70-13,572

BROTHERSON, Jack DeVon, 1938-
SPECIES COMPOSITION, DISTRIBUTION, AND PHYTOSOCIOLOGY OF KALSOW PRAIRIE, A MESIC TALL-GRASS PRAIRIE IN IOWA.

Iowa State University, Ph.D., 1969
Botany

University Microfilms, Inc., Ann Arbor, Michigan

SPECIES COMPOSITION, DISTRIBUTION, AND PHYTOSOCIOLOGY OF KALSOW PRAIRIE, A MESIC TALL-GRASS PRAIRIE IN IOWA

by

Jack DeVon Brotherson

A Dissertation Submitted to the

Graduate Faculty in Partial Fulfillment of

The Requirements for the Degree of

DOCTOR OF PHILOSOPHY

Major Subject: Plant Ecology

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa

1969

TABLE OF CONTENTS

INTRODUCTION

> There are prairies three, six, ten, and twenty leagues in length, and three in width, surrounded by forests of the same extent; beyond these, the prairies begin again, so that there is as much of one sort of land as of the other. Sometimes we saw the grass very short, and, at other times five or six feet high; hemp, which grows naturally there, reaches a height of eight feet.
>
> A settler would not there spend ten years in cutting down and burning trees; on the day of his arrival, he could put his plough into the ground. --Louis Jolliet--

> These are the finest and most fertile countries in the world...From time to time there are vast prairies where the grass is ten or twelve feet high at all seasons...No settler arriving in the country will not find at first enough to support plenteously a large family, or will not, in less than two years' time be as comfortably settled as in any place in Europe. --Douay--

Of such are the accounts of explorers and settlers of presettlement Iowan vegetation (Dondore, 1926). A government survey started in March, 1832, when Iowa was still a territory, and completed in August 1859, first documented the original extent of this vast grassland area. This survey indicated that in the 1850's grassland covered about 85% of Iowa (U.S. Government, 1868; Hayden, 1945; Hewes, 1950; and Dick-Peddie, 1955). Today there are only a few tracts of this once vast Iowa prairie remaining.

Provision for state owned prairies was made in 1933 when the Iowa State Conservation Commission prepared a report known as the Iowa Twenty-five Year Conservation Plan. In a section of this report the following proposal is recommended:

> Prairie Preserve--Recommended. Along the railroad rights-of-way, and here and there in small patches throughout the state, unbroken virgin prairie sod is still to be found. Some of these will be saved because they lie within protected areas, or simply because the ground cannot be used for farm purposes. But somewhere in Iowa a large enough original tract of prairie vegetation should be secured in order to save, under control of

> the state, the characteristic landscape, and wild flowers, and wild life of the native prairies. Several tracts ranging from forty to three hundred acres have been found by the survey. The Conservation Plan includes a Prairie Preserve which will be one of the remaining original areas, or which may be produced by purchase of semiwaste land and bringing it back to prairie condition in a few years' time. (Hayden, 1945)

Four prairies are now owned by state agencies which were purchased and set aside as natural areas with the intent that the various typical landscapes, wild flowers, and wild life of the native tall-grass prairie region be preserved for posterity. It was also intended that these areas would be useful as game and wild life sanctuaries; as examples of the native prairie soil types, where comparisons could be made with cultivated soils of the same soil association; as reserves of prairie where scientific investigations could be made on problems concerning the native vegetations, floras and faunas of the various topographic, climatic, and prairie districts throughout Iowa. Therefore, they were meant to serve as a reference point by which future generations could compare the influences of man on Iowa since settlement (Hayden, 1946; Moyer, 1953; Aikman, 1959; Landers, 1966).

One such area is Kalsow Prairie, 160 acres of unplowed grassland in Pocahontas County, Iowa. Criteria for its purchase dictated that this area satisfy the requirements of a game preserve, contain one or more soil types of an association, and include several regional vegetation types (Hayden, 1946). The prairie was purchased in 1949 by the State Conservation Commission at a cost of $32,000 from Otto C. Kalsow (State Conservation Commission, 1968). Since its purchase in 1949 it has been the object of several studies on the nature and description of its vegetation, soils, management, insects, response to fire, mammals, and nematodes (Moyer, 1953; Ehrenreich, 1957; Esau, 1968; Richards, 1969; Brennan, 1969; Norton and Ponchillia, 1968; Schmitt, 1969).

This investigation was undertaken to provide information on the phytosociology of this particular prairie in relation to edaphic and topographic variation and to disturbance. It includes information on species composition and distribution, factors affecting the distributional patterns of these species, community types, and interrelationships within and between these communities.

More specifically, the objectives of this study are:

1. To make an inventory of plant species on Kalsow Prairie.
2. To compare the present vegetation with that which existed at the time of earlier studies.
3. To describe the prairie vegetation as a prelude to detailed studies of soil, fire, decomposition, mammals, fungi and other aspects of ecosystem dynamics.
4. To determine sub-communities by the use of ordination and classification techniques.
5. To map species distributional patterns and relate these patterns to other species and to topographic and edaphic features of the landscape.
6. To provide information on the natural vegetation of Kalsow Prairie for use in scientific and educational endeavors and purely esthetic approaches to this once great expanse of grassland.

LITERATURE REVIEW

Early accounts by the first explorers, surveyors, and settlers in the Midwest describe three major types of landscape in Iowa: (1) woodland, (2) well-drained prairie, and (3) poorly-drained prairie and marsh (Dondore, 1926; Berry, 1927; Hewes, 1950). The woodlands were confined to the stream valleys and adjacent slopes, while the prairie was said to occupy the remaining portions of the land (Berry, 1927; Hewes, 1950). The well-drained prairie was the most extensive except in portions of the state subjected to late Wisconsin glaciation. Here the poorly-drained prairie and marsh were more common (Hewes, 1950; Hewes, 1951; Hewes and Frandson, 1952). The well-drained prairie was described as highly fertile (Dondore, 1926; Berry, 1927), whereas the poorly-drained prairie was filled with water most of the season and "capable of producing nothing but wild rice, frogs, and mosquitoes" (Hewes and Frandson, 1952).

The first recorded botanical study of Iowa prairie came before 1850 and gave attention mainly to the collection, identification and listing of plant species found within the prairie. Information such as collection locations, general soil conditions, and maps were included (Nicollet, 1845; Ellsworth, 1924). Numerous studies, published after the early 1900's, have contributed much to our knowledge of the prairie flora (Shimek, 1911; Shimek, 1915; Steiger, 1930; Hayden, 1943; Freckmann, 1966). These studies included species lists and generally have brought together floristic data of value toward the completion of a state flora. Cratty (1933) produced the first checklist of the Iowa flora, yet Gilly (1948) commented that much is yet to be done before such a work is a reality. Moyer (1953) and Monson (1959) have reviewed the progress of such a work. The latter produced an annotated checklist with keys to the families, genera, and species of spermatophytes of north-central Iowa. Such floristic studies have led to the development of our present knowledge and understanding of tall-grass prairie ecology in Iowa.

References to the prairies are many, concerning floristics, origin, composition, seasonal aspects, classification, and phytosociology. Shimek (1925) includes an extensive bibliography and discussion of early works including Pound and Clements (1898), Harvey (1908), Shimek (1911, 1915), Sampson (1921), Gleason (1922) and Shantz (1923). These works were largely concerned with the extent, distribution, floristic composition, persistence, and early classification of prairie vegetation. In most cases only general reference is made to the environment (i.e., climate, soils, topography, etc.).

The characteristics of Iowa prairie in terms of vegetation types, structure, and general ecology of the dominant species was the subject of several papers during the 1930's and 1940's (Steiger, 1930; Rydberg, 1931; Weaver and Fitzpatrick, 1934; Hayden, 1943). These authors recognized the existence of six major types of grassland or vegetative communities and generally concluded that water relations, as affected by climate, soil and topography, are responsible for local variations in the structure and distribution of prairie vegetation. Weaver and Fitzpatrick (1934) state:

> In varying the water relations of soil and air they merely bring about changes in the groupings of the dominant grasses and accompanying segregations and rearrangements of the forbs.

The major grassland types as alluded to in the above studies were labeled "Consociations" after Weaver and Clements (1938) and were designated as follows:

1. Big Bluestem type (*Andropogon gerardi*)--found on the lower moist slopes and well aerated lowlands.

2. Slough Grass type (*Spartina pectinata*)--found on poorly aerated and wet soils of sloughs and natural drainage systems.

3. Tall Panic Grass-Wildrye type (*Panicum virgatum* and *Elymus canadensis*)--found to occur on soils intermediate between Slough Grass and Big Bluestem types.

4. Little Bluestem type (*Andropogon scoparius*)--most important upland type (well drained soils).

5. Needle Grass type (*Stipa spartea*)--found on the uplands often occurring as a narrow zone following the shoulders of the ridges.

6. Prairie Dropseed type (*Sporobolus heterolepis*)--found locally on the dryest upland sites.

Moyer (1953), Aikman and Thorne (1956), Ehrenreich (1957), and Kennedy (1969) in recent studies present ecological and taxonomic descriptions of four state-owned native prairie tracts. All accounts contain extensive reviews of prairie literature. The vegetation complex as treated in these studies is limited basically to upland prairie. The studies also include information on soils, microclimate, topography, and management. Aikman (1959) has reviewed in some detail the state of prairie research in Iowa.

Investigations involving the distribution of individual species within the prairie association began with the work of Shimek (1911, 1915, 1925). Weaver (1930) and Weaver and Fitzpatrick (1932) discuss the role of the major grasses and forbs within the community. Steiger (1930) and Cain and Evans (1952) mapped the spatial distributions of several species. They conclude that the principal factors affecting the local distribution patterns of prairie species are as follows: (1) microclimatic conditions,

(2) edaphic variations, (3) the biology of the species concerned, particularly methods of reproduction and dispersal, (4) the relations of the species and other organisms, animal as well as plant, occurring in the community, and (5) the element of chance in the dispersal and establishment of new individuals. Local distribution patterns of species have been of interest to many ecologists. Several methods, all designed to detect departures from randomness, have been reviewed by Kershaw (1964) and Sanders (1969).

Species in general show varying degrees of aggregation or association due to exhibited preferences for or tolerances of certain environmental conditions. The distributional patterns and interactions of the component species of a community express its phytosociological structure. Studies of grassland phytosociology have been concerned with either classification or ordination of basic species groups (Crawford and Wishart, 1968).

Classification methods for expressing quantitatively the associations between different species or groups of species have been the subject of numerous papers. The works of Calvert (1922) and Gleason (1925) are the first major contributions, the latter being the first to use 2 x 2 contingency tables to measure association. Other methods proposing to delineate associated species or groups of species are those of Forbes (1925), Nash (1950), Goodall (1952), Cole (1949, 1957), Fager (1957), Harberd (1960), Odum et al. (1960), and Beals (1960). These methods describe several association indices which have been used in phytosociological studies by Dice (1945), McIntosh (1957), Bray (1956), Shanks (1953), Goodall (1954), DeVries (1953), Hale (1955), and McIntosh (1962).

In the use of classification methods several authors have used the digital computer for data handling. This has led to the development of methods which simplify procedures and reduce greatly the amount of manual labor necessary to complete large scale studies.

Such methods generally employ the R and Q techniques developed in factor analysis. R-techniques treat the stands (or vegetation samples) as individuals and the species as attributes. Analysis data represent correlations between all possible pairs of species as they occur in different stands. Therefore if species A,B,C,... are found in stands 1,2,3,... and are designated as $a_1,a_2,a_3,\ldots,$ $b_1,b_2,b_3,\ldots,$ $c_1,c_2,c_3,\ldots$etc., this technique involves correlations between such sets of pairs as a_1,b_1; a_2,b_2;a_3,b_3,...etc. Q-techniques treat the species as individuals and the stands as attributes, examining all possible pairs of stands in terms of the occurrence of different species in two stands. Thus Q-techniques involve an estimation of similarity or dissimilarity between stands and utilize correlations between such sets of species as a_1,a_2;b_1,b_2;c_1,c_2;.... R-techniques result in the ordination of species in n-dimensional space while Q-techniques result in the ordination of stands in n-dimensional space. The attempt is to classify vegetation by identifying discontinuities or similarities between sample groups. Sample sets are detected by sample homogeneity or by the occurrence of groups of coincident species. The use of computers and the theory of these classification techniques are covered in Williams and Lambert (1960, 1961a, 1961b, 1962), Lambert and Williams (1962), Greig-Smith (1964), Lance and Williams (1965, 1966), Edwards and Gavalli-Sforza (1965), Orloci (1967), and Crawford and Wishart (1966, 1967, 1968).

Measurements of community similarity on the basis of total species composition began with the efforts of Jaccard (1902, 1908). This approach, including the papers of Gleason (1920) and Sorenson (1948), was an attempt to group stands of vegetation by consideration of qualitative or quantitative similarity of species composition. From these and other efforts has developed the concept of the "coefficient of community." Such a concept is the basis for nearly all proposed ordination techniques. Sanders (1969) suggested that of the many methods used in ordination the best known is that of Curtis and McIntosh (1951). Their technique is called the "continuum-index" and is one example of a linear ordination method. The continuum concept has been reviewed extensively by McIntosh (1967). Other studies involving the use of linear ordination schemes are those of Whitford and Salamun (1954), Clausen (1957), Bray and Curtis (1957), Curtis (1959), Looman and Campbell (1960), Dix and Butler (1960), Christensen (1963) and Brotherson (1967). In the use of these linear ordination schemes, edaphic, climatic and other environmental factors have often been plotted against the ordination of the stands. Early attempts of single factor correlation had led some authors to question the relevance of considering single environmental factors apart from the environmental complex (Goodall, 1954; Williams, 1954; Whittaker, 1956). Bray and Curtis (1957) introduced a three-dimensional ordination to counter these objections. Other studies have reviewed this approach and in some instances introduced new methods (Gittins, 1965a, 1965b; Orloci, 1966; and Austin and Orloci, 1966). More recent papers have since coupled these three-dimensional techniques with the concepts of classification reviewed earlier (Gittins, 1965c; Kershaw, 1968; and Crawford and Wishart, 1968). These studies first classify the existing vegetation into homogenous groups and then ordinate the groups into multi-dimensional arrays. The ordination is a means of representing the variation both within and between the terminal groups of the classification procedures. Crawford and Wishart (1968) indicate a definite need for the combination and use of both techniques.

METHODS

General

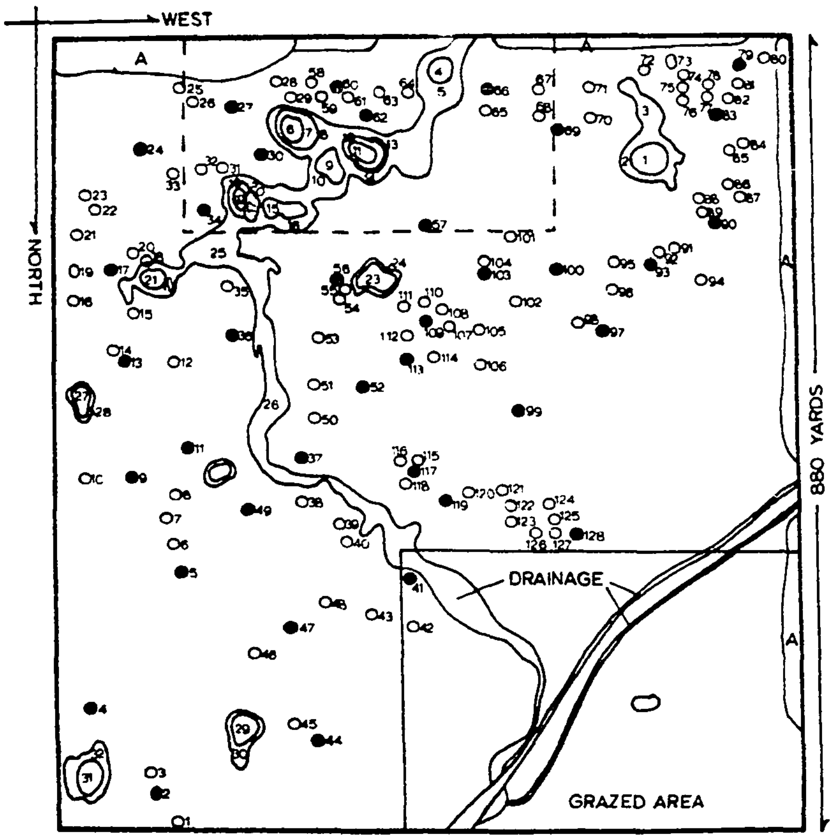
This study was begun in the spring of 1967 and continued through the following year (1968) and into the summer of 1969. The study site (Kalsow Prairie) is one of four state-owned Iowa prairies. It is located five miles northwest of Manson, Iowa, and comprises the NE $\frac{1}{4}$ of Section 36, Belleville Township, T 90N, R 32W, Pocahontas County. It occurs in a part of north central Iowa which was glaciated during the most recent advances of the Wisconsin Glacier and within the Clarion-Nicollet-Webster soil association area (Ruhe, 1969). The area was chosen for study on the basis of its vegetational composition (i.e., floristic richness and the presence of several plant community types). These vegetation types or sub-communities (Figure 1) were studied periodically throughout the summers of 1967 and 1968. The vegetational data and the topographic and edaphic information were collected during these visits. Data analysis was completed during the winters and summers of 1968 and 1969.

The Vegetation

Taxonomy

Voucher specimens were collected in duplicate throughout the growing seasons of 1967 and 1968. All specimens were identified and identical sets have been deposited in the herbaria of Iowa State University, Ames, Iowa and the Brigham Young University, Provo, Utah. Nomenclature follows Pohl (1966) for the grasses, Gilly (1946) for the sedges, and Gleason (1952) for the forbs.

Figure 1. Map of Kalsow Prairie showing locations of potholes and drainage, Mima mounds, old pasture, border weed communities, and 20-acre intensive study area



MAP OF THE KALSOW PRAIRIE

O MIMA MOUNDS
● MIMA MOUNDS ADJACENT TO WHICH THE PRAIRIE WAS SAMPLED
A AREAS AFFECTED BY SOIL DRIFT FROM ADJACENT FIELDS
– – 20 ACRES OF PRAIRIE INVOLVED IN SOIL AND PLANT DISTRIBUTION STUDIES
POTHOLES AND DRAINAGE

Community types

Kalsow Prairie contains within its boundaries five vegetation types or sub-communities. These vegetation units were identified and delimited as follows (Figures 1 and 2):

1. Upland prairie--includes the major portion of the study area on the ridges and adjacent lower slopes.

2. Potholes and drainage--found in the swales and lowlands of the study site.

3. Mima mounds--found scattered over the entire 160 acres of the prairie.

4. Grazed pasture--includes about 35 acres in the northwest corner of the study site.

5. Border weed communities--found forming rather narrow margins along the south and west fences of the prairie.

The vegetation of these community types was analyzed using two separate approaches. The first involved the identification and listing of all species found within their boundaries. The second utilized random plots to determine percent cover, composition, and interspecific relationships of species within these sub-communities.

Quadrat analysis

The vegetation of each area was sampled by using a 20 x 50 cm (1000 cm^2) quadrat (Figure 3). The quadrats were located on a restricted basis to reduce bias and to keep adjacent quadrats at fairly equal distances apart. The number of samples varied with the community types, but a total of 4494 quadrats was taken on the entire prairie. Sampling was done between August 1 and September 15 each year when most species had reached their maximum growth. Cover estimates were made for each quadrat through use of Daubenmire's (1959) method. This method employs the

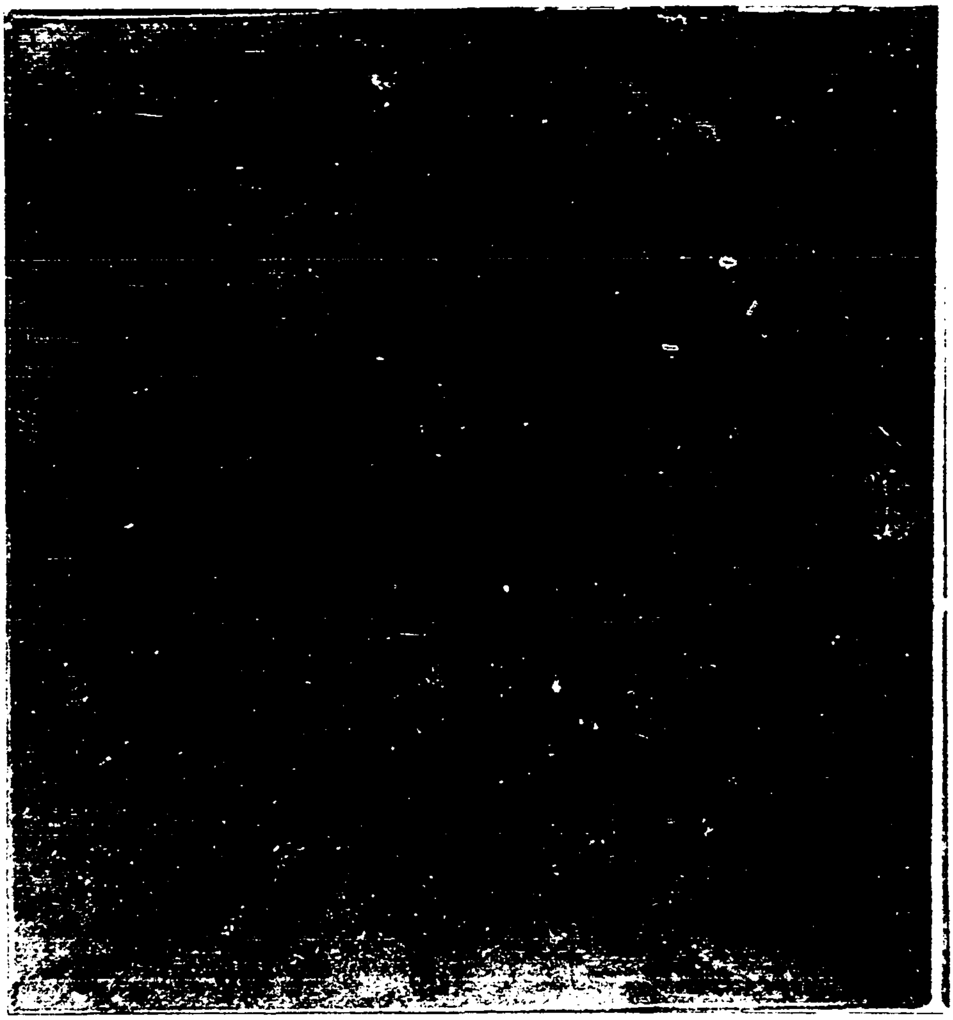


Figure 2. Aerial photograph of Kalsow Prairie taken August 31, 1953, U. S. Department of Agriculture, photo number B22-2M-35

following cover classes:

Cover class	Range (%)	Midpoint of range (%)
1	0-5	2.5
2	6-25	15.0
3	26-50	37.5
4	51-75	62.5
5	76-95	85.0
6	96-100	97.5

The midpoints of the ranges were used in calculation.

Coverage was determined separately for all species overlapping the plot regardless of where the individuals were rooted. Coverage was projected to include the perimeter of overlap of each species regardless of superimposed canopies of other species. The canopies of different species are commonly interlaced or superimposed over the same area; therefore coverage percents often total greater than 100 percent.

Community analysis

Upland prairie   Data taken to describe this community were obtained from two sources. The first source involved 444 samples taken adjacent to 37 selected Mima mounds. Each mound was bisected by two transects oriented in north-south and east-west directions. Quadrats were then taken along these transects (Figure 4) starting at the mound edge and progressing into the adjacent prairie. A total of 12 quadrats was taken adjacent to each mound, three in each direction. The quadrats were placed at 12-foot intervals. The second source involved samples taken from 20 acres of the prairie (Figure 1) involved in plant distribution studies. These quadrats were taken at 30-foot intervals along a grid covering the total area.

Pothole and drainage   Analysis of these areas was accomplished by dividing the sites into sub-units or zones (Figure 1) based on location and dominant species. Each sub-unit was then sampled by randomly locating a starting point and then placing a quadrat every 10 feet along a transect. Twenty quadrats were taken for each zone. One pothole and drainage complex was mapped by vegetation zones using a plain table mapping procedure described by Phillips (1959).

Mima mounds These sites were first located (Figure 1) and permanently identified by a numbered stake placed at the west edge of the mound. Every mound was then sampled starting at the northeast corner of the mound and gridding the mound with quadrats placed every three steps. The number of samples varied with the size of the mound ranging from 5 on the smallest to 45 on the largest. A total of 1549 samples was taken on 128 mounds. Mound dimensions were taken in north-south and east-west directions, and areas (in square feet) were obtained through the use of the ellipse area formula:

$$A = \pi ab$$

A is the area; $\pi = 3.1417$; a is the length; and b is the width of the mound.

Grazed pasture This area was divided into 30 equal-sized blocks (Figure 5) with individual blocks measuring 60 feet by 78 feet. Each block was sub-sampled 20 times by quadrats placed at 10-foot intervals along an S-shaped transect. A quadratic surface was then fitted to summary data in an attempt to discover the direction of movement of prairie plants into this area. The statistical model used in this analysis is as follows:

$$Y = \beta_0 + \beta_1 X_1 + \beta_{11} X_1^2 + \beta_2 X_2 + \beta_{22} X_2^2 + \beta_{12} X_1 X_2 + \epsilon_i$$

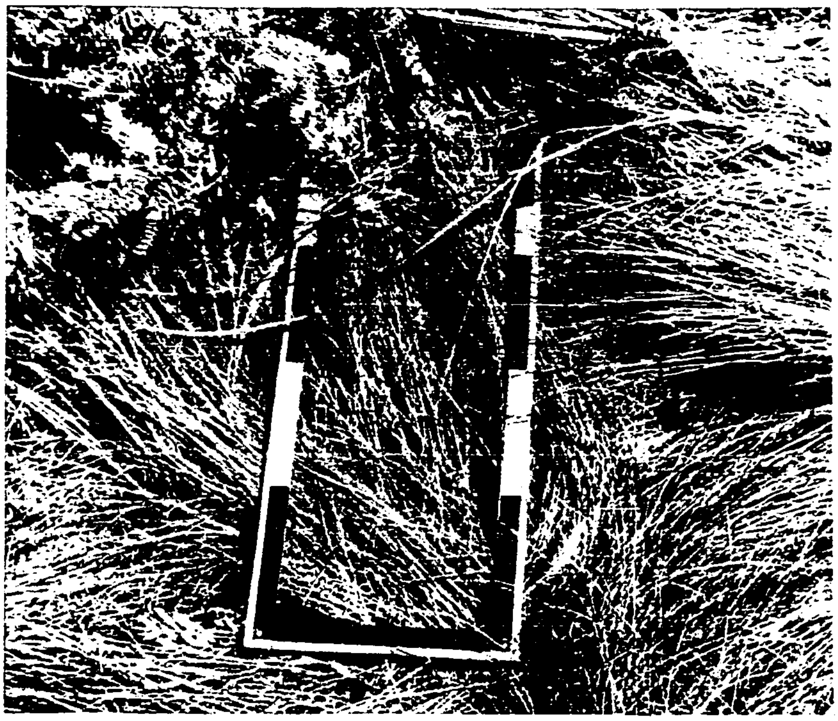


Figure 3. Quadrat (20 x 50 cm inside dimensions) used in vegetation sampling

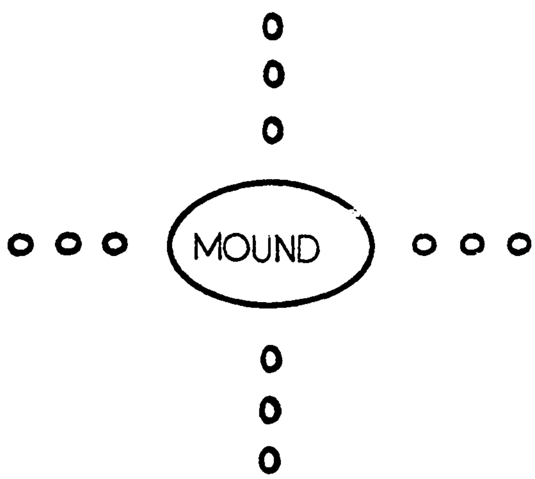


Figure 4. Location of plots in upland prairie adjacent to selected Mima mounds

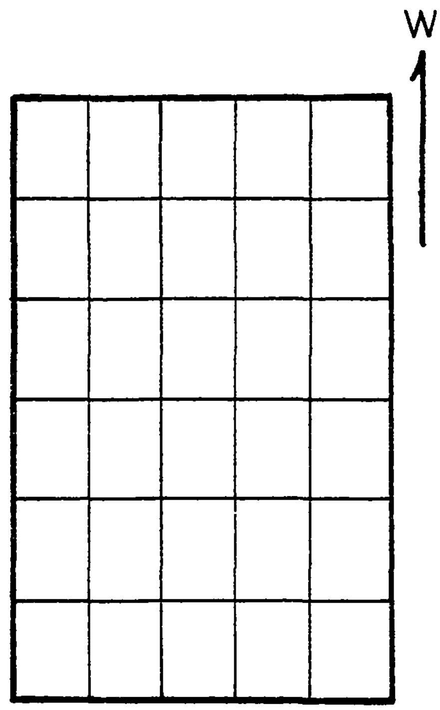


Figure 5. Blocking technique used in sampling grazed pasture

where: Y = estimated mean value from the regression of average cover data

β = population regression coefficient

ϵ = error variable

and

X_1 = north-south direction variable

X_2 = east-west direction variable

Border weed communities These areas were divided into one, two, and three or more year-old weed communities based on the year of dust deposition. They were then sampled by placing a quadrat every ten feet along transects oriented by use of a Brunton compass. In communities adjacent to the south fence transects were oriented east-west and in communities adjacent to the west fence transects were oriented north-south. A total of 227 quadrats was taken in these communities.

Selected environmental analysis

Plant distribution study This study was conducted in August of 1968. A 20-acre plot of prairie (Figure 1) containing a large segment of potholes and drainage was selected and staked off in a 30 x 30-foot grid. Each 900 square-foot block was then surveyed and a presence list compiled for all plant species found within the area. A total of 968 blocks was thus surveyed, and distribution data were tabulated for 160 species.

Topography study Topographic readings were taken at 968 points and recorded in tenths of feet on the same 20-acre grid. Points were located at the corners of the 900 square foot plots. Elevation data were also taken for a 1000-foot transect (Figure 6). Readings were taken at 10-foot intervals along this transect. Changes in dominant vegetation were also recorded as they were intersected by the transect.

Soil mapping   Soils were mapped on the 20-acre intensive study area. Mapping was done in cooperation with the Iowa State University Soils Survey under the supervision of Dr. Thomas E. Fenton, with Mr. J. Herbert Huddleston doing the actual mapping in the field. Mr. Huddleston's mapping criteria for decisions on soil series deliniation were as follows:

A   Clarion--typical well drained soil on convex ridges. Surface color 10YR 2/2 - 3/2; subsoil color 10YR 4'3 - 5'4.

A⁻   Clarion-Nicollet--an intergrade with respect to drainage as interpreted from the color profile. Surface is still 10YR 2/2 - 3/2, but the subsoil colors are duller, not exceeding /3 chroma. Profile is not mottled as in Nicollet.

N   Nicollet--typical Nicollet, 10YR 2/1 - 2/2 surface color, /2 chromas in the subsoil, which is mottled. Depth to carbonates generally greater than 30 inches.

Na   Calcareous Nicollet--as above, but calcareous at some depth less than 30 inches.

W   Webster--typical Webster with black (N2/ - 10YR 2/1) surface colors and gray (10YR 4/1 - 4/2 - 5/2) subsoil colors. Depth to gray subsoil ranges from 23-41 inches, but is commonly 30-35 inches. Carbonates occur at some depth below 22 inches, but the usual range in depth to carbonates is 22-36 inches. Some soils identified as Webster are non-calcareous in the entire probe depth (42 inches).

Wh   Heavy Webster--typical colors of Webster but heavier textures, stronger development in the B and a lack of carbonates in 42 inches. In many places spots of Wh are included in the regular Webster mapping unit. On the other hand some areas identified as regular Webster but non-calcareous to 36 inches or more might better have been called heavy Webster. The Webster soils, as mapped, include a rather broad range of texture and depths to carbonates, which could be more precisely subdivided only with further investigations.

N⁻   Webster-Nicollet--an intergrade whose surface color and friability is like Nicollet but whose subsoil is darker or grayer than true Nicollet. The soil is drier than Webster.

Nā Calcareous Webster-Nicollet--as above but calcareous somewhere above 22 inches.

H Harps--typical Harps, a loamy, weakly developed soil that effervesces strongly to violently from the surface downward. Calcium carbonate equivalent probably in the range 20-40 percent.

C Canisteo--this is essentially calcareous Webster. As mapped, it may be non-calcareous in the surface, but carbonates must be detected somewhere in the 0-15 inch layer. It has lower calcium carbonate equivalent, heavier textures, and stronger development than Harps.

H^{-} Harps-Canisteo--an intergrade that has either Harps-like characteristics in the surface and becomes more Canisteo-like with depth or Canisteo-like surface characteristics and a Harps-like subsoil.

Wa Webster-Canisteo--an intergrade in which carbonates are first detected in the 15-22 inch layer. All other characteristics of Wa, W, and C are essentially the same.

C^{-} Inverted Canisteo-Heavy Webster--this represents a rather peculiar condition that tends to occur as a narrow band around the potholes. The surface is moderately to strongly calcareous, but carbonates decrease with depth to a non-calcareous, heavy, well developed subsoil like that of heavy Webster.

G Glenco--a poorly drained soil that occupies small potholes, the outer portions of large potholes, or connecting drainage-ways. It has a black, highly organic surface but a gray, mineral, heavy, well-developed subsoil. In many respects it is similar to heavy Webster except for the organic surface and lack of grit and pebbles. Depth to carbonates is generally greater than 42 inches, but may be up to 36 inches.

Ga Calcareous Glenco--Glenco that becomes calcareous above 36 inches. It usually lacks the heavy texture and good development of regular Glenco as well.

O Okoboji--a black, mucky silt loam, very weakly developed soil occurring in the deepest areas of the potholes.

GO Glenco-Okoboji--an intergrade that may have the heavy textures of Glenco, but is darker, more organic, less well developed, and wetter than Glenco.

Seventeen soil series were recognized and mapped in the field utilizing soil samples obtained with a 42-inch hand probe.

Data analysis

General descriptive data Data collected from quadrat studies, mapping studies, soil studies and topographic studies were used to describe generally the vegetation of each area. Frequency values and average cover values were determined for all species in every stand. Frequency values were determined by use of the following formula:

$$\text{Frequency } (\%) = \frac{\text{Number of plots of occurrence}}{\text{Total number of plots sampled}} \times 100$$

Cover values were determined by summing the midpoints of the cover-class ranges and dividing by the number of sample quadrats in the stand.

Ordination analysis An ordination technique proposed by Orloci (1966) was employed to ordinate vegetation units within the different sub-communities listed above. Raw data were first summarized by hand calculation and then transferred to punch cards. This technique was programmed for use on an IBM S360 Mod 65 computer by Mr. Rodger Mrachek, research assistant working under Dr. David Jowett of the Statistics Department, Iowa State University. Through this technique the entities to be ordinated (i.e., plant species or stands of vegetation) are projected as points into n-dimensional space. Such points are positioned by attribute scores through the application of the R and Q-techniques of factor analysis described previously. Once established this multidimensional array of points is then reduced to a three dimensional system. This is accomplished by selecting the two most different stands or species and placing one at zero and the other at some distance along the abscissa. All other stands or species under consideration are then positioned linearly in relationship to these two extremes. This action thus establishes the X-axis. The above process is repeated until all points have been established in three dimensional space (i.e., Y and Z axes have been added). Coordinate values for the X, Y and Z axes are given as output from the computer.

<u>Interspecific association analysis</u> Expressions of interspecific association were attempted utilizing Cole's Index (1949). Step one in the computation of the index involves the accumulation of 2 x 2 contingency tables (Figure 7). Actual calculation of the index involves the following three sets of formulas:

when $ad \geq bc$:

$$C_7 \pm \sigma_c = \frac{ad - bc}{(a + b)(b + d)} \pm \sqrt{\frac{(a + c)(c + d)}{n(a + b)(b + c)}}$$

when $bc > ad$ and $d \leq a$:

$$C_7 \pm \sigma_c = \frac{ad - bc}{(a + b)(a + c)} \pm \sqrt{\frac{(b + d)(c + d)}{n(a + b)(a + c)}}$$

when $bc > ad$ and $a > d$:

$$C_7 \pm \sigma_c = \frac{ad - bc}{(b + d)(c + d)} \pm \sqrt{\frac{(a + b)(a + c)}{n(b + d)(c + d)}}$$

where C_7 = Cole's Index of Interspecific Association

$_c$ = standard deviation Cole's Index

n = total number of samples

and a, b, c and d represent the four cells of the 2 x 2 contingency table.

