grama

Blue grama is well adapted to grazing by domestic livestock as is evidenced by its abundance on areas of heavy grazing pressure. Grazing apparently had no effect on the pattern exhibited by this species at the scales measurable with the methods used. The analysis shows similar curves for all areas sampled (Fig. 5). The sharp rise at the larger block sizes reflects a change in frequency along the length of the transects (Greig-Smith, 1964). This trend in abundance may indicate that a larger scale of pattern exists in the area sampled, but is too large to be measured with a transect 25.6 m long. A scale of pattern this size would be the result of environmental or soil differences, and not attributable to grazing intensities.

Only the analysis for the heavy grazed treatment shows a peak at the intermediate block sizes. The peak shown at block size 16 (16 dm) seems to be due to a reciprocal pattern imposed upon blue grama by plains pricklypear. Although blue grama does grow within the clumps of cactus, it necessarily exists at a lower frequency within these clumps due to the area occupied by the cactus. Similar reciprocal patterns have been distinguished in grasslands (Ashby, 1948). Kershaw (1958, 1959) found reciprocal patterns that were due primarily to soil depth.

Although no definite scale of pattern can be distinguished among the grazing treatments, the intensity of the heterogeneity shows a definite decrease as the stage of succession tends toward climax. This result is similar to that found by Barnes and Stanbury (1951) and Anderson (1967). Greig-Smith (1964) hypothesized that the intensity of pattern would decrease with succession state and also an enlargement of the scale of pattern would take place as an area of vegetation tended toward climax. Both of these hypotheses seem to fit the pattern of blue grama on these five sites.

Plains pricklypear

Plains pricklypear's primary means of propagation is by rhizomes. During a wet year, new plants emerge from rhizomes and seeds may germinate, but unless favorable conditions follow in successive years, these seedlings seem to die before they mature. One of the many effects of grazing is increased temperature and dryness of the soil surface. The effect of trampling with grazing must also be taken into account. This makes it difficult for seedling cactus to survive in the intermediate areas between established clumps. The result of these factors is a highly intense clumping of cactus in the heavy grazed pasture. This clumping becomes less severe as grazing pressure decreases and conditions for seedling establishment becomes more favorable (Table III). In the lighter grazed pastures, cactus plants are numerous, but they tend to be small and, on the whole, cover values are less than in the heavier grazed pastures (Klipple and Costello, 1960). This decrease in cover must be attributed to the increased competition provided by grass species as grazing is decreased.

The analysis of pattern reveals two scales of pattern on each site (Fig. 6). The smaller scale at block size 2 (2 dm) to 8 (8 dm) is due to the reproductive habit of the species. This scale does not appear as pronounced peaks on the graph as would be expected. It is possible that this may be due to limitations of the technique (Kershaw, 1964) or to variations in the scale of the pattern (Kershaw, 1957). The larger scale, block size 16 (16 dm) to 64 (64 dm), must be attributed to variations in the distributions of the clumps and individual cacti. At this scale it is likely that the causal factors are not morphological or sociological, but must be attributed to complex environmental factors such as soil and microclimatological differences (Greig-Smith, 1961a).

Needleleaf sedge

The frequency values of needleleaf sedge exhibit no significant changes on the grazed areas, but decrease where protected from grazing. The three grazing areas and the 10-year exclosures show only one pattern scale, which occurs at block size 16 (16 dm) to 32 (32 dm). Only the 30-year exclosure differs in that two peaks are present. The smaller peak occuring at block size 16 (16 dm), corresponds to the peaks found in the grazed area analyses. The large scale peak occurs at block size 64 (64 dm). The smaller scale peak at block size 16 (16 dm) to 32 (32 dm) is due most likely to the environmental effects on the plant. The pattern scale analysis indicates that grazing does not seem to influence the scale of the environmental pattern. This is expected since the frequency values are approximately the same on the grazed areas. The presence of a larger scale in the 30-year exclosure and a decrease in frequency indicate that needleleaf sedge is retreating to the areas more favorable for growth. The fact that the pattern intensity also decreases on the protected areas supports the observation.

Scarlet globemallow

Scarlet globemallow is not rhizomatous as are the other three species tested, but it spreads by means of seeds. This plant is a good forage species, and the effects of grazing are readily seen (Table II). Neither the scale or the intensity of the pattern shows a trend with grazing treatment. Two scales of pattern are discernible in each pasture, a small scale at block size 4 (4 dm) to 8 (8 dm) and a larger scale at block size 32 (32 dm) to 64 (64 dm). The smaller scale is probably the result of the spread of seed from a single plant or a small group of plants. Grazing does not seem to affect either intensity or scale of pattern. At the larger scale, seed dispersal does not seem to be a causal factor since the vegetation appears to have stabilized after 30 years of controlled grazing (Fig. 4). It is likely, then, that this large scale pattern is the result of a complex of environmental factors rather than grazing intensity (Greig-Smith, 1964).

## SUMMARY AND CONCLUSIONS

A study to determine plant pattern characteristics was conducted on the International Biological program's (Grassland Biome) Pawnee Site. Five areas were selected for this investigation. Three of these areas were grazed at light, medium, and heavy intensities. The two remaining areas were protected from grazing, one for 10 years and one for 30 years. All of these areas were located on upland sites, and were on soils of the Vona and Ascalon soil series.

Within each of the selected areas, 8 transects were sampled. These transects were located on a restricted randomized basis, i.e., the starting points of the transects were randomly located within the sites but their directions were selected so that half were North-South and half were East-West oriented. Transects were 25.6 m long and 1 dm wide. They consisted of 256 contiguous units 1 $dm^2$ in size, which were subdivided into 1/16 $dm^2$ subunits. The frequency of all plant species occuring within these 1/16 $dm^2$ subunits was recorded. Rooted frequency was used for all species except plains pricklypear.

The data were analyzed for pattern in accordance with an adaptation by Kershaw (1958) of an earlier method used by Greig-Smith (1952). Pattern intensity was determined by use of the procedure recommended by Kershaw (1970). Frequency data used in the pattern analysis was also used to establish the successional stage of each of the areas.

It was assumed that grazing intensity caused a regression in the successional state of a grassland. This was confirmed by frequency data obtained from the five sites. Blue grama, the most prevalent species on the areas sampled, provided the best indication of the successional stage of the site. The grazed pastures showed an increase in frequency of blue grama with an increase in grazing pressure. The 30-year exclosure revealed the lowest frequency of blue grama. The 10-year exclosures had a high frequency of blue grama which may be due to its spread when initially protected from grazing. Other preferred grass species such as western wheatgrass, needle-and-thread, and sand dropseed were practically absent from the heavier grazed pastures, but showed increased abundance under light or no grazing.

Perennial shrubs such as broom snakeweed, fringed sagewort, and rubber rabbitbush were abundant on the exclosed and lightly grazed areas, but were only incidental on the heavy grazed pasture. Plains pricklypear was present in higher frequency on the exclosures and lighter grazed areas. This species is normally thought to increase under heavy grazing conditions. The higher frequencies observed on the light grazed and exclosed pastures may be due to the dispersion characteristics of plains pricklypear.

Perennial forbs were generally more abundant on lightly grazed pastures as compared to medium or heavy grazed pastures. One of the more preferred forbs, scarlet globemallow, did not show a significant increase as a result of protection from grazing.

Annual grasses and forbs were generally more abundant where grazing was heavy.

From this information the five sites selected for sampling were confirmed to be in distinct successional stages resulting from intensity of grazing. The lighter the grazing or the longer the time of exclosure the nearer the area approached a climax condition.