Tests of statistical significance were performed by means of the Chi-square test. The Chi-squares were computed by the formula:

$$X^2 = \frac{(ad - bc)^2 n}{(a + b)(a + c)(c + d)(b + d)}$$

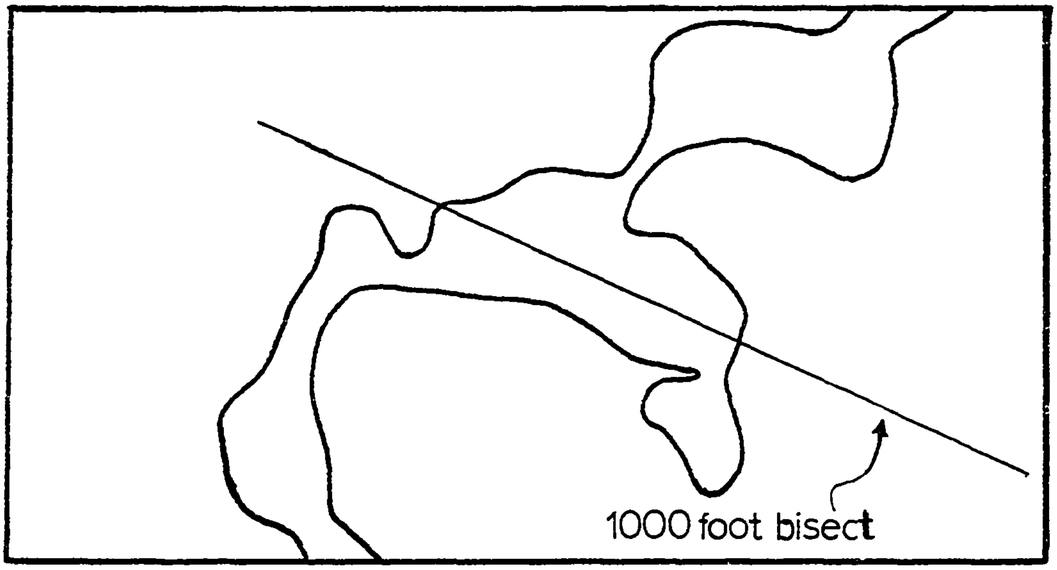


Figure 6. Location of 1000-foot bisect in 20-acre intensive study area from SE corner toward the NW

		SPECIES A		
		Present	Absent	
SPECIES B	Present	a	b	a + b
	Absent	c	d	c + d
		a + c	b + d	n

Figure 7. Contingency table (2 x 2) used in Cole's Index analysis

where X^2 = Chi-square value

n = number of samples

and a, b, c and d represent the different cells of the 2 x 2 contingency table.

In all cases a single degree of freedom was used. Chi-square values greater than 3.84 were considered to be significant at the 5% level, while values greater than 6.63 were considered to be significant at the 1% level.

Data representation   Graphic representation of data obtained from topographic studies and from ordination analysis was drawn by the computer. Such representation was accomplished through the use of a plotting technique developed and programmed by Mr. Howard Jesperson, Agricultural Experiment Station, Iowa State University.

RESULTS AND DISCUSSION

Upland Prairie

Information on 105 species sampled in the upland regions of Kalsow Prairie is presented in Table 1. Cover, composition (i.e., based on cover), and frequency values of Sporobolus heterolepis, Andropogon gerardi, Poa pratensis, and Panicum leibergii indicate these are the dominant grasses of the upland sites. Important or sub-dominant forbs include Solidago canadensis, Solidago rigida, Helianthus grosseserratus, Amorpha canescens, Aster ericoides, Desmodium canadense, Zizia aurea, Helianthus laetiflorus, Aster laevis, Ratibida columnifera, Ceanothus americanus, and Rosa suffulta.

Average cover values (Table 1) ranged from a high of 25.42 for Sporobolus heterolepis to a low of 0.01 for several species. Percentage frequency values, on the other hand, ranged from 73.1 for Andropogon gerardi to 0.1 for many species. No tests of correlation were made between average cover values and percentage frequency, but those species showing the highest cover values generally showed correspondingly higher percentage frequency values.

Field observations strongly support the data in Table 1 that Sporobolus heterolepis is the dominant plant of the upland prairie. This would place Kalsow Prairie within the "Consociation" designated by Weaver and Fitzpatrick (1934) as the Prairie Dropseed type (Sporobolus heterolepis) because of the large extent of the area that is upland prairie. Weaver and Fitzpatrick (1934) described this particular consociation as being the least extensive and least important tall-grass sub-community. It was found to occupy drier upland sites and included the two sub-dominants Stipa spartea and Andropogon scoparius. Although these two species were present (Table 1), they were not found in sufficient quantity to be labeled sub-dominants. The important grass species found with Sporobolus heterolepis in this study (i.e., Andropogon gerardi, Poa pratensis, and Panicum leibergii) suggest that the present day upland regions of Kalsow Prairie are vegetatively distinct from the Prairie Dropseed Consociation of similar areas described earlier by Weaver. Both the species and their characteristics suggest that this difference is due either to change in the original vegetation, to differences in community characteristics or to variations in the more recently glaciated land. Poa pratensis, for example, is an introduced species whose characteristics are such that it is able to compete well within the environment of the prairie protected from fire and under conditions of grazing, mowing and other disturbance is known to increase in importance (Weaver, 1954). Andropogon gerardi, on the other hand, is a native grass described by Weaver and Fitzpatrick (1934) as the dominant of the most extensive tall-grass consociation which occupied the lowlands and lower moist slopes of the tall-grass prairie region.

Historical information as well as evidence obtained in this study (Figures 1, 8, 9 and 75) indicates that much of the Kalsow Prairie has been subjected to mowing, grazing to some extent, and abundant pocket gopher activity. The distribution of Mima mounds on the upland prairie is shown in Figures 1 and 9, and pocket gopher (Geomys bursarius) activity on a selected 20-acre tract of the prairie is shown in Figure 8. Both Mima mounds and pocket gopher activity are widely scattered across

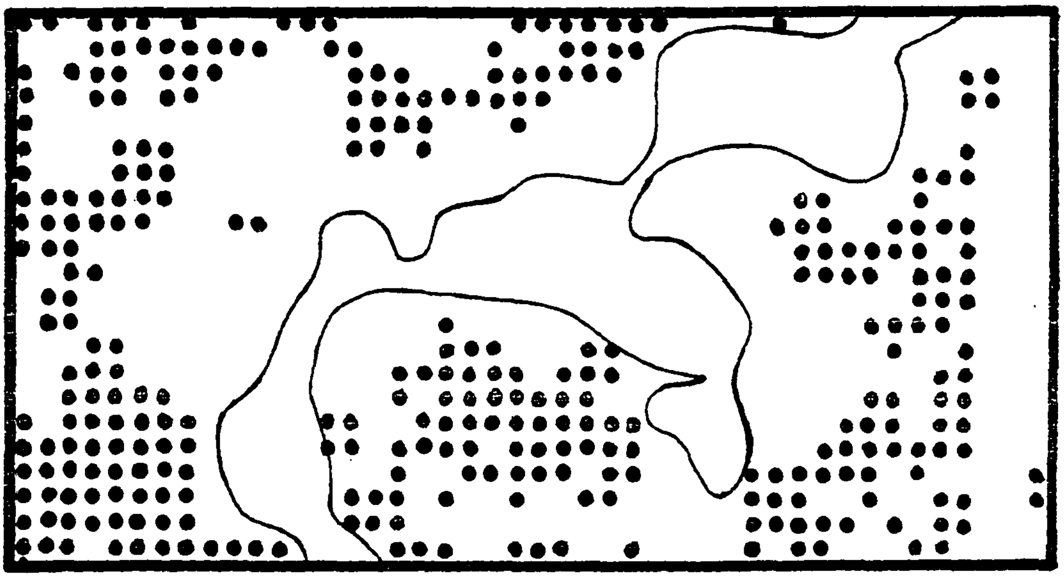


Figure 8. Distribution of pocket gopher (Geomys bursarius) activity in the 20-acre intensive study plot

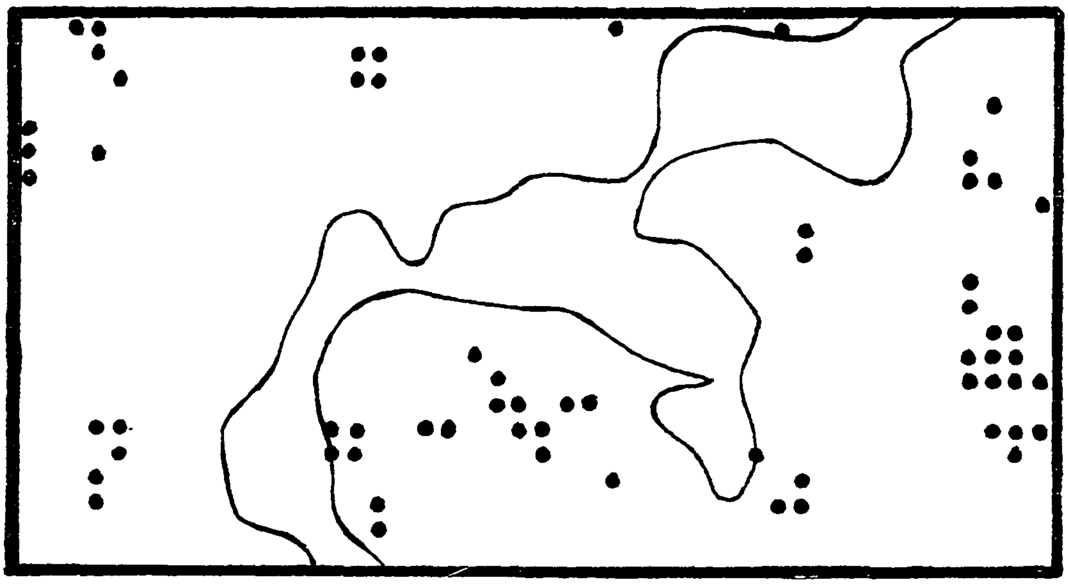


Figure 9. Distribution of Mima mound influences in the 20-acre intensive study plot

Table 1. Cover, composition, and frequency percentages for species sampled on upland prairie sites

Species	% Cover	% Composition	% Frequency	% Frequency[a]
Sporobolus heterolepis	25.42	27.81	66.7	85.0
Andropogon gerardi	15.93	17.43	73.1	87.5
Poa pratensis	12.36	13.52	54.5	90.0
Solidago canadensis	4.12	4.51	38.9	15.0
Solidago rigida	2.57	2.81	19.4	5.0
Panicum leibergii	2.56	2.80	34.0	12.5
Helianthus grosseserratus	2.30	2.52	31.6	10.0
Amorpha canescens	2.08	2.28	15.0	27.5
Aster ericoides	1.99	2.19	40.7	37.5
Desmodium canadense	1.66	1.82	23.0	5.0
Zizia aurea	1.62	1.77	36.1	67.5
Helianthus laetiflorus	1.49	1.63	11.4	7.5
Aster laevis	1.30	1.42	16.9	7.5
Ratibida columnifera[b]	1.26	1.39	20.6	10.0
Ceanothus americanus	1.15	1.26	.9	2.5
Rosa suffulta	1.07	1.17	18.4	45.0
Lysimachia hybrida	.84	.92	.7	5.0
Convolvulus sepium	.76	.83	1.2	2.5
Silphium laciniatum	.72	.79	12.4	15.0
Achillea lanulosa	.68	.74	11.7	45.0
Galium obtusum	.65	.71	29.1	5.0
Spartina pectinata	.60	.66	10.3	17.5
Artemisia ludoviciana	.59	.65	4.4	2.5
Comandra umbellata	.59	.65	9.1	45.0
Andropogon scoparius	.52	.57	1.7	85.0
Fragaria virginiana	.52	.57	20.7	7.5
Physalis heterophylla	.47	.51	2.1	
Elymus canadensis	.45	.49	19.4	12.5
Stipa spartea	.45	.49	6.6	20.0
Aster simplex	.43	.47	13.1	
Muhlenbergia racemosa	.37	.40	11.2	
Panicum virgatum	.36	.39	12.1	75.0
Senecio pauperculus	.36	.39	9.3	
Lithospermum canescens	.35	.38	13.0	17.5
Heliopsis helianthoides	.31	.34	5.8	17.5
Psoralea argophylla	.29	.32	3.8	5.0
Solidago missouriensis	.28	.31	2.7	5.0
Apocynum sibiricum	.27	.30	3.3	
Asclepias tuberosa	.26	.28	3.5	2.5

[a]Figures taken from Moyer (1953) for comparison purposes

[b]Determined after completion of manuscript to be Ratibida pinnata

Table 1. (Continued)

Species	% Cover	% Composition	% Frequency	% Frequency[a]
Setaria viridis	.23	.25	.7	
Cirsium altissimum	.23	.25	4.6	17.5
Sorghastrum nutans	.21	.23	5.4	42.5
Liatris pycnostachya	.21	.23	9.8	27.5
Petalostemum purpureum	.20	.22	29.5	32.5
Pycnanthemum virginianum	.20	.22	7.0	5.0
Lythrum alatum	.20	.22	.6	
Phlox pilosa	.16	.18	6.3	10.0
Physalis virginiana	.16	.18	3.1	7.5
Viola pedatifida	.14	.15	5.5	5.0
Setaria lutescens	.13	.14	.5	
Viscia americana	.12	.13	4.7	7.5
Lathyrus venosus	.12	.13	2.5	5.0
Equisetum kansanum	.11	.12	4.7	42.5
Eryngium yuccifolium	.11	.12	1.0	2.5
Petalostemum candidum	.11	.12	3.9	7.5
Baptisia leucophaea	.09	.10	.7	15.0
Asclepias syriaca	.07	.08	1.4	
Ambrosia artemisifolia	.06	.07	1.4	
Baptisia leucantha	.06	.07	.7	
Carex gravida	.06	.07	2.0	
Oxalis stricta	.06	.07	.9	
Teucrium canadense	.06	.07	1.7	
Viola sp.	.06	.07	3.2	
Gentiana andrewsii	.05	.06	1.1	2.5
Potentilla arguta	.05	.06	.5	
Scutellaria leonardii	.05	.06	2.2	
Thalictrum dasycarpum	.05	.06	1.6	7.5
Lespedeza capitata	.04	.04	1.0	2.5
Solidago riddellii	.04	.04	2.4	
Anemone cylindrica	.03	.03	.5	35.0
Helenium autumnale	.03	.03	.8	
Pedicularis canadensis	.03	.03	1.2	22.5
Bouteloua curtipendula	.03	.03	.9	7.5
Chenopodium album	.02	.02	.2	
Lathyrus palustris	.02	.02	1.1	
Liatris aspera	.02	.02	.8	25.0
Lycopus americanus	.02	.02	.7	
Lysimachia chiliata	.02	.02	.6	
Mentha arvensis	.02	.02	.4	
Solidago gymnospermoides	.02	.02	1.4	5.0
Vernonia fasiculata	.02	.02	.3	
Taraxacum officinale	.02	.02	.9	

Table 1. (Continued)

Species	% Cover	% Composition	% Frequency	% Frequency[a]
Echinacea pallida	.02	.02	.4	10.0
Agropyron repens	.01	.01	.5	
Agropyron smithii	.01	.01	1.2	2.5
Anemone canadensis	.01	.01	1.7	
Arabis hirsuta	.01	.01	.1	
Asclepias sullivantii	.01	.01	.2	5.0
Asclepias verticillata	.01	.01	.4	2.5
Astragalus canadensis	.01	.01	.3	
Cicuta maculata	.01	.01	.3	10.0
Helianthus maximiliani	.01	.01	.6	
Juncus tenuis	.01	.01	.1	
Lactuca scariola	.01	.01	.4	
Lysimachia quadriflora	.01	.01	.8	
Panicum capillare	.01	.01	.1	
Phleum pratense	.01	.01	.6	85.0
Rudbeckia hirta	.01	.01	.3	
Veronicastrum virginicum	.01	.01	.1	
Allium sp.	.01	.01	.1	
Aster novae-angliae	.01	.01	.4	
Cacalia tuberosa	.01	.01	.1	
Prenanthes racemosa	.01	.01	.7	
Solidago nemoralis	.01	.01	2.6	2.5
Trifolium pratense	.01	.01	.1	12.5

the prairie. The Mima mounds are poorly understood areas of disturbance to be discussed later. Other disturbance areas are along the south and west boundaries of the prairie where dust from adjacent plowed fields has been deposited in depths up to two or three feet (Figure 1).

The distribution of soil types in the 20-acre intensive study site is shown in Figure 75. From this map it can be seen that much of the 20 acres is of lowland soil types. In fact, a large part of the upland prairie may occupy lowland soil types. The disturbance will give possible explanation to the high incidence of Poa pratensis found with

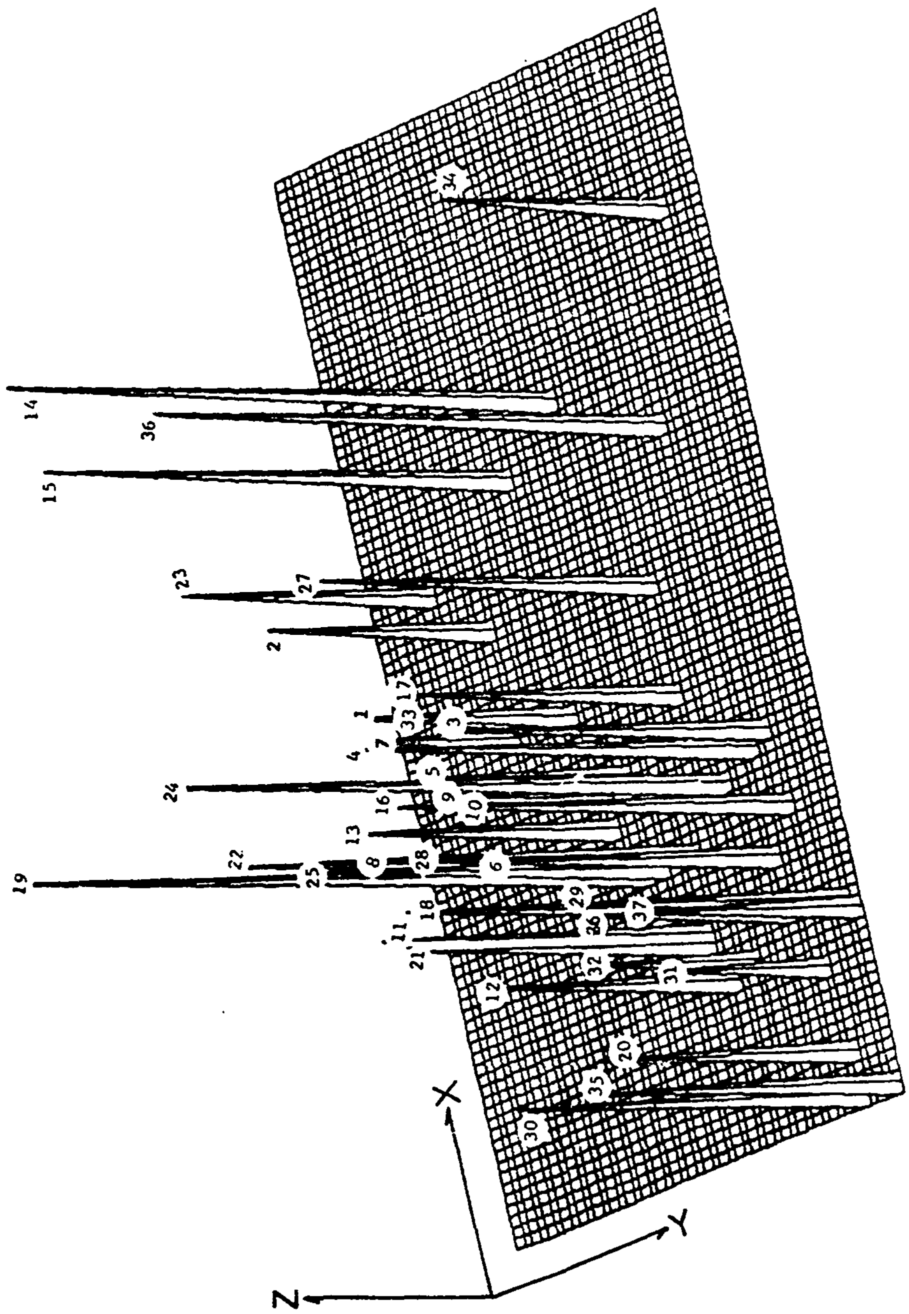
Sporobolus heterolepis while the large tracts of lowland soil types might well explain the abundance of Andropogon gerardi.

Why Sporobolus heterolepis is found growing in such abundance on the lowland areas is difficult to explain, but it might be due to the high amount of calcareous soil types found within Kalsow Prairie (Figure 75). Early studies (Weaver and Fitzpatrick, 1934; Shimek, 1925) suggest the distribution of Sporobolus heterolepis as restricted to driest uplands. Because these areas often show a lack of soil profile development or outcroppings of parent material often high in carbonates (Oschwald, et al., 1965) it is feasible that Sporobolus heterolepis is adapted to grow on soils of high carbonate content and that it might easily be extended to lowland soils high in carbonate content.

Moyer (1953), in a study of the Kalsow Prairie vegetation, gave percentage frequency values for many of the species included in Table 1 of this paper. His figures are reported in column four of Table 1 for comparison. These figures suggest that there have been some changes in the vegetation of the upland prairie since 1953. Some of the species which show increases in percentage frequency in the past 16 years are Solidago canadensis, Solidago rigida, Panicum leibergii, Helianthus grosseserratus, Desmodium canadense, Galium obtusum, and Fragaria virginiana. Species which show decreases in percentage frequency over this same period are Phleum pratense, Poa pratensis, Zizia aurea, Rosa suffulta, Andropogon scoparius, Panicum virgatum, Sorghastrum nutans, Equisetum kansanum, Anemone cylindrica, Liatris aspera, and Sporobolus heterolepis. Such changes are not easily explained but might be related to general fluctuations over a period of years of the vegetation, to fluctuations in climatic conditions (i.e., time and duration of rainfall, drought, etc.), to interspecific competition, to differences in the technique and intensity of sampling, and to the possible influence of slight disturbance upon the prairie due to increased populations of pocket gophers, dust accumulation from adjacent fields, public visitors, and management practices. Further discussion of these changes will be covered in the discussion of Mima mounds.

To describe in greater detail the interrelationships of species in the upland prairie a three-dimensional stand and species ordination treatment was attempted using Orloci's (1966) method. The results are shown in Figures 10, 11, and 14. Data used in the ordination were from the 444 samples of upland prairie taken adjacent to 37 selected Mima mounds. These 37 sites are shown as points in three-dimensional space in Figure 10 and as dots in two-dimensional space in Figure 11. Initially, attempts were made to place the individual sites into specific groups. Groups were designated on the basis of where the stands fell when plotted in three-dimensional space (i.e., those sites which fell close together were considered to be the most similar and were placed within the same group). Attempts to understand the meaning of such groupings were unsuccessful. Further attempts to understand the ordering pattern led to the conclusion that discrete grouping within these upland prairie regions is not feasible. It appears that the ordering of the stands into three-dimensional space was controlled by the response of several of the major species to environmental gradients. Of these species, Andropogon gerardi (Figure 12) and Sporobolus heterolepis (Figure 13) were plotted against the X and Y coordinates of the ordination and as

Figure 10. Three-dimensional ordination of upland prairie adjacent to selected Mima mounds, numbers indicating sample sites


X
Y
Z
14
36
15
23
27
2
1
17
33
3
4
7
5
24
16
9
10
13
22
8
28
6
19
25
29
18
37
11
36
21
32
31
12
20
35
30
34

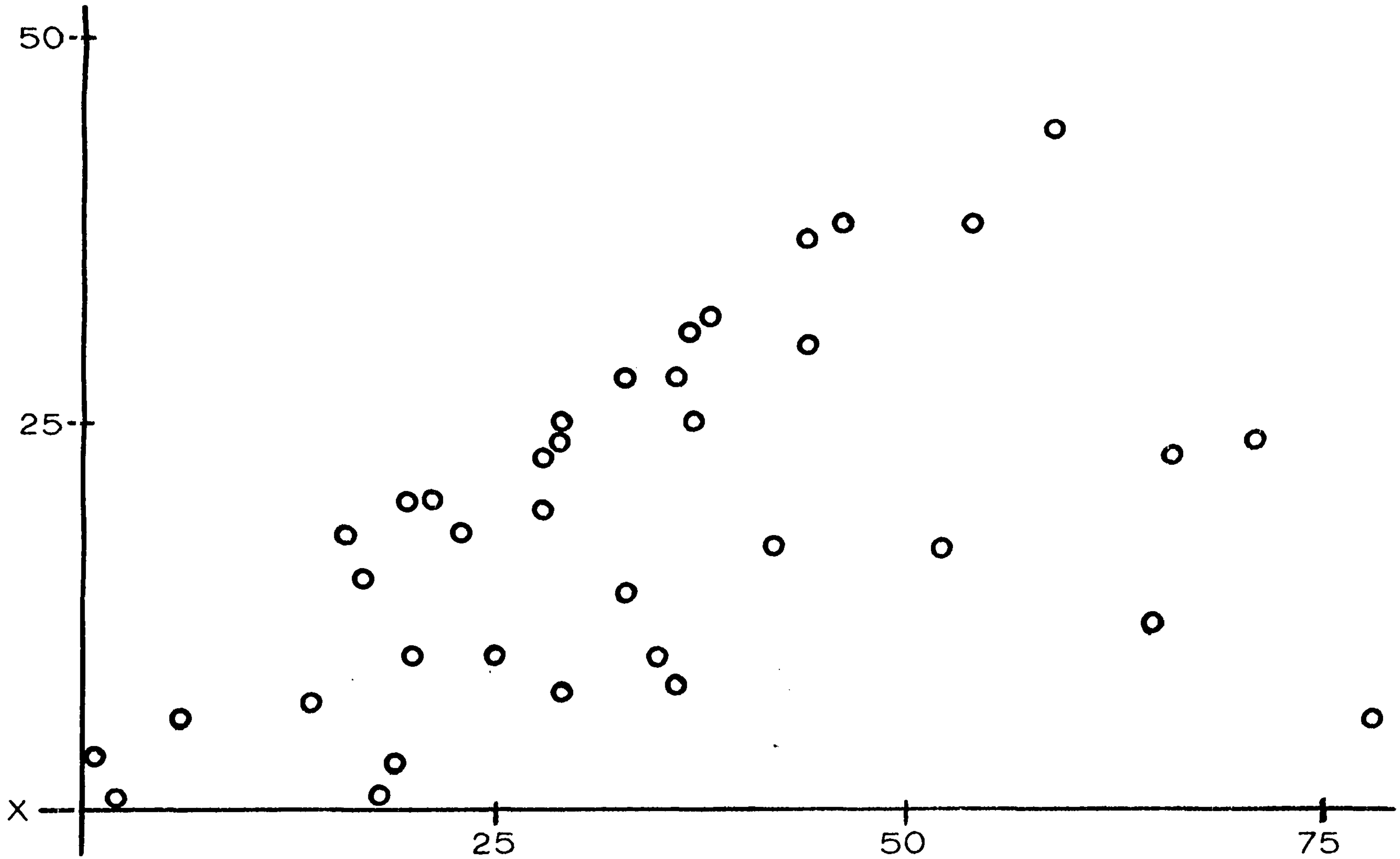


Figure 11. Two-dimensional ordination of upland prairie adjacent to selected Mima mounds, factors responsible for pattern unknown

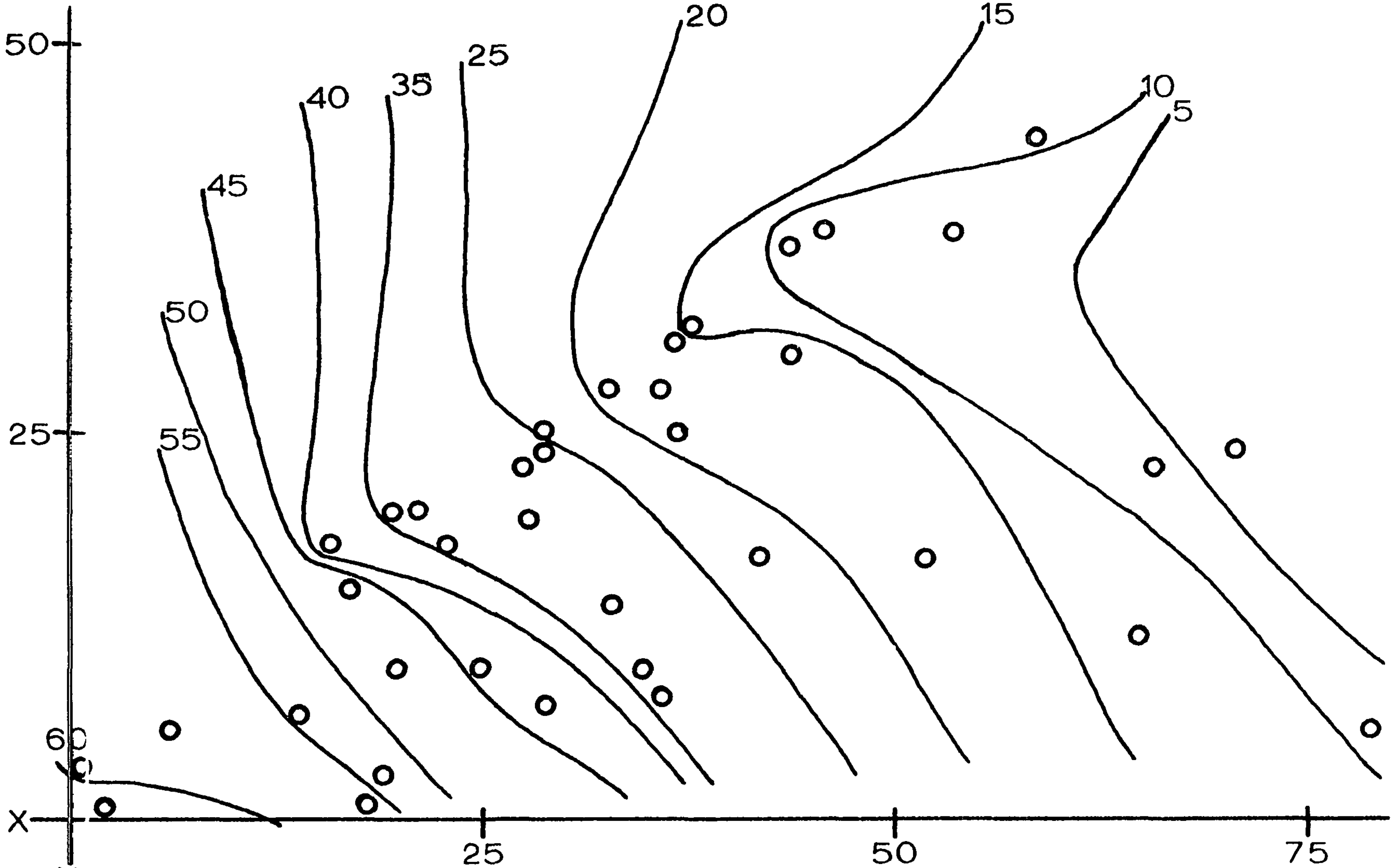


Figure 12. Two-dimensional ordination of upland prairie with percentage cover values of *Sporobolus heterolepis* for each site shown relating indirectly to the Y-axis

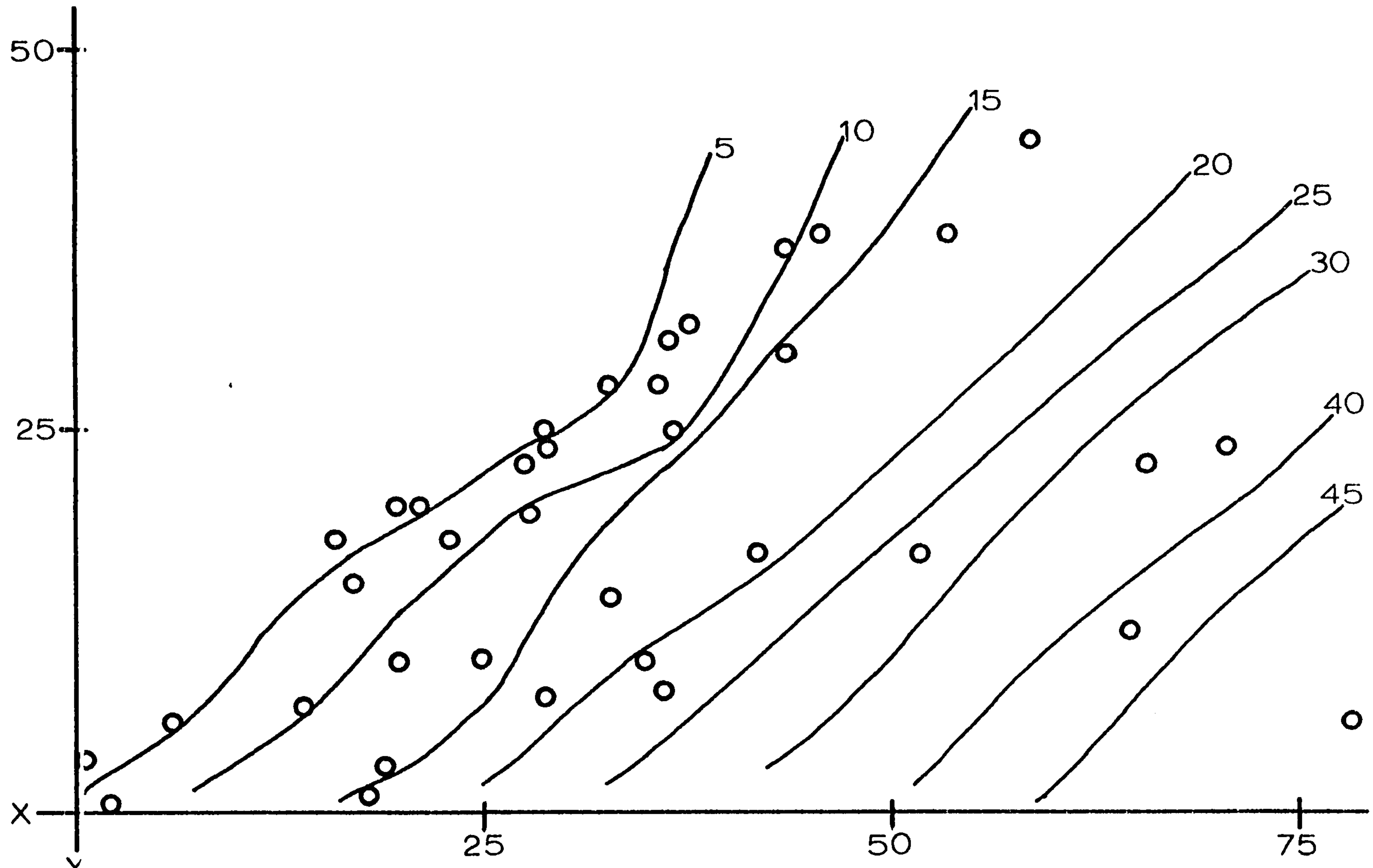


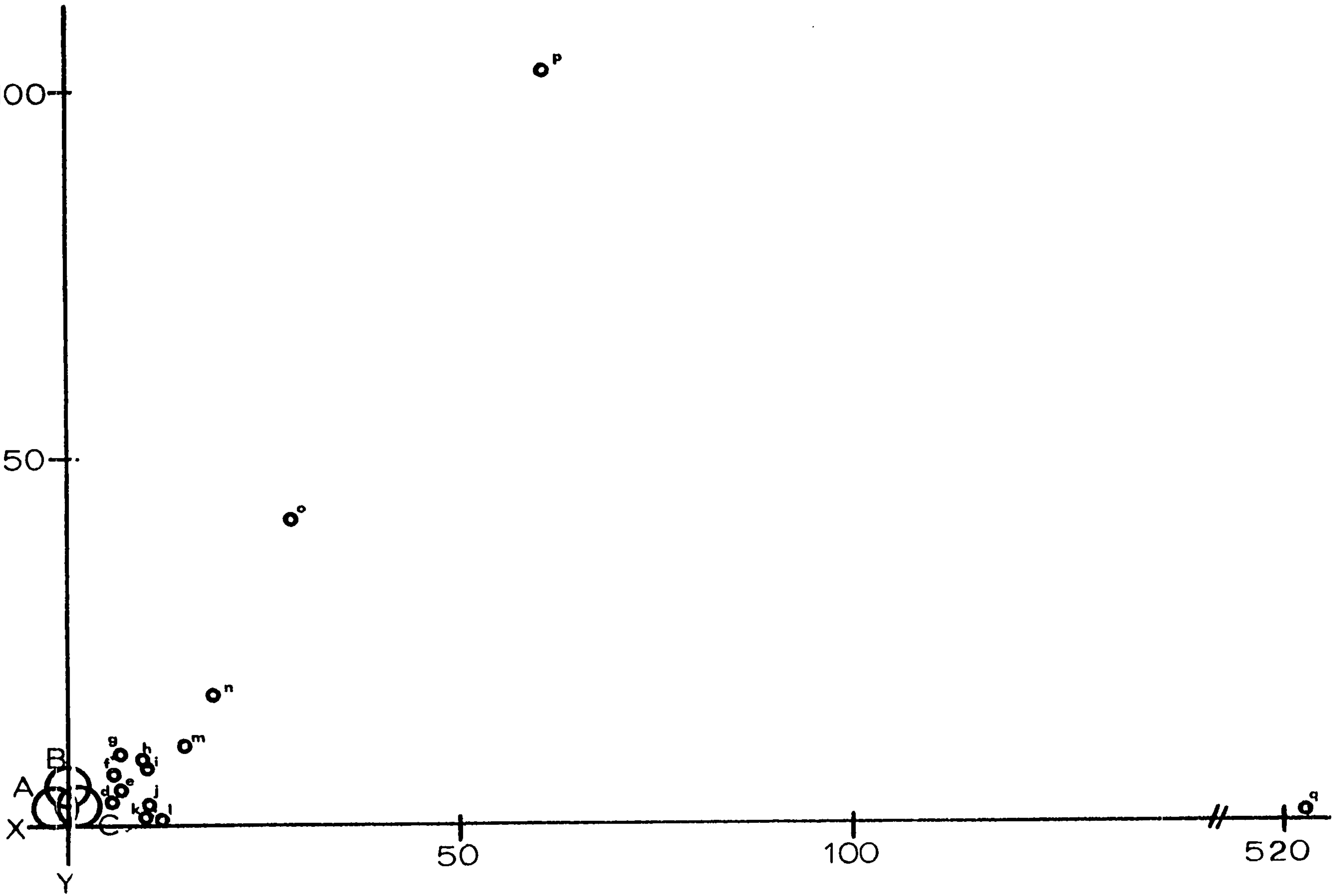
Figure 13. Two-dimensional ordination of upland prairie with percentage cover values of *Andropogon gerardi* for each site shown relating directly to the X-axis

can be seen both species show continuous distribution in relationship to the axes. Stands plotted near the origin and adjacent to the Y-axis were found to be from drier sites while those found away from the origin were found on wetter, more moist sites. These facts tend to support the hypothesis that the vegetation of upland prairie is basically a continuum as earlier described by Curtis (1955) and Dix and Butler (1960). Kennedy (1969), in studying an upland prairie in Guthrie County, Iowa, also concluded that prairie vegetation there is best described through the use of the continuum-index concept.

Attempts at environmental factor correlation with the ordination axes were not made since only general information on environmental gradients was available. It seems, however, that these axes represent environmental gradients and that the ordering of stands or species along these axes is accomplished through the response of the different stands or species to certain factors such as moisture, carbonates, or other soil characteristics.

The species ordination is shown in Figure 14. Spartina pectinata and Ceanothus americanus are the most different entities on the X-axis and Andropogon gerardi is the most distinct entity on the Y-axis. Other species having distinct distribution patterns are Physalis virginiana, Silphium laciniatum, Oxalis stricta, Amorpha canescens, Solidago missouriensis, Desmodium canadense, Helianthus grosseserratus, Aster ericoides, Vicia americana, Pycnanthemum virginianum, Ratibida columnifera, Aster laevis, and Helianthus laetiflorus. All other species either showed no definite distribution patterns or were too rare to establish a meaningful order. The circles A, B, and C in Figure 14

Figure 14. Two-dimensional ordination of species found in upland prairie study sites, factors responsible for patterns unknown. A, B, and C = clusters of species not showing distinct distribution patterns, d = *Helianthus laetiflorus*, e = *Aster laevis*, f = *Ratibida columnifera*, g = *Pycnanthemum virginianum*, h = *Aster ericoides*, i = *Vicia americana*, j = *Helianthus grosseserratus*, k = *Desmodium canadense*, l = *Amorpha canescens*, m = *Oxalis stricta*, n = *Silphium laciniatum*, o = *Physalis virginiana*, p = *Andropogon gerardi*, q = *Spartina pectinata*



100
50
X
Y
A
B
C
a b c d e f g h i j k l m n o p q
50
100
520

represent the points where 76 of the 92 species fell. This ordering of species has not delineated associated groups but has pointed out those species which exhibit peculiar distribution patterns or which show a definite response to one or several environmental stimuli. Sanders (1969) found that the R-analysis of Orloci (1966) did give him some fairly distinct groups of associated species as well as groups of species which could not be considered associated. Collins (1968) used the technique to identify taxa which were distinct and different and used them as indicator species in his interpretation of the ecological relationships of fossil diatom populations. It is evident from Figure 14 that the method has not provided information on groups of associated species but rather has indicated taxa which are distinct and therefore may have some usefulness as indicator species.

Attempts to discover groups of positively associated species within the upland regions of Kalsow Prairie were made using Cole's Index (1949). Those species showing positive association with other taxa are shown in Table 2. A total of 298 significant associations were found. Some species, such as Achillea lanulosa, Agropyron smithii, Amorpha canescens, Andropogon gerardi, Asclepias tuberosa, Carex gravida, Comandra umbellata, Helenium autumnale, Lespedeza capitata, Phleum pratense, and Solidago gymnospermoides exhibit positive association with only a limited number of species. Other species, however, show positive association with a large number of species. Some of these species are Aster ericoides, Desmodium canadense, Fragaria virginiana, Galium obtusum, Helianthus grosseserratus, Poa pratensis, Solidago canadensis, Solidago rigida, Sporobolus heterolepis, and Zizia aurea. Many species showed no

Table 2. Cole's Index values expressing positive interspecific association on upland prairie

Species	Species	X^{2a}	C_7^b	σ_7^c
Achillea lanulosa	Andropogon gerardi	18.77	.73	.17
	Aster ericoides	6.84	.22	.08
	Poa pratensis	5.03	.27	.11
	Solidago rigida	13.41	.21	.05
	Sporobolus heterolepis	11.06	.51	.15
Agropyron repens	Carex gravida	4.91	.22	.09
	Convolvulus sepium	7.04	.44	.16
	Physalis heterophylla	5.31	.22	.09
Agropyron smithii	Andropogon gerardi	5.96	.73	.29
	Aster ericoides	8.97	.45	.15
	Galium obtusum	4.33	.34	.16
	Helianthus grosseserratus	5.43	.43	.18
	Muhlenbergia racemosa	24.25	.27	.05
	Petalostemum purpureum	8.26	.20	.06
	Pycnanthemum virginianum	5.65	.18	.07
	Solidago canadensis	13.22	.53	.14
	Solidago riddellii	25.22	.24	.04
Ambrosia artemisifolia	Asclepias syriaca	83.22	.43	.04
	Helianthus grosseserratus	5.12	.23	.10
	Senecio pauperculus	155.77	.77	.06
	Setaria lutescens	58.48	.28	.03
	Setaria viridis	165.69	.57	.04
	Stipa spartea	4.00	.24	.12
	Taraxacum officinale	172.49	.55	.04
Amorpha canescens	Andropogon gerardi	15.62	.51	.13
	Panicum leibergii	28.29	.24	.04
	Solidago rigida	19.00	.20	.04
	Sporobolus heterolepis	41.54	.77	.11
Andropogon gerardi	Aster ericoides	126.73	.18	.01
	Poa pratensis	176.68	.30	.02
	Solidago canadensis	85.47	.15	.01
	Sporobolus heterolepis	238.41	.46	.02
Andopogon scoparius	Comandra umbellata	10.40	.21	.06
	Lithospermum canescens	19.30	.35	.08
	Panicum leibergii	5.62	.41	.17
	Petalostemum purpureum	7.53	.18	.06
	Phlox pilosa	11.12	.19	.05

[a]Chi-square

[b]Cole's Index

[c]Standard deviation Cole's Index

Table 2. (Continued)

Species	Species	X^2	C_7	σ_7
	Solidago rigida	6.01	.25	.10
	Sporobolus heterolepis	8.23	.77	.26
	Zizia aurea	5.23	.31	.13
Anemone canadensis	Artemisia ludoviciana	5.53	.19	.08
	Petalostemum candidum	6.16	.19	.07
	Poa pratensis	5.57	.80	.33
	Solidago missouriensis	25.23	.16	.03
Apocynum sibiricum	Aster simplex	14.68	.26	.06
	Calamagrostis canadensis	102.95	.70	.06
	Carex aquatilis	44.71	.35	.05
	Carex retrorsa	70.51	.55	.06
	Carex lasiocarpa	66.57	.39	.04
	Fragaria virginiana	3.83	.38	.19
	Heliopsis helianthoides	4.39	.27	.12
	Polygonum coccimeum	15.26	.18	.04
	Spartina pectinata	13.73	.18	.05
Artemisia ludoviciana	Aster ericoides	4.53	.42	.19
	Convolvulus sepium	51.32	.22	.03
	Helianthus laetiflorus	14.98	.28	.07
	Poa pratensis	15.37	.78	.19
Asclepias sullivantii	Elymus canadensis	5.94	.67	.27
Asclepias syriaca	Aster simplex	4.71	.38	.17
	Cirsium altissimum	5.77	.21	.08
	Desmodium canadense	9.84	.66	.21
	Equisetum kansanum	6.87	.21	.08
	Lithospermum canescens	8.15	.31	.10
	Rosa suffulta	9.99	.32	.10
	Senecio pauperculus	47.45	.43	.06
	Taraxacum officinale	25.23	.20	.04
	Thalictrum dasycarpum	12.88	.23	.06
Asclepias tuberosa	Aster ericoides	4.80	.27	.12
	Desmodium canadense	17.17	.42	.10
	Elymus canadensis	9.21	.29	.09
	Sporobolus heterolepis	17.15	.92	.22
	Zizia aurea	7.13	.30	.11
Asclepias verticillata	Lithospermum canescens	14.39	1.00	.26
Aster ericoides	Helianthus grosseserratus	17.76	.17	.03
	Poa pratensis	105.26	.46	.04
	Solidago canadensis	49.17	.22	.03
	Sporobolus heterolepis	70.97	.49	.05
	Zizia aurea	40.95	.19	.02
Aster laevis	Desmodium canadense	23.69	.30	.06
	Panicum leibergii	53.78	.36	.04
	Poa pratensis	27.26	.54	.10
	Sporobolus heterolepis	9.76	.41	.13

Table 2. (Continued)

Species	Species	X^2	C_7	σ_7
Aster simplex	Calamagrostis canadensis	42.41	.21	.03
	Carex gravida	34.75	.21	.03
	Carex retrorsa	30.80	.17	.03
	Fragaria virginiana	4.89	.19	.08
	Galium obtusum	54.31	.37	.05
	Helianthus grosseserratus	95.05	.56	.05
	Poa pratensis	7.48	.58	.21
	Senecio pauperculus	61.08	.19	.02
	Silphium laciniatum	32.99	.29	.05
	Spartina pectinata	34.20	.32	.05
Bouteloua curtipendula	Comandra umbellata	5.23	.29	.12
	Helianthus laetiflorus	7.18	.41	.15
	Phlox pilosa	7.47	.31	.11
Calamagrostis canadensis	Carex aquatilis	427.86	.50	.02
	Carex retrorsa	580.80	.74	.03
	Carex lasiocarpa	404.31	.45	.02
	Phalaris arundinacea	171.76	.20	.01
	Polygonum coccineum	64.45	.18	.02
	Spartina pectinata	154.17	.30	.02
Carex atherodes	Carex retrorsa	18.21	.27	.06
	Polygonum coccineum	370.61	.87	.04
	Scirpus fluviatilis	145.67	.34	.02
Carex aquatilis	Carex retrorsa	469.33	.88	.04
	Carex lasiocarpa	406.70	.59	.02
	Phalaris arundinacea	57.45	.16	.01
	Polygonum coccineum	33.93	.17	.02
	Spartina pectinata	66.04	.26	.03
Carex gravida	Desmodium canadense	17.26	.49	.11
	Fragaria virginiana	30.76	.64	.11
	Galium obtusum	21.59	.56	.11
	Helianthus grosseserratus	36.90	.71	.11
	Liatris pycnostrachya	8.21	.22	.07
	Muhlenbergia racemosa	4.90	.23	.10
	Petalostemum purpureum	9.82	.23	.07
	Silphium laciniatum	19.94	.30	.06
	Solidago canadensis	6.94	.57	.21
Carex lasiocarpa	Lathyrus palustris	110.24	1.00	.09
	Lysimachia hybrida	147.33	1.00	.08
	Phalaris arundinacea	92.24	.21	.02
	Polygonum coccineum	27.12	.17	.03
	Spartina pectinata	72.67	.30	.03
Carex retrorsa	Carex lasiocarpa	465.71	.50	.02
	Phlaris arundinacea	158.23	.20	.01
	Polygonum coccineum	79.04	.20	.02
	Spartina pectinata	117.52	.27	.02

Table 2. (Continued)

Species	Species	X^2	C_7	σ_7
Cirsium altissimum	Fragaria virginiana	8.78	.21	.07
	Galium obtusum	7.65	.29	.10
	Helianthus grosseserratus	8.53	.34	.11
	Petalostemum candidum	8.80	.15	.05
	Physalis virginiana	24.36	.28	.05
	Solidago canadensis	5.09	.21	.09
Comandra umbellata	Desmodium canadense	47.92	.50	.07
	Elymus canadensis	11.91	.23	.06
	Fragaria virginiana	15.97	.26	.06
	Panicum leibergii	16.18	.24	.05
	Petalostemum purpureum	19.78	.18	.03
	Poa pratensis	10.28	.39	.12
	Ratibida columnifera	26.47	.26	.05
	Solidago rigida	15.47	.23	.05
	Sporobolus heterolepis	15.25	.62	.15
	Zizia aurea	28.32	.43	.08
	Solidago nemoralis	32.92	.17	.02
Convolvulus sepium	Poa pratensis	5.30	.66	.28
Desmodium canadense	Elymus canadensis	80.81	.27	.02
	Fragaria virginiana	75.91	.40	.04
	Galium obtusum	81.55	.43	.04
	Helianthus grosseserratus	26.91	.24	.04
	Muhlenbergia racemosa	31.07	.23	.04
	Poa pratensis	38.84	.34	.05
	Solidago rigida	20.28	.21	.04
	Sporobolus heterolepis	99.46	.70	.06
	Zizia aurea	66.09	.29	.03
Elymus canadensis	Fragaria virginiana	72.47	.27	.03
	Galium obtusum	21.27	.26	.05
	Poa pratensis	44.15	.39	.05
	Sporobolus heterolepis	42.70	.49	.07
Equisetum kansanum	Heliopsis helianthoides	7.25	.19	.07
	Lithospermum canescens	20.66	.20	.04
	Petalostemum candidum	11.42	.21	.06
	Phlox pilosa	6.58	.19	.07
	Sporobolus heterolepis	20.81	.83	.18
	Zizia aurea	11.12	.31	.09
Eryngium yuccifolium	Panicum leibergii	7.80	.31	.11
	Rosa suffulta	10.29	.22	.06
	Solidago rigida	4.57	.24	.11
	Sporobolus heterolepis	7.90	.85	.30
Fragaria virginiana	Galium obtusum	69.59	.39	.04
	Helianthus grosseserratus	40.39	.31	.04
	Muhlenbergia racemosa	37.67	.26	.04
	Poa pratensis	29.55	.33	.05

Table 2. (Continued)

Species	Species	X^2	C_7	σ_7
	Solidago canadensis	13.28	.33	.08
	Sporobolus heterolepis	39.10	.48	.07
	Zizia aurea	4.89	.18	.08
Galium obtusum	Helianthus grosseserratus	91.71	.35	.03
	Muhlenbergia racemosa	25.27	.21	.04
	Silphium laciniatum	41.48	.17	.02
	Solidago canadensis	13.09	.31	.08
	Zizia aurea	5.17	.18	.07
Gentiana andrewsii	Heliopsis helianthoides	12.46	.45	.12
	Liatris pycnostachya	4.04	.26	.13
	Lithospermum canescens	4.52	.40	.18
	Zizia aurea	4.34	.71	.34
Helenium autumnale	Helianthus grosseserratus	15.18	.88	.22
	Lythrum alatum	48.25	.19	.02
	Muhlenbergia racemosa	10.43	.22	.06
	Poa pratensis	11.28	.86	.25
	Pycnanthemum virginianum	7.30	.25	.09
	Senecio pauperculus	40.42	.62	.09
	Solidago canadensis	5.32	.41	.17
Helianthus grosseserratus	Solidago canadensis	73.49	.21	.02
Helianthus laetiflorus	Panicum leibergii	42.24	.37	.05
	Phlox pilosa	25.63	.18	.03
	Sporobolus heterolepis	5.53	.36	.15
Helianthus maximiliani	Scutellaria leonardii	11.06	.19	.05
	Taraxacum officinale	11.06	.19	.05
Heliopsis helianthoides	Poa pratensis	6.77	.52	.19
	Pycnanthemum virginianum	20.89	.32	.07
	Ratibida columnifera	6.37	.21	.08
	Solidago canadensis	8.97	.41	.13
Lactuca scariola	Pedicularis canadensis	12.13	.19	.05
	Rosa suffulta	7.31	.35	.12
Lathyrus palustris	Lysimachia hybrida	35.58	.24	.04
	Senecio pauperculus	3.94	.21	.10
	Silphium laciniatum	10.63	.46	.14
	Spartina pectinata	14.78	.39	.10
	Viola sp.	6.30	.23	.08
Lespedeza capitata	Lithospermum canescens	12.60	.45	.12
	Panicum leibergii	3.80	.38	.19
	Rosa suffulta	5.52	.28	.11
	Silphium laciniatum	5.93	.28	.11
Liatris aspera	Physalis virginiana	21.69	.40	.08
Liatris pycnostachya	Poa pratensis	6.21	.24	.09
	Silphium laciniatum	17.79	.19	.04
	Solidago canadensis	17.40	.28	.06
	Sporobolus heterolepis	39.56	.78	.12

Table 2. (Continued)

Species	Species	X^2	C_7	σ_7
	Zizia aurea	26.25	.32	.06
Lithospermum canescens	Panicum leibergii	26.20	.25	.04
	Sporobolus heterolepis	37.09	.81	.13
	Zizia aurea	23.59	.33	.06
Lycopus americanus	Lythrum alatum	52.06	.21	.02
	Senecio pauperculus	18.03	.43	.10
	Spartina pectinata	19.71	.43	.09
Lysimachia hybrida	Muhlenbergia racemosa	5.77	.60	.25
	Polygonum coccineum	53.59	1.00	.13
	Scirpus fluviatilis	95.59	.83	.08
	Spartina pectinata	13.03	.64	.17
	Viola sp.	9.00	.31	.10
Lysimachia quadriflora	Muhlenbergia racemosa	8.08	.22	.07
	Pedicularis canadensis	54.24	.50	.06
	Petalostemum purpureum	4.08	.20	.09
	Poa pratensis	4.41	.63	.30
	Senecio pauperculus	17.76	.48	.11
Lythrum alatum	Senecio pauperculus	5.70	.27	.11
	Spartina pectinata	6.37	.28	.11
Mentha arvensis	Phalaris arundinacea	6.67	.21	.08
	Polygonum coccineum	6.64	.30	.11
Muhlenbergia racemosa	Zizia aurea	7.48	.25	.09
Panicum capillare	Pycnanthemum virginianum	20.53	.20	.04
	Senecio pauperculus	27.20	.24	.04
	Silphium laciniatum	12.59	.20	.05
	Solidago canadensis	6.31	.21	.08
	Zizia aurea	11.91	.28	.08
Panicum leibergii	Poa pratensis	12.96	.24	.06
	Sporobolus heterolepis	56.41	.65	.08
Panicum virgatum	Poa pratensis	12.96	.24	.06
	Sporobolus heterolepis	56.41	.65	.08
Pedicularis canadensis	Pycnanthemum virginianum	37.72	.49	.07
	Senecio pauperculus	5.78	.22	.09
	Solidago rigida	5.11	.29	.12
	Zizia aurea	20.45	.79	.17
Petalostemum candidum	Ratibida columnifera	4.02	.21	.10
	Rosa suffulta	4.27	.23	.10
Petalostemum purpureum	Poa pratensis	11.86	.34	.09
	Solidago canadensis	16.33	.28	.06
	Solidago rigida	20.61	.22	.04
	Sporobolus heterolepis	30.35	.71	.12
	Zizia aurea	24.91	.33	.06
Phalaris arundinacea	Polygonum coccineum	78.87	.41	.04
	Spartina pectinata	25.65	.26	.05
Phleum pratense	Phlox pilosa	5.50	.34	.14

Table 2. (Continued)

Species	Species	X^2	C_7	σ_7
	Ratibida columnifera	7.39	.73	.26
Phlox pilosa	Ratibida columnifera	8.27	.25	.08
	Sporobolus heterolepis	7.60	.64	.23
Physalis virginiana	Rosa suffulta	5.93	.21	.08
	Solidago rigida	4.93	.32	.14
Poa pratensis	Sporobolus heterolepis	54.66	.31	.04
Polygonum coccineum	Scirpus fluviatilis	350.08	.37	.01
Potentilla arguta	Solidago missouriensis	5.48	.30	.12
Psoralea argophylla	Stipa spartea	6.50	.18	.07
Pycnanthemum virginianum	Senecio pauperculus	30.62	.19	.03
	Silphium laciniatum	25.56	.21	.04
	Solidago canadensis	25.73	.31	.06
	Sporobolus heterolepis	11.25	.39	.11
	Zizia aurea	7.48	.69	.25
Ratibida columnifera	Sporobolus heterolepis	22.69	.48	.10
	Zizia aurea	19.66	.23	.05
Rosa suffulta	Sporobolus heterolepis	13.85	.54	.14
Rudbeckia hirta	Solidago rigida	7.17	.75	.28
Senecio pauperculus	Solidago canadensis	51.17	.42	.05
	Taraxacum officinale	100.89	.32	.03
Setaria lutescens	Setaria viridis	525.50	.89	.03
Silphium laciniatum	Solidago canadensis	4.85	.34	.15
	Spartina pectinata	15.95	.21	.05
	Sporobolus heterolepis	32.83	.52	.09
	Viola sp.	38.07	.19	.03
	Zizia aurea	43.57	.31	.04
Solidago canadensis	Sporobolus heterolepis	21.62	.28	.06
Solidago gymnospermoides	Solidago rigida	3.87	.22	.11
	Sporobolus heterolepis	8.50	.86	.29
	Zizia aurea	9.77	.47	.15
Solidago rigida	Sporobolus heterolepis	96.94	.84	.08
Sorghastrum nutans	Sporobolus heterolepis	17.68	.81	.19
	Zizia aurea	5.46	.23	.09
Sporobolus heterolepis	Zizia aurea	130.17	.19	.01
Viola sp.	Zizia aurea	8.97	.35	.11
Panicum implicatum	Solidago nemoralis	8.63	.19	.06

significant association or expressed values of high negative association. Positive values of Cole's Index indicate that species occur together more often than would otherwise be expected due to chance (Hale, 1955;

Hurlbert, 1969). Therefore, through the use of such an index one can deduce groups of species which consistently show positive values of association with one another. Figures 15, 16 and 17 were constructed from values taken from Table 2 to illustrate the existence of such groups within the upland prairie. In all three cases one species was picked and the corresponding figure was then built up around this species.

Potholes and Drainage

Marean and Jones (1903) gave the following description of the landscape in central Iowa:

> Low knolls are separated by saucerlike depressions in which impounded water often stands the year around. In many cases these low-lying areas have been reclaimed by artificial drainage, but in the main rainwater which falls upon the upland has to escape by seepage or evaporation. Little ponds and marshes are found in almost innumerable places scattered all over the country.

These saucerlike depressions have been estimated as covering more than 50 percent of that part of Iowa subjected to late Wisconsin glaciation (Hewes, 1950). They were early recognized as supporting a distinct vegetation from that of the adjacent upland prairie (Yapp, 1909; Sherff, 1912; Shimek, 1915; and Berry, 1927). The grasses of these areas were described as being "ten to twelve feet tall all season" (Dondore, 1926). These and later descriptions indicate that the potholes and drainage ways were often characterized by very discrete zones of vegetation (Sherff, 1912; Shimek, 1915; Schaffner, 1926, Hayden, 1943; and Trauger, 1967). Mainly three to four zones were recognized yet in all cases little information was given on the relationships of these zones to one another either floristically or spatially. Some authors

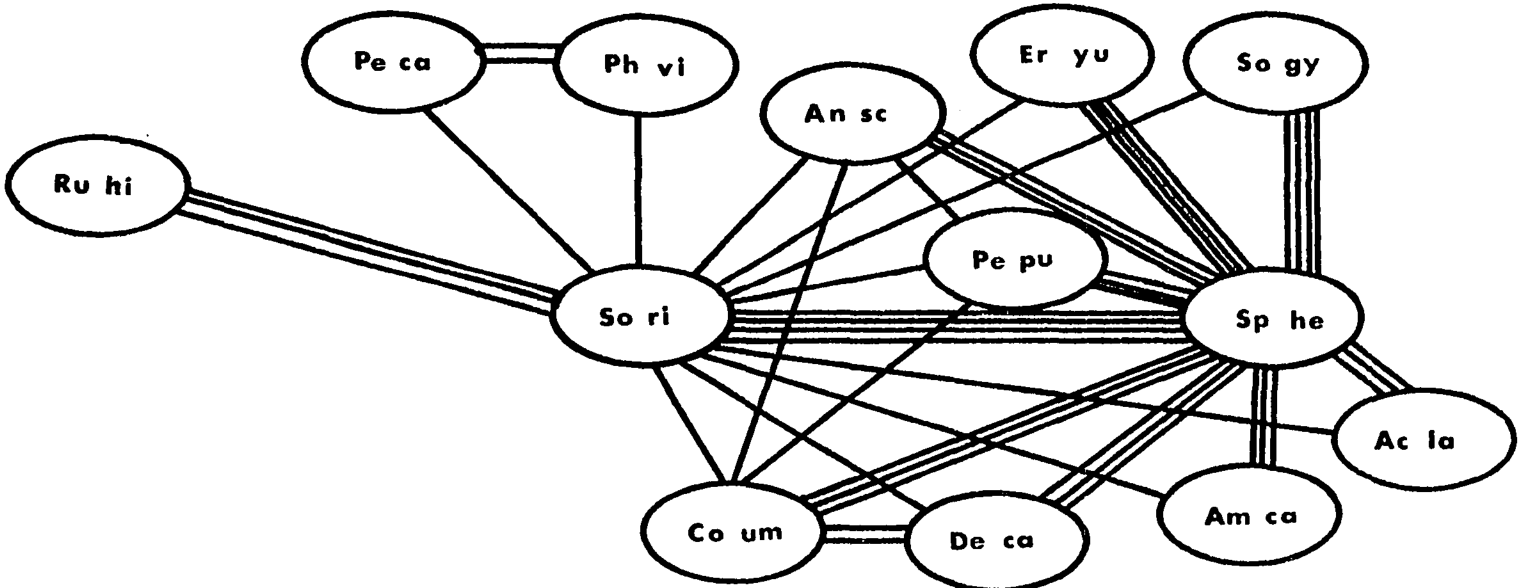
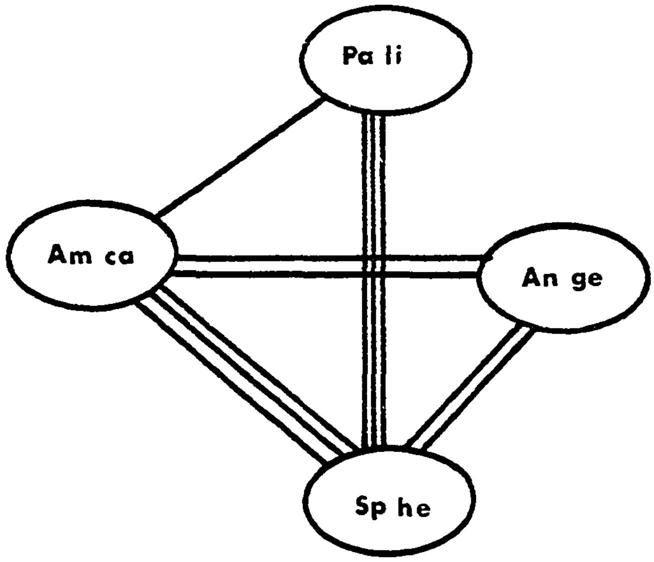
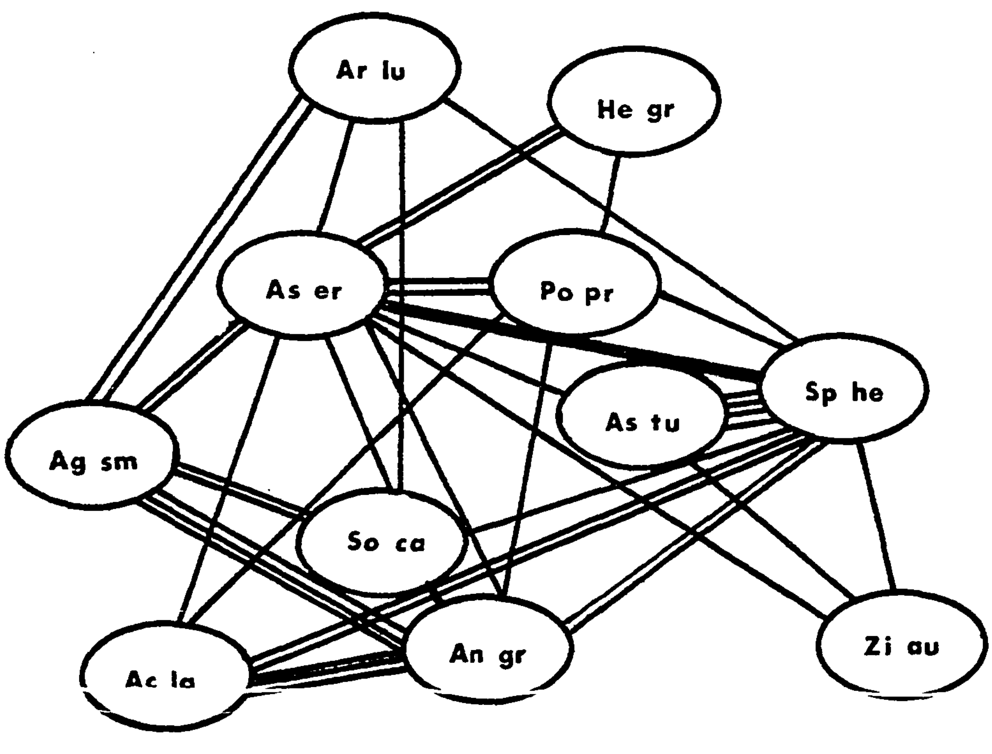


Figure 15. *Solidago rigida* and associated species of upland prairie as determined by Cole's (1949) Index, the more lines between species, the greater the association. So ri = *Solidago rigida*, Ru hi = *Rudbeckia hirta*, Pe ca = *Pedicularis canadensis*, Ph vi = *Physalis virginiana*, An sc = *Andropogon scoparius*, Er yu = *Eryngium yuccifolium*, Pe pu = *Petalostemum purpureum*, So gy = *Solidago gymnospermoides*, Sp he = *Sporobolus heterolepis*, Ac la = *Achillea lanulosa*, Am ca = *Amorpha canescens*, De ca = *Desmodium canadense*, Co um = *Comandra umbellata*

Figure 16. *Amorpha canescens* and associated species of upland prairie as determined by Cole's (1949) Index, the more lines between the species, the greater the association; Am ca = *Amorpha canescens*, Pa li = *Panicum leibergii*, An ge = *Andropogon gerardi*, Sp he = *Sporobolus heterolepis*

Figure 17. *Aster ericoides* and associated species of upland prairie as determined by Cole's (1949) Index, the more lines between the species, the greater the association; As er = *Aster ericoides*, Ar lu = *Artemisia ludoviciana*, He gr = *Helianthus grosseserratus*, Po pr = *Poa pratensis*, As tu = *Asclepias tuberosa*, Sp he = *Sporobolus heterolepis*, Zi au = *Zizia aurea*, An gr = *Andropogon gerardi*, So ca = *Solidago canadensis*, Ac la = *Achillea lanulosa*, Ag sm = *Agropyron smithii*


Pa li
Am ca
An ge
Sp he


Ar lu
He gr
As er
Po pr
Sp he
As tu
Ag sm
So ca
Zi au
Ac la
An gr

(Sherff, 1912; Schaffner, 1926; and Hayden, 1943), however, indicated that succession was taking place in these areas and proposed the following successional scheme:

I	Pond center
II	Sedge zone
III	Slough grass zone
IV	Dry margin of slough grass
V	_Andropogon gerardi_
VI	Upland prairie

There is within the boundaries of Kalsow Prairie a complex of potholes and corresponding drainage ways (Figures 1 and 2). These areas are found scattered throughout the 160 acres at different elevations. They also vary in depth and degree of fill. These characteristics make them extremely useful in the studies of plant succession on such areas as well as for studies involving zonation. All 14 potholes found within the prairie exhibited typical zonation (Figures 18 and 19). Figure 19 represents the zonation patterns of a pothole and drainage complex found within the 20 acres used for intensive study (Figure 1).

The mapping was done according to a plain table method described by Phillips (1959). Boundaries were located by placing stakes along the edges of the zones as indicated by the dominant plant within each zone. A total of 36 zones was sampled as found within the 14 potholes marked on Figure 1. Each zone was sub-sampled 20 times for cover and then averaged to obtain a characteristic vegetation for every zone. The 36 zones were then ordinated into three-dimensional space using Orloci's (1966) method (Figures 20 and 21).

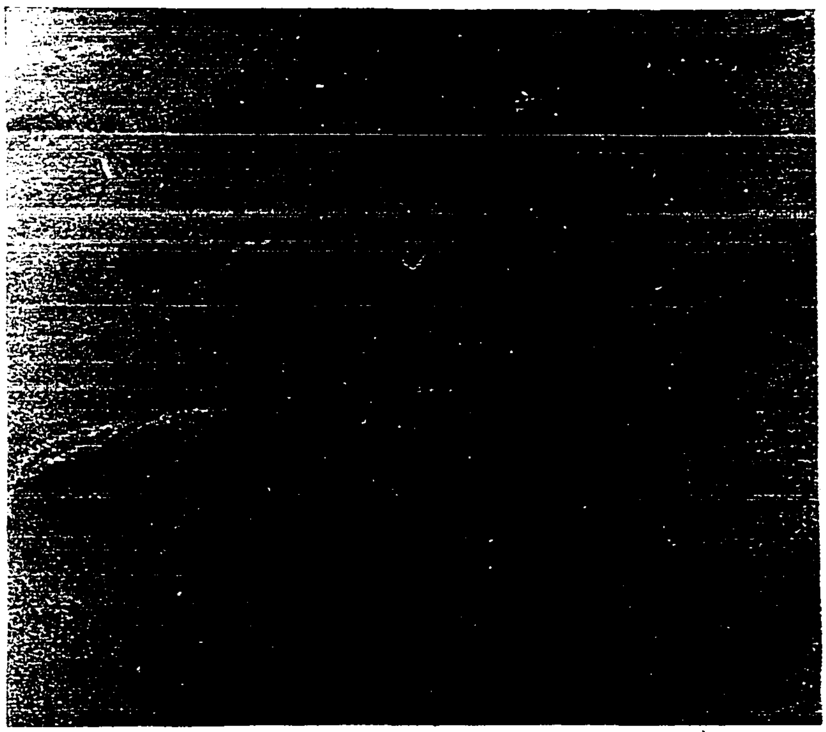


Figure 18. Aerial photograph of pothole and drainage zonation in eastern half of 20-acre intensive study area

Figure 19. Map of pothole and drainage zonation of the 20-acre intensive study area, numbers corresponding to groups of associated species from Table 3

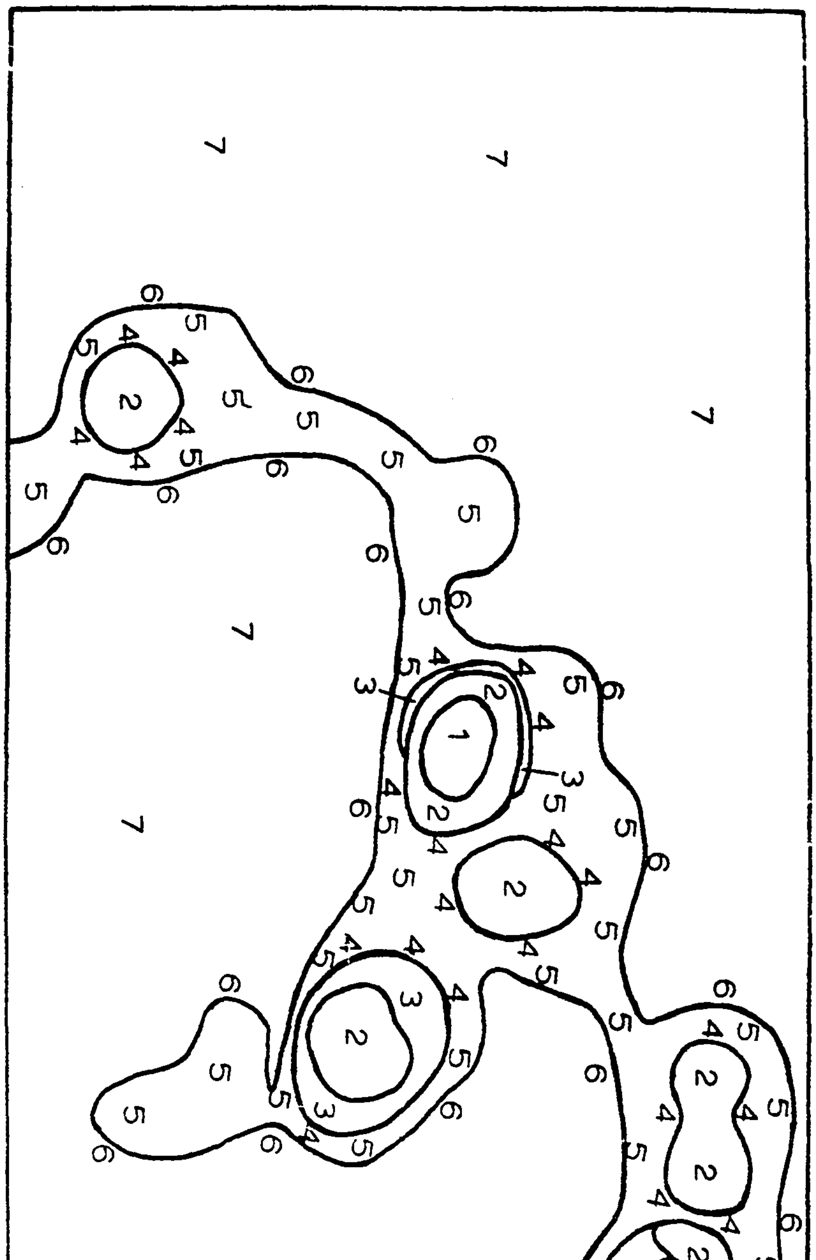
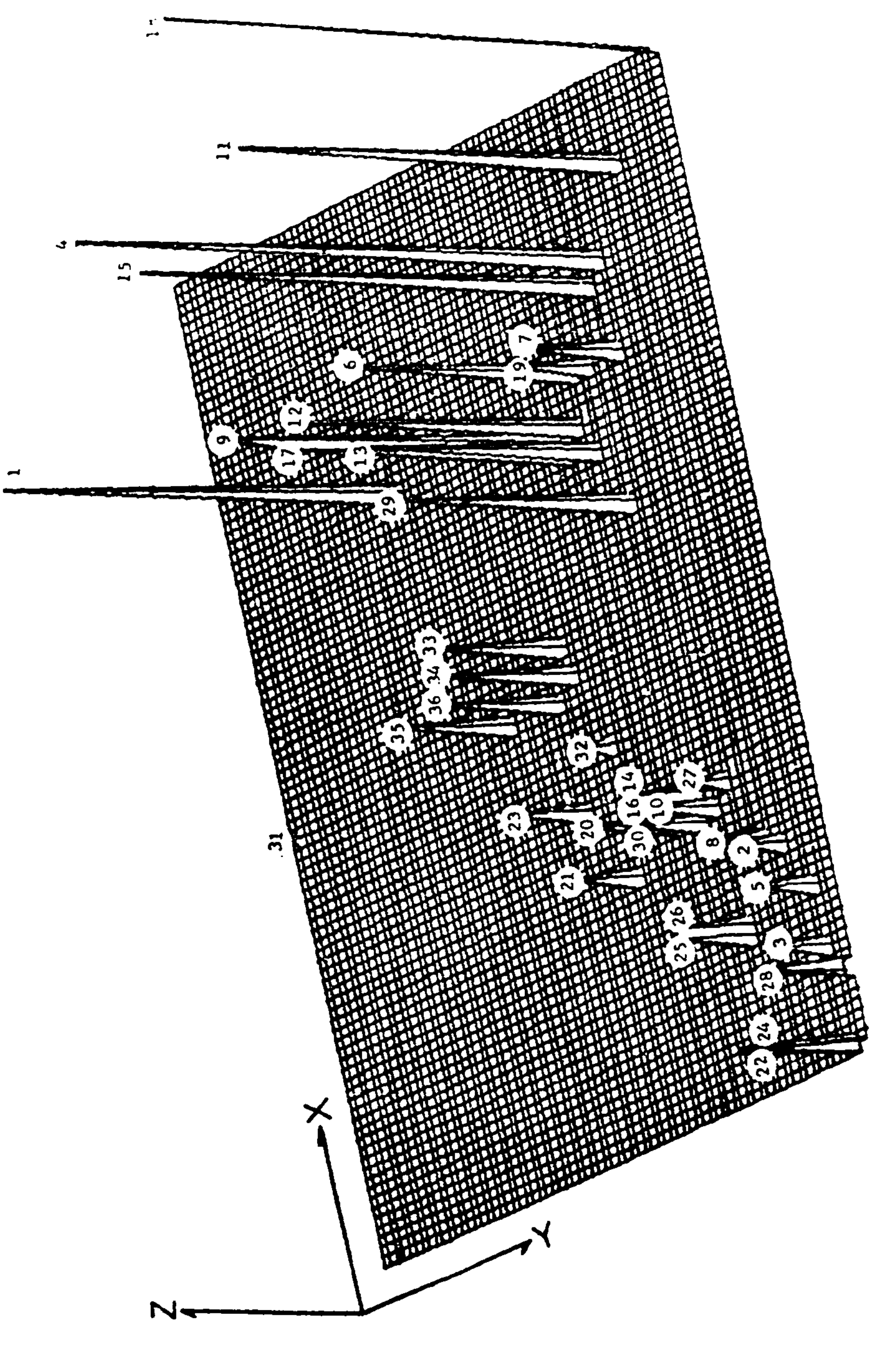

WEST
NORTH

Figure 20. Three-dimensional ordination of pothole and drainage zones found in Kalsow Prairie, with numbers corresponding to pothole and drainage numbers from Figure 1 except 33-36 which are prairie edge areas


X
Y
Z
1
4
11
15
6
7
19
9
12
17
13
29
33
34
36
35
31
32
27
14
16
10
23
20
30
8
2
21
5
26
25
3
28
24
22

Following the ordination the individual zones were then grouped into six units as shown in Figure 21. This procedure is contrary to that followed in the analysis of the upland prairie data, but it was felt that such an approach was justified because each zone represents a rather discrete vegetational unit. After grouping, the data belonging to each new unit were averaged and placed in Table 3. These six units correspond in reality to the six zones mapped in Figure 19. Table 3 is so designed that column 1 through column 6 represent values from the center of each pothole to the transition to upland prairie, respectively. The positioning of each species within Table 3 was done by assigning those species with the highest values for Group 1 at the top and those species with the highest values for Group 6 at the bottom of the list. It was then possible to determine from the table the characteristic distributional patterns of many of the species as well as their positions of importance within each zone (i.e., Helianthus grosseserratus is restricted to Groups 5 and 6 and is the dominant species of Group 6).