The four species selected for the pattern analysis, blue grama, needleleaf sedge, plains pricklypear and scarlet globemallow were determined to be nonrandomly distributed by the pattern analysis. This nonrandomness was in the form of various degrees of clumping. Three of the species, blue grama, plains pricklypear, and needleleaf sedge, propagated primarily by means of rhizomes. Only plains pricklypear exhibited a small scale pattern which could be attributed to the morphology of the plant. Scarlet globemallow spreads by seed and it was found that small scale clumping was detectable and could be attributed to the seed dispersal characteristics of the plant.

The pattern detected at the medium scales seems to be the effect of the environment created by the differing grazing intensities. The medium scale pattern exhibited by plains pricklypear is a result of the environmental changes caused by domestic cattle grazing. The pattern of this species, seems to impose a reciprocal pattern on such species as blue grama. The three species, plains pricklypear, needleleaf sedge, and scarlet globemallow, show clumping at the larger block sizes. It is likely that patterns at this scale are due to environmental factors, but no changes that can be attributed to the effect of grazing could be found.

The intensity of pattern values calculated for these species is independent of either the scale of pattern or the abundance of the plant. On all sites except the 10-year exclosures the intensity of the pattern of the rhizomatous species decreased as the site approached a climax condition. The reason the 10-year exclosures did not follow this trend is probably due to the abundance of blue grama at this stage of secondary succession. The only species that spreads by seed, scarlet globemallow, showed no trend due to successional state.

## LITERATURE CITED

Anderson, Derek J. 1961a. The structure of some upland plant communities in Caernarvonshire. II. The pattern shown by _Vaccinium myrtillus_ and _Calluna vulgaris_. J. of Ecol. 49:731-738.

Anderson, Derek J. 1961b. The structure of some upland plant communities in Caernarvonshire. I. The pattern shown by _Pteridium aquilinum_. J. of Ecol. 49:369-376.

Anderson, Derek J. 1965. Studies on structure in plant communities. I. An analysis of limestone grassland in Monk's Dale, Derbyshire. J. of Ecol. 53:97-107.

Anderson, Derek J. 1967. Studies on structure in plant communities. III. Data on pattern in colonizing species. J. of Ecol. 55:397-404.

Ashby, E. 1948. Statistical ecology. II. A reassessment. Bot. Rev. 14:222-234.

Barnes, H. and F. A. Stanbury. 1951. A statistical study of plant distribution during the colonization and early development of vegetation on china clay residues. J. of Ecol. 39:171-181.

Blackman, G. E. 1935. A study by statistical methods of the distribution of species in grassland associations. Ann. Bot. Lond. 49:749-777.

Blackman, G. E. 1942. Statistical and ecological studies in the distribution of species in plant communities. I. Dispersion as a factor in the study of changes in plant populations. Ann. Bot. Lond., N. S. 6:351-370.

Chadwick, M. J. 1960. _Nardus stricta_, a weed of hill grazings. The Biology of Weeds. Blackwell Sci. Pub., Oxford.

Clapham, A. R. 1936. Over-dispersion in grassland communities and the use of statistical methods in plant ecology. J. of Ecol. 24:232-251.

Cooper, C. F. 1960. Changes in Vegetation, Structure, and Growth of South-Western Pine Forests Since White Settlement. Ecol. Monographs. 30:129-164.

Cooper, C. F. 1961. Pattern in ponderosa pine forests. Ecol. 42:493-499.

David, F. N. and P. G. Moore. 1954. Notes on contagious distributions in plant populations. Ann. Bot. Lond. N. S. 18:47-53.

Duncan, D. B. 1955. Multiple range and multiple F tests. Biometrics 11:1-42.

Gleason, H. A. 1920. Some applications of the quadrat method. Bull. Torrey Bot. Club. 47:21-33.

Goodall, D. W. 1961. Objective methods for the classification of vegetation. IV. Pattern and minimal area. Aust. J. Bot. 9:162-193.

Goodall, D. W. 1963. Pattern analysis and minimal area-some further comments. J. of Ecol. 51:705-710.

Greig-Smith, P. 1952. The use of random and contiguous quadrats in the study of the structure of plant communities. Ann. Bot. 16: 293-316.

Greig-Smith, P. 1957. Quantitative Plant Ecology. Butterworths, London. 191 pp.

Greig-Smith, P. 1961a. Data on pattern within plant communities. I. The analysis of pattern. J. of Ecol. 49:695-702.

Greig-Smith, P. 1961b. Data on pattern within plant communities. II. Amophila arenaria (L.) Link. J. of Ecol. 49:703-708.

Greig-Smith, P. 1964. Quantitative Plant Ecology. Second edition. Butterworths, London. 256 pp.

Greig-Smith, P. and K. A. Kershaw. 1958. The significance of pattern in vegetation. Vegetatio. 8:189-192.

Greig-Smith, P., K. A. Kershaw, and D. J. Anderson. 1963. The analysis of pattern in vegetation; a comment on a paper by D. W. Goodall. J. of Ecol. 51:223-229.

Hyder, D. N., R. E. Bement, E. E. Remmenga and C. Terwilliger, Jr. 1966. Vegetation-Soils and Vegetation-Grazing Relations from Frequency Data. J. Range Manage. 19:11-17.

Kershaw, K. A. 1957. The use of cover and frequency in the detection of pattern in plant communities. Ecol. 38:291-299.

Kershaw, K. A. 1958. An investigation of the structure of a grassland community. I. The pattern of Agrostis tenuis. J. of Ecol. 46:571-592.

Kershaw, K. A. 1959. An investigation of the structure of a grassland community. II. The pattern of Dactylis glomerata, Lolium perenne and Trifolium repens. III. Discussion and conclusions. J. of Ecol. 47:31-53.

Kershaw, K. A. 1960a. Cyclic and pattern phenomena as exhibited by Alchemilla alpina. J. of Ecol. 48:443-453.

Kershaw, K. A. 1960b. The detection of pattern and association. J. of Ecol. 48:233-242.

Kershaw, K. A. 1962a. Quantitative ecological studies from Landmannahellir, Iceland. I. Eriophorum angustifolium. J. of Ecol. 50:163-169.

Kershaw, K. A. 1962b. Quantitative ecological studies from Landmannahellir, Iceland. II. The rhizome behavior of Carex bigelowii and Calamagrostis neglecta. J. of Ecol. 50:171-179.

Kershaw, K. A. 1962c. Quantitative ecological studies from Landmannahellir, Iceland. III. Variation of performance in Carex bigelowii. J. of Ecol. 50:393-399.

Kershaw, Kenneth A. 1963. Pattern in vegetation and its causality. Ecol. 44:377-388.

Kershaw, K. A. 1964. Quantitative and Dynamic Plant Ecology. Arnold Press. Great Britain. 183 pp.

Kershaw, K. A. 1970. An emphirical approach to the estimation of pattern intensity from density and cover data. Ecol. 51:729-734.

Klipple, G. E. and David F. Costello. 1960. Vegetation and Cattle Responses to Different Intensities of Grazing on Short-Grass Ranges on the Central Great Plains. U.S.D.A. Tech. Bull. No. 1216. 82 pp.

McGinnies, W. G. 1934. The relation between frequency index and abundance as applied to plant populations in a semi-arid region. Ecol. 15:263-282.

Moore, P. G. 1953. A test for non-randomness in plant populations. Ann. Bot. Lond. N. S. 17:57-62.

Owen, Myrfyn and D. J. Harberd. 1970. Vegetational pattern in a stable grassland community. J. of Ecol. 58:399-408.