The species of these different zones were also ordinated into three-dimensional space (Figure 22). Here again the ordination did not yield groups of associated taxa but rather picked out eight species exhibiting distinct and different distributional patterns and placed all others within the areas covered by the circles A, B, and C. When the results of Figure 22 are compared with those of Table 3 it can be seen that those species picked by this method as indicator species are those taxa which represent the dominants or sub-dominants of Groups 1 through 6.

A 1000-foot bisect of the area shown in Figures 6 and 19 was taken in an effort to correlate the distribution of the dominants of each zone with

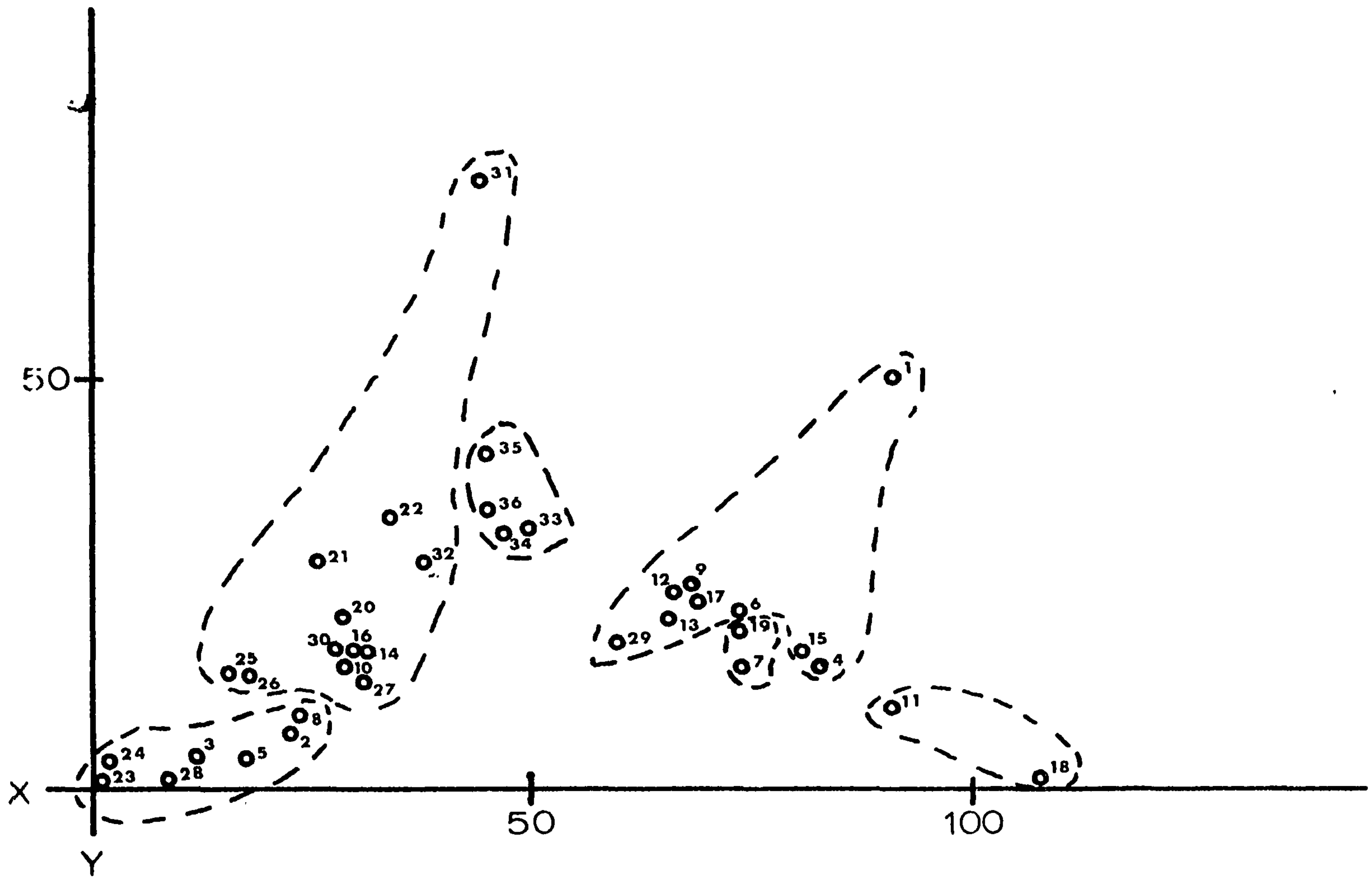


Figure 21. Two-dimensional ordination of pothole and drainage zones of Kalsow Prairie, grouped as shown in Table 3 with factors responsible for ordination unknown

Figure 22. Two-dimensional ordination of species found in pothole and drainage areas of Kalsow Prairie; A, B, and C = clusters of species not showing distinct distribution patterns, d = *Polygonum coccineum* (usually in center of pothole), e = *Scirpus fluviatilis*, f = *Carex atherodes*, g = *Lysimachia hybrida*, h = *Spartina pectinata*, i = *Carex aquatilis*, j = *Carex lasiocarpa*, k = *Calamagrostis canadensis* (usually in outer zone of pothole complex)

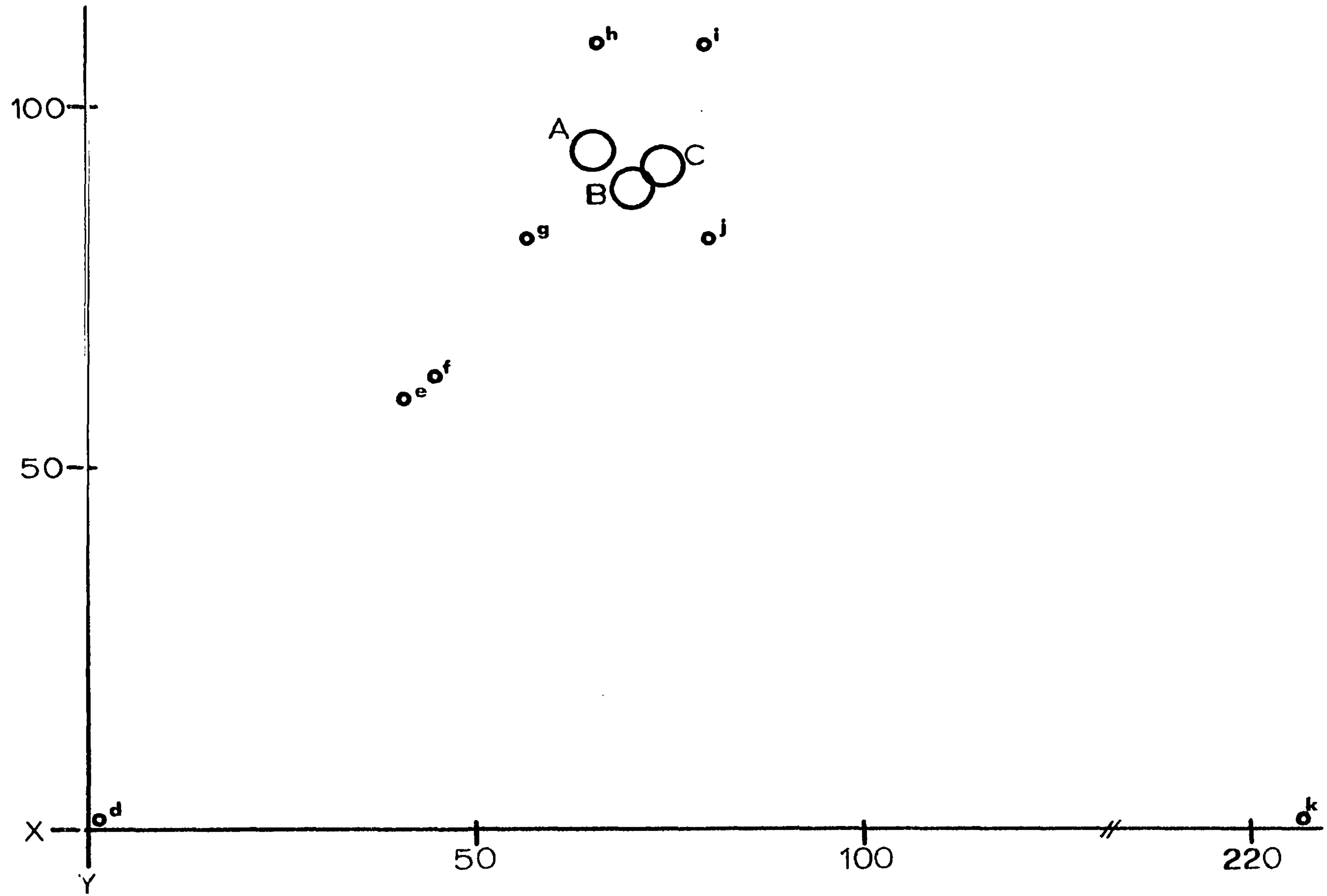

100
50
X
Y
50
100
220
A
B
C
d
e
f
g
h
i
j
k

Table 3. Average percentage cover values in the six groups according to Orloci ordination for the pothole and drainage communities

Species	1	2	3	4	5	6
Polygonum coccineum[a]	66.15	26.74	31.15	5.27	2.58	.57
Lysimachia hybrida[a]	19.50	.39	--	.55	.36	.07
Scirpus fluviatilis[a]	5.55	22.94	1.55	.11	--	--
Carex atherodes[a]	2.45	10.56	53.45	.06	.12	--
Spartina pectinata[a]	--	1.89	.80	17.54	12.53	2.20
Carex aquatilis[a]	--	1.44	.75	14.51	3.42	6.05
Carex retrorsa	--	.80	.20	3.27	2.10	.02
Phalaris arundinacea	.05	.39	--	2.64	2.21	--
Sagittaria latifolia	--	--	--	1.21	.01	--
Eleocharis sp.	--	.20	.05	.73	.29	--
Calamagrostis canadensis[a]	--	2.60	3.15	26.73	57.10	6.42
Apocynum sibiricum	--	.40	--	.98	2.08	.75
Lycopus americanus	--	.24	--	.18	1.36	1.07
Convolvulus sepium	--	--	--	.16	.14	.12
Teucrium canadense	--	.41	--	.10	.76	.60
Carex meadii	--	--	--	.01	.26	--
Iris virginica	--	--	--	.01	.14	--
Asclepias incarnata	--	--	--	.07	.01	--
Hordeum jubatum	--	--	--	.01	--	--
Rumex crispus	--	--	--	.01	--	--
Panicum capillare	--	--	--	--	--	.02
Cirsium altissimum	--	--	--	--	--	.02
Asclepias sullivantii	--	--	--	--	--	.05
Zizia aurea	--	--	--	.01	--	.07
Pycnanthemum virginianum	--	--	--	--	--	.10
Elymus canadensis	--	--	--	.01	--	.15
Thalictrum dasycarpum	--	--	--	--	--	.15
Helenium autumnale	--	--	--	.01	--	.20
Helianthus laetiflorus	--	--	--	--	--	.20
Anemone cylindrica	--	--	--	--	--	.20
Solidago rigida	--	--	--	--	--	.20
Gentiana andrewsii	--	--	--	.01	.02	.20
Agrostis hiemalis	--	--	--	--	--	.22
Heliopsis helianthoides	--	--	--	--	--	.22
Cicuta maculata	--	--	--	--	--	.22
Lythrum alatum	--	--	--	.01	.21	.22
Aster ericoides	--	--	--	--	--	.25
Panicum virgatum	--	--	--	--	.07	.25
Lathyrum palustris	--	--	--	.02	.06	.35
Silphium laciniatum	--	--	--	--	--	.37

[a]species picked by the three-dimensional ordination as indicator species

Table 3. (Continued)

Species	1	2	3	4	5	6
Eryngium yuccifolium	--	--	--	--	--	.40
Desmodium canadense	--	--	--	--	--	.40
Liatris pycnostachya	--	--	--	--	--	.55
Vernonia fasiculata	--	--	--	.24	.53	.55
Rosa suffulta	--	--	--	.32	.10	.72
Fragaria virginiana	--	--	--	--	.01	1.32
Senecio pauperculus	--	--	--	--	--	1.52
Solidago gymnospermoides	--	--	--	--	.17	1.70
Andropogon gerardi	--	--	--	--	--	2.20
Poa pratensis	--	--	--	.58	.60	2.35
Solidago canadensis	--	--	--	.01	.01	3.05
Sporobolus heterolepis	--	--	--	--	--	4.07
Aster simplex	.40	--	--	.86	2.01	5.22
Galium obtusum	--	--	--	.35	1.56	5.65
Carex lasiocarpa[a]	--	.55	1.15	5.55	7.43	10.15
Helianthus grosseserratus	--	--	--	.65	1.98	13.10

elevation and topography. This information has been summarized in Figure 23. The bisect data showed that changes in elevation of 6 to 12 inches very often produced changes in the distribution patterns of the zone dominants.

Attempts to pick groups of associated species through the application of Cole's Index are shown in Table 4 and in Figures 24 and 25. Figure 24a represents a clearly definable cluster and includes the dominant species of Groups 1 through 3 of Table 3. These species are Carex atherodes, Lysimachia hybrida, Polygonum coccineum, and Scirpus fluviatilis. Figures 24b and 25 show several definable clusters and include the taxa found in Groups 4 through 6 of Table 3. The cluster designated by A in Figure 25 contains entirely those species found in Groups 4 and 5 of Table 3. Those clusters identified by the letters B and C of this same

Figure 23. Correlation of dominant species of each zone from potholes and drainages with changes in elevation along bisect through 20-acre intensive study area; 1 = *Sporobolus heterolepis*, 2 = *Helianthus grosseserratus*, 3 = *Calamagrostis canadensis*, 4 = *Carex atherodes*, 5 = *Scirpus fluviatilis*, 6 = *Polygonum coccineum*

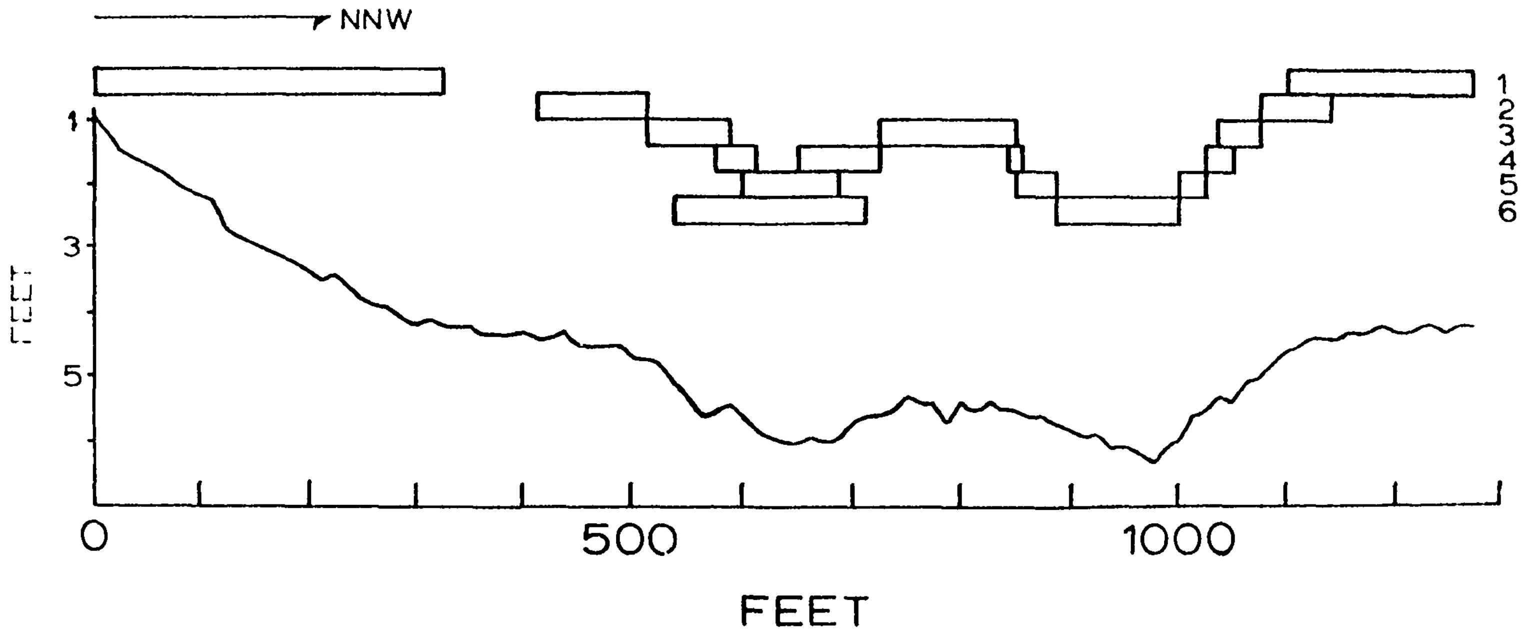

NNW
1
3
5
FEET
1
2
3
4
5
6
0
500
1000
FEET

Table 4. Cole's Index values expressing positive interspecific association in pothole and drainage communities

Species	Species	X^{2a}	$C_7{}^b$	$\sigma_7{}^c$
Andropogon gerardi	Eryngium yuccifolium	119.80	.30	.02
	Liatris pycnostachya	130.35	.38	.03
	Sporobolus heterolepis	65.90	.22	.02
Anemone cylindrica	Fragaria virginiana	89.71	.19	.02
	Panicum virgatum	84.61	.24	.02
	Thalictrum dasycarpum	91.73	.33	.03
Apocynum sibiricum	Calamagrostis canadensis	41.22	.68	.10
	Carex lasiocarpa	30.42	.57	.10
	Carex retrorsa	9.44	.18	.05
	Spartina pectinata	19.63	.37	.08
Aster simplex	Calamagrostis canadensis	36.47	.56	.09
	Carex lasiocarpa	31.79	.51	.09
	Galium obtusum	212.39	.51	.03
	Helianthus grosseserratus	231.49	.51	.03
	Poa pratensis	85.80	.18	.01
	Spartina pectinata	19.10	.31	.07
Calamagrostis canadensis	Carex aquatilis	49.30	.17	.02
	Carex lasiocarpa	338.21	.68	.03
	Carex retrorsa	81.33	.19	.02
	Spartina pectinata	200.44	.41	.02
Carex atherodes	Polygonum coccineum	153.47	.93	.07
	Scirpus fluviatilis	120.34	.47	.04
Carex meadii	Rosa suffulta	28.47	.38	.07
Carex aquatilis	Carex lasiocarpa	73.33	.49	.05
	Carex retrorsa	53.85	.24	.03
	Spartina pectinata	19.61	.20	.04
Carex lasiocarpa	Carex retrorsa	111.72	.70	.06
	Spartina pectinata	183.90	.40	.02
Carex retrorsa	Spartina pectinata	43.76	.35	.05
Convolvulus sepium	Galium obtusum	8.76	.39	.13
Desmodium canadense	Aster ericoides	54.86	.28	.03
	Liatris pycnostachya	87.08	.42	.04
	Ratibida columnifera	200.56	.28	.02
	Senecio pauperculus	189.69	.71	.05
Eleocharis sp.	Phalaris arundinacea	28.62	.25	.04
Elymus canadensis	Aster ericoides	65.57	.33	.04

[a]Chi-square

[b]Cole's Index

[c]Standard deviation Cole's Index

Table 4. (Continued)

Species	Species	X^2	C_7	σ_7
	Galium obtusum	4.34	.39	.18
	Helianthus grosseserratus	30.83	1.00	.18
	Lathyrus palustris	62.34	.49	.06
	Desmodium canadense	64.57	.33	.04
	Liatris pycnostachya	44.21	.32	.04
	Senecio pauperculus	33.25	.32	.05
	Thalictrum dasycarpum	91.73	.33	.03
Eryngium yuccifolium	Sporobolus heterolepis	54.86	.28	.03
Fragaria virginiana	Andropogon gerardi	37.61	.19	.03
	Galium obtusum	46.46	.70	.10
	Helianthus grosseserratus	104.86	1.00	.09
	Poa pratensis	19.29	.25	.05
	Senecio pauperculus	37.61	.19	.03
	Solidago canadensis	30.90	.27	.04
	Sporobolus heterolepis	75.87	.19	.02
Galium obtusum	Helianthus grosseserratus	242.41	.60	.03
	Poa pratensis	86.58	.20	.02
	Spartina pectinata	13.73	.29	.07
Helenium autumnale	Helianthus grosseserratus	5.54	.60	.25
Helianthus grosseserratus	Poa pratensis	131.97	.25	.02
	Solidago canadensis	112.89	.20	.01
Iris virginica	Poa pratensis	7.38	.29	.10
	Rosa suffulta	23.11	.32	.06
	Vernonia fasiculata	8.39	.29	.10
Lathyrus palustris	Poa pratensis	9.53	.20	.06
	Solidago gymnospermoides	62.18	.30	.03
	Thalictrum dasycarpum	75.89	.18	.02
Liatris pycnostachya	Senecio pauperculus	44.56	.29	.04
	Sporobolus heterolepis	248.50	.50	.03
Lysimachia hybrida	Polygonum coccineum	16.21	.61	.15
	Scirpus fluviatilis	16.11	.34	.08
Lythrum alatum	Vernonia fasiculata	5.46	.20	.08
Panicum virgatum	Poa pratensis	14.89	.29	.07
	Teucrium canadense	45.63	.39	.05
Poa pratensis	Solidago canadensis	92.29	.30	.03
Polygonum coccineum	Scirpus fluviatilis	223.30	.32	.02
Rosa suffulta	Andropogon gerardi	42.51	.21	.03
	Solidago canadensis	35.46	.30	.05
Solidago canadensis	Senecio pauperculus	160.63	.30	.02
Zizia aurea	Desmodium canadense	132.56	.66	.05

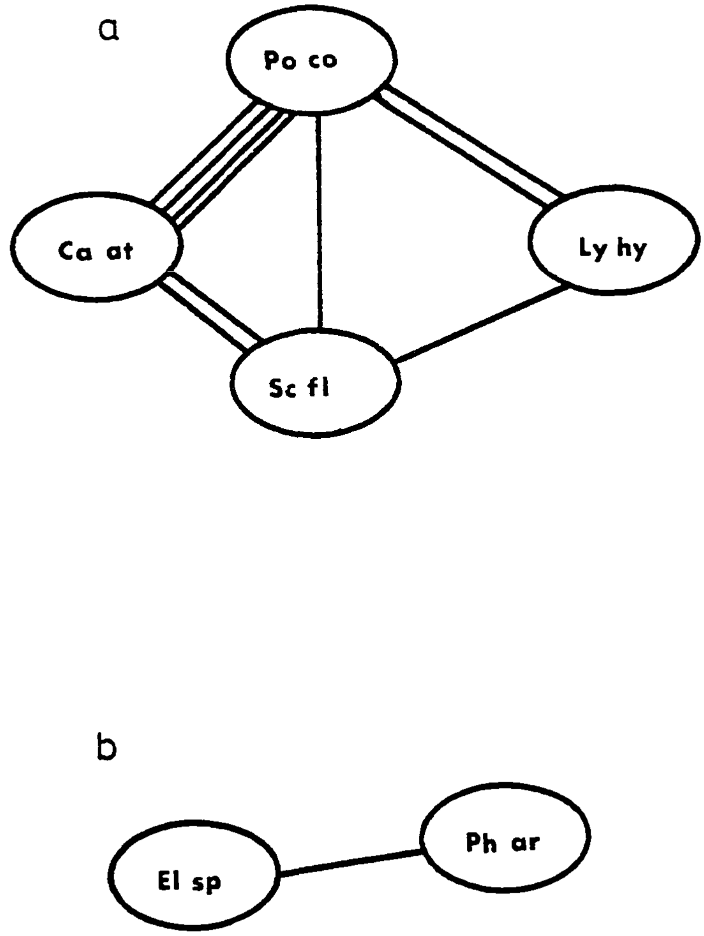


Figure 24. Associated species of potholes and drainage, Groups 1 and 2 (Table 3) as determined by Cole's (1949) Index; (a) Ca at = Carex atherodes, Po co = Polygonum coccineum, Ly hy = Lysimachia hybrida; (b) El sp = Eleocharis sp., Ph ar = Phalaris arundinacea

Figure 25. Associated species of potholes and drainage, Groups 3-6 (Table 3) as determined by Cole's (1949) Index, the more lines between species, the greater the association; groups A, B, and C are basic clusters; Ca aq = Carex aquatilis, Ca re = Carex retrorsa, Sp pe = Spartina pectinata, Ap si = Apocynum sibiricum, Ca ca = Calamagrostis canadensis, Ca la = Carex lasiocarpa, As si = Aster simplex, Ga ob = Galium obtusum, He gr = Helianthus grosseserratus, Fr vi = Fragaria virginiana, So ca = Solidago canadensis, Po pr = Poa pratensis, Ca me = Carex meadii, Ro su = Rosa suffulta, An ge = Andropogon gerardi, La pa = Lathyrus palustris, So gy = Solidago gymnospermoides, Th da = Thalictrum dasycarpum, Ir vr = Iris virginica, Ve fa = Vernonia fasiculata, Ly al = Lythrum alatum, Pa vi = Panicum virgatum, Te ca = Teucrium canadense, An cy = Anemone cylindrica, El ca = Elymus canadensis, As er = Aster ericoides, Li py = Liatris pycnostachya, De ca = Desmodium canadense, Zi au = Zizia aurea, Ra co = Ratibida columnifera, Se pa = Senecio pauperculus, Er yu = Eryngium yuccifolium, Sp he = Sporobolus heterolepis

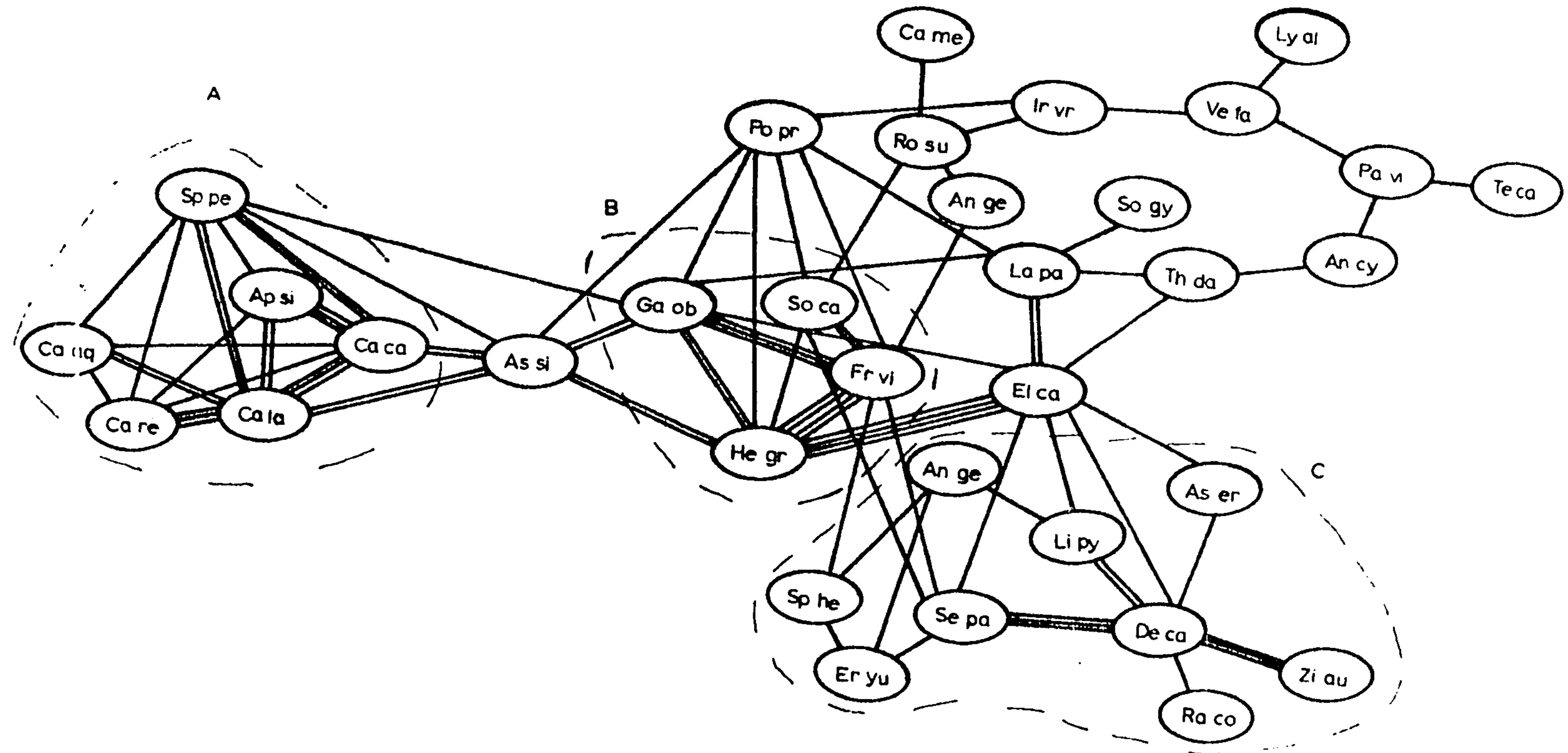

A
B
C
Sp pe
Ap si
Ca aq
Ca ca
Ca re
Ca la
As si
Po pr
Ca me
Ro su
Ir vr
Ve fa
Ly al
Pa vi
Te ca
An ge
So gy
La pa
Th da
An cy
Ga ob
So ca
Fr vi
El ca
He gr
An ge
As er
Li py
Sp he
Se pa
De ca
Zi au
Er yu
Ra co

figure contain only plants found in Group 6 of Table 3 and correspond in reality to the prairie edge. Cluster A and Clusters B and C are bridged by a single species (Aster simplex) which is found growing mainly along the border between Groups 5 and 6 of Table 3.

The vegetation of the potholes and drainage ways of Kalsow Prairie can best be described as a series of five zones each of which exhibit different spatial and floristic properties. This characteristic zonation can be expected to repeat itself from pothole to pothole when controlling environmental factors are found to be similar. The zones themselves are best described by starting at the center of the potholes and moving toward the prairie edge. Zone 1 (Group 1 of Table 3, etc.) is found at the center of the deepest potholes and is dominated chiefly by Polygonum coccineum and Lysimachia hybrida. Zone 2 is found to completely encircle zone 1 and is characterized by the dominants Polygonum coccineum and Scirpus fluviatilis. Zone 3 is found as a very narrow band which encircles zone 2 or occurs as rather wide patches in areas of equivalent elevation. It is characterized chiefly by Carex atherodes. Zones 4 and 5 are best distinguished in potholes and drainage ways which are somewhat shallow. Zone 4 most often occupies the center of these shallow depressions while being surrounded by zone 5. Zone 4 is characterized by the species Spartina pectinata, Carex aquatilis, and Calamagrostis canadensis. Zone 5 is distinguished by the dominant species Calamagrostis canadensis and by a few other participating species (i.e., Apocynum sibiricum, Lycopus americanus, Teucrium canadense, Carex meadii, and Iris virginica). Zone 6 of Table 3 is, of course, the prairie edge and is characterized mainly by the presence of Helianthus grosseserratus.

It seems that these zones represent in some measure a successional sequence which is controlled basically by the degree of fill of the potholes and consequently by related moisture regimes. The successional scheme parallels in many respects a scheme proposed by earlier authors (Sherff, 1912; Schaffner, 1926; and Hayden, 1943). The following successional sequence is thus proposed beginning at the pothole centers:

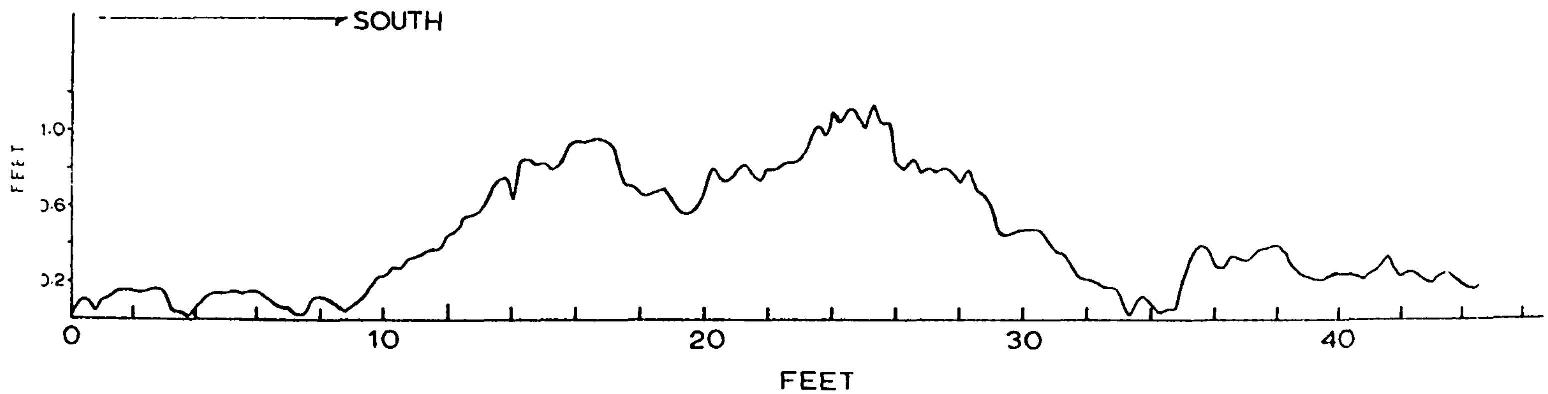
I	*Polygonum coccineum-Lysimachia hybrida* zone
II	*Polygonum coccineum-Scirpus fluviatilis* zone
III	*Carex atherodes-Polygonum coccineum* zone
IV	*Spartina pectinata-Carex aquatilis-Calamagrostis canadensis* zone
V	*Calamagrostis canadensis* zone
VI	Upland prairie edge

The actuality of this scheme is based on the repeatability of the zonation pattern as found within the potholes of Kalsow Prairie. Evidence for change or fluctuations in pothole vegetation paralleling this sequence will depend on the results obtained from long term studies.