Phillips, M. E. 1953. Studies in the quantitative morphology and ecology of Eriophorum angustifolium Roth.: I. The rhizome system. J. Ecol. 41:295-318.

Pielou, E. C. 1969. An Introduction to Mathematical Ecology. Wiley-Interscience. New York. 286 pp.

Scurfield, G. 1956. Note of experimental ecology and the use of a biological flora. Vegetatio 7:3-8.

Svedburg, T. 1922. Ettidrag tillde statiska metodernas anvandning inom voxtbiologien. Svensk bot Tidskr. 16:1-8. (cf. Kershaw, 1964).

Thompson, H. R. 1955. Spatial point processes with application to ecology. Biometrika 42:102-115.

Thompson, H. R. 1958. The statistical study of plant distribution patterns using a grid of quadrats. Aust. J. Bot. 6:322-342.

Watt, A. S. 1947a. Pattern and process in the plant community. J. of Ecol. 35:1-22.

Watt, A. S. 1947b. Contributions to the ecology of braken (Pteridium aquilinum). IV. The structure of the community. New Phytol. xlvi. 98.

Whitford, P. B. 1949. Distribution of woodland plants in relation to succession and clonal growth. Ecol. 30:199-208.

# APPENDICES

# APPENDIX A

Codes and scientific names of plants found on the study sites.

| Code name | Scientific name |
|---|---|
| Agsm | *Agropyron smithii* Rydb. |
| Arfr | *Artemisia frigida* Willd. |
| Arlo | *Aristida longiseta* Steud. |
| Asmi | *Astragalus missouriensis* Nutt. |
| Asta | *Aster tanacetifolius* H.B.K. |
| Baop | *Bahia oppositifolia* (Nutt.) Dc. |
| Bogr | *Bouteloua gracilis* (H.B.K.) Lag. |
| Buda | *Buchloe dactyloides* (Nutt.) Engelm. |
| Cael | *Carex eleocharis* Bailey |
| Cafi | *Carex filifolia* Nutt. |
| Chle | *Chenopodium leptophyllum* Nutt. |
| Chna | *Chrysothamnus nauseosus* (Pall.) Britt. |
| Chvi | *Chrysothamnus viscidiflorus* |
| Eref | *Eriogonum effusum* Nutt. |
| Evnu | *Evolvulus nuttallianus* Roem. + Schult. |
| Gaco | *Gaura coccinea* Nutt. ex Pursh. |
| Gila | *Gilia laxiflora* (Coult.) Osterh. |
| Gisp | *Gilia spicata* Nutt. |
| Gusa | *Gutierrezia sarothrae* (Pursh) Britt. + Rusby |
| Hasp | *Haploppappus spinulosus* (Pursh) Dc. |
| Hevi | *Heterotheca villosa* (Pursh) Skinners |
| Lare | *Lappula redowskii* (Hornem.) Greene |

| Code name | Scientific name |
|---|---|
| Lede | Lepidium densiflorum Schrad. |
| Liin | Lithospermum incisum Lehm. |
| Lyju | Lygodesmia juncea (Pursh) D. Don. |
| Mavi | Mammillaria vivipara (Nutt.) Haw. |
| Mufi | Muhlenbergia filiculmis vasey |
| Muto | Muhlenbergia torreyi (Kunth) Hitchc. |
| Oeco | Oenothera cornoptifolia Torr. + Gray |
| Oppo | Opuntia polyacantha Haw. |
| Plpu | Plantago purshii |
| Pste | Psoralea tenuiflora Pursh |
| Saka | Salsola kali tenuiflora Tausch. |
| Scbr | Scutellaria brittonii Porter |
| Sihy | Sitanion hysterix (Nutt.) J. G. Smith |
| Spco | Sphaeralcea coccinea (Pursh) Rydb. |
| Spcr | Sporobolus cryptandrus (Torr.) A. Gray |
| Stco | Stipa comata Trin. and Rupr. |
| Tapa | Talinum parviflorum Nutt. |
| Thme | Thelasperma megapotamicum (Spreng.) Kuntze |
| Thtr | Thelasperma trifidum (Poir.) Britt. |
| Tose | Townsendia sericea Hook. |
| Troc | Tradescantia occidentalis (Britt.) Smyth |
| Vuoc | Vulpia octoflora Walt. |

# APPENDIX B

Table B-1. Frequencies of plants found in the 30-year exclosure.

| Species | Transect Number | | | | | | | | Mean | Std. Dev. |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | | |
| Agsm | 0.39 | 0.12 | | 0.39 | 1.17 | 16.79 | 12.89 | 0.78 | 4.07 | 6.30 |
| Arfr | | 3.51 | 3.12 | 0.39 | | 1.95 | 0.78 | 1.17 | 1.36 | 1.27 |
| Arlo | 7.42 | 3.12 | 14.06 | 9.76 | 7.42 | 4.30 | 9.38 | 2.34 | 7.22 | 3.66 |
| Asta | 0.39 | | | | | | 0.39 | | 0.10 | .17 |
| Bogr | 88.67 | 89.45 | 78.52 | 89.06 | 83.59 | 83.98 | 82.81 | 92.58 | 86.08 | 4.29 |
| Cael | 8.59 | 12.89 | 8.59 | 15.23 | 4.30 | 24.61 | 14.06 | 1.56 | 11.23 | 6.72 |
| Cafi | 1.17 | | | 1.56 | 0.78 | 1.56 | | 1.95 | 0.88 | .75 |
| Chna | | 1.17 | | 0.39 | | | | | 0.19 | .39 |
| Eref | 2.34 | | 0.78 | 0.78 | | 0.78 | 1.17 | 0.78 | 0.83 | .74 |
| Gaco | | | | 0.78 | 0.78 | | 0.39 | | 0.24 | .33 |
| Gusa | 1.17 | 1.49 | | | 0.39 | 0.39 | 0.78 | 0.78 | 0.62 | .49 |
| Hevi | | | 0.39 | 0.39 | 0.78 | | | | 0.19 | .27 |
| Lare | 0.39 | | | 0.78 | | 0.39 | | | 0.19 | .27 |
| Lede | 1.56 | 2.34 | 1.95 | 2.34 | 2.34 | 0.39 | 1.56 | | 1.56 | .84 |
| Liin | | | | | | | | 0.78 | 0.10 | .25 |
| Oeco | | 0.39 | | | | 0.39 | | 1.17 | 0.24 | .38 |
| Oppo | 24.61 | 12.11 | 21.48 | 19.14 | 21.09 | 8.20 | 19.92 | 17.19 | 17.97 | 5.02 |
| Plpu | 1.17 | 0.39 | 0.39 | | | 1.17 | 0.39 | | 0.44 | .45 |
| Pste | | 0.39 | 0.78 | 0.39 | | 0.39 | | 0.78 | 0.34 | .30 |
| Saka | 0.39 | 0.39 | 1.56 | | 0.78 | 0.78 | 0.78 | 1.56 | 0.78 | .52 |
| Sihy | 1.17 | | | | | | | | 0.14 | .39 |
| Spco | 11.33 | 14.45 | 14.06 | 31.64 | 27.73 | 9.38 | 17.58 | 18.36 | 18.07 | 7.31 |
| Spcr | 5.61 | 1.95 | 1.95 | 2.34 | 2.34 | 11.12 | 4.69 | | 3.75 | 3.22 |
| Stco | 9.76 | 16.79 | 9.76 | 4.69 | 1.56 | 10.16 | 5.86 | 5.08 | 7.96 | 4.38 |
| Thtr | 1.17 | 4.70 | 3.51 | 3.51 | 3.51 | 0.39 | 4.69 | 1.95 | 2.93 | 1.75 |
| Tose | | | | 0.39 | | | | | 0.05 | .13 |
| Troc | | 3.51 | 0.78 | 3.51 | 4.29 | 4.68 | | 2.73 | 2.44 | 1.78 |
| Vuoc | 2.34 | 1.95 | 2.73 | 1.17 | 1.17 | 1.95 | 0.39 | 2.34 | 1.76 | .73 |