Mima Mounds

Scattered across the 160 acres of Kalsow Prairie are numerous small circular mounds of soil ranging in diameter from 6 to 72 feet with a microrelief of from 6 to 36 inches (Figure 26). They support a different vegetation than the surrounding prairie (Figure 27). Such mounds, originally thought to be Indian burial mounds (Davids, 1967), have been known to exist for many years. Their origin has frequently been contested in scientific literature where they are often referred to as "Mima mounds." They have been considered the result of fossorial mammal

Figure 26. Microrelief, determined in July, 1968, of Mound 14 (Figure 1), a typical Mima mound, Kalsow Prairie


SOUTH
FEET
1.0
0.6
0.2
0
10
20
30
40
FEET

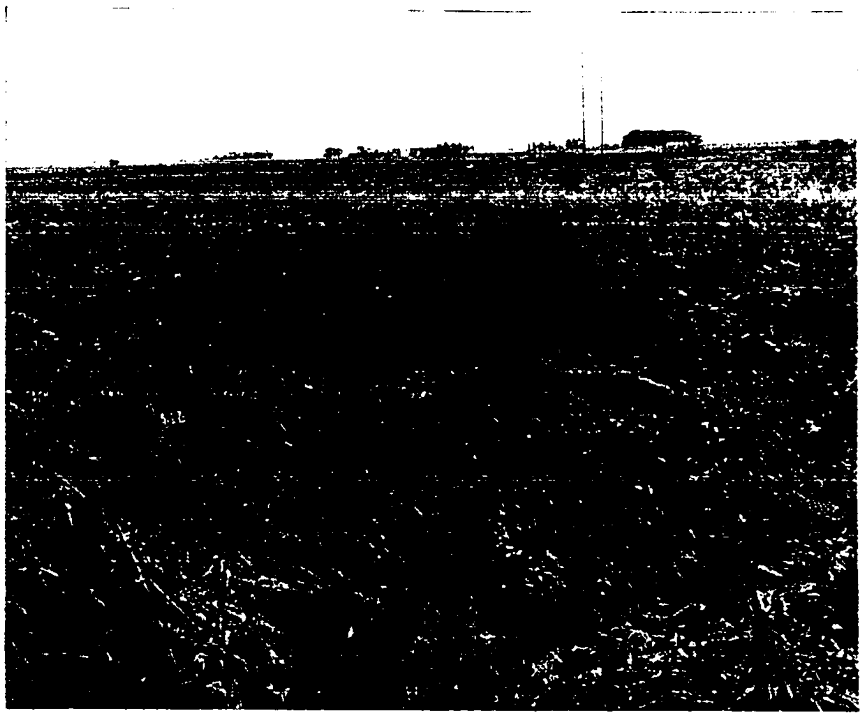


Figure 27. Mima mound number 33 (Figure 1), showing typical growth of annual and biennial weeds, Kalsow Prairie

activity, hydrostatic pressure, wind deposition, or several ground-frost phenomena (Scheffer, 1947; Thorp, 1949; Tester and Marshall, 1961; Hansen, 1962; and Davids, 1967). Scheffer (1958), McGinnies (1960) and Ross et al. (1968), in reviews of mound development, indicate that none of the hypotheses concerning their origin is universally accepted. Ross et al. (1968) indicate that this disagreement is probably due to the description of different causes or combinations of causes at different locations.

The Mima mounds of Kalsow Prairie are low, rounded mounds of loose, non-stratified soil which occur most frequently on the higher, better-drained soils. Their origin is at present not well understood, but it seems that they are most likely initiated by activity of the pocket gopher (Geomys bursarius) and other animals. Once initiated they might then be affected and enlarged by the differential expansion and contraction of their soils and by wind deposition of dust carried in from the adjacent cultivated fields. Continued use by pocket gophers and other burrowing mammals is evidenced by an abundance of recent soil pushed out from burrows in and about the mounds.

A vegetation analysis of several mounds picked randomly as a representative sample of the mound phenomena on the Kalsow Prairie showed that the number of plant species supported by the mounds was only slightly greater than that of the surrounding prairie (i.e., mounds = 51 species, adjacent prairie = 49 species). Of these, 38 or 75% of the sampled species were found in common on mounds and prairie. Those species showing cover values greater than one are placed in Table 5.

Table 5. Average percentage cover values in mound and adjacent prairie areas for all species with a percent cover greater than one

Species	% Cover (prairie)	% Cover (mounds)
[a]1 Sporobolus heterolepis	53.60	.04
1 Amorpha canescens	2.00	.83
Andropogon scoparius	1.00	
2 Zizia aurea	1.20	.83
Aster laevis	1.10	.04
Solidago rigida	1.30	.10
2 Panicum leibergii	3.00	1.80
3 Aster ericoides	3.00	4.00
Andropogon gerardi	14.00	11.85
3 Ratibida columnifera	1.00	2.90
Achillea lanulosa	.93	2.40
4 Physalis heterophylla	.04	1.90
Rosa suffulta	.80	1.70
4 Convolvulus sepium	.10	1.90
Asclepias syriaca		1.10
Agropyron repens		1.40
Ambrosia artemisifolia		4.30
5 Solidago canadensis	3.00	8.36
5 Poa pratensis	8.00	45.26

[a]These numbers are the adaptation numbers assigned to the different indicator species

Indicator species were chosen as representative of the two areas and assigned adaptation numbers according to the method of Dix and Butler (1960). This information was then used to compute Plot Index Values (P.I.V.) for the two areas and thus separate them spatially as shown in Figure 28. The Plot Index Values were computed by use of the following equation:

$$\text{P.I.V.} = \frac{\text{Sum (percent cover of each indicator species x its adaptation \#)}}{\text{Sum (percent cover of each indicator species)}}$$

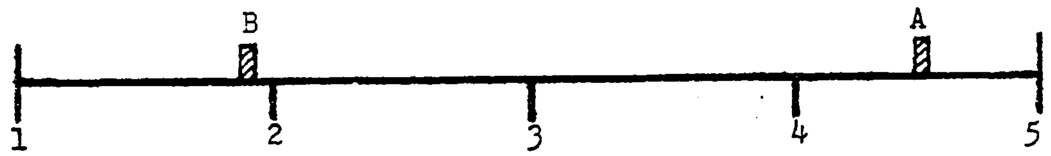


Figure 28. Linear ordination of the Mima mound and adjacent prairie vegetation according to their plot index values. A = Mima mounds, B = adjacent prairie

This spatial separation (Figure 28) and Table 5 indicate definite differences in the vegetation of the two areas. To further strengthen the hypothesis that the vegetation changes from the mounds to the prairie, a similarity index was computed for the two areas utilizing Sorensen's (1948) index of similarity. The following equation was used:

$$K = \frac{2w}{a + b} \times 100$$

K is the index of similarity between the two areas; a represents the sum of the cover percentages of all species in the prairie; b represents a similar figure for the mounds; and w represents that part of the cover common to the species found in both areas.

The value of K was calculated to be 35.2% which means that the mound vegetation and the adjacent prairie vegetation have a similarity of 35%. Similarity values reported by Curtis (1959) for a series of communities in Wisconsin showed extremes from 34.1 to 70.3. It seems, therefore, that mounds are quite distinct from the prairie.

The relationship of mound vegetation to adjacent prairie has not been extensively investigated (Ross et al., 1968). Attempts to describe such relationships in the present study revealed that the mounds are associated with changes in the surrounding prairie vegetation. These changes were investigated by sampling prairie vegetation adjacent to 37 of the 128 mounds studied. Two transects, one oriented north-south and the other east-west, were extended through each mound. The adjacent prairie vegetation was sampled along these transects starting at the mound boundary and extending into the prairie. Twelve samples at 12-foot intervals were taken adjacent to each mound as shown in Figure 4. Cover estimates were recorded for each species present in the quadrat. The resulting data were analyzed by grouping all quadrats found at equal intervals from the mounds and averaging them to obtain percentage cover values for all participating species (Table 6). A similar analysis was also completed by grouping all quadrats located on the north, south, east, and west sides of the mounds and again averaging to obtain percentage cover values for all participating species (Table 7). In both cases it is evident that the mounds have provided a new microenvironment to which some prairie species respond. Some species (Table 6) show a positive response by appearing almost exclusively on the mounds or by increasing in importance from the prairie toward the mound. Species showing this type of response were Achillea lanulosa, Agropyron repens, Ambrosia artemisifolia, Asclepias syriaca, Aster ericoides, Chenopodium album, Convolvulus sepium, Elymus canadensis, Fragaria virginiana, Galium obtusum, Helianthus grosseserratus, Helianthus laetiflorus, Heliopsis helianthoides, Oxalis stricta, Physalis heterophylla, Poa pratensis, Ratibida columnifera, Rosa suffulta, Solidago canadensis, and Spartina pectinata. Other species showed a negative response decreasing in importance as the mound is approached from the prairie. These species were Amorpha canescens, Aster laevis, Baptisia leucantha, Comandra umbellata, Eryngium yuccifolium, Lathyrus venosus, Liatris pycnostachya, Silphium laciniatum, Solidago rigida, Sporobolus heterolepis and Zizia aurea. Another response is exhibited by Andropogon gerardi. It increases in importance as you move toward the mound then drops sharply in average percentage cover as you reach the mound proper. Other species showing this same kind of response were Andropogon scoparius, Bouteloua curtipendula, Desmodium canadense, and Lithospermum canescens.

Evidence from Table 7 indicates that several species also showed some response to small differences in microrelief as associated with aspect. Species showing preference for the southern aspect were Amorpha canescens, Andropogon scoparius, Asclepias tuberosa, Aster ericoides, Comandra umbellata, Lithospermum canescens, Panicum leibergii, Petalostemum candidum, Poa pratensis, Solidago missouriensis, and Stipa spartea. Species showing preference for the north side of the mounds were Anemone cylindrica, Asclepias syriaca, Convolvulus sepium, Sorghastrum nutans, and Vicia americana.

It seems the mounds, however slight in microrelief, provide sufficient modification of the prairie to allow striking patterns of vegetational change to emerge. In one aspect the mounds provide habitats which exhibit different levels of disturbance (i.e., the amount of actual disturbance decreases as you leave the mound and proceed into the prairie). The response of several species to the disturbance factor would tend to support the hypothesis made in the discussion on upland prairie that the changes which have occurred in the prairie since 1953 were in effect caused by some degree of disturbance. Several of the species which showed

Table 6. Effects of Mima mounds on cover values of the surrounding upland prairie vegetation

Species	Mound	12 ft.	24 ft.	36 ft.
Achillea lanulosa	.74	.50	.59	.51
Agropyron repens	1.16	.02	.02	.03
Agropyron trachycaulum	.01	.00	.00	.00
Ambrosia artemisifolia	1.91	.02	.02	.00
Ambrosia trifida	.41	.00	.00	.00
Amorpha canescens	.41	1.94	2.01	1.35
Amphicarpa bracteata	.14	.02	.00	.00
Andropogon gerardi	7.69	18.72	14.66	12.80
Andropogon scoparius	.01	1.37	.42	.46
Anemone canadensis	.00	.00	.00	.02
Anemone cylindrica	.01	.10	.06	.02
Apocynum sibiricum	.07	.10	.00	.12
Arabis hirsuta	.01	.00	.00	.00
Artemisia ludoviciana	.61	.49	.30	.25
Asclepias sullivantii	.01	.00	.00	.00
Asclepias syriaca	1.18	.17	.02	.00
Asclepias tuberosa	.35	.51	.19	.03
Asclepias verticillata	.04	.03	.02	.00
Aster ericoides	3.96	2.23	2.50	1.82
Aster laevis	.97	1.60	1.76	.81
Aster simplex	.51	.30	.20	.24
Astragalus canadensis	.00	.02	.02	.00
Baptisia leucantha	.05	.10	.17	.02
Baptisia leucophaea	.00	.00	.10	.10
Bouteloua curtipendula	.03	.07	.05	.02
Caenothus americanus	.00	.00	.00	.10
Calamagrostis canadensis	.01	.00	.00	.02
Carex gravida	.19	.10	.07	.16
Carex aquatilis	.00	.02	.00	.00
Carex retrorsa	.00	.00	.00	.02
Chenopodium album	.77	.02	.00	.00
Cicuta maculata	.00	.00	.03	.00
Cirsium altissimum	.50	.03	.19	.15
Cirsium arvense	.25	.00	.00	.00
Comandra umbellata	.06	.23	.27	.34
Convolvulus sepium	3.13	.53	.28	.22
Desmodium canadense	1.25	2.21	1.91	1.79
Echinacea pallida	.00	.00	.00	.02
Elymus canadensis	1.22	.42	.47	.39
Elymus virginicus	.06	.00	.00	.00
Equisetum kansanum	.07	.07	.14	.07
Erigeron strigosus	.01	.00	.00	.00
Eryngium yuccifolium	.01	.10	.14	.02

Table 6. (Continued)

Species	Mound	12 ft.	24 ft.	36 ft.
Euphorbia serpyllfolia	.01	.00	.00	.00
Fragaria virginiana	.83	.79	.63	.41
Galium obtusum	.93	.74	.69	.54
Gentiana andrewsii	.00	.02	.05	.15
Helianthus grosseserratus	4.13	1.72	1.67	2.36
Helianthus laetiflorus	1.59	1.52	1.23	1.03
Helianthus maximiliani	.46	.14	.02	.00
Heliopsis helianthoides	1.32	.51	.37	.63
Juncus tenuis	.00	.02	.00	.00
Kochia scoparia	.13	.00	.00	.00
Lactuca scariola	.12	.00	.00	.02
Lathyrus palustris	.02	.00	.03	.02
Lathyrus venosus	.13	.20	.19	.07
Lespedeza capitata	.00	.02	.04	.04
Liatris aspera	.06	.02	.04	.04
Liatris pycnostachya	.01	.20	.19	.29
Lithospermum canescens	.24	.57	.54	.37
Lysimachia chiliata	.08	.03	.02	.03
Lysimachia hybrida	.00	.10	.02	.10
Lysimachia quadriflora	.00	.00	.02	.02
Muhlenbergia racemosa	.40	.51	.69	.39
Oenothera biennis	.11	.00	.00	.00
Oxalis stricta	1.42	.08	.02	.02
Panicum capillare	.27	.00	.00	.00
Panicum leibergii	2.02	3.13	3.89	2.52
Panicum virgatum	.62	.52	.39	.54
Pedicularis canadensis	.00	.00	.02	.03
Petalostemum candidum	.02	.19	.10	.25
Petalostemum purpureum	.02	.25	.35	.20
Phleum pratensis	.01	.00	.03	.03
Phlox pilosa	.19	.25	.41	.20
Physalis heterophylla	1.24	.12	.08	.02
Physalis virginiana	.35	.10	.14	.07
Poa pratensis	40.47	10.14	7.64	6.69
Polygonum convolvulus	.14	.00	.00	.00
Polygonum ramosissimum	.09	.00	.00	.00
Potentilla arguta	.09	.00	.10	.02
Psoralea argophylla	.15	.14	.24	.10
Pycnanthemum virginianum	.00	.07	.00	.19
Ratibida columnifera	3.08	2.19	1.30	1.49
Rosa suffulta	2.48	1.20	1.49	1.50
Scutellaria leonardii	.03	.03	.04	.02
Senecio pauperculus	.13	.03	.03	.14
Setaria lutescens	.62	.00	.02	.00

Table 6. (Continued)

Species	Mound	12 ft.	24 ft.	36 ft.
Setaria viridis	.03	.00	.00	.00
Silphium laciniatum	.02	.39	.54	.69
Solanum nigrum	.09	.00	.00	.00
Solidago canadensis	10.73	5.03	3.80	4.51
Solidago gymnospermoides	.00	.02	.00	.02
Solidago missouriensis	.11	.23	.35	.20
Solidago rigida	.47	1.37	2.50	1.47
Sorghastrum nutans	.00	.10	.27	.65
Spartina pectinata	.94	.37	.32	.24
Sporobolus heterolepis	1.05	22.61	31.00	33.97
Stipa spartea	.25	.59	.89	.49
Taraxacum officinale	.00	.10	.00	.00
Thalictrum dasycarpum	.01	.00	.00	.00
Tradescantia bracteata	.01	.00	.00	.00
Trifolium pratense	.05	.00	.02	.00
Viola pedatifida	.19	.27	.19	.27
Viola sp.	.13	.07	.10	.05
Vicia americana	.11	.30	.07	.14
Zizia aurea	1.44	2.08	2.47	1.65

increased importance since Moyer's (1953) work (i.e., Solidago canadensis, Panicum leibergii, Helianthus grosseserratus, Desmodium canadense, Galium obtusum, and Fragaria virginiana) also showed a corresponding increase in importance as you approach the mounds from the prairie. Likewise, some of the species which decreased in importance in the past 16 years (i.e., Zizia aurea, Sorghastrum nutans, and Sporobolus heterolepis) also decreased as disturbance increased. Several species, Andropogon gerardi, Andropogon scoparius, Bouteloua curtipendula, and Lithospermum canescens, indicated positive response to slight disturbance but negative response to heavier disturbance.

It seems, therefore, that mounds or other forms of disturbance affect vegetation changes in the prairie which, when considered over a

Table 7. Effects of Mima mounds on cover values of the surrounding upland prairie vegetation in relation to aspect

Species	Mound	North	South	East	West
Achillea lanulosa	.74	.56	.38	.68	.56
Agropyron repens	1.16	.02	.00	.05	.02
Ambrosia artemisifolia	1.91	.02	.02	.00	.00
Amorpha canescens	.41	2.16	2.68	1.24	2.07
Amphicarpa bracteata	.41	.00	.00	.02	.00
Andropogon gerardi	7.69	16.24	15.16	16.64	13.22
Andropogon scoparius	.01	.45	1.28	.86	.45
Anemone canadensis	.00	.00	.00	.02	.00
Anemone cylindrica	.01	.11	.05	.07	.05
Apocynum sibiricum	.07	.11	.00	.07	.00
Artemisia ludoviciana	.61	.36	.25	.45	.34
Asclepias syriaca	1.18	.16	.05	.00	.02
Asclepias tuberosa	.35	.14	.74	.02	.11
Asclepias verticillata	.04	.02	.00	.02	.02
Aster ericoides	3.96	2.09	2.52	2.00	2.17
Aster laevis	.97	1.31	1.31	1.62	1.55
Aster simplex	.51	.14	.11	.27	.47
Astragalus canadensis	.00	.05	.00	.00	.00
Baptisia leucantha	.05	.00	.00	.29	.14
Bouteloua curtipendula	.03	.02	.02	.09	.05
Calamagrostis canadensis	.01	.11	.00	.02	.00
Carex brevoir	.19	.00	.11	.23	.05
Carex aquatilis	.00	.00	.02	.00	.00
Carex lasiocarpa	.00	.00	.00	.02	.00
Chenopodium album	.77	.00	.00	.00	.02
Cicuta maculata	.00	.00	.00	.00	.05
Cirsium altissimum	.50	.09	.07	.07	.20
Comandra umbellata	.06	.20	.50	.45	.23
Convolvulus sepium	3.13	.63	.25	.23	.47
Desmodium canadense	1.25	1.78	1.91	1.89	2.16
Echinacea pallida	.00	.00	.02	.02	.00
Elymus canadensis	1.22	.43	.63	.45	.25
Equisetum kansanum	.07	.11	.11	.09	.07
Eryngium yuccifolium	.01	.05	.00	.14	.14
Fragaria virginiana	.83	.59	.70	.68	.65
Galium obtusum	.93	.88	.86	.52	.68
Gentiana andrewsii	.00	.05	.14	.02	.05
Helianthus grosseserratus	4.13	2.41	2.18	2.09	1.01
Helianthus laetiflorus	1.59	.97	1.26	1.58	1.22
Helianthus maximiliani	.46	.16	.00	.05	.02
Heliopsis helianthoides	1.32	.43	.52	.92	.27
Juncus tenuis	.00	.00	.00	.02	.00
Lactuca scariola	.12	.02	.00	.00	.00

Table 7. (Continued)

Species	Mound	North	South	East	West
Lathyrus palustris	.02	.02	.00	.05	.02
Lathyrus venosus	.13	.07	.14	.23	.05
Lespedeza capitata	.00	.07	.00	.07	.02
Liatris aspera	.06	.00	.02	.09	.05
Liatris pycnostachya	.01	.16	.29	.23	.27
Lithospermum canescens	.24	.43	.74	.41	.45
Lysimachia chiliata	.08	.00	.05	.05	.02
Lysimachia hybrida	.00	.00	.16	.02	.00
Lysimachia quadriflora	.00	.00	.00	.02	.02
Muhlenbergia racemosa	.40	.56	.47	.36	.79
Oxalis stricta	1.42	.02	.02	.07	.05
Panicum leibergii	2.02	2.97	4.35	2.57	2.68
Panicum virgatum	.62	.36	.63	.65	.41
Pedicularis canadensis	.00	.00	.00	.05	.05
Petalostemum candidum	.02	.18	.27	.14	.11
Petalostemum purpureum	.02	.14	.16	.52	.29
Phleum pratense	.01	.05	.02	.02	.02
Phlox pilosa	.19	.34	.18	.45	.20
Physalis heterophylla	1.24	.00	.14	.11	.23
Physalis virginiana	.35	.14	.07	.16	.14
Poa pratensis	40.47	7.55	9.89	7.76	6.42
Potentilla arguta	.09	.02	.02	.14	.00
Psoralea argophylla	.15	.09	.20	.32	.09
Pycnanthemum virginianum	.00	.05	.05	.05	.07
Ratibida columnifera	3.08	1.37	1.80	2.00	1.60
Rosa suffulta	2.48	1.55	1.55	.83	1.22
Scutellaria leonardii	.03	.05	.02	.07	.02
Senecio pauperculus	.13	.18	.02	.07	.05
Setaria lutescens	.62	.00	.02	.00	.00
Silphium laciniatum	.02	.29	.61	.36	.90
Solidago canadensis	10.73	5.50	4.28	4.12	4.08
Solidago gymnospermoides	.00	.00	.00	.07	.00
Solidago missouriensis	.11	.20	.52	.27	.11
Solidago rigida	.47	1.94	1.64	1.46	2.03
Sorghastrum nutans	.00	.95	.14	.16	.27
Spartina pectinata	.94	.14	.45	.56	.25
Sporobolus heterolepis	1.05	32.30	27.03	24.28	36.03
Stipa spartea	.25	.18	.50	.38	.38
Taraxacum officinale	.00	.14	.00	.00	.00
Trifolium pratense	.05	.00	.00	.02	.00
Viola pedatifida	.19	.27	.27	.29	.16
Viola sp.	.13	.07	.09	.02	.14
Vicia americana	.11	.36	.18	.09	.14
Zizia aurea	1.44	2.45	2.05	2.30	2.36

period of years, may alter the original structure and composition of its vegetation. Whether such changes would be permanent or temporary is a question that can be answered only by long term studies set up to follow the fluctuations of the prairie vegetation and its environment.

Analysis of the mound vegetation as a unit was attempted using Orloci's (1966) method of ordination. Each mound was considered as a stand of vegetation and all 128 mounds were projected into three-dimensional space (Figure 29). This analysis placed the 128 mounds into a relatively linear relationship in the X, Y, and Z planes (Figure 29). This indicated that only two to three factors could be responsible for the placing of each mound into this sort of an alignment in relation to all the other mounds. Further study indicated that alignment was closely related to the two species Poa pratensis and Solidago canadensis. Poa pratensis was responsible for alignment of the X-axis (Figure 31) and Solidago canadensis was responsible for alignment of the Y-axis (Figure 30). Because no environmental measurements were taken, it was impossible to tell what causative factors these two species were linked to. It appears, however, that the vegetation of the mounds fits the concept of a continuum and that perhaps the controlling environmental factors would be related to the age of the mound and the degree of disturbance.

By ordinating the species of the mounds into three-dimensional space (Figure 32), it was found that only those species having irregular distribution patterns were isolated. The most different species were Poa pratensis, Solidago canadensis, Solanum nigrum, Andropogon gerardi, Aster ericoides, Helianthus grosseserratus, Convolvulus sepium, Helianthus laetiflorus, Desmodium canadense, Ambrosia artemisifolia, Panicum leibergii,

Figure 29. Three-dimensional ordination of 128 Mima mounds found in Kalsow Prairie; factors responsible for ordination unknown

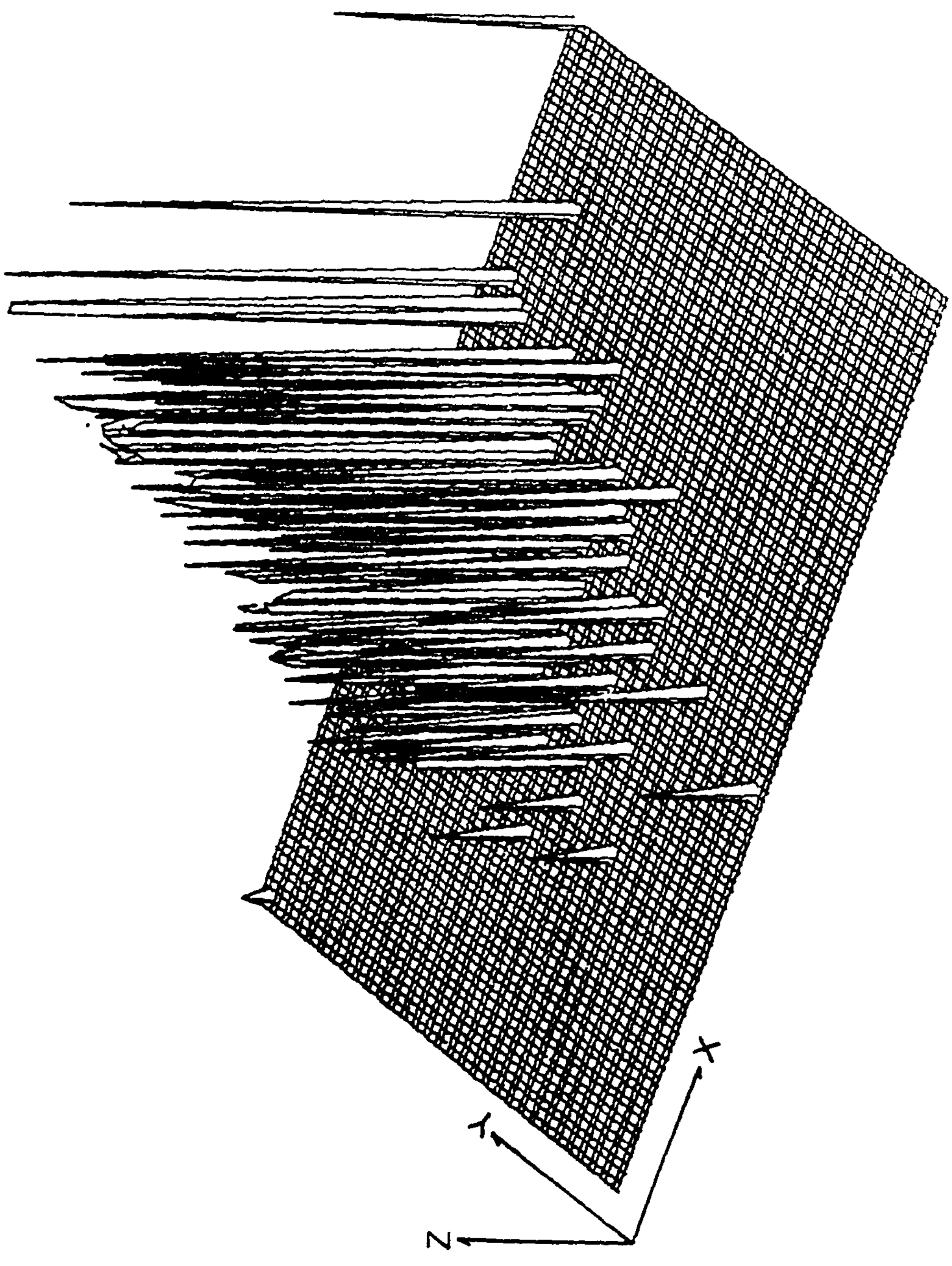
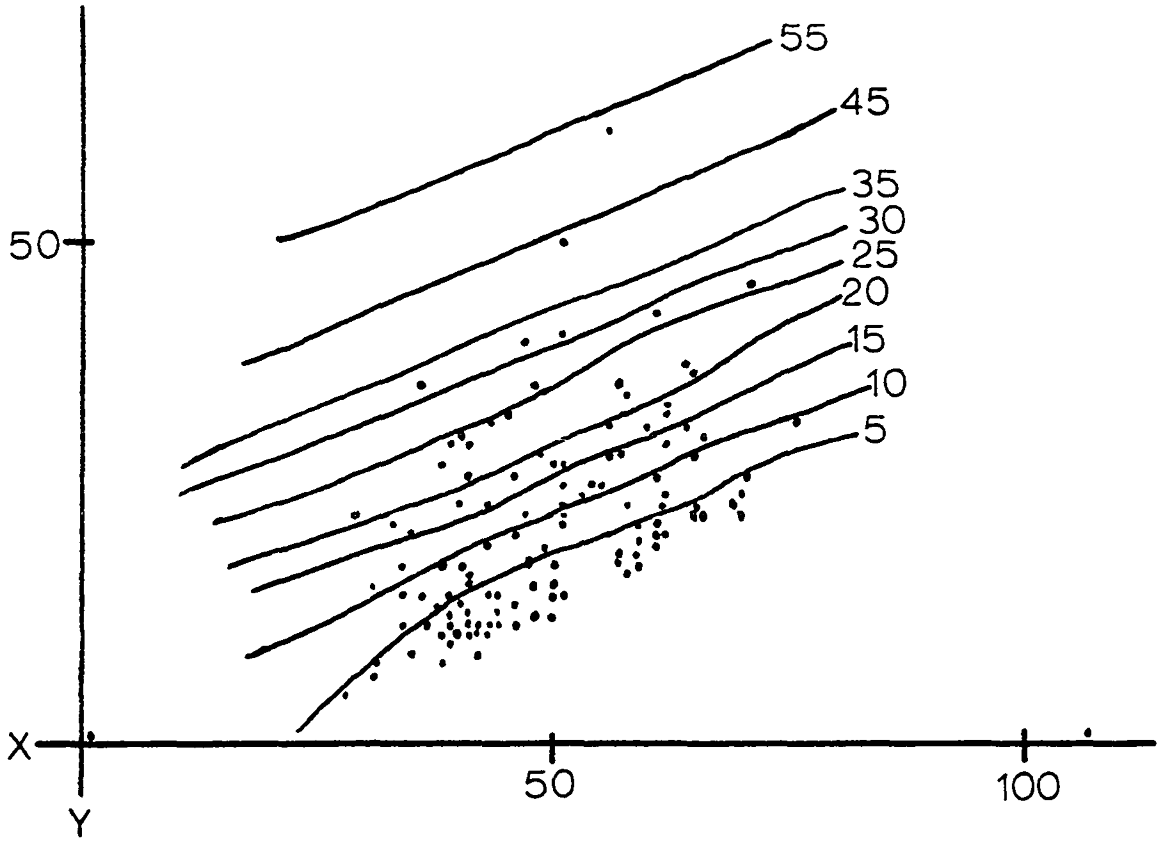

X
Y
Z

Figure 30. Two-dimensional ordination of Mima mounds with percentage cover values of _Solidago canadensis_ shown relating indirectly to the Y-axis

Figure 31. Two-dimensional ordination of Mima mounds with percentage cover values of _Poa pratensis_ shown relating directly to the X-axis


55
45
35
30
25
20
15
10
5
50
X
50
100
Y

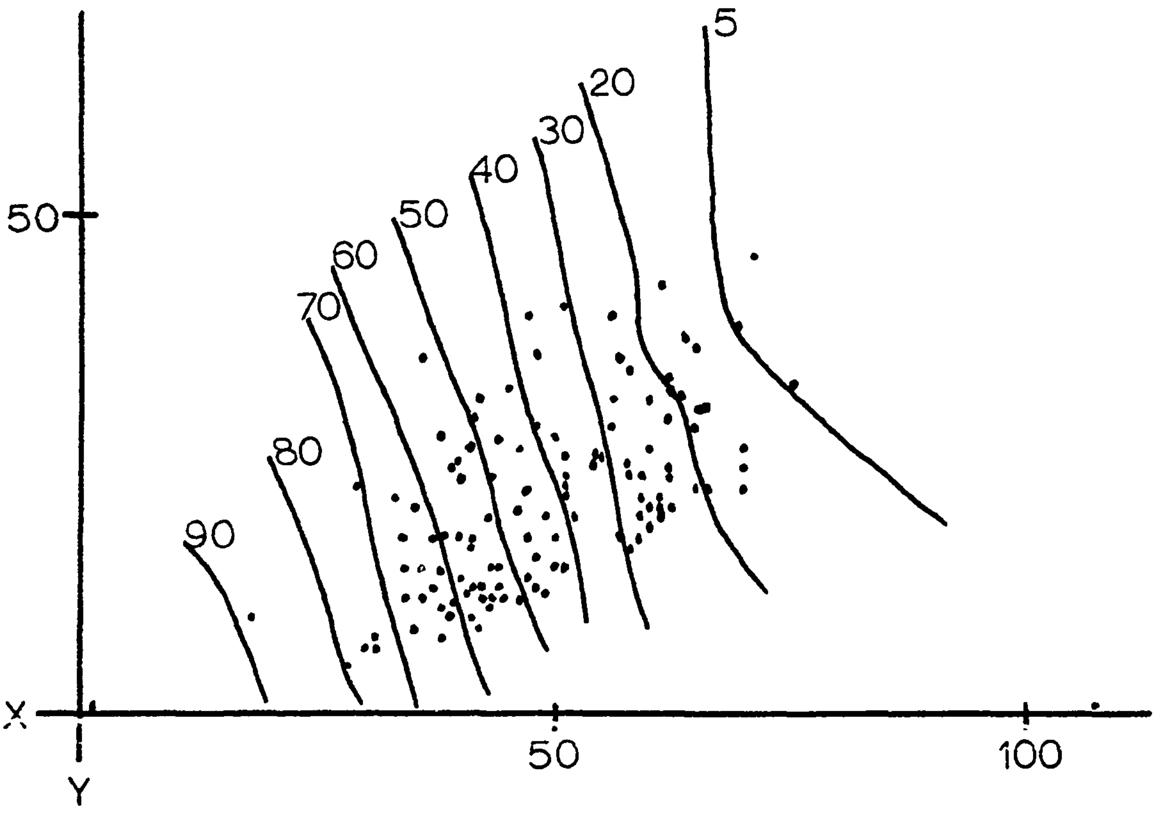
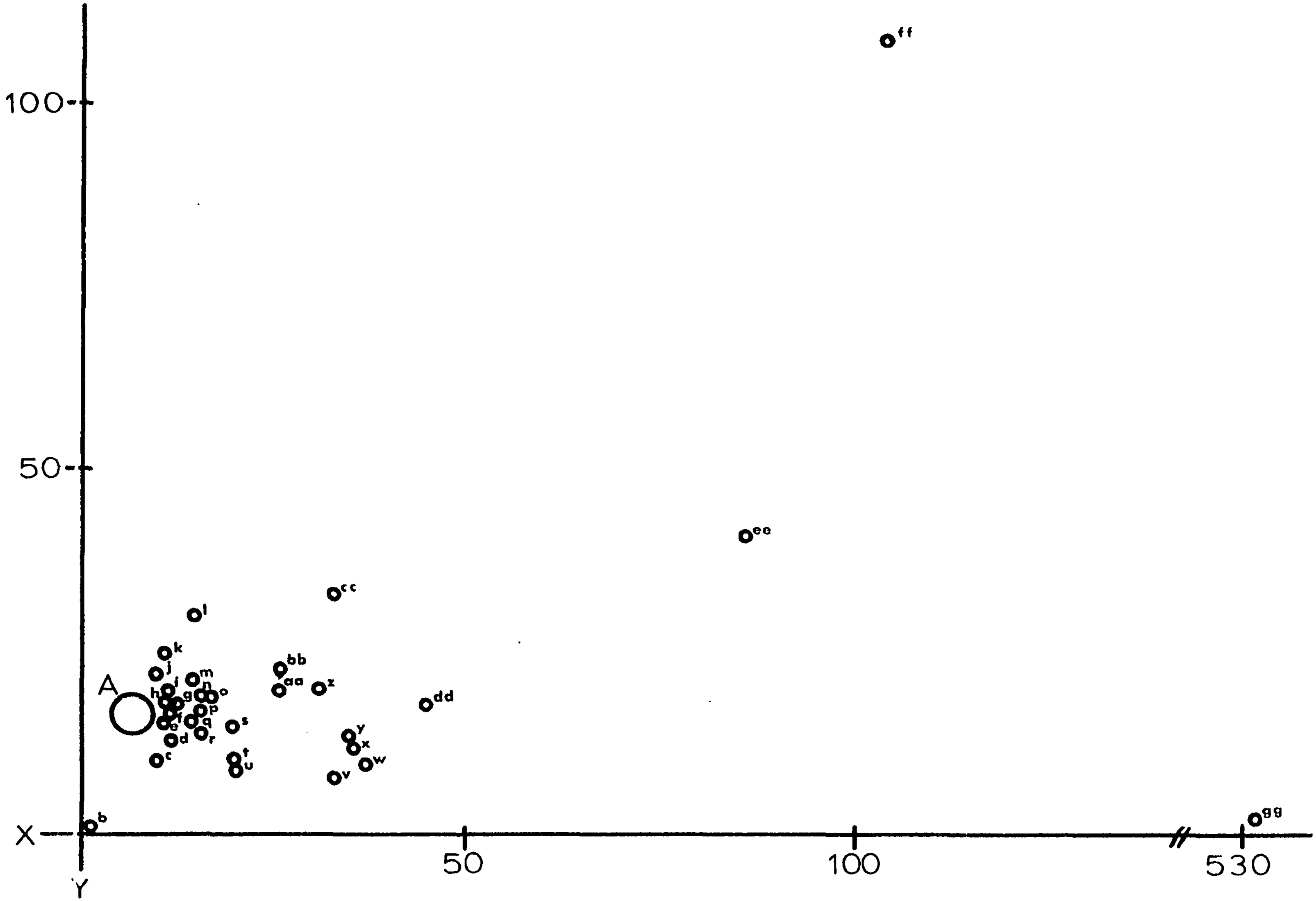

5
20
30
40
50
60
70
80
90
50
X
50
100
Y

Figure 32. Two-dimensional ordination of species found in the Mima mound study; A = cluster of species not showing distinct distribution patterns, b = Solanum nigrum, c = Ambrosia trifida, d = Agropyron repens, e = Amorpha canescens, f = Chenopodium album, g = Fragaria virginiana, h = Achillea lanulosa, i = Asclepias syriaca, j = Spartina pectinata, k = Panicum virgatum, l = Zizia aurea, m = Heliopsis helianthoides, n = Physalis heterophylla, o = Elymus canadensis, p = Aster laevis, q = Oxalis stricta, r = Artemisia ludoviciana, s = Sporobolus heterolepis, t = Aster simplex, u = Galium obtusum, v = Ambrosia artemisifolia, w = Convolvulus sepium, x = Helianthus laetiflorus, y = Desmodium canadense, z = Ratibida columnifera, aa = Panicum leibergii, bb = Rosa suffulta, cc = Helianthus grosseserratus, dd = Aster ericoides, ee = Andropogon gerardi, ff = Solidago canadensis, gg = Poa pratensis



100
50
X
Y
50
100
530
A
a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q
r
s
t
u
v
w
x
y
z
aa
bb
cc
dd
ee
ff
gg

Ratibida columnifera, Rosa suffulta, and Zizia aurea. Again it was found that the two species Poa pratensis and Solidago canadensis were responsible for alignment of the X and Y-axes.

To further understand the relationships of mound vegetation, interspecific association values were computed for all possible pairs of species (Table 8). Out of 7200 possible combinations only 78 or about 1% showed any degree of positive association. Four basic clusters or groups of species within these 78 positive association units are illustrated in Figures 33 and 34. These four clusters are designated as A, B, C, and D in Figure 34. Cluster "A" has as its center Solidago rigida and as associated species: Carex gravida, Monarda fistulosa, Senecio pauperculus, Aster simplex, Solanum nigrum, Apocynum sibiricum, Panicum virgatum, and Spartina pectinata. Cluster "B" has for its center a unit of three species: Desmodium canadense, Fragaria virginiana, and Helianthus grosseserratus. These are then associated with several other species only on a very limited basis (i.e., 20 to 40 percent). Cluster "C" has as its center Zizia aurea and as associated species: Lythrum alatum, Pedicularis canadensis, Petalostemum candidum, and Lysimachia hybrida. Here again Zizia aurea and its associated species are weakly associated with several other species. Cluster "D" is basically a discrete unit including Lycopus americanus, Lysimachia hybrida, and Spartina pectinata. In all cases the above clusters appear to be composed of species which are generally found on lowland prairie soils or bordering potholes and drainageways. This would indicate that the mounds as shown by these groups might be somewhat more moist than the adjacent prairie. There seems to be little indication that these groups

Table 8. Cole's Index values expressing positive interspecific association in Mima mound communities

Species	Species	X^{2a}	$C_7{}^b$	$\sigma_7{}^c$
Agropyron repens	Convolvulus sepium	48.20	.45	.06
Amorpha canescens	Panicum leibergii	37.20	.49	.07
	Sporobolus heterolepis	24.82	.19	.03
Andropogon gerardi	Poa pratensis	8.82	.63	.21
Apocynum sibiricum	Solidago canadensis	5.04	.33	.14
	Spartina pectinata	15.77	.21	.05
Artemisia ludoviciana	Convolvulus sepium	16.97	.19	.04
Asclepias tuberosa	Panicum virgatum	12.68	.17	.04
Aster laevis	Panicum leibergii	23.91	.19	.03
Aster simplex	Elymus canadensis	5.99	.19	.07
	Helianthus grosseserratus	54.44	.35	.04
	Ratibida columnifera	8.92	.17	.05
	Solidago canadensis	17.50	.45	.11
Bouteloua curtipendula	Convolvulus sepium	3.80	.36	.18
	Lithospermum canescens	14.34	.23	.06
	Panicum leibergii	4.13	.30	.14
	Phlox pilosa	9.26	.21	.07
	Zizia aurea	4.10	.21	.10
Carex gravida	Fragaria virginiana	3.91	.19	.09
	Physalis virginiana	17.76	.25	.05
	Solidago canadensis	7.54	.65	.23
Chenopodium album	Elymus canadensis	7.69	.18	.06
Cirsium altissimum	Panicum capillare	39.39	.17	.02
Comandra umbellata	Desmodium canadense	14.88	.20	.05
	Fragaria virginiana	17.87	.26	.06
	Galium obtusum	22.35	.29	.06
	Panicum leibergii	10.20	.32	.09
	Sporobolus heterolepis	28.49	.25	.04
Desmodium canadense	Fragaria virginiana	230.53	.45	.02
	Galium obtusum	239.96	.46	.02
	Helianthus grosseserratus	75.32	.29	.03
	Panicum virgatum	55.13	.17	.02
	Ratibida columnifera	20.91	.19	.04
	Solidago canadensis	8.52	.22	.07
	Spartina pectinata	79.85	.24	.02
	Zizia aurea	87.88	.31	.03

[a]Chi-square

[b]Cole's Index

[c]Standard deviation Cole's Index

Table 8. (Continued)

Species	Species	X^2	C_7	σ_7
Equisetum kansanum	Helianthus laetiflorus	13.69	.34	.09
Eryngium yuccifolium	Viola pedatifida	75.09	.82	.09
Fragaria virginiana	Galium obtusum	137.95	.30	.02
	Helianthus grosseserratus	71.48	.24	.02
Galium obtusum	Helianthus grosseserratus	72.33	.24	.02
	Panicum virgatum	75.68	.17	.01
	Zizia aurea	68.88	.24	.02
Helianthus maximiliani	Panicum leibergii	4.31	.23	.11
Kochia scoparia	Physalis heterophylla	9.38	.42	.13
Lactuca scariola	Phlox pilosa	5.36	.17	.07
Lathyrus palustris	Ratibida columnifera	5.58	.36	.15
	Solidago rigida	5.68	.19	.08
Liatris pycnostachya	Lithospermum canescens	19.50	.36	.08
	Petalostemum purpureum	23.57	.19	.03
	Psoralea argophylla	11.75	.18	.05
	Solidago rigida	7.77	.25	.08
	Sporobolus heterolepis	6.69	.24	.09
Lithospermum canescens	Panicum leibergii	16.28	.25	.06
Lycopus americanus	Lysimachia chiliata	145.04	.66	.05
	Spartina pectinata	9.46	.62	.20
Lysimachia chiliata	Spartina pectinata	40.75	.60	.09
	Zizia aurea	12.21	.40	.11
Lythrum alatum	Zizia aurea	20.90	.70	.15
Monarda fistulosa	Solidago canadensis	5.17	1.00	.43
Oenothera biennis	Panicum capillare	102.87	.33	.03
Panicum virgatum	Solidago canadensis	20.30	.37	.08
	Spartina pectinata	27.11	.15	.02
Pedicularis canadensis	Zizia aurea	26.42	1.00	.19
Petalostemum candidum	Zizia aurea	10.36	.30	.09
Polygonum ramosissimum	Rumex crispus	71.91	.22	.02
Potentilla arguta	Viola pedatifida	7.62	.17	.06
Senecio pauperculus	Solidago canadensis	6.56	.70	.27
	Solidago rigida	4.90	.17	.07
	Spartina pectinata	10.20	.31	.09
	Zizia aurea	8.91	.36	.12
Silphium laciniatum	Solidago rigida	7.60	.19	.06
	Spartina pectinata	11.51	.30	.08
	Viola sp.	97.96	.42	.04
	Zizia aurea	9.31	.33	.10
Solanum nigrum	Solidago canadensis	4.29	.51	.24
Solidago rigida	Zizia aurea	23.58	.19	.03
Viola sp.	Zizia aurea	17.37	.30	.06

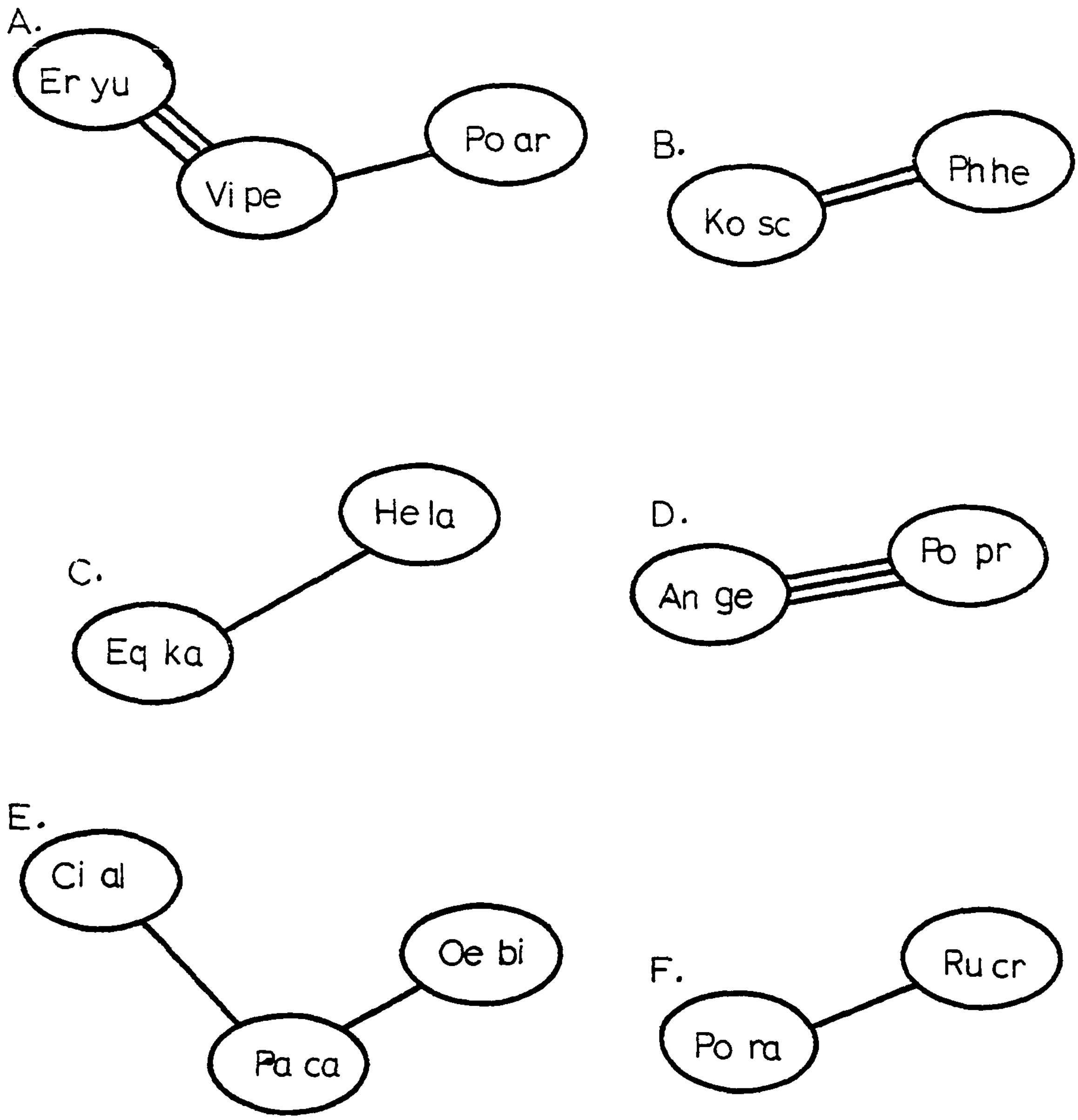
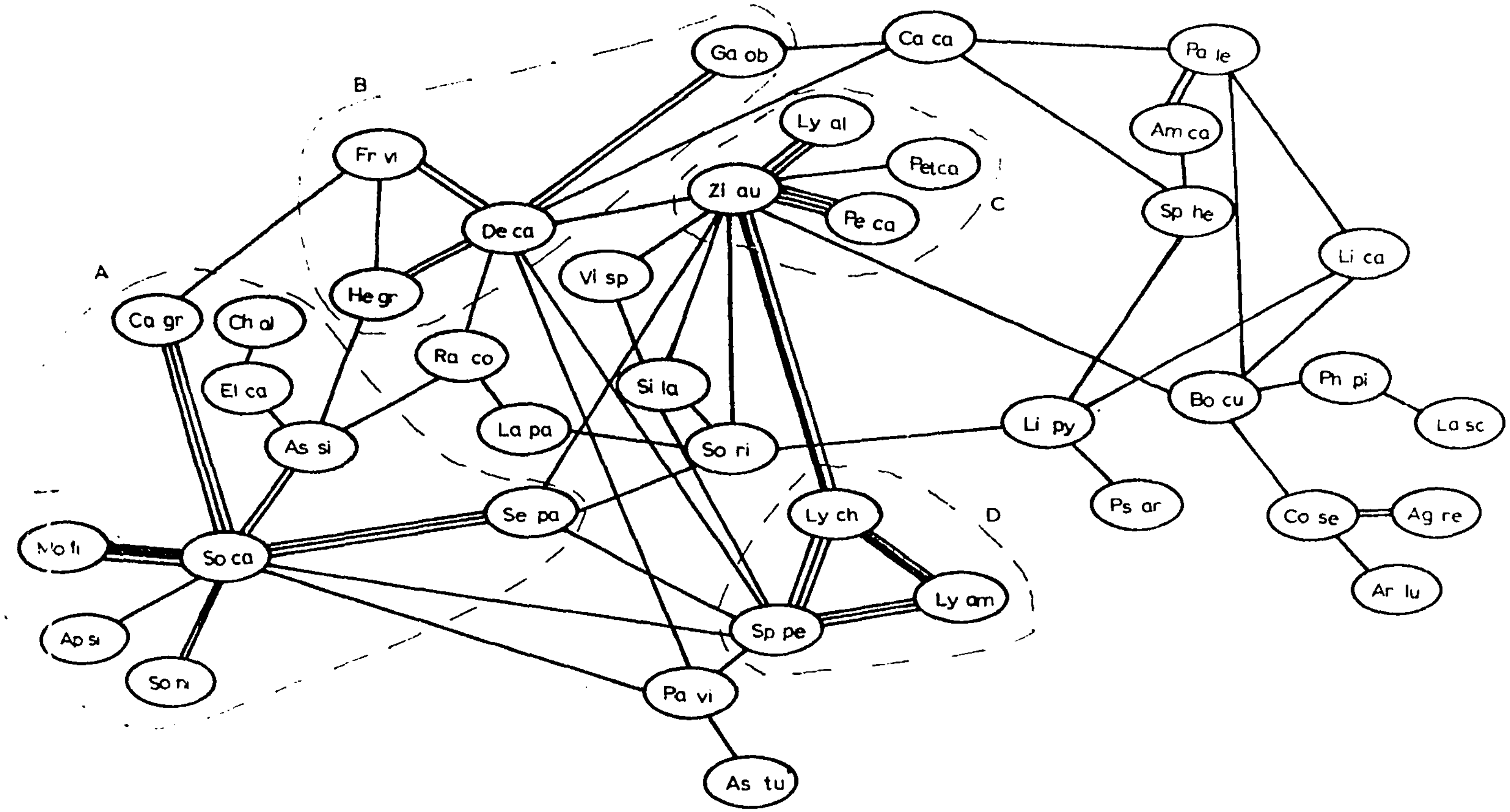


Figure 33. Association of species found in the Mima mound study, Halsow Prairie, as determined by Cole's (1949) Index, the more lines between species, the greater the association; (A) Er yu = Eryngium yuccifolium, Vi pe = Viola podatifida, Po ar = Potentilla arguta, (B) Ko sc = Kochia scoparia, Ph he = Physalis heterophylla, (C) Eq ka = Equisetum kansanum, He la = Helianthus laetiflorus, (D) An ge = Andropogon gerardi, Po pr = Poa pratensis, (E) Ci al = Cirsium altissimum, Pa ca = Panicum capillare, Oe bi = Oenothera biennis, (F) Po ra = Polygonum ramosissimum, Ru cr = Rumex crispus

Figure 34. Association of species found in the Mima mound study, Kalsow Prairie, as determined by Cole's (1949) Index, the more lines between species, the greater the association; groups A, B, C, and D are basic clusters; Ag re = *Agropyron repens*, Am ca = *Amorpha canescens*, Ap si = *Apocynum sibiricum*, Ar lu = *Artemisia ludoviciana*, As si = *Aster simplex*, As tu = *Asclepias tuberosa*, Bo cu = *Bouteloua curtipendula*, Ca ca = *Calamagrostis canadensis*, Ca gr = *Carex gravida*, Ch al = *Chenopodium album*, Co se = *Convolvulus sepium*, De ca = *Desmodium canadense*, El ca = *Elymus canadensis*, Fr vi = *Fragaria virginiana*, Ga ob = *Galium obtusum*, He gr = *Helianthus grossoserratus*, Mo fi = *Monarda fistulosa*, Pa le = *Panicum leibergii*, Pa vi = *Panicum virgatum*, Pe ca = *Pedicularis canadensis*, Pet ca = *Petalostemum candidum*, Ph pi = *Phlox pilosa*, Ps ar = *Psoralea argophylla*, La pa = *Lathyrus palustris*, La sc = *Lactuca scariola*, Li ca = *Lithospermum canescens*, Li py = *Liatris pycnostachya*, Ly al = *Lythrum alatum*, Ly am = *Lycopus americanus*, Ly ch = *Lysimachia chiliata*, Ra co = *Ratibida columnifera*, Se pa = *Senecio pauperculus*, Si la = *Silphium laciniatum*, Sp he = *Sporobolus heterophylla*, Sp pe = *Spartina pectinata*, So ni = *Solanum nigrum*, So ca = *Solidago canadensis*, So ri = *Solidago rigida*, Vi sp = *Viola* sp., Zi au = *Zizia aurea*



A
B
C
D
Ga ob
Ca ca
Pa le
Fr vi
Ly al
Pe ca
Am ca
Zi au
Pe ca
Sp he
De ca
Vi sp
Li ca
He gr
Ca gr
Ch al
Ra co
Si la
El ca
Ph pi
Bo cu
La sc
La pa
Li py
As si
So ri
Ps ar
Ly ch
Se pa
Co se
Ag re
Mo fi
So ca
Ly am
Ar lu
Ap si
Sp pe
So ri
Pa vi
As tu

are associated with mound size, degree of disturbance, or mound position in relation to slope.

It appears that once a mound is formed, a new microenvironment is created which affects directly the structure and stability of the surrounding prairie. This effect is shown in the response of many species to the creation of these new habitats. The factors deemed most influential in affecting these new habitats are disturbance and microrelief. Field observations indicate that the mounds represent microsuccession sites and cause changes in the prairie vegetation to earlier stages in the sere. This hypothesis is supported by the fact that in all cases studied, the vegetation of the mounds included a number of weed species (annuals, biennials and some perennials) which are recognized as pioneer species. The resulting mound vegetation appears to be made up of a mixture of these pioneer species and species from the prairie which respond favorably to mound disturbance. Present evidence also indicates that mound vegetation is undergoing succession which may be repeatedly set back by more disturbance. It seems that mound vegetation is strongly influenced in its basic composition by the adjacent prairie flora.

Grazed Pasture

Occupying the northwest corner of Kalsow Prairie is an area of 35 acres once used by earlier owners as a pasture (Figure 1). At the acquisition of the rest of the prairie in 1949 these 35 acres were purchased also and added to the prairie. All old fences were removed, and the full 160 acres were enclosed as a unit. The intention was to encourage the native plants found adjacent to the pasture to serve as a seed source and thus eventually this 35 acres would return to native prairie. The state of the vegetation on the pasture in 1949 is unknown since no studies or descriptions were made of it at that time; however, Weaver (1954) indicates that prairies, when subjected to grazing over long periods of time, tend to degenerate. He states that under grazing conditions the prairie flora is generally phased out and replaced by species which are better adapted to the pressure of close grazing and trampling. Such plants are generally referred to as increasers and include *Poa pratensis*, *Solidago canadensis*, *Verbena stricta* and several other inedible forbs in this region. Field observations on several nearby pastures used for grazing support Weaver's (1954) conclusions. Therefore, it seems that the 1949 pasture vegetation could well have been dominated by *Poa pratensis*, *Solidago canadensis*, and *Verbena stricta*. The cover values from Table 9 tend to support this conclusion.

Aerial photographs in 1968 (Figure 35) of the Kalsow Prairie indicate that vegetation patterns along the old fence lines which at one time separated the grazed portion of Kalsow Prairie from the prairie proper are still very visible. This would indicate that rather sharp lines of demarcation still exist between the grazed pasture and the adjacent prairie vegetation. The pasture does, however, include as part of its vegetation (Table 9) a number of prairie species. Investigation of the advance of these prairie species into the pasture was accomplished by dividing the pasture into 30 equal-sized blocks and then sub-sampling the vegetation of each block. Average cover values were computed for all plants found within each block. A quadratic surface was then fitted to eleven treatments (Tables 9 and 10) in attempts to define as nearly as

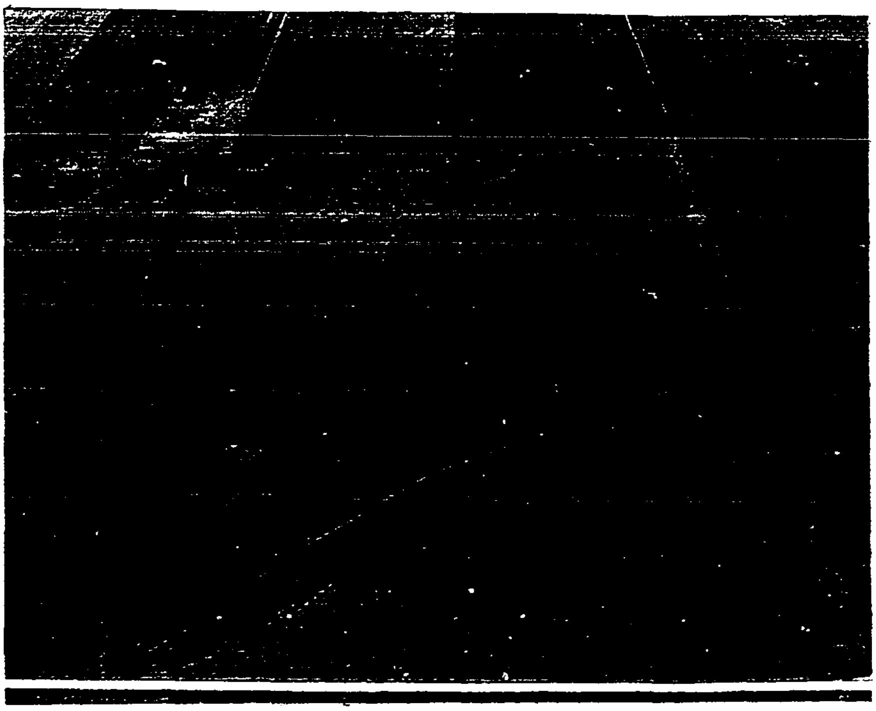


Figure 35. Aerial photograph of western half of Kalsow Prairie (facing south), showing old fence line and drainage pattern in the grazed pasture in foreground

Table 9. Occurrence and percent average cover of plant species in the grazed area of Kalsow Prairie. The numbers 1-11 correspond to the identification numbers of the different treatments found in Table 10, an X indicating occurrence

Species	Ave. % cover	1	2	3	4	5	6	7	8	9	10	11
Achillea lanulosa	.17						X					
Agropyron repens	.02						X	X				
Ambrosia artemisifolia	.58					X	X					
Ambrosia trifida	.01						X					
Andropogon gerardi	34.01			X			X			X		
Anemone cylindrica	.01						X	X	X	X		
Apocynum sibiricum	.01						X	X			X	
Artemisia ludoviciana	.03						X	X	X	X		
Asclepias incarnata	.01						X	X			X	
Asclepias syriaca	.36						X	X				
Asclepias verticillata	.01						X	X				
Aster ericoides	.94				X		X	X				
Aster laevis	.01						X	X	X	X		
Aster novae-angliae	.03						X	X	X	X		
Aster simplex	.46						X	X	X	X	X	
Bouteloua curtipendula	.01						X	X	X	X		
Bromus inermis	.38						X					
Carex retrorsa	.02						X	X			X	
Carex lasiocarpa	.14						X	X			X	
Chenopodium album	.01						X					
Cirsium altissimum	.03						X	X				
Cirsium arvense	.74						X					
Convolvulus sepium	.03						X					
Desmodium canadense	.03						X	X	X	X		
Elymus canadensis	.01						X	X	X	X		
Equisetum arvense	.01						X				X	
Equisetum kansanum	.06						X	X				
Fragaria virginiana	.08						X	X	X	X	X	
Galium obtusum	.16						X	X	X	X	X	
Gentiana andrewsii	.01						X	X	X	X	X	
Glychorriza lepidota	.04						X	X	X	X	X	
Helenium autumnale	.01						X	X	X	X	X	
Helianthus grosseserratus	.79						X	X	X	X		
Helianthus laetiflorus	.03						X	X	X	X		
Helianthus maximiliani	.15						X	X	X	X		
Heliopsis helianthoides	.03						X	X	X	X		
Lactuca scariola	.01						X					
Liatris pycnostachya	.01						X	X	X	X		
Lysimachia chiliata	.05						X	X	X	X	X	
Lythrum alatum	.01						X	X	X	X	X	
Melilotus alba	.05						X					

Table 9. (Continued)

Species	Ave. % cover	1	2	3	4	5	6	7	8	9	10	11
Mentha arvensis	.03						X	X			X	
Muhlenbergia racemosa	.08						X	X	X	X		
Panicum virgatum	.05						X	X	X	X	X	
Petalostemum purpureum	.01						X	X	X	X		
Phleum pratense	.01						X					
Phlox pilosa	.01						X	X	X	X		
Physalis heterophylla	.15						X	X	X	X		
Physalis virginiana	.01						X	X	X	X		
Poa pratensis	51.03	X					X					X
Polygonum coccineum	.01						X	X			X	
Ratibida columnifera	.12						X	X	X	X		
Rosa blanda	.01						X	X	X	X		
Rosa suffulta	.17						X	X	X	X		
Scirpus atrovirens	.33						X	X			X	
Scutellaria leonardii	.01						X	X	X	X		
Senecio pauperculus	.01						X	X	X	X		
Setaria lutescens	.12						X					
Solidago canadensis	20.97		X				X					X
Solidago rigida	.42						X	X	X	X		
Spartina pectinata	.45						X	X			X	
Sporobolus heterolepis	.06						X	X	X	X		
Teucrium canadense	.03						X	X			X	
Trifolium pratense	.03						X					
Vernonia fasiculata	.01						X	X			X	
Viola pedatifida	.05						X	X	X	X		
Viola sp.	.08						X	X	X	X		
Vicia americana	.01						X	X	X	X		
Zizia aurea	.03						X	X	X	X		

possible the influx into the pasture of prairie species. Corresponding changes in the state of the pasture species were also examined by this method. Analysis showed (Table 10) nine of the eleven treatments to possess R^2 values greater than .57, R^2 being interpreted to indicate that proportion of the variation about the fitted surface which is accounted for by regression. Data from Table 10, used to construct diagrams (Figure 36) of the fitted surfaces, indicate that there has been

Table 10. Beta values and their levels of significance for the fitting of a quadratic surface to 30 acres of grazed prairie

Species	Ident. no.	B_0	B_1	B_{11}	B_2	B_{22}	B_{12}	X_3 [a]	X_4 [b]	R^2
Poa pratensis	1	46.45^{**}	5.64^{**}	$.67^{ns}$	5.06^{**}	$-.06^{ns}$	$-.15^{ns}$	-3.99^{ns}	36.95^{*}	.85
Solidago canadensis	2	20.76^{**}	$.88^{*}$	$.08^{ns}$	$.47^{ns}$	$.06^{ns}$	$-.04^{ns}$	-1.32^{ns}	-20.11^{**}	.57
Andropogon gerardi	3	44.05^{**}	-6.16^{**}	-1.02^{*}	-3.27^{**}	$-.16^{ns}$	$-.06^{ns}$	-9.02^{ns}	-25.15^{ns}	.73
Aster ericoides	4	1.35^{**}	$- .01^{ns}$	$- .04^{ns}$	$- .06^{ns}$	$-.01^{ns}$	$.02^{ns}$	$- .19^{ns}$	$- .54^{ns}$	.12
Ambrosia artemisifolia	5	$.28^{ns}$	$.06^{ns}$	$.02^{ns}$	$- .02^{ns}$	$.01^{ns}$	$.00^{ns}$	$.45^{ns}$	1.94^{ns}	.09
Numbers of species	6	9.26^{**}	$- .32^{ns}$	$- .04^{ns}$	$- .11^{ns}$	$.06^{ns}$	$-.05^{ns}$	4.58^{**}	$- .54^{ns}$	.61
All prairie	7	3.36^{**}	$- .15^{ns}$	$.06^{ns}$	$- .44^{**}$	$.02^{ns}$	$-.03^{ns}$	5.63^{**}	$- 5.48^{ns}$	.78
High prairie	8	2.03^{*}	$- .34^{*}$	$.03^{ns}$	$- .20^{ns}$	$-.02^{ns}$	$.01^{ns}$	3.41^{**}	2.35^{ns}	.66

[a] Drainage

[b] *Cirsium arvense*

** Significant at the 1% level

* Significant at the 5% level

ns nonsignificant

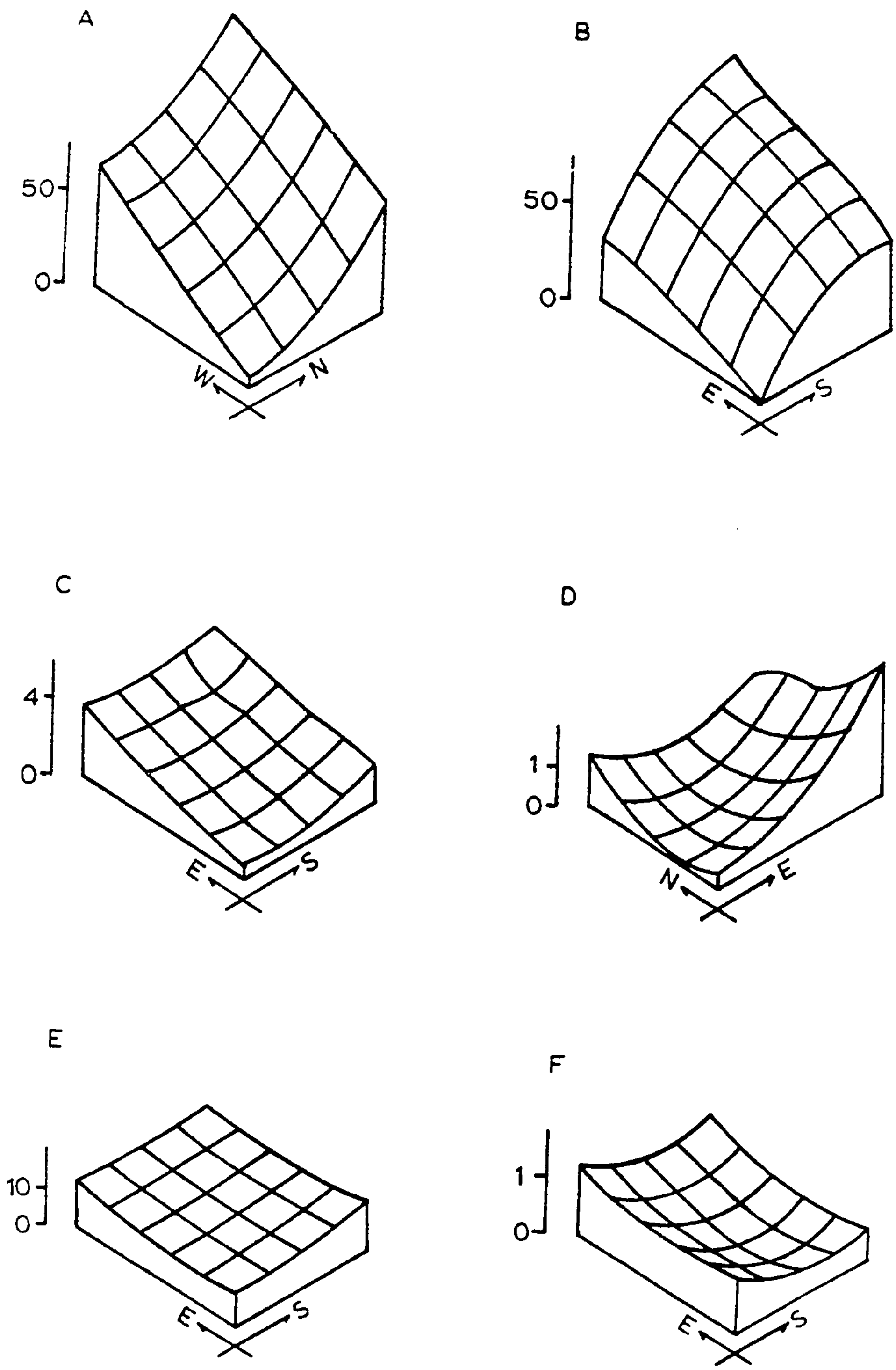
Table 10. (Continued)

Species	Ident. no.	B_0	B_1	B_{11}	B_2	B_{22}	B_{12}	X_3	X_4	R^2
Andropogon gerardi and high prairie	9	47.42^{**}	-6.66^{**}	$-.95^{*}$	-3.72^{**}	$-.23^{ns}$	$.06^{ns}$	-5.48^{ns}	-22.71^{ns}	.76
Low prairie	10	$-.02^{ns}$	$-.10^{ns}$	$.04^{ns}$	$-.13^{ns}$	$.03^{ns}$	$.04^{ns}$	3.83^{**}	$-.82^{ns}$	.85
Solidago canadensis and Poa pratensis	11	63.77^{**}	7.07^{**}	$.79^{*}$	5.59^{**}	$.17^{ns}$	$-.36^{ns}$	-5.31^{ns}	16.85^{ns}	.86

a definite movement of prairie species into the pasture. Figures 36b and 36c show this movement. Figure 36b represents the fitted surface of Andropogon gerardi, and Figure 36c represents a composite of all native prairie species found within the pasture except Andropogon gerardi and Solidago canadensis. Other treatments showing this same kind of surface were 8 (high prairie) and 9 (Andropogon gerardi-high prairie) (Table 9). Figure 36a is the fitted surface of Poa pratensis. This figure is almost a mirror image of the surface representing the advance of Andropogon gerardi; thus it is interpreted to represent the retreat of Poa pratensis. Figures 36d, 36e, and 36f represent low prairie, number of species, and Ambrosia artemisifolia (Table 10). Of these treatments "low prairie" represents a composite of all species common to the drainage areas of native prairie vegetation (Table 9). No suggestion of directional movements of these lowland species can be seen in Figure 36d, but it is interesting to note that the R^2 value for this treatment is .85 and that the treatment is also highly correlated with the drainage factor. The "numbers of species" treatment represented an unsuccessful attempt to discover if the areas nearest the prairie-pasture boundary exhibited greater numbers of species than areas away from the prairie. From Figures 36e and Table 9 it seems that this condition is more closely related to the presence of drainage ways than to the proximity of sites to the prairie-pasture border.

Field observations indicated that there existed an apparent front of the Andropogon gerardi influx into the old pasture. It was of interest to know if this front was an invasion front dependent on time or if it was being restricted in its present position by some environmental factor.

Figure 36. Fitted quadratic surfaces of grazed pasture data demonstrating influx of prairie plants into the area; A = percentage cover of *Poa pratensis*; B = percentage cover of *Andropogon gerardi*; C = composite of upland prairie species; D = composite of lowland prairie and drainage species; E = number of species; F = percentage cover of *Ambrosia artemisifolia*


A
50
0
W
N
B
50
0
E
S
C
4
0
E
S
D
1
0
N
E
E
10
0
E
S
F
1
0
E
S

A contour map, constructed from the cover values of Andropogon gerardi as found within each of the original 30 units (Figure 37), shows the distribution of Andropogon gerardi to be a wave front extending into the pasture from the pasture-prairie border. It seems, therefore, that the observed front is an actual invasion apart from the restriction of environmental factors.

Cole's Index analysis of the pasture data yielded only 11 pairs of positively associated taxa (Table 11). Illustration of these associations revealed three basic clusters. The most prominent cluster (Figure 38a) includes Andropogon gerardi as its center and Achillea lanulosa, Poa pratensis, Solidago canadensis, and Aster ericoides as associated species. Figure 38b illustrates a second cluster which includes species common only to the drainage ways of the pasture: Aster simplex, Carex meadii, Fragaria virginiana, Galium obtusum, Helianthus grosseserratus, Panicum virgatum, and Spartina pectinata. There was on one part of the pasture a small area characterized by Cirsium arvense. Figure 38c represents a cluster of species found within this particular vegetative unit.

It appears that the prairie is in the processes of reestablishing itself within the boundaries of this 35 acres of old pasture. The process is slow as evidenced by old fence lines which are still very visible and by the fact that Andropogon gerardi makes up about 90% of the cover given to the area by prairie species. In another ten years it is likely that the area will be completely dominated by Andropogon gerardi, but it seems doubtful that the area will return to the vegetation type now represented by the major portion of Kalsow Prairie in the next 100 years.