Table B-2. Frequencies of plants found in the 10-year exclosures.

| Species | Transect Number | | | | | | | | Mean | Std. Dev. |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | | |
| Agsm | | | | | 1.17 | 12.50 | 5.47 | 3.12 | 2.78 | 4.11 |
| Arfr | | | | | 0.39 | | | | 0.04 | .13 |
| Arlo | 0.39 | 3.51 | 5.08 | 7.03 | 0.39 | 1.56 | | 2.73 | 2.59 | 2.36 |
| Asmi | | | | | | 0.78 | | | 0.10 | .26 |
| Asta | 1.17 | | 0.39 | | 0.39 | | | 0.39 | 0.29 | .38 |
| Astragalus Spp. | | 0.39 | 0.78 | | | | | | 0.15 | .27 |
| Bogr | 94.92 | 95.70 | 96.09 | 94.53 | 97.66 | 95.70 | 98.05 | 90.62 | 95.41 | 3.01 |
| Buda | | | | | 34.76 | 36.33 | 11.33 | 9.76 | 11.52 | 14.53 |
| Cael | 2.34 | | 13.67 | 12.50 | 41.41 | 32.81 | 25.05 | 3.91 | 16.21 | 14.21 |
| Chle | 0.39 | 0.39 | 0.39 | | 0.39 | | | 0.39 | 0.24 | .19 |
| Chvi | | | | | | | 1.17 | 3.91 | 0.64 | 1.30 |
| Eref | | 0.39 | | | | | | | 0.05 | .13 |
| Evnu | 0.39 | | | | 0.39 | | 1.95 | 1.56 | 0.54 | .73 |
| Gaco | 1.95 | | | | | | 1.17 | | 0.39 | .70 |
| Gusa | | | | | 0.78 | 0.39 | | 4.69 | 0.73 | 1.52 |
| Hasp | | | | | | 0.39 | | | 0.05 | .13 |
| Hevi | | | | | | 0.78 | | | 0.10 | .26 |
| Lare | 0.78 | | 0.39 | 0.39 | 0.39 | | | | 0.24 | .27 |
| Lede | 7.03 | 3.12 | 3.90 | 7.03 | 8.20 | 5.86 | 8.59 | 7.81 | 6.44 | 1.87 |
| Mufi | | | | | | | | 0.78 | 0.10 | .26 |
| Oppo | 12.89 | 20.70 | 11.33 | 8.20 | 7.81 | 10.94 | 10.55 | 6.64 | 11.13 | 4.10 |
| Plpu | 0.78 | 1.17 | 1.17 | 3.12 | 2.73 | 0.78 | 0.39 | | 1.27 | 1.03 |
| Pste | 0.78 | | | | | | | | 0.10 | .25 |
| Saka | 0.78 | 2.34 | 2.34 | 1.56 | | | | 0.78 | 1.07 | .82 |
| Scbr | | | | | | | | 1.56 | 0.19 | .52 |
| Spco | 13.28 | 10.55 | 8.20 | 5.86 | 14.45 | 10.94 | 19.53 | 22.27 | 13.13 | 5.18 |
| Spcr | 3.91 | 1.17 | | 0.39 | 0.78 | | 3.91 | | 1.27 | 1.57 |
| Stco | | | 1.17 | | | | | | 0.15 | .38 |
| Tapa | 0.39 | | | | | | | | 0.05 | .13 |
| Thtr | | 1.95 | 1.56 | | | | | | 0.44 | .77 |
| Vuoc | 11.72 | 16.41 | 9.38 | 20.70 | 7.03 | 7.81 | 6.25 | 12.11 | 11.43 | 5.91 |

Table B-3. Frequencies of plants found in the heavy grazed pasture.

| Species | Transect Number | | | | | | | | Mean | Std. Dev. |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | | |
| Agsm | | 0.78 | | | 0.39 | 0.39 | | | 0.15 | .27 |
| Arlo | 1.17 | 0.39 | 2.34 | | 1.56 | 5.47 | | | 1.37 | 1.75 |
| Asmi | | 0.39 | | | 0.39 | | 0.78 | | 0.20 | .27 |
| Asta | 0.39 | | | | | | | | 0.05 | .13 |
| Baop | 0.78 | 0.39 | 2.73 | | 2.73 | | | | 0.83 | 1.13 |
| Bogr | 99.22 | 96.48 | 97.66 | 99.61 | 98.83 | 97.27 | 96.87 | 98.83 | 98.10 | 1.10 |
| Buda | 1.95 | 13.67 | 8.59 | 0.39 | | 0.78 | 23.05 | 25.39 | 9.23 | 9.75 |
| Cael | 28.12 | 31.25 | 19.53 | 24.61 | 30.86 | 37.89 | 11.72 | 21.48 | 25.68 | 7.62 |
| Cafi | | 0.39 | 0.39 | 2.73 | 8.89 | | 0.78 | | 1.66 | 2.89 |
| Chle | | | | | | 2.34 | 0.39 | 1.56 | 0.54 | .84 |
| Eref | 1.56 | 2.34 | | 0.78 | 0.39 | 2.34 | | | 0.93 | .95 |
| Gaco | | 1.17 | 1.17 | 2.73 | 2.34 | | 1.17 | | 1.07 | 1.00 |
| Gisp | | | | | 0.78 | | | | 0.10 | .26 |
| Gusa | | | | | | | 0.39 | | 0.05 | .13 |
| Hasp | | | 0.78 | | 0.39 | | | | 0.15 | .27 |
| Hevi | | | | | | | 0.39 | | 0.05 | .12 |
| Lare | 1.17 | 0.39 | 0.78 | 0.39 | | 0.39 | | | 0.39 | .39 |
| Lede | 5.86 | 4.69 | 4.30 | 4.30 | 0.78 | 7.03 | | 1.56 | 2.56 | 2.35 |
| Mavi | | | | | | | 0.78 | | 0.10 | .26 |
| Muto | | 3.90 | | | | | | | 0.48 | 1.29 |
| Oeco | | | 0.39 | | | | | | 0.05 | .13 |
| Oppo | 4.30 | 3.13 | 8.98 | 9.77 | 3.52 | 4.30 | 7.03 | 8.59 | 6.20 | 2.50 |
| Penstemon Spp. | | | | | 0.78 | 0.39 | | | 0.15 | .27 |
| Plpu | 5.08 | 3.90 | 2.34 | 1.17 | 1.56 | 9.37 | 3.90 | 0.78 | 3.63 | 2.63 |
| Pste | | 0.39 | 0.78 | 1.95 | | | | | 0.39 | .64 |
| Saka | 0.78 | 1.56 | 0.78 | 1.95 | 0.39 | 0.39 | 0.39 | 3.51 | 1.22 | 1.02 |
| Senecio Spp. | | | 0.39 | 0.78 | | 2.34 | | | 0.44 | .76 |
| Spco | 7.81 | 4.69 | 8.98 | 7.42 | 8.59 | 12.11 | 4.30 | 3.52 | 7.18 | 2.69 |
| Spcr | 1.17 | | | | | | | | 0.15 | .39 |
| Tose | 3.51 | 0.39 | 1.17 | 1.17 | 1.56 | 2.34 | | | 1.27 | 1.13 |
| Vuoc | 9.37 | 10.54 | 8.59 | 10.16 | 3.12 | 10.94 | 7.03 | 6.25 | 8.25 | 2.48 |