Figure 37. *Andropogon gerardi* invasion of grazed pasture indicated by lines representing percentage cover values

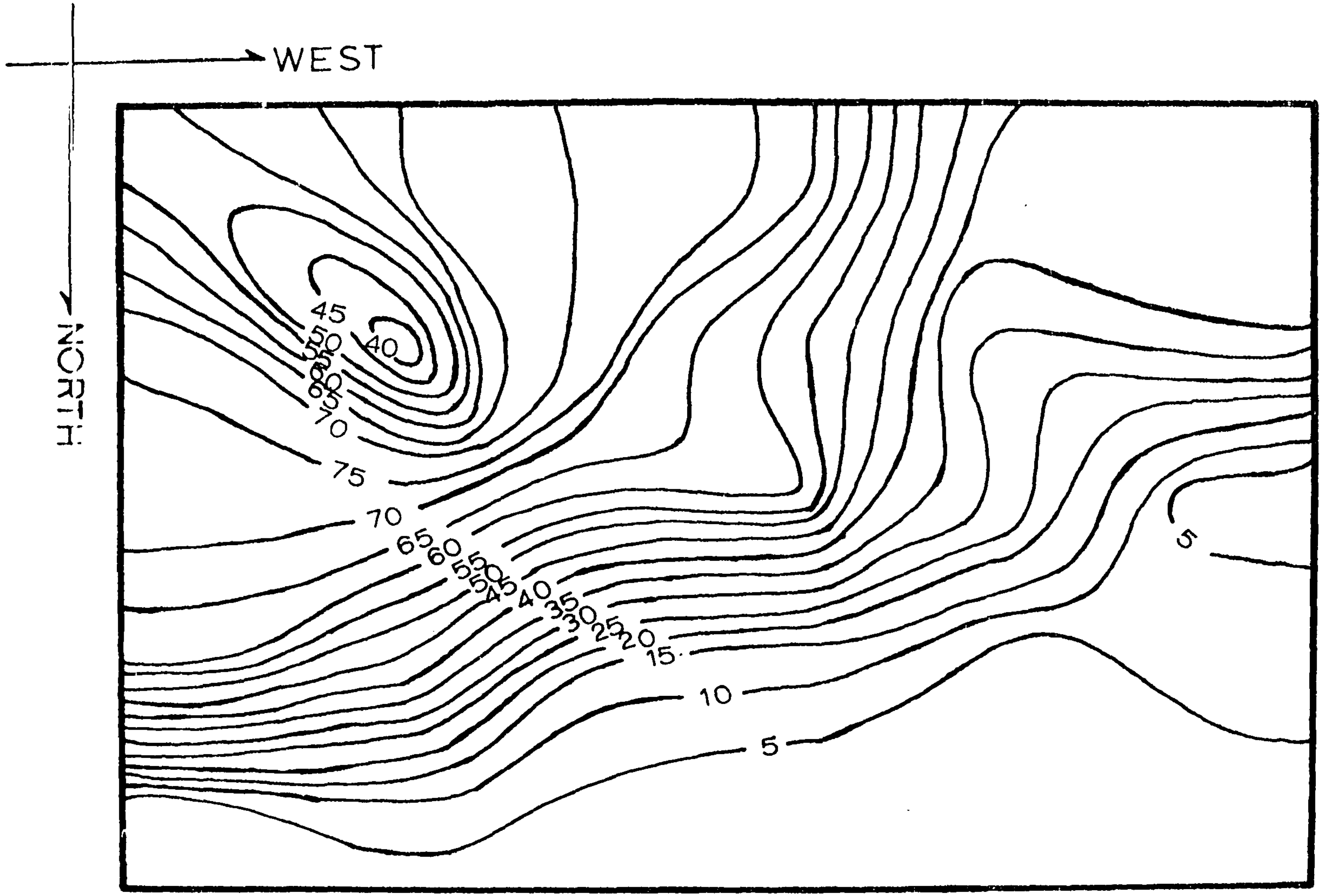

WEST
NORTH
40
45
50
55
60
65
70
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
5

Figure 38. Association groups of species found in grazed pasture, as determined by Cole's (1949) Index, the more lines between species, the greater the association; (A) Ac la = *Achillea lanulosa*, An ge = *Andropogon gerardi*, As er = *Aster ericoides*, Po pr = *Poa pratensis*, So ca = *Solidago canadensis*; (B) As si = *Aster simplex*, Ca gr = *Carex gravida*, Fr vi = *Fragaria virginiana*, Ga ob = *Galium obtusum*, He gr = *Helianthus grosseserratus*, Pa vi = *Panicum virgatum*; (C) As sy = *Asclepias syriaca*, As ve = *Asclepias verticillata*, Ci ar = *Cirsium arvense*; (D) Ra co = *Ratibida columnifera*, So ri = *Solidago rigida*; (E) As la = *Aster laevis*, Ph he = *Physalis heterophylla*

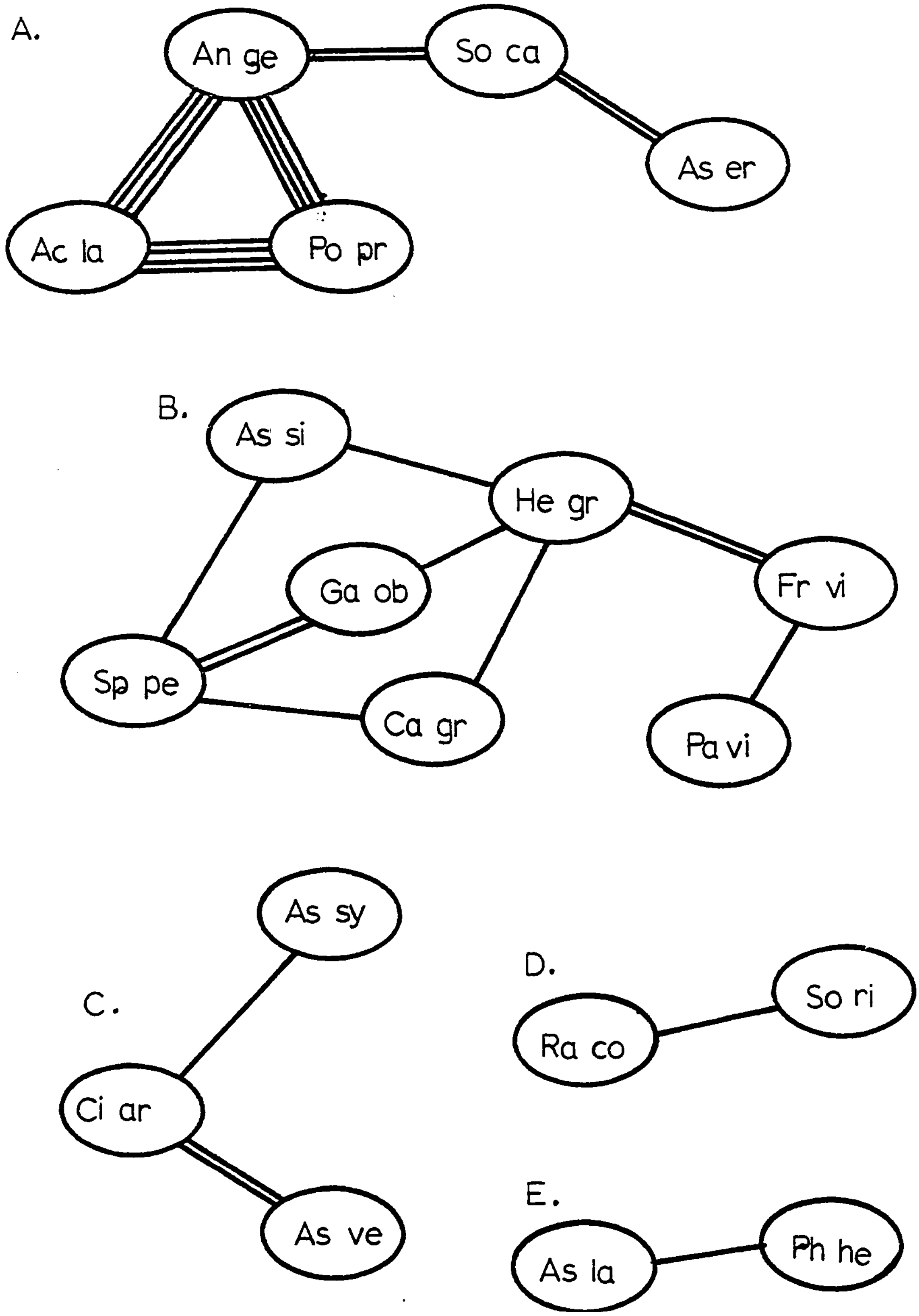

A.
An ge
So ca
As er
Ac la
Po pr
B.
As si
He gr
Ga ob
Fr vi
Sp pe
Ca gr
Pa vi
C.
As sy
Ci ar
As ve
D.
Ra co
So ri
E.
As la
Ph he

Table 11. Cole's Index values expressing positive interspecific association in the grazed pasture

Species	Species	X^{2a}	C_7^b	σ_7^c
Achillea lanulosa	Andropogon gerardi	11.25	.88	.26
Andropogon gerardi	Poa pratensis	4.52	1.00	.47
	Solidago canadensis	19.54	.42	.09
Asclepias syriaca	Cirsium arvense	9.94	.12	.03
Asclepias verticillata	Cirsium arvense	33.87	.65	.11
Aster ericoides	Solidago canadensis	3.67	.52	.26
Aster laevis	Physalis heterophylla	7.56	.18	.06
Aster simplex	Helianthus grosseserratus	16.70	.18	.04
	Spartina pectinata	31.16	.22	.03
Fragaria virginiana	Helianthus grosseserratus	19.00	.57	.12
	Panicum virgatum	28.45	.19	.03
Galium obtusum	Helianthus grosseserratus	15.51	.20	.05
	Spartina pectinata	86.59	.43	.04
Ratibida columnifera	Solidago rigida	4.97	.20	.09
Scirpus atrovirens	Helianthus grosseserratus	24.35	.38	.07
	Spartina pectinata	11.94	.24	.06

[a]Chi-square

[b]Cole's Index

[c]Standard deviation Cole's Index

Border Weed Communities

Lying adjacent to the south and west fences of Kalsow Prairie are large cultivated fields. During late October and early November of 1966 and 1967 these fields were plowed, according to common farming practices in the area. In the springs of 1967 and 1968 high winds deposited soil from the fields in depths, accumulated from previous years also, up to three feet along the south and west boundaries of the prairie (Figure 1). Usually this deposition was in rather narrow strips 10 to 15 feet wide, but in one case near the southeast corner of Kalsow Prairie the width of the deposition exceeded 60 feet.

With this deposition of soil several new communities characterized by the abundance of annual and biennial weeds were introduced into the Kalsow Prairie (Figure 39a). Field observations revealed five types of weed communities associated with the origin and with the age of the deposits. Table 12 includes a list of species and their percentage cover values as found within these five communities.

Community number 1 originated from soil blown in from an adjacent field in soybeans the previous year. It was characterized by Chenopodium album, Amaranthus tamariscinus, Setaria viridis, Ambrosia artemisifolia, and Polygonum persicaria. The species are listed in their order of importance in the community.

Community number 2 originated from soil blown in from an area in corn the previous year. Column 1 represents the 1967 sampling and column 2 represents the 1968 sampling. In 1967 the community was dominated by a foxtail community (Setaria lutescens and Setaria viridis) with smaller amounts of the following broad-leaved weeds: Amaranthus tamariscinus, Chenopodium album, Polygonum pennsylvanicum, and Helianthus annuus. In 1968 there had been an apparent shift in the importance of several species in the community even though still heavily dominated by the foxtails. Setaria lutescens and Helianthus annuus increased in importance while Setaria viridis, Amaranthus tamariscinus, Chenopodium album, and Polygonum pennsylvanicum decreased. Solidago canadensis, a perennial, showed up in the vegetation with an average cover value of 8.00.

Communities 3 and 4 were mowed in the spring of 1968. Column 2 values of both communities in Table 12 represents resampling of the

Figure 39a. Weed community dominated in foreground by Setaria lutescens and Setaria viridis along edge of Kalsow Prairie

Table 12. Percentage cover values of species found in five weed communities on Kalsow Prairie and recorded changes in two of these communities as affected by mowing

Species	1	2		3		4		5
	1968	1967	1968	1967	1968[a]	1967	1968[a]	1967
Agropyron smithii						.75		
Amaranthus retroflexus		.13		8.71	29.59	1.50	6.75	
Amaranthus tamariscinus	27.88	10.75		33.11	2.89			
Ambrosia artemisifolia	7.38		2.88	.46	1.29		3.50	
Ambrosia trifida		.75	.75	10.18	5.38	76.60	81.05	15.20
Amorpha canescens		4.63	2.63		.32			
Andropogon gerardi				.21	.21			
Apocynum sibiricum	.75							
Asclepias sullivantii				.21		.75		
Asclepias syriaca	.75	.36		1.00	.21	.13	3.00	2.50
Aster ericoides			.13	.54				
Brassica nigra		.75		.54				
Bromus inermis				4.18	5.75	16.50		82.50
Calamagrostis canadensis				.04				
Carex gravida				.04		11.75		
Chenopodium album	62.38	7.25	1.50	2.25	9.69	.13	3.75	
Convolvulus sepium	.42	.75	1.63	.64	1.39	.25		4.38
Echinochloa crusgalli		.75		2.57				
Elymus canadensis				.04	.04	.13		
Equisetum kansanum					.07	.13		
Euphorbia serpyllfolia				.04				
Helianthus annuus		3.75	9.25					
Helianthus grosseserratus			3.88	.86	.21	1.88		
Helianthus laetiflorus			5.50	.07	.21			.21
Kochia scoparia				2.29	9.43			
Lathyrus venosus		.88	.13					
Lathyrus palustris			.13					
Muhlenbergia racemosa					.61		.25	
Oxalis stricta		.13		1.14				
Panicum capillare	.13							
Panicum virgatum			.13					
Physalis heterophylla		.75	1.63	.46	.21			.21
Physalis virginiana					.43			
Poa pratensis				10.61	4.60	4.63		2.50
Polygonum coccineum				.04				
Polygonum convolvulus				.46	.57			
Polygonum pennsylvanicum	.75	5.63	.38	8.29	10.86	6.25		

[a]Mowed

Table 12. (Continued)

Species	1	2		3		4		5
	1968	1967	1968	1967	1968[a]	1967	1968[a]	1967
Polygonum persicaria	2.38			5.29	.46			
Portulaca oleracea				.29				
Psoralea argophylla		.13	.13					
Rosa suffulta		.88	4.50	1.07	.82			
Setaria lutescens		38.75	53.50	31.18	4.15		1.50	
Setaria viridis	7.88	36.13	32.38	28.32	20.27		12.50	
Solidago canadensis			8.00	2.29	2.05	.25	1.25	
Spartina pectinata				.04		.13		
Teucrium canadense					.46			
Trifolium pratensis				.04				
Veronicastrum virginicum		.13						
Vicia americana		.13	.13	.04				

communities after such treatment. Community number 3 is located along the south and west fence of Kalsow Prairie and represents a community two or more years old which received various amounts of new dust from the adjacent fields in the spring, 1967. Therefore, it bears the characteristics of communities of several ages. Species characteristic of younger communities and also the dominants of the area were *Amaranthus tamariscinus*, *Setaria lutescens*, *Setaria viridis*, *Polygonum pennsylvanicum*, and *Polygonum persicaria*. Species indicating age in the community were *Ambrosia trifida*, *Poa pratensis*, *Bromus inermis*, *Solidago canadensis*, and *Rosa suffulta*. Mowing of the area apparently did have some effect on the vegetation of the community as is evidenced by increases in the importance of several species (i.e., *Amaranthus retroflexus*, *Chenopodium album*, and *Kochia scoparia*). Several species showing corresponding decreases in importance were *Amaranthus tamariscinus*, *Polygonum persicaria*, Setaria lutescens and Setaria viridis. It is not certain that those changes can be fully or even partially attributed to the effect of mowing because no unmowed areas were available for comparison and because any changes would also most certainly be confounded by new deposits of dust in 1968.

Community 4 is located along the west fence and is characterized by the dominant Ambrosia trifida. Other important species were Bromus inermis, Poa pratensis, Carex gravida and Polygonum pennsylvanicum. The effects of mowing are again unassessable, but it is interesting to note how drastically a disturbance can result in a shift in the importance of several species (Table 12).

Community 5 represents an area which has been relatively stable for some time. It is dominated almost exclusively by Bromus inermis. Other important species were Ambrosia trifida, Convolvulus sepium, and Poa pratensis.

Analysis involving Orloci's (1966) ordination procedure showed no trends when the individual samples were ordinated but did isolate species showing irregular distribution patterns (Figure 39b). These species were Amaranthus retroflexus, Amaranthus tamariscinus, Ambrosia artemisifolia, Ambrosia trifida, Bromus inermis, Chenopodium album, Kochia scoparia, Polygonum pennsylvanicum, Polygonum persicaria, Rosa suffulta, Setaria lutescens and Setaria viridis. These species are in all cases either dominants or sub-dominants of the basic weed communities described in Table 12.

Data from Cole's Index (Table 13) revealed two basic clusters or groups of positively associated species. The largest cluster (Figure 40a)

Figure 39b. Two-dimensional ordination of species bound in weed communities; A = cluster of species not showing distinct distribution patterns, b = Bromus inermis, c = Ambrosia trifida, d = Ambrosia artemisifolia, e = Kochia scoparia, f = Rosa suffulta, g = Polygonum persicaria, h = Chenopodium album, i = Polygonum pennsylvanicum, j = Amaranthus retroflexus, k = Amaranthus tamariscinus, l = Setaria lutescens, m = Setaria viridis

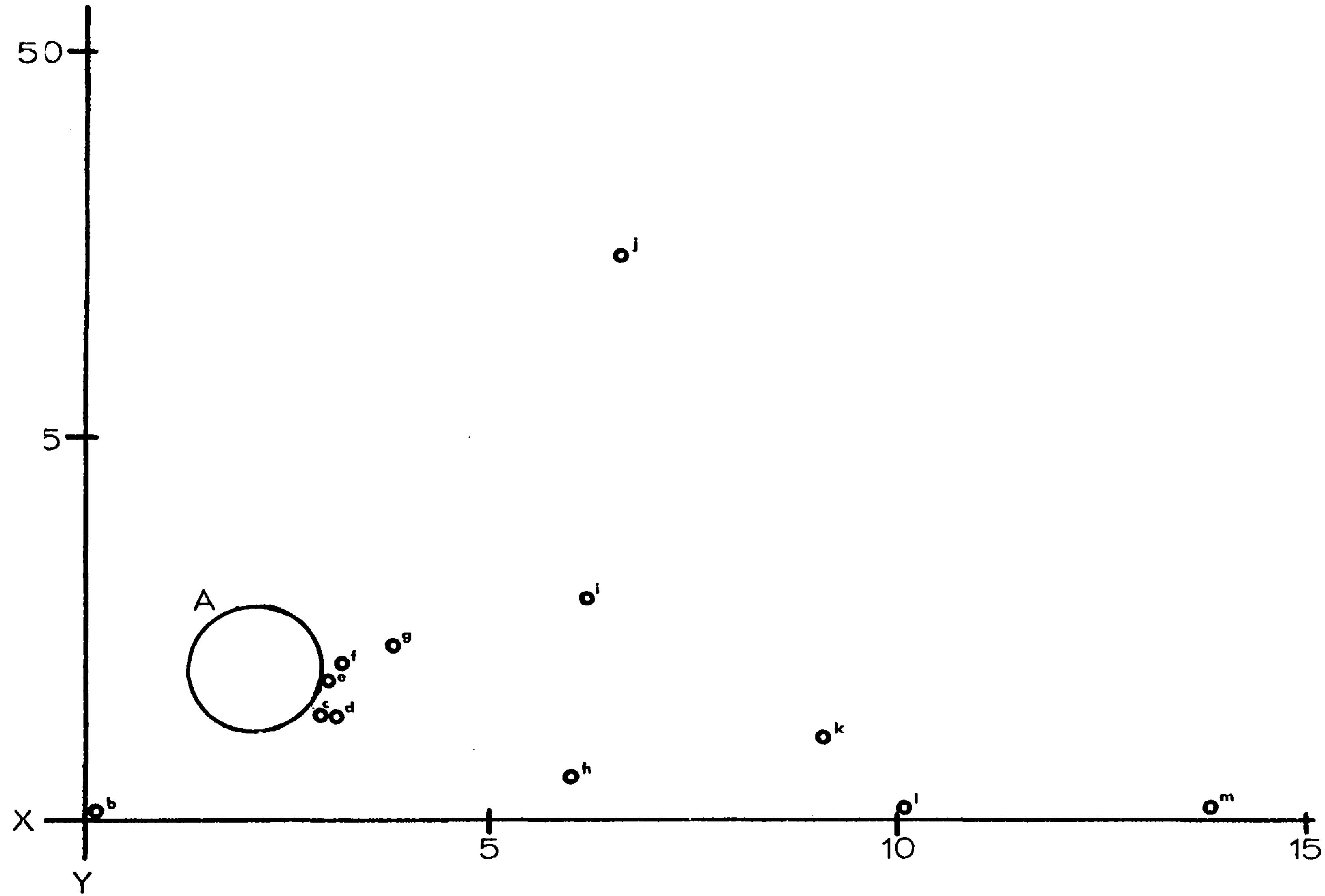

50
5
X
Y
5
10
15
A
b
c
d
e
f
g
h
i
j
k
l
m

Table 13. Cole's Index values expressing positive interspecific association in border weed communities

Species	Species	X^{2a}	$C_7^{\,b}$	$\sigma_7^{\,c}$
Amaranthus retroflexus	Polygonum pennsylvanicum	22.14	.29	.06
	Setaria viridis	19.66	.77	.17
Amaranthus tamariscinus	Setaria lutescens	28.90	.51	.09
	Setaria viridis	19.95	.67	.14
Ambrosia artemisifolia	Chenopodium album	3.88	.24	.12
Ambrosia trifida	Poa pratensis	32.36	.20	.03
Chenopodium album	Setaria viridis	14.69	.69	.18
Echinochloa crusgalli	Setaria lutescens	9.91	.85	.27
Helianthus laetiflorus	Solidago canadensis	5.98	.26	.10
Oxalis stricta	Poa pratensis	9.93	.32	.10
	Polygonum persicaria	4.54	.28	.13
Physalis heterophylla	Solidago canadensis	5.40	.78	.33
Poa pratensis	Solidago canadensis	7.30	.20	.07
Polygonum convolvulus	Setaria lutescens	4.32	1.00	.48
Polygonum pennsylvanicum	Setaria lutescens	8.93	.36	.11
	Setaria viridis	24.43	.93	.18
Polygonum persicaria	Setaria lutescens	4.45	.40	.18
	Setaria viridis	5.86	.73	.29
Rosa suffulta	Setaria lutescens	9.26	.69	.22
Setaria lutescens	Setaria viridis	58.43	.81	.10

[a]Chi-square

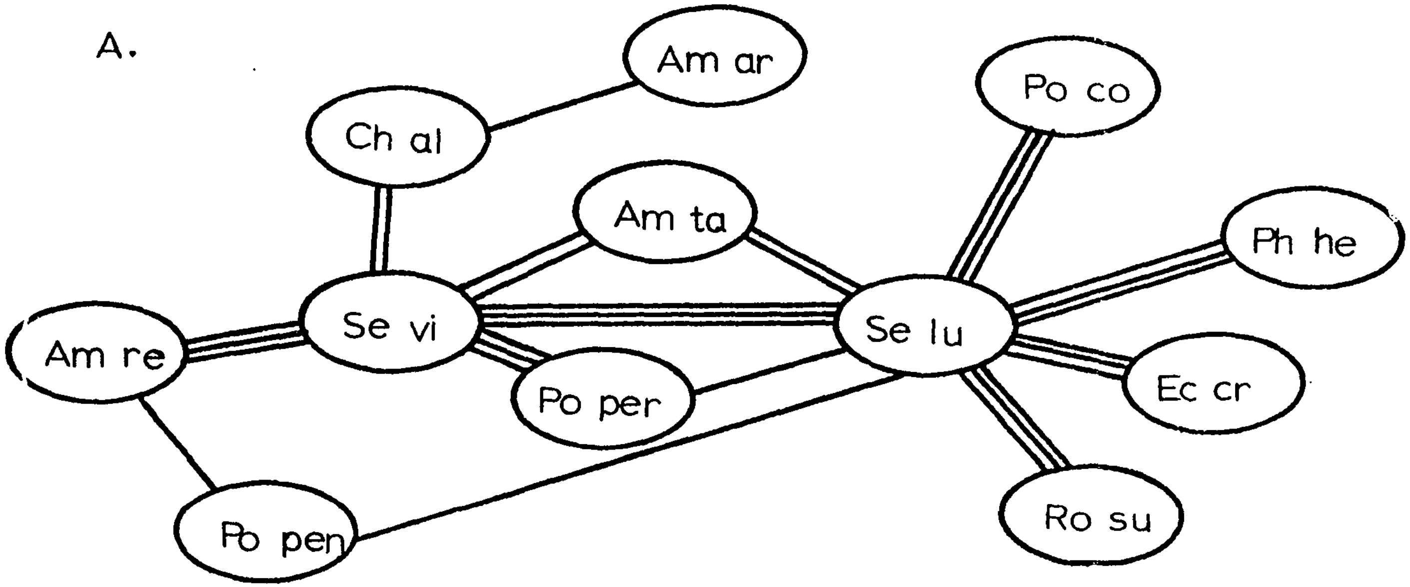
[b]Cole's Index

[c]Standard deviation Cole's Index

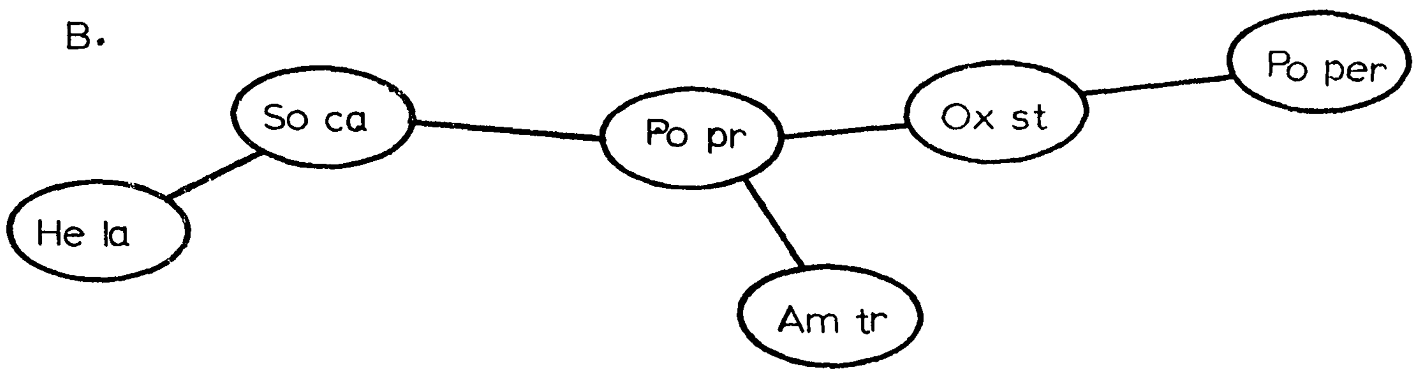
has for a nucleus the two species Setaria lutescens and Setaria viridis. Associated with these species were Amaranthus retroflexus, Amaranthus tamariscinus, Ambrosia artemisifolia, Chenopodium album, Echinochloa crusgalli, Physalis heterophylla, Polygonum convolvulus, Polygonum pennsylvanicum, Polygonum persicaria, and Rosa suffulta. A second cluster, poorly defined (Figure 40b), had for its center Poa pratensis. Its associated species were Ambrosia trifida, Helianthus laetiflorus, Oxalis stricta, Polygonum persicaria and Solidago canadensis.

Figure 40. Association groups of species found in weed communities as determined by Cole's (1949) Index, the more lines between species, the greater the association; (A) Am ar = *Ambrosia artemisifolia*, Am re = *Amaranthus retroflexus*, Am ta = *Amaranthus tamariscinus*, Ch al = *Chenopodium album*, Ec cr = *Echinochloa crusgalli*, Ph he = *Physalis heterophylla*, Po co = *Polygonum convolvulus*, Po pen = *Polygonum pennsylvanicum*, Po per = *Polygonum persicaria*, Ro su = *Rosa suffulta*, Se lu = *Setaria lutescens*, Se vi = *Setaria viridis*; (B) Am tr = *Ambrosia trifida*, He la = *Helianthus laetiflorus*, Ox st = *Oxalis stricta*, Po per = *Polygonum persicaria*, Po pr = *Poa pratensis*, So ca = *Solidago canadensis*

A.


Am ar
Ch al
Po co
Am ta
Ph he
Am re
Se vi
Se lu
Po per
Ec cr
Po pen
Ro su

B.


So ca
Po pr
Ox st
Po per
He la
Am tr

The vegetation of these border communities is undoubtedly a result of the interaction of several factors, but the most important influence is the fall plowing of adjacent cultivated fields and the resulting deposition of dust from these fields. The existence of several types of weed communities appears to be associated with age, depth of deposit, time of most recent dust accumulation, and source of dust. The soil from areas supporting different cultivated crops gave rise to different types of weed communities which changed in basic vegetative structure as they aged. Soil blown in from fields originally in corn supported mainly foxtail communities, whereas soil from soybean fields supported mostly broad-leaved weeds the first year.

In mixed stands or weed communities such as those described above few species are at their potential maximum. Palmblad (1968) indicates that this limitation is regulated first by the number of available microenvironments suitable to germination and second by self-controlled germination, mortality, and individual plasticity. Such sources of variation help explain differences found in the border communities and also aid in understanding the changes which took place in communities 3 and 4 between 1967 and 1968. New depositions or disturbances would provide new microenvironments for germination. When no further disturbance occurs it is possible that differences in self-inhibition, self-controlled germination, mortality, and ecological amplitude between species could well cause reduction of certain annual weedy species and their replacement by others or by perennials or biennials during a growing season.

Selected Environmental Studies

Twenty acres of the prairie adjacent to its southern boundary (Figure 1) were selected for intensive study of the distribution of plant species in relation to soils and topography. The area was chosen because it included within its boundaries a representation of all vegetation types occurring on Kalsow Prairie. The area was staked on a 30 x 30-foot grid which placed 968 points within the 20 acres. From these points all factors included in this study were examined.

The presence of all plant species found in the area was recorded in relation to each 900 square-foot section of the grid. From these presence figures distribution maps for 160 species were constructed. Examples of these maps are shown in Figures 41 through 74. These figures illustrate examples of distribution patterns often shared by several species. Andropogon gerardi (Figure 44) illustrates a type of pattern typical of many species commonly found in the upland prairie. This pattern indicates that these species have wide ecological amplitudes and are limited basically by conditions peculiar to the drainage areas of the prairie. Other species which showed similar distribution patterns were Aster ericoides, Elymus canadensis, Equisetum kansanum, Lithospermum canescens, Petalostemum purpureum, Poa pratensis, Ratibida columnifera, Rosa suffulta, Solidago canadensis, Solidago rigida, Sporobolus heterolepis, and Zizia aurea.

A pattern closely resembling that of Andropogon gerardi but also showing limited distribution on the higher and drier ridges of the area is that exemplified by Silphium laciniatum (Figure 50). Species included under this type of pattern were Desmodium canadense, Fragaria virginiana, Galium obtusum, Helianthus grosseserratus, Heliopsis helianthoides, Liatris pycnostachya, Panicum virgatum, and Spartina pectinata.

The pattern shown by Ambrosia artemisifolia (Figure 42) is limited to the border weed communities. Other species found limited to these areas were Amaranthus tamariscinus, Ambrosia trifida, Brassica nigra, Chenopodium album, Helianthus annuus, Polygonum pennsylvanicum, Polygonum persicaria, Setaria lutescens, and Setaria viridis.

Figure 43 (Amorpha canescens) illustrates a pattern common to species limited to growth on the ridges and lower slopes of the area. This would correspond to areas composed mainly of Clarion, Nicollet and Webster soil types (Figure 75). When compared with the pattern exhibited by Andropogon gerardi this type shows a narrowing ecological amplitude and decrease in the ability of species exhibiting this type of pattern to compete in lowland areas. Other species showing this type of pattern were Achillea lanulosa, Arabis hirsuta, Asclepias syriaca, Asclepias tuberosa, Aster laevis, and Panicum leibergii.

Several species found limited in distribution to the mid and upland slopes of the prairie exemplify the pattern shown by Solidago nemoralis (Figure 45). These species were Eryngium yuccifolium, Solidago gymnospermoides, Solidago riddellii, and Viola pedatifida. Such species show rather narrow ecological amplitudes when compared with the groups discussed earlier.

Another group exhibiting rather narrow ranges in distribution are characterized by the patterns shown in Figures 54 and 55. These species, Artemisia ludoviciana, Ceanothus americanus, Echinacea pallida, Helianthus *laetiflorus*, *Lathyrus venosus*, *Lespedeza capitata*, *Liatris aspera*, *Petalostemum candidum*, *Potentilla arguta*, *Psoralea argophylla*, *Solidago missouriensis*, and *Stipa spartea*, are found occupying the ridges and drier sites of the prairie. This would correspond to the Clarion, Clarion-Nicollet, and Nicollet areas of Figure 75.

A final group of species limited from growth in the drainage areas of the prairie show a pattern characteristic of those found in Figure 41 (*Agropyron smithii*) and Figure 49 (*Helenium autumnale*). Here again the ecological amplitudes of these species are narrow when compared with *Andropogon gerardi* or *Sporobolus heterolepis*. As can be seen the distribution of these species corresponds closely to the borders of the pothole and drainage complex; thus these species mainly occupy soils which are characterized by being highly calcareous to the surface. Other species exhibiting this type of distribution are *Agrostis alba*, *Aster simplex*, *Lycopus americanus*, *Lysimachia quadriflora*, *Lythrum alatum*, *Senecio pauperculus* and *Viola* sp.

Species restricted in occurrence to the potholes and drainage ways of the area were found to exhibit two types of distributional patterns. The first, shown by *Calamagrostis canadensis* in Figure 46, corresponds generally to the shallower areas of the drainage system. The pattern shown by Figure 46 also includes the species *Apocynum sibiricum*, *Asclepias incarnata*, *Carex aquatilis*, *Carex lasiocarpa*, *Carex retrorsa*, *Phalaris arundinacea*, *Teucrium canadense*, and *Vernonia fasiculata*. The areas covered by these species correspond generally to the Glenco soils as shown in Figure 75. The second, illustrated by *Carex atherodes* and *Scirpus fluviatilis* in Figures 47 and 48, is more restricted in extent than the above and corresponds to the deeper areas within the drainage system. Species occupying areas equivalent to those shown in Figures 47 and 48 were Lysimachia hybrida, Polygonum coccineum, and Mentha arvensis. These areas correspond to Glenco-Okoboji and Okoboji soil locations as shown in Figure 75.

In several cases it was noted that two species belonging to the same genus showed opposing patterns of distribution. Examples of this phenomenon are illustrated by the species Aster laevis and Aster simplex, Figures 51 and 52; Helianthus grosseserratus and Helianthus laetiflorus, Figures 59 and 60; and Liatris aspera and Liatris pycnostachya, Figures 61 and 62.

Other species were shown to have patterns corresponding to the distribution of Mima mounds found within the area (Figure 9). Such patterns are shown by Convolvulus sepium (Figure 56) and by Oxalis stricta (Figure 65).