Table B-4. Frequencies of plants found in the medium grazed pasture.

| Species | Transect Number | | | | | | | | Mean | Std. Dev. |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | | |
| Agsm | | | | | | 3.20 | | 4.30 | 0.94 | 1.65 |
| Arlo | 0.78 | 3.90 | 14.06 | 3.90 | 3.90 | 10.94 | 7.42 | 9.37 | 6.78 | 4.16 |
| Arfr | | | 1.17 | | | | 0.39 | | 0.19 | .39 |
| Asmi | 0.39 | | | | | | | | 0.05 | .13 |
| Asta | 0.39 | | | 0.39 | | | 2.34 | 0.39 | 4.39 | .74 |
| Astragalus Spp. | | | | | | | 0.39 | | 0.05 | .13 |
| Baop | 3.90 | | | | 1.17 | | 1.56 | 2.34 | 1.12 | 1.34 |
| Bogr | 94.14 | 91.80 | 92.97 | 98.44 | 96.87 | 94.92 | 91.02 | 94.53 | 94.94 | 2.32 |
| Buda | 0.78 | | 3.52 | | | 10.94 | 11.72 | | 3.37 | 4.73 |
| Cael | 51.95 | 32.42 | 42.97 | 12.11 | 2.73 | 21.87 | 51.95 | 16.80 | 29.10 | 17.35 |
| Cafi | 0.39 | | | | | | | | 0.05 | .13 |
| Chle | | | 0.39 | 0.39 | | 0.39 | 0.39 | 0.78 | 0.92 | .25 |
| Chna | | 0.39 | | | | | | | 0.05 | .13 |
| Gaco | | 0.78 | 0.78 | | 0.39 | 0.39 | | | 0.29 | .32 |
| Gisp | 0.78 | 0.39 | | | | | | 0.78 | 0.24 | .33 |
| Gusa | | | | | 0.39 | | | 0.39 | 0.10 | .16 |
| Lare | | | | | 0.39 | 0.39 | | | 0.10 | .16 |
| Lede | 0.78 | 0.39 | 1.95 | 1.56 | 1.17 | 1.56 | 4.30 | | 1.46 | 1.23 |
| Mavi | | | 0.39 | | | | | | 0.05 | .13 |
| Oppo | 5.47 | 5.86 | 4.30 | 5.86 | 4.69 | 5.08 | 4.30 | 4.30 | 4.98 | .64 |
| Plpu | 3.51 | 4.30 | 2.73 | 5.47 | 2.73 | 3.51 | 6.25 | 5.47 | 4.25 | 1.25 |
| Saka | | 0.39 | 1.56 | | | | 0.39 | 0.39 | 0.34 | .49 |
| Spco | 4.30 | 1.17 | 5.47 | 2.34 | 3.52 | 6.25 | 8.59 | 0.39 | 4.00 | 2.56 |
| Spcr | | | 8.98 | 2.34 | | 1.95 | 1.56 | 0.78 | 1.95 | 2.79 |
| Tapa | | | | 1.95 | | 0.39 | | 0.39 | 0.34 | .63 |
| Vuoc | 5.47 | 1.17 | 9.76 | 7.81 | 16.80 | 10.16 | 12.89 | 7.81 | 8.98 | 9.04 |

Table B-5. Frequencies of plants found in the light grazed pasture.

| Species | Transect Number | | | | | | | | Mean | Std. Dev. |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | | |
| Arlo | 4.68 | 2.34 | 1.56 | 8.59 | 0.78 | 1.17 | 7.03 | 5.86 | 4.00 | 2.77 |
| Asta | | | | 0.39 | | 0.39 | 1.17 | | 0.29 | .38 |
| Astragalus Spp. | | | | | 0.39 | 0.39 | | | 0.10 | .16 |
| Baop | | 1.17 | | 0.78 | | | | | 0.24 | .43 |
| Bogr | 98.44 | 99.61 | 78.52 | 94.53 | 98.83 | 98.44 | 93.36 | 82.81 | 93.07 | 7.53 |
| Buda | | | 36.33 | | | 10.16 | | | 5.81 | 12.00 |
| Cael | 7.42 | 31.64 | 33.59 | 32.42 | 39.06 | 30.47 | 28.52 | 32.42 | 29.44 | 8.80 |
| Cafi | | | 1.17 | 4.30 | | | 4.30 | | 1.22 | 1.81 |
| Chle | 3.91 | | | | | | | 0.39 | 0.53 | 1.28 |
| Chna | | 0.78 | | | | | | 0.78 | 0.19 | .33 |
| Eref | | | | | | | | 1.95 | 0.24 | .64 |
| Gaco | 0.39 | | 5.08 | | 0.39 | 1.17 | 2.73 | | 1.22 | 1.69 |
| Gusa | | | 1.95 | | 0.39 | | 3.90 | 0.78 | 0.88 | 1.30 |
| Gila | 3.12 | | | | | | | | 0.39 | 1.03 |
| Gisp | | | 0.78 | | | | | | 0.10 | .26 |
| Hasp | | | 1.17 | | | | | | 0.14 | .39 |
| Lare | 0.39 | | | | | 0.39 | 0.39 | 3.90 | 0.63 | 1.25 |
| Lede | 1.95 | 2.43 | 6.25 | 7.81 | 2.73 | 1.17 | 3.12 | 0.39 | 3.23 | 2.37 |
| Lomation Spp. | 0.39 | 0.78 | | | | | | | 0.15 | .27 |
| Lyju | | | | | | | 0.78 | | 0.10 | .26 |
| Mavi | | | 0.39 | | | | | | 0.04 | .13 |
| Muto | | | | 3.12 | | | 2.73 | 0.78 | 0.83 | 1.24 |
| Oeco | | | | 0.39 | 1.17 | 5.08 | | 7.42 | 1.76 | 2.68 |
| Oppo | 12.50 | 7.42 | 10.55 | 19.53 | 11.72 | 10.16 | 17.58 | 3.52 | 11.62 | 4.81 |
| Plpu | 1.95 | 0.78 | 0.39 | 6.25 | 1.17 | 1.17 | 0.39 | 0.39 | 1.56 | 1.84 |
| Pste | | 0.39 | 1.17 | 1.17 | | | | 0.39 | 0.39 | .47 |
| Saka | | | 0.39 | 2.34 | 1.17 | 1.56 | 1.17 | 7.42 | 1.76 | 2.26 |
| Sihy | 0.39 | | | | | | | | 0.04 | .13 |
| Spco | 13.28 | 16.41 | 15.23 | 13.28 | 16.02 | 17.58 | 21.48 | 18.75 | 16.50 | 2.59 |
| Spcr | 2.73 | 0.78 | | | 10.16 | 4.30 | 1.56 | 16.80 | 4.54 | 5.58 |
| Stco | | | | 4.30 | | | 0.39 | 0.39 | 0.63 | 1.39 |
| Thme | | 0.39 | 0.78 | 4.30 | 0.39 | | | | 0.73 | 1.37 |
| Thtr | | | | | 4.30 | | 2.34 | 3.12 | 1.22 | 1.65 |
| Tose | | | | | 0.39 | | | | 0.04 | .12 |
| Vuoc | 8.59 | 3.90 | 7.42 | 15.23 | 1.95 | 7.03 | 3.90 | 8.20 | 7.03 | 3.81 |

## APPENDIX C

Mean square values using a 1/2 dm by 1 dm basic unit.

### Mean Square Values for BOGR

| Block Size | Exc. 30-year | Exc. 10-year | L.G. | M.G. | H.G. |
|---|---|---|---|---|---|
| 1 | 17.16 | 17.52 | 20.24 | 21.99 | 16.55 |
| 2 | 28.72 | 37.59 | 43.66 | 33.00 | 28.60 |
| 4 | 80.90 | 62.33 | 49.61 | 87.68 | 65.49 |
| 8 | 128.20 | 96.70 | 76.34 | 89.40 | 73.63 |
| 16 | 159.95 | 122.54 | 175.61 | 89.58 | 101.02 |
| 32 | 213.78 | 27.86 | 66.38 | 392.44 | 60.44 |
| 64 | 452.15 | 9.56 | 499.69 | 550.06 | 140.94 |
| 128 | 625.00 | 26.25 | 6.88 | .31 | .00 |
| | | | | | |
| 1 | 19.10 | 18.60 | 19.69 | 19.32 | 18.03 |
| 2 | 29.97 | 30.63 | 53.71 | 43.31 | 35.83 |
| 4 | 59.00 | 44.66 | 62.87 | 67.37 | 56.37 |
| 8 | 117.77 | 55.22 | 81.10 | 89.16 | 42.23 |
| 16 | 164.70 | 92.60 | 69.10 | 71.31 | 397.77 |
| 32 | 102.11 | 199.48 | 57.95 | 370.75 | 317.94 |
| 64 | 1278.69 | 72.31 | 1519.87 | 231.25 | 153.56 |
| 128 | 256.00 | 1064.37 | 168.00 | 210.25 | 210.25 |

### Mean Square Values for OPPO

| Block Size | Exc. 30-year | Exc. 10-year | L.G. | M.G. | H.G. |
|---|---|---|---|---|---|
| 1 | 6.40 | 2.23 | 1.69 | .78 | 1.66 |
| 2 | 10.01 | 7.50 | 4.02 | 2.40 | 2.21 |
| 4 | 14.16 | 10.90 | 4.80 | 1.18 | 5.63 |
| 8 | 21.15 | 7.40 | 6.39 | 2.21 | 5.24 |
| 16 | 27.14 | 11.75 | 10.52 | 6.04 | 4.67 |
| 32 | 15.12 | 28.00 | 3.68 | 5.59 | 5.36 |
| 64 | 8.00 | .86 | .85 | 7.66 | 2.08 |
| 128 | 159.39 | 29.57 | 19.14 | 1.41 | 8.63 |
| | | | | | |
| 1 | 3.79 | 2.16 | 2.29 | 1.24 | 1.24 |
| 2 | 6.66 | 3.16 | 4.45 | 2.12 | 1.68 |
| 4 | 9.21 | 5.23 | 3.54 | 7.25 | 3.36 |
| 8 | 14.23 | 4.98 | 6.26 | 9.39 | 5.32 |
| 16 | 18.30 | 4.15 | 3.59 | 8.80 | 4.96 |
| 32 | 4.39 | 3.29 | 5.98 | 9.21 | 2.79 |
| 64 | .14 | 1.06 | 24.57 | 4.32 | 8.46 |
| 128 | 28.22 | 11.39 | 8.27 | 4.25 | 16.50 |

Mean Square Values for CAEL

| Block Size | Exc. 30-year | Exc. 10-year | L.G. | M.G. | H.G. |
|---|---|---|---|---|---|
| 1 | .87 | .36 | 1.78 | 2.04 | 2.01 |
| 2 | 1.40 | .48 | 3.00 | 3.03 | 2.54 |
| 4 | 2.31 | .83 | 4.52 | 3.60 | 5.54 |
| 8 | 6.15 | .31 | 3.38 | 4.25 | 11.18 |
| 16 | 8.43 | .92 | 4.91 | 8.68 | 10.34 |
| 32 | 21.93 | 2.64 | 11.71 | 51.32 | 32.64 |
| 64 | 2.91 | 8.00 | 148.68 | 6.96 | 10.18 |
| 128 | 10.16 | .56 | 6.57 | 20.82 | 16.50 |
| 1 | 1.36 | 1.99 | 3.39 | 1.36 | 1.27 |
| 2 | 2.03 | 2.03 | 5.21 | 1.70 | 2.27 |
| 4 | 5.59 | 2.40 | 4.89 | 2.35 | 4.03 |
| 8 | 11.27 | 3.28 | 13.31 | 2.68 | 1.63 |
| 16 | 3.36 | 6.62 | 12.22 | 2.60 | 7.83 |
| 32 | 21.79 | 8.98 | 88.24 | 11.37 | 25.23 |
| 64 | 33.25 | 15.58 | 314.16 | 14.95 | 8.52 |
| 128 | 208.44 | 1.89 | 30.94 | .06 | 1.56 |

Mean Square Values for SPCO

| Block Size | Exc. 30-year | Exc. 10-year | L.G. | M.G. | H.G. |
|---|---|---|---|---|---|
| 1 | 1.06 | .37 | .73 | .12 | .21 |
| 2 | .82 | .47 | .85 | .12 | .49 |
| 4 | 1.36 | .36 | .85 | .19 | .30 |
| 8 | .90 | .46 | 1.01 | .10 | .41 |
| 16 | .39 | .50 | .46 | .06 | .15 |
| 32 | .12 | .38 | 1.14 | .24 | .15 |
| 64 | .66 | .78 | .18 | .23 | 1.07 |
| 128 | 3.06 | .14 | 1.13 | .39 | 1.89 |
| 1 | .82 | 1.45 | .92 | .19 | .34 |
| 2 | .68 | 1.61 | .86 | .23 | .30 |
| 4 | .61 | 1.09 | 1.09 | .13 | .17 |
| 8 | .54 | 1.16 | .89 | .47 | .34 |
| 16 | 1.34 | 2.36 | 2.56 | .30 | .44 |
| 32 | 1.39 | 1.88 | .89 | .15 | .20 |
| 64 | .02 | .70 | 1.04 | 2.57 | .79 |
| 128 | 7.22 | 2.64 | 4.25 | .10 | .77 |

APPENDIX D

Mean square values using a 1 dm square basic unit.

Mean Square Values for (BOGR)

| Block Size | Exc. 30-year | Exc. 10-year | L.G. | M.G. | H.G. |
|---|---|---|---|---|---|
| 1 | 68.42 | 73.47 | 113.37 | 71.50 | 69.77 |
| 2 | 133.55 | 111.58 | 164.87 | 163.41 | 123.70 |
| 4 | 139.92 | 171.34 | 128.62 | 212.94 | 140.31 |
| 8 | 200.98 | 130.69 | 164.69 | 190.50 | 356.00 |
| 16 | 401.80 | 132.87 | 235.37 | 436.87 | 681.62 |
| 32 | 433.00 | 138.75 | 213.25 | 862.00 | 274.00 |
| 64 | 1974.56 | 716.00 | 295.50 | 1473.00 | 152.50 |
| 128 | 2364.31 | 264.00 | 756.00 | 2916.00 | 7722.00 |

Mean Square Values for (OPPO)

| Block Size | Exc. 30-year | Exc. 10-year | L.G. | M.G. | H.G. |
|---|---|---|---|---|---|
| 1 | 23.25 | 10.16 | 7.21 | 5.27 | 3.73 |
| 2 | 25.49 | 14.11 | 11.11 | 9.15 | 9.77 |
| 4 | 64.92 | 17.11 | 12.87 | 11.12 | 10.28 |
| 8 | 40.71 | 11.39 | 20.74 | 10.48 | 5.30 |
| 16 | 30.43 | 16.93 | 11.49 | 19.19 | 8.62 |
| 32 | 10.48 | 3.01 | 38.66 | 12.68 | 7.27 |
| 64 | 164.16 | 2.46 | 26.51 | 14.85 | 28.76 |
| 128 | 38.29 | 13.60 | 26.27 | 1.56 | .06 |

Mean Square Values for (CAEL)

| Block Size | Exc. 30-year | Exc. 10-year | L.G. | M.G. | H.G. |
|---|---|---|---|---|---|
| 1 | 2.59 | 2.48 | 7.16 | 4.39 | 4.70 |
| 2 | 8.14 | 3.50 | 9.58 | 6.06 | 8.43 |
| 4 | 17.00 | 5.00 | 19.58 | 11.72 | 15.73 |
| 8 | 11.59 | 9.32 | 16.68 | 17.12 | 29.94 |
| 16 | 55.81 | 7.20 | 115.06 | 73.87 | 54.91 |
| 32 | 28.45 | 39.39 | 104.02 | 96.96 | 21.04 |
| 64 | 155.52 | 8.70 | 85.78 | 27.75 | 22.36 |
| 128 | 54.39 | 1.27 | 6.25 | 30.94 | 33.79 |

Mean Square Values for (SPCO)

| Block Size | Exc. 30-year | Exc. 10-year | L.G. | M.G. | H.G. |
|---|---|---|---|---|---|
| 1 | 1.93 | 1.93 | 1.68 | .41 | .82 |
| 2 | 2.30 | 1.42 | 1.73 | .35 | .59 |
| 4 | 2.07 | 2.09 | 1.96 | .52 | .94 |
| 8 | 3.36 | 5.65 | 3.62 | .19 | .51 |
| 16 | 1.14 | 3.91 | 2.60 | .40 | .36 |
| 32 | .87 | 2.79 | 4.63 | 2.07 | 2.39 |
| 64 | 17.33 | 9.03 | 4.88 | .91 | 3.66 |
| 128 | .66 | 3.52 | 5.63 | .88 | .06 |

# APPENDIX E

## Plant Pattern Data

Plant pattern data collected in 1970 at the Pawnee Site is Grassland Biome data set A2U007B. An explanation of the data format and an example of the data follow.

| Columns | Contents |
|---|---|
| 1- 2 | Day |
| 3- 4 | Month |
| 5- 6 | Year |
| 7- 8 | Treatment (MG = medium grazing, LG = light grazing, HG = heavy grazing, EX = fertilizer) |
| 9-10 | Plot number |
| 11-12 | The letters PL |
| 13-16 | Code (CIRC = begin an enclosed area, CLOS = end an enclosed area, PONT = a point measurement) |
| 17-20 | Plant genus/species |
| 21 | The letter X |
| 22-24 | X-coordinate |
| 25 | The letter Y |
| 26-28 | Y-coordinate |
| 29-30 | Physiographic location (UP = upland, LO = lowland) |

*** EXAMPLE OF DATA ***

```
         1         2         3         4         5         6         7         8
12345678901234567890123456789012345678901234567890123456789012345678901234567890

061670MG04PLCIRCBOGRX184Y196UP
061670MG04PL    BOGRX392Y196UP
061670MG04PL    BOGRX292Y181UP
061670MG04PL    BOGRX392Y168UP
061670MG04PL    BOGRX379Y163UP
061670MG04PL    BOGRX372Y151UP
061670MG04PL    BOGRX367Y146UP
061670MG04PL    BOGRX360Y147UP
061670MG04PL    BOGRX359Y159UP
061670MG04PL    BOGRX345Y164UP
061670MG04PL    BOGRX338Y156UP
061670MG04PL    BOGRX337Y148UP
061670MG04PL    BOGRX329Y147UP
061670MG04PL    BOGRX322Y149UP
061670MG04PL    BOGRX314Y157UP
061670MG04PL    BOGRX306Y157UP
061670MG04PL    BOGRX313Y164UP
061670MG04PL    BOGRX300Y172UP
061670MG04PL    BOGRX286Y168UP
061670MG04PL    BOGRX275Y162UP
061670MG04PL    BOGRX271Y149UP
061670MG04PL    BOGRX271Y137UP
061670MG04PL    BOGRX273Y130UP
061670MG04PL    BOGRX265Y127UP
061670MG04PL    BOGRX266Y117UP
061670MG04PL    BOGRX254Y115UP
061670MG04PL    BOGRX251Y124UP
061670MG04PL    BOGRX250Y135UP
061670MG04PL    BOGRX245Y143UP
061670MG04PL    BOGRX234Y144UP
061670MG04PL    BOGRX235Y131UP
061670MG04PL    BOGRX241Y121UP
061670MG04PL    BOGRX247Y104UP
061670MG04PL    BOGRX234Y095UP
061670MG04PL    BOGRX220Y090UP
061670MG04PL    BOGRX218Y075UP
061670MG04PL    BOGRX210Y061UP
061670MG04PL    BOGRX208Y047UP
061670MG04PL    BOGRX213Y038UP
061670MG04PL    BOGRX224Y030UP
061670MG04PL    BOGRX230Y025UP
061670MG04PL    BOGRX229Y011UP
061670MG04PL    BOGRX240Y010UP
061670MG04PL    BOGRX249Y005UP
```

```
061670MG04PL        BOGRX252Y000UP
061670MG04PL        BOGRX215Y001UP
061670MG04PL        BOGRX193Y001UP
061670MG04PL        BOGRX187Y022UP
061670MG04PL        BOGRX180Y033UP
061670MG04PL        BOGRX168Y037UP
061670MG04PL        BOGRX158Y032UP
061670MG04PL        BOGRX157Y030UP
061670MG04PL        BOGRX150Y030UP
061670MG04PL        BOGRX150Y037UP
061670MG04PL        BOGRX152Y038UP
061670MG04PL        BOGRX135Y032UP
061670MG04PL        BOGRX134Y036UP
061670MG04PL        BOGRX137Y048UP
061670MG04PL        BOGRX133Y061UP
061670MG04PL        BOGRX124Y075UP
061670MG04PL        BOGRX133Y103UP
061670MG04PL        BOGRX157Y121UP
061670MG04PL        BOGRX161Y139UP
061670MG04PL        BOGRX159Y146UP
061670MG04PL        BOGRX170Y151UP
061670MG04PL        BOGRX173Y161UP
061670MG04PL        BOGRX185Y168UP
061670MG04PL        BOGRX188Y190UP
061670MG04PLCLOSBOGRX186Y196UP
061670MG04PLCIRCBOGRX120Y196UP
061670MG04PL        BOGRX102Y196UP
061670MG04PL        BOGRX108Y191UP
061670MG04PLCLOSBOGRX116Y192UP
061670MG04PLCIRCBOGRX127Y161UP
061670MG04PL        BOGRX133Y157UP
061670MG04PL        BOGRX143Y154UP
061670MG04PL        BOGRX144Y159UP
061670MG04PL        BOGRX137Y165UP
061670MG04PL        BOGRX135Y174UP
061670MG04PLCLOSBOGRX129Y172UP
061670MG04PLCIRCBOGRX087Y176UP
061670MG04PL        BOGRX081Y175UP
061670MG04PL        BOGRX085Y168UP
061670MG04PLCLOSBOGRX090Y172UP
061670MG04PLPONTCAELX074Y178UP
061670MG04PLPONTCAELX022Y180UP
061670MG04PLPONTCAELX033Y179UP
061670MG04PLPONTCAELX036Y172UP
061670MG04PLPONTCAELX028Y157UP
061670MG04PLPONTCAELX026Y162UP
061670MG04PLPONTENTHX037Y143UP
061670MG04PLPONTSPCOX123Y150UP
061670MG04PLPONTCAELX097Y132UP
061670MG04PLPONTCAELX096Y134UP
061670MG04PLPONTCAELX097Y132UP
061670MG04PLCIRCBOGRX087Y130UP
061670MG04PL        BOGRX083Y120UP
061670MG04PL        BOGRX073Y114UP
061670MG04PL        BOGRX068Y106UP
061670MG04PL        BOGRX058Y107UP
```

```
061670MG04PL    BOGRX044Y106UP
061670MG04PL    BOGRX044Y116UP
061670MG04PL    BOGRX044Y131UP
061670MG04PL    BOGRX044Y143UP
061670MG04PL    BOGRX058Y148UP
061670MG04PL    BOGRX070Y144UP
061670MG04PLCLOSBOGRX084Y139UP
061670MG04PLPONTCAELX059Y115UP
061670MG04PLPONTENTHX057Y124UP
061670MG04PLPONTENTHX051Y091UP
061670MG04PLPONTENTHX053Y088UP
061670MG04PLPONTCAELX069Y072UP
061670MG04PLCIRCBOGRX000Y100UP
061670MG04PL    BOGRX000Y028UP
061670MG04PL    BOGRX011Y020UP
061670MG04PL    BOGRX020Y005UP
061670MG04PL    BOGRX031Y000UP
061670MG04PL    BOGRX082Y000UP
061670MG04PL    BOGRX072Y011UP
061670MG04PL    BOGRX054Y006UP
061670MG04PL    BOGRX042Y007UP
061670MG04PL    BOGRX050Y036UP
061670MG04PL    BOGRX057Y050UP
061670MG04PL    BOGRX062Y063UP
061670MG04PL    BOGRX040Y078UP
061670MG04PL    BOGRX016Y097UP
061670MG04PLCLOSBOGRX005Y104UP
061670MG04PLPONTCAELX007Y057UP
061670MG04PLPONTCAELX029Y009UP
061670MG04PLPONTCAELX072Y027UP
061670MG04PLPONTCAELX071Y029UP
061670MG04PLPONTCAELX085Y067UP
061670MG04PLPONTCAELX097Y056UP
061670MG04PLPONTCAELX110Y040UP
061670MG04PLPONTCAELX122Y007UP
061670MG04PLPONTCAELX116Y008UP
061670MG04PLPONTCAELX123Y004UP
061670MG04PLPONTCAELX136Y040UP
061670MG04PLPONTPLPUX164Y088UP
061670MG04PLPONTFFOCX165Y079UP
061670MG04PLPONTFFOCX165Y075UP
061670MG04PLPONTCAELX231Y157UP
061670MG04PLPONTCAELX242Y156UP
061670MG04PLPONTCAFLX145Y147UP
061670MG04PLPONTCAELX277Y139UP
061670MG04PLPONTCAELX269Y159UP
061670MG04PLPONTCAELX270Y161UP
061670MG04PLPONTCAELX273Y161UP
061670MG04PLPONTCAELX286Y159UP
061670MG04PLPONTCAELX277Y139UP
061670MG04PLPONTCAELX274Y170UP
061670MG04PLPONTCAELX279Y177UP
061670MG04PLPONTCAELX274Y191UP
061670MG04PLPONTCAELX283Y173UP
061670MG04PLPONTCAELX287Y172UP
```

```
061670MG04PLPONTCAELX289Y171UP
061670MG04PLPONTOPPOX362Y166UP
061670MG04PLPONTCAELX297Y112UP
061670MG04PLPONTFFOCX329Y121UP
061670MG04PLPONTCAELX242Y042UP
061670MG04PLPONTCAELX225Y039UP
061670MG04PLPONTCAELX225Y037UP
061670MG04PLPONTCAELX224Y036UP
061670MG04PLPONTCAELX249Y018UP
061670MG04PLPONTASTAX255Y020UP
061670MG04PLPONTCAELX256Y026UP
061670MG04PLPONTCAELX269Y030UP
061670MG04PLPONTCAELX285Y034UP
061670MG04PLPONTCAELX276Y051UP
061670MG04PLCIRCBOGRX394Y135UP
061670MG04PL    BOGRX389Y120UP
061670MG04PL    BOGRX390Y104UP
061670MG04PL    BOGRX380Y108UP
061670MG04PL    BOGRX380Y123UP
061670MG04PL    BOGRX373Y131UP
061670MG04PL    BOGRX345Y110UP
061670MG04PL    BOGRX357Y095UP
061670MG04PL    BOGRX372Y096UP
061670MG04PL    BOGRX375Y084UP
061670MG04PL    BOGRX360Y069UP
061670MG04PL    BOGRX344Y055UP
061670MG04PL    BOGRX335Y042UP
061670MG04PL    BOGRX324Y045UP
061670MG04PL    BOGRX328Y060UP
061670MG04PL    BOGRX320Y060UP
061670MG04PL    BOGRX313Y045UP
061670MG04PL    BOGRX302Y047UP
061670MG04PL    BOGRX302Y063UP
061670MG04PL    BOGRX307Y072UP
061670MG04PL    BOGRX328Y071UP
061670MG04PL    BOGRX329Y079UP
061670MG04PL    BOGRX322Y086UP
061670MG04PL    BOGRX325Y096UP
061670MG04PL    BOGRX312Y098UP
061670MG04PL    BOGRX294Y097UP
061670MG04PL    BOGRX273Y077UP
061670MG04PL    BOGRX266Y062UP
061670MG04PL    BOGRX270Y046UP
061670MG04PL    BOGRX252Y025UP
061670MG04PL    BOGRX257Y018UP
061670MG04PL    BOGRX266Y004UP
061670MG04PL    BOGRX266Y000UP
061670MG04PL    BOGRX280Y000UP
061670MG04PL    BOGRX271Y009UP
061670MG04PL    BOGRX280Y022UP
061670MG04PL    BOGRX294Y032UP
061670MG04PL    BOGRX300Y019UP
061670MG04PL    BOGRX038Y010UP
061670MG04PL    BOGRX311Y000UP
061670MG04PL    BOGRX325Y000UP
```

```
061670MG04PL         BOGRX319Y009UP
061670MG04PL         BOGRX319Y019UP
061670MG04PL         BOGRX324Y015UP
061670MG04PL         BOGRX333Y003UP
061670MG04PL         BOGRX343Y012UP
061670MG04PL         BOGRX355Y022UP
061670MG04PL         BOGRX358Y025UP
061670MG04PL         BOGRX357Y034UP
061670MG04PL         BOGRX362Y032UP
061670MG04PL         BOGRX068Y026UP
061670MG04PL         BOGRX381Y029UP
061670MG04PL         BOGRX379Y038UP
061670MG04PL         BOGRX373Y052UP
061670MG04PL         BOGRX371Y063UP
061670MG04PL         BOGRX374Y075UP
061670MG04PL         BOGRX387Y074UP
061670MG04PL         BOGRX394Y073UP
061670MG04PLCLOSBOGRX394Y124UP
061670MG04PLPONTCAELX313Y060UP
061670MG04PLPONTLAREX266Y071UP
061670MG04PLPONTCAELX368Y143UP
```