Many factors affect the distribution of a species within the community. It has been shown that individuals of different taxa seldom have identical spatial arrangements within an area (Greig-Smith, 1964), yet as shown above, the distribution patterns of some species may be similar and often show overlapping boundaries. Such species may be closely associated due to preferences for similar microenvironments or as in the case of Andropogon gerardi because of wide ecological amplitude. Generally these differences in the local distribution of species have been attributed to local microenvironments (i.e., Mima mounds, animal burrows, ridge tops, and drainage ways), interspecific competition (i.e., allelopathy, shade tolerance, etc.), species biology (i.e., modes

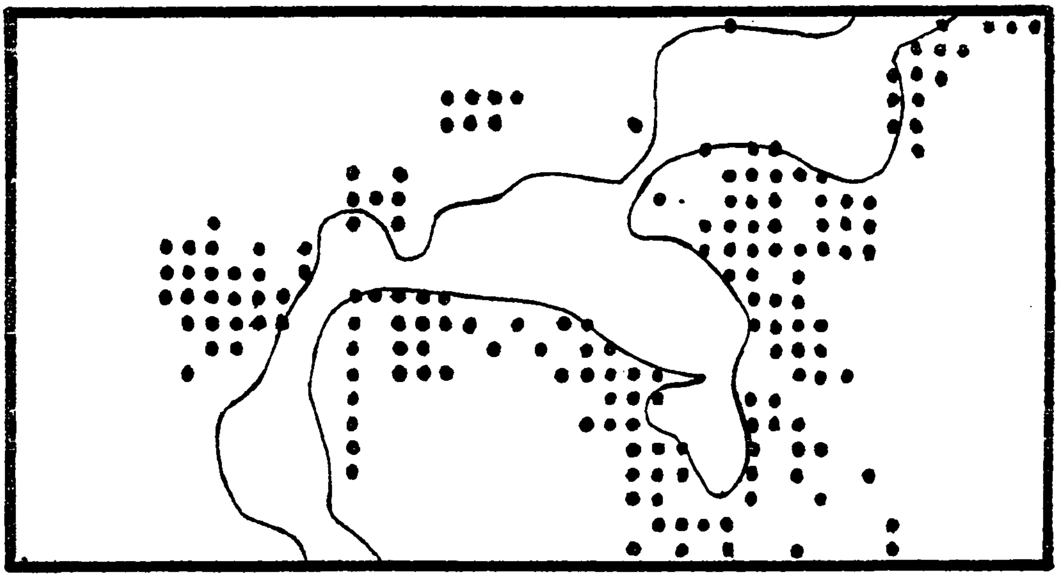


Figure 41. Distribution pattern of Agropyron smithii in the 20-acre intensive study plot

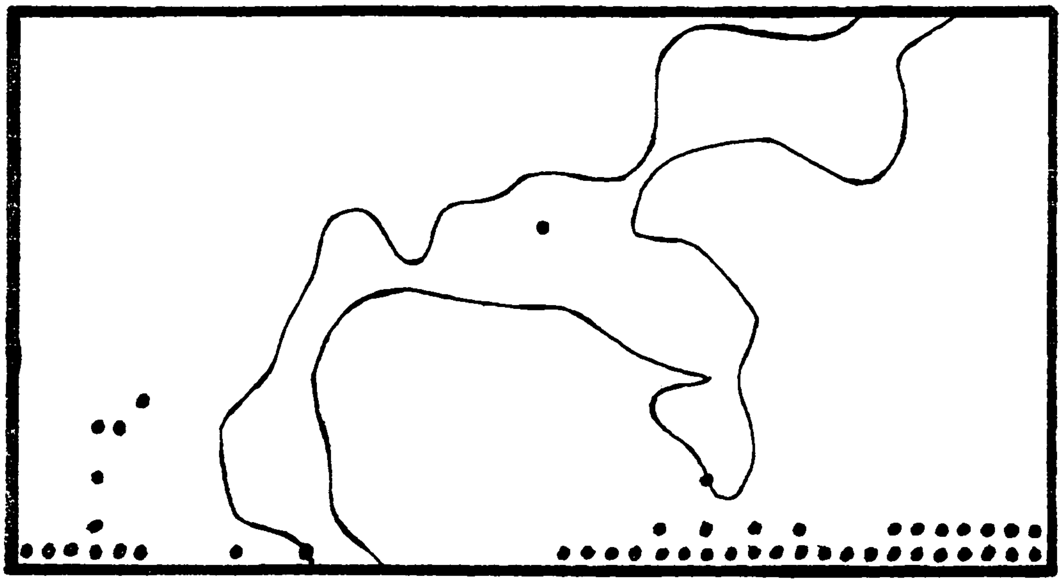


Figure 42. Distribution pattern of Ambrosia artemisifolia in the 20-acre intensive study plot

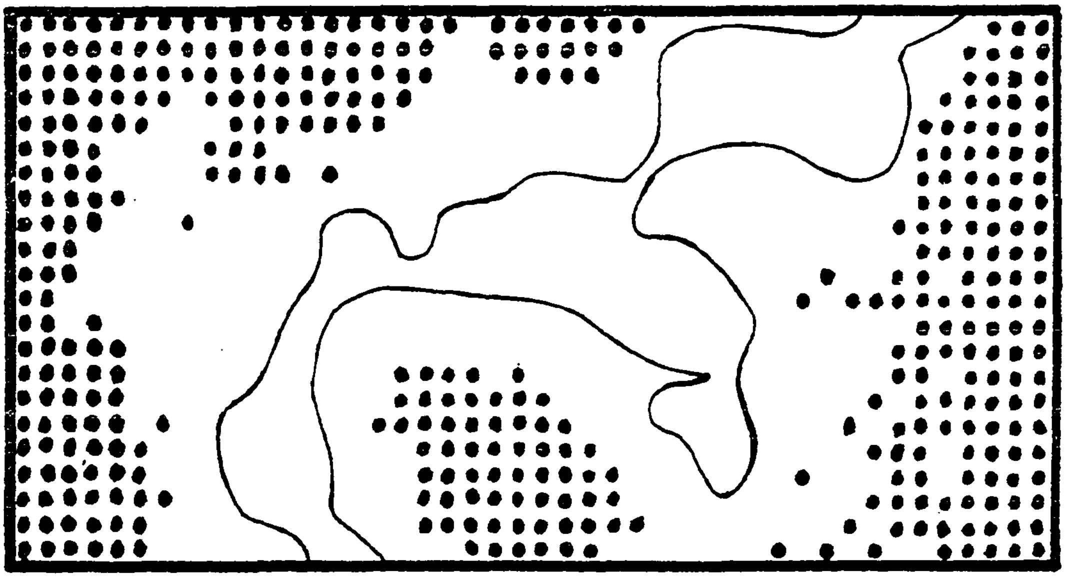


Figure 43. Distribution pattern of Amorpha canescens in the 20-acre intensive study plot

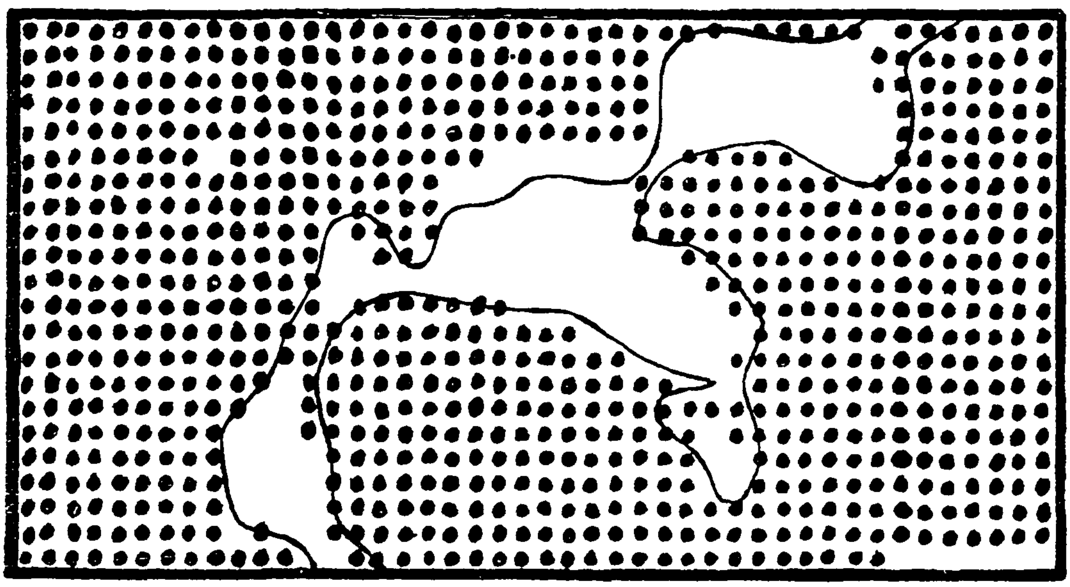


Figure 44. Distribution pattern of Andropogon gerardi in the 20-acre intensive study plot

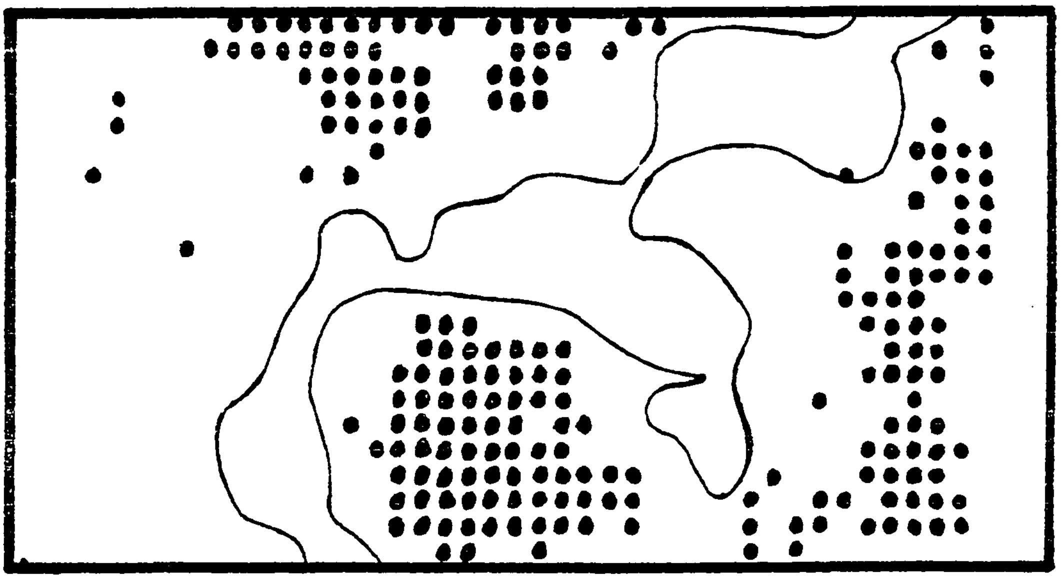


Figure 45. Distribution pattern of Solidago nemoralis in the 20-acre intensive study plot

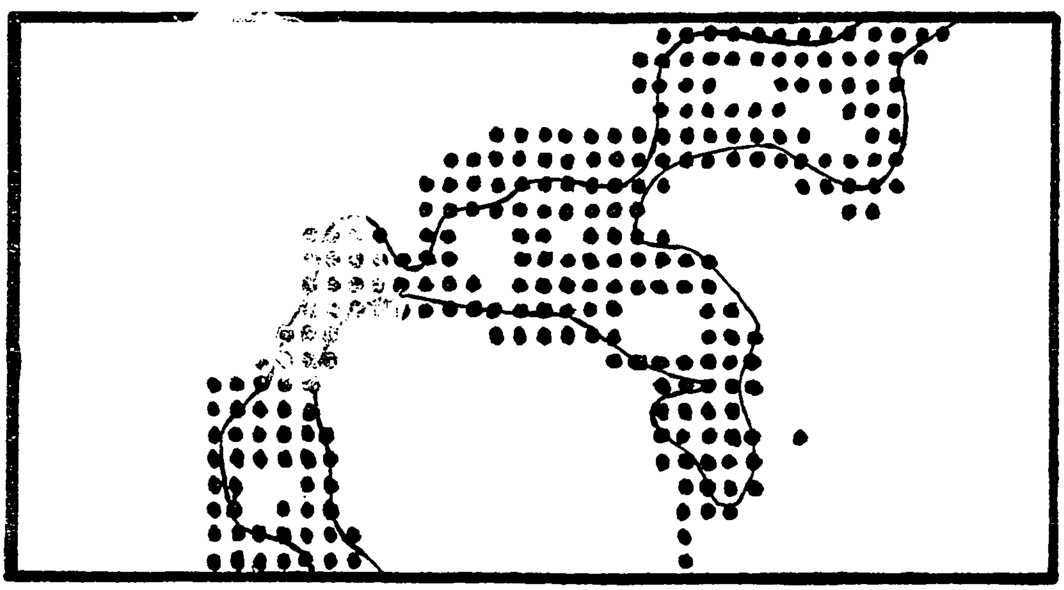


Figure 46. Distribution pattern of Calamagrostis canadensis in the 20-acre intensive study plot

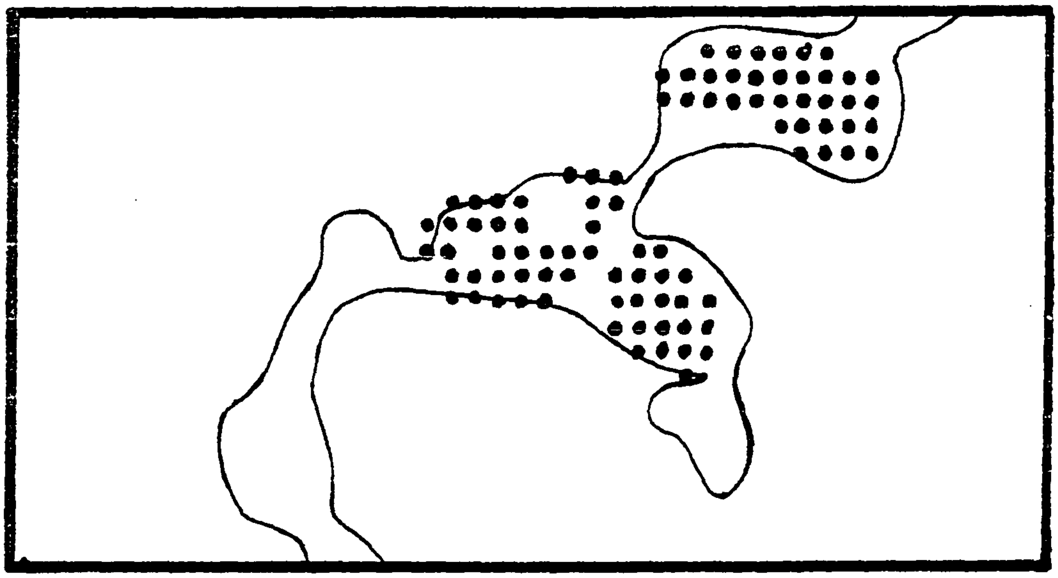


Figure 47. Distribution pattern of Carex atherodes in the 20-acre intensive study plot

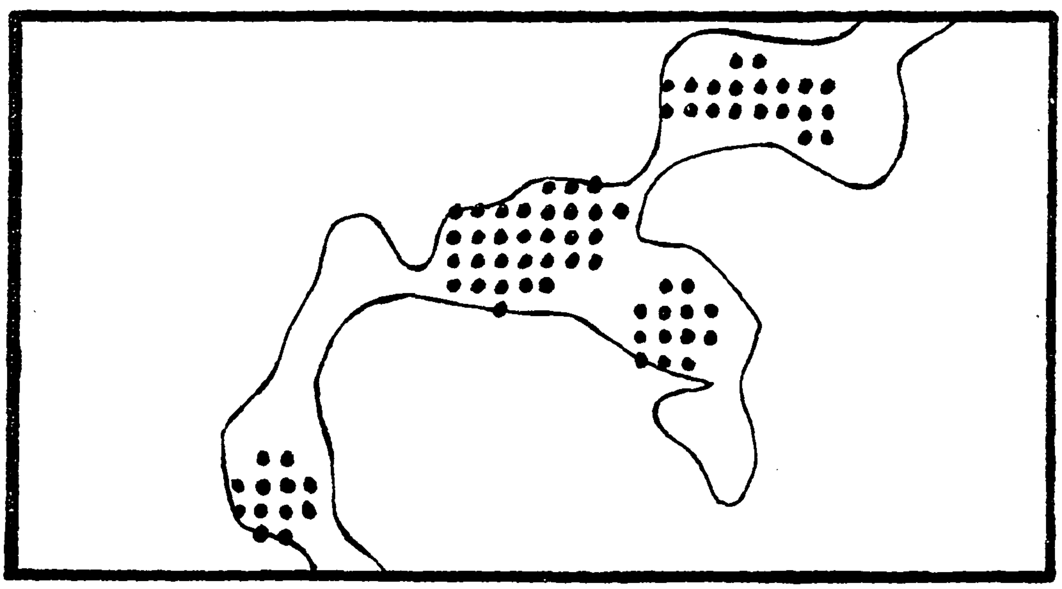


Figure 48. Distribution pattern of Scirpus fluviatilis in the 20-acre intensive study plot

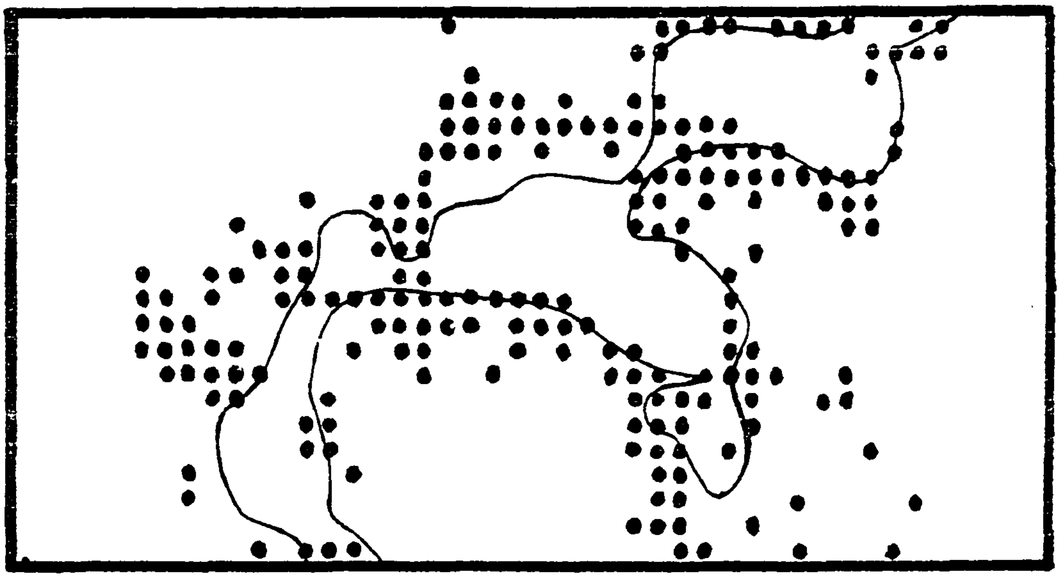


Figure 49. Distribution pattern of Helenium autumnale in the 20-acre intensive study plot

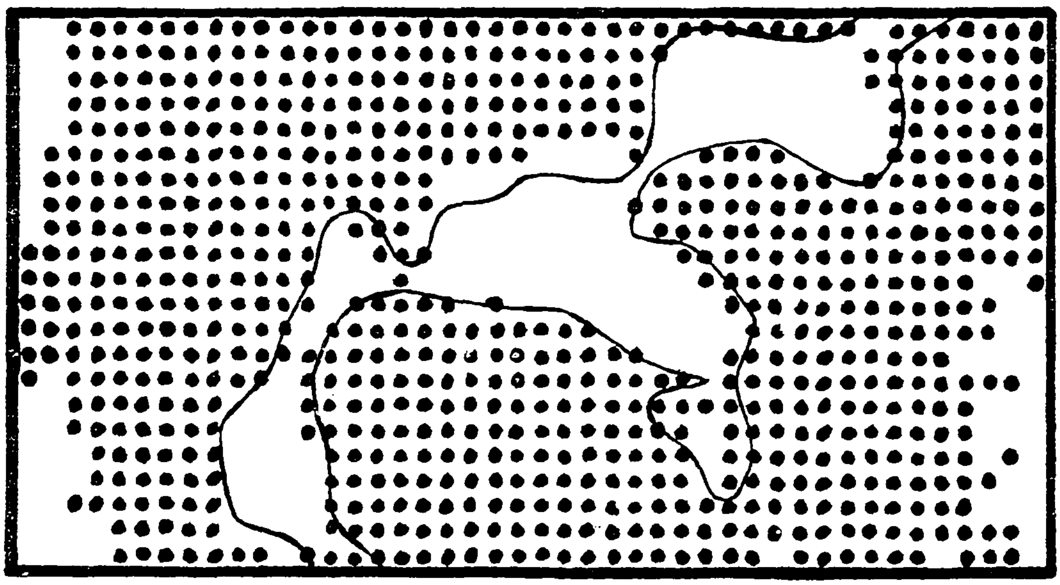


Figure 50. Distribution pattern of Silphium laciniatum in the 20-acre intensive study plot

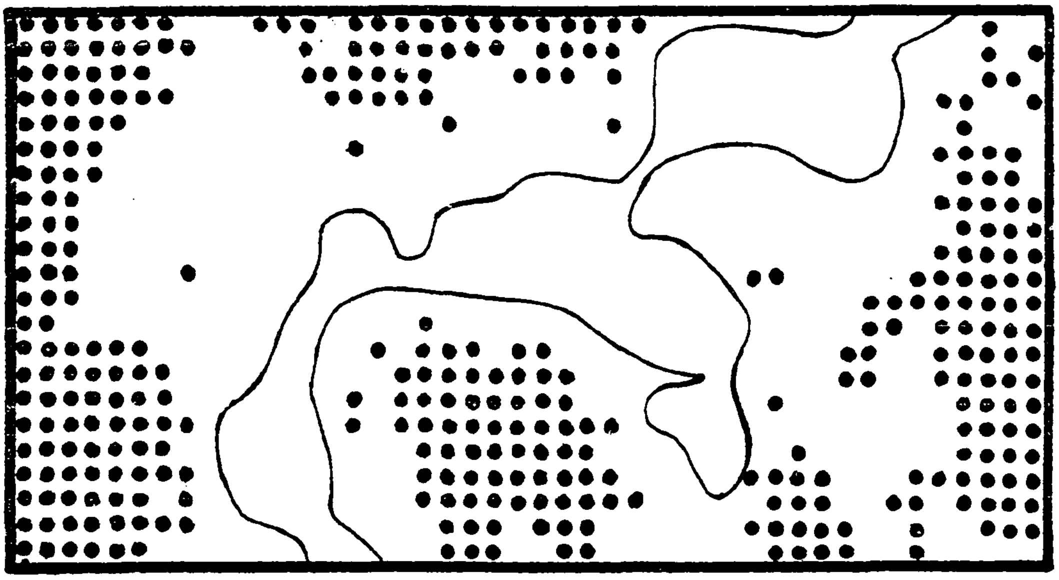


Figure 51. Distribution pattern of Aster laevis in the 20-acre intensive study plot

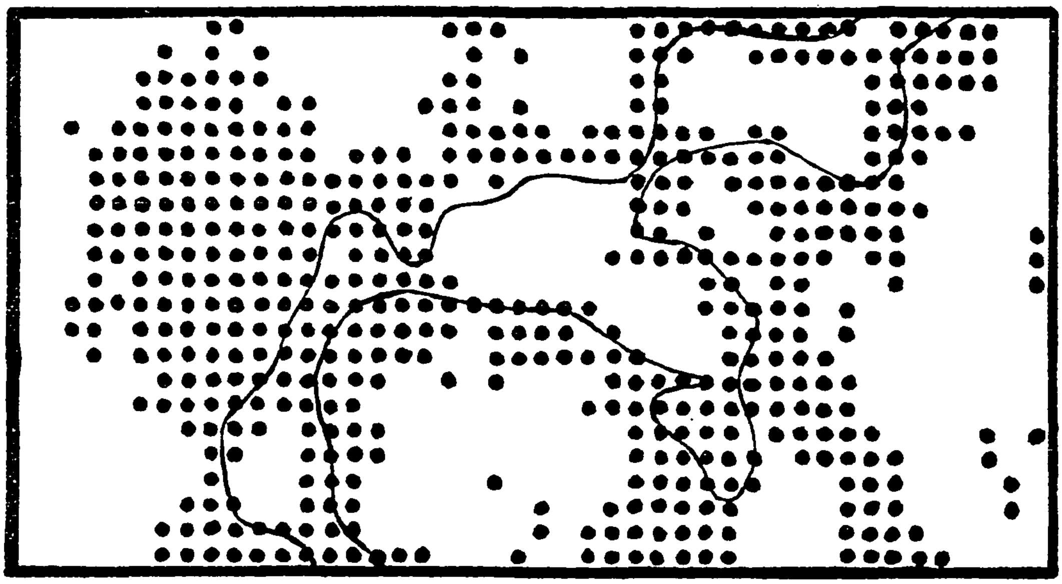


Figure 52. Distribution pattern of Aster simplex in the 20-acre intensive study plot

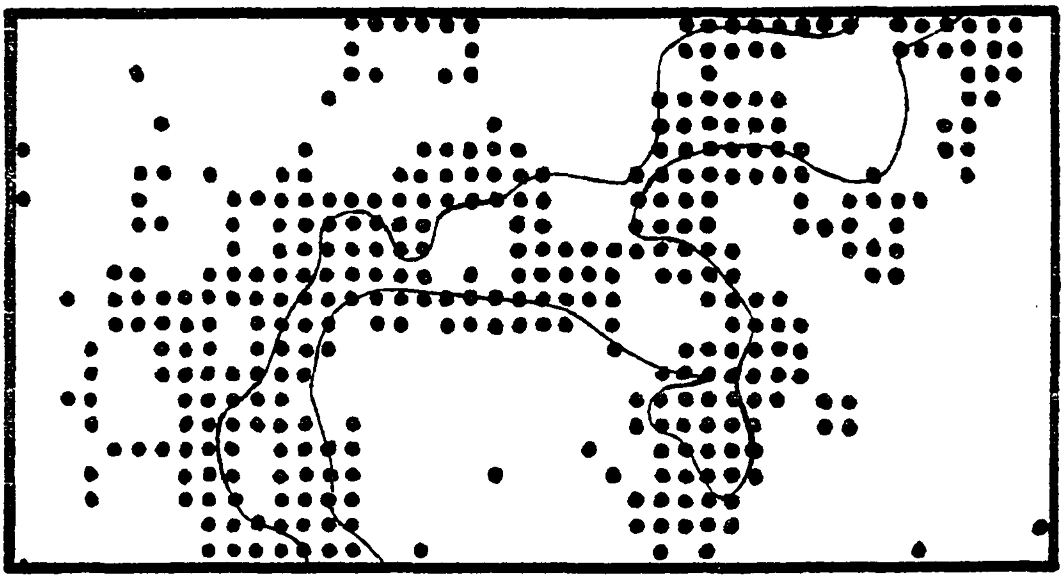


Figure 53. Distribution pattern of Apocynum sibiricum in the 20-acre intensive study plot

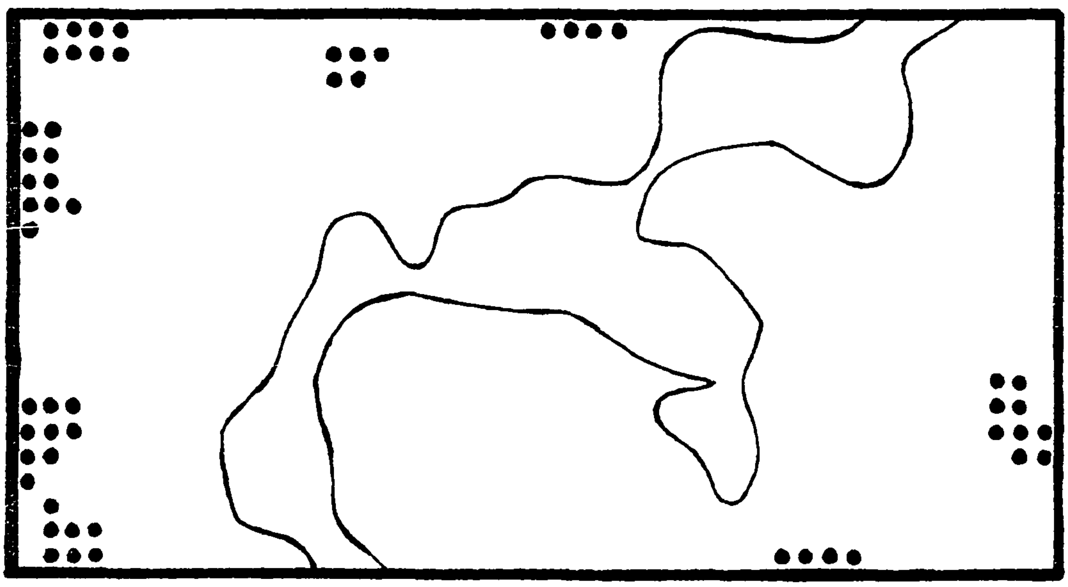


Figure 54. Distribution pattern of Artemisia ludoviciana in the 20-acre intensive study plot

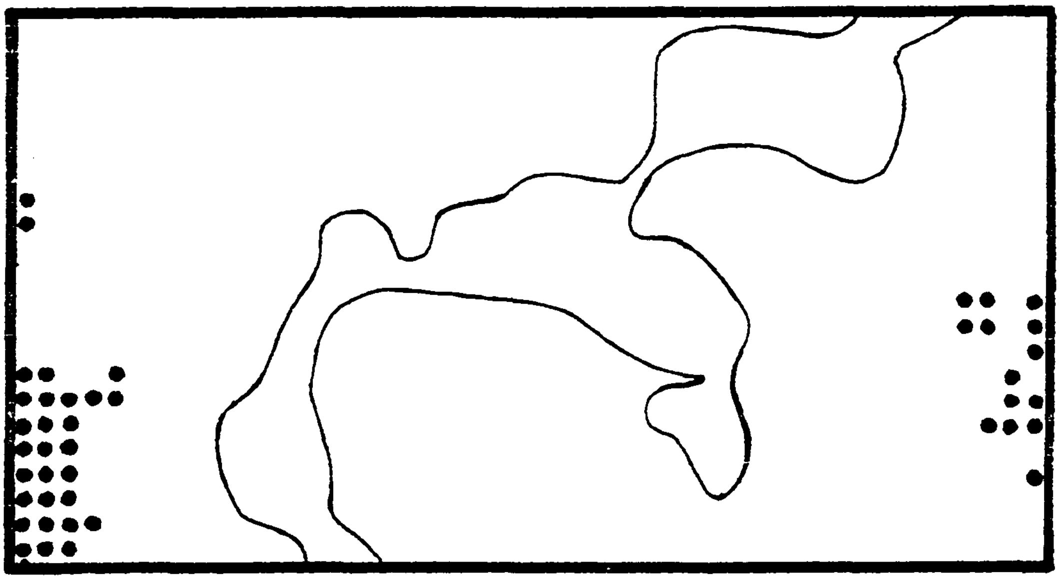


Figure 55. Distribution pattern of Ceanothus americanus in the 20-acre intensive study plot

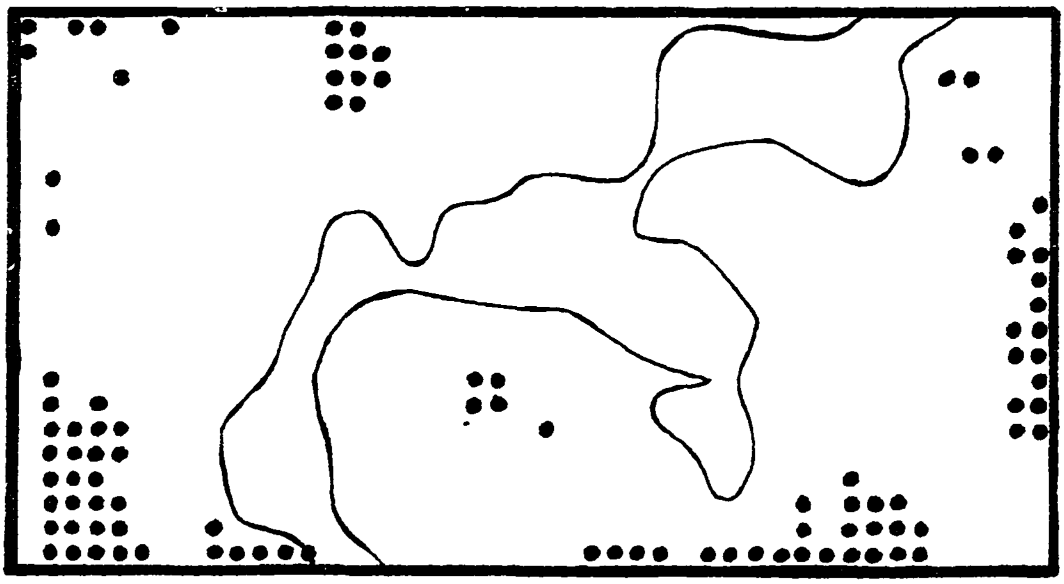


Figure 56. Distribution pattern of Convolvulus sepium in the 20-acre intensive study plot

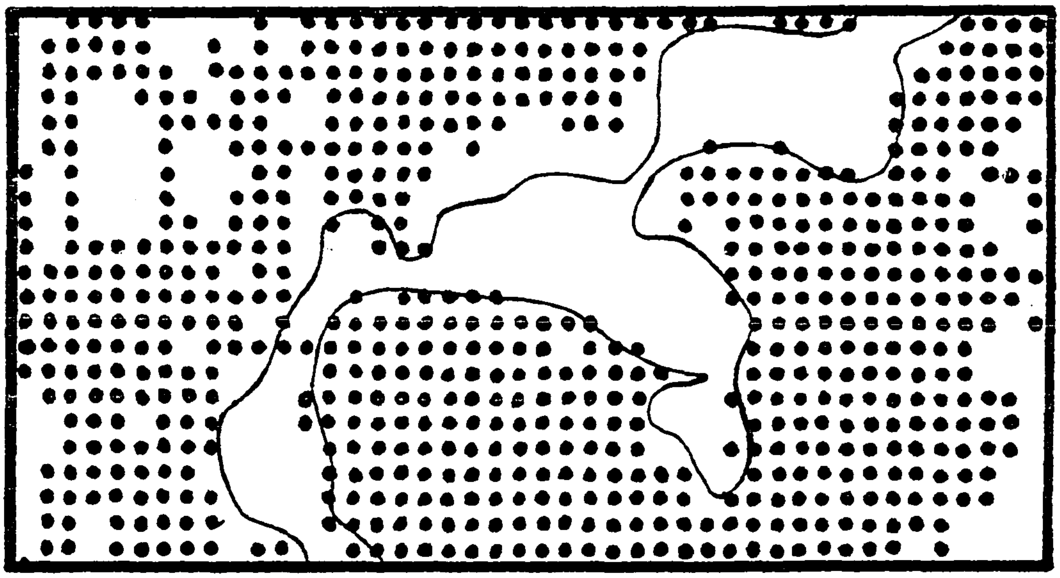


Figure 57. Distribution pattern of Desmodium canadense in the 20-acre intensive study plot

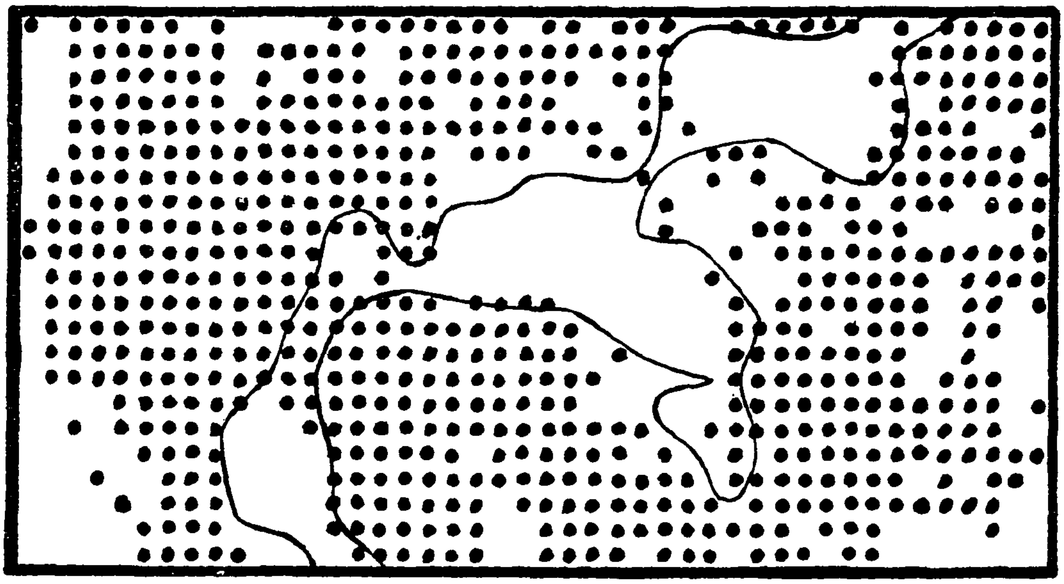


Figure 58. Distribution pattern of Fragaria virginiana in the 20-acre intensive study plot

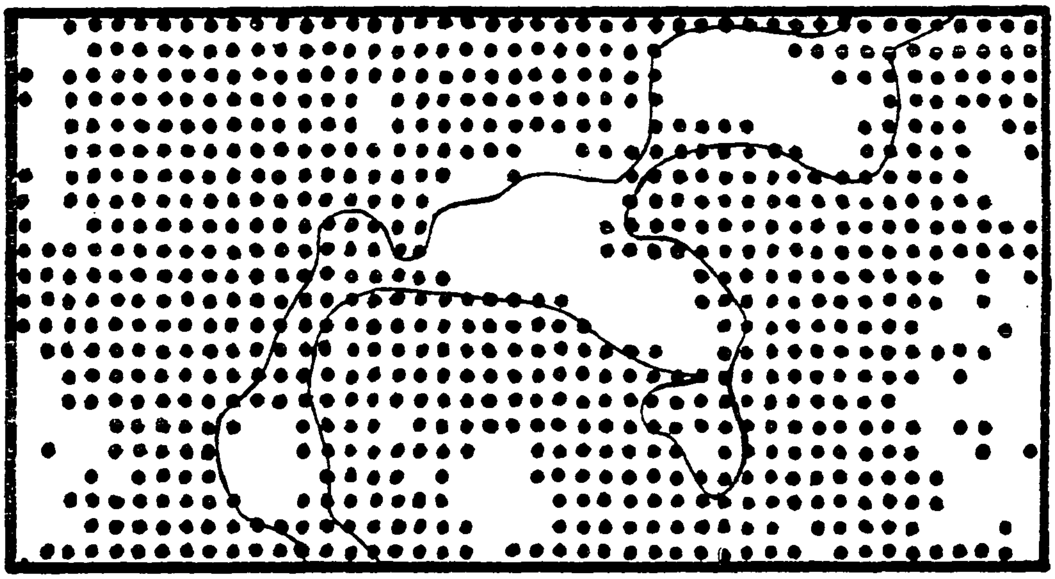


Figure 59. Distribution pattern of Helianthus grosseserratus in the 20-acre intensive study plot

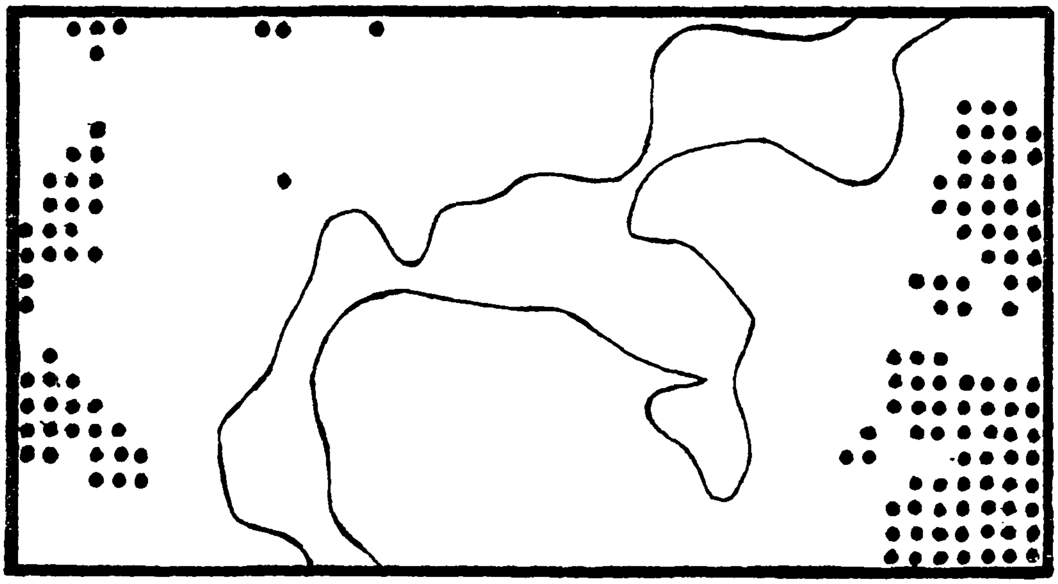


Figure 60. Distribution pattern of Helianthus laetiflorus in the 20-acre intensive study plot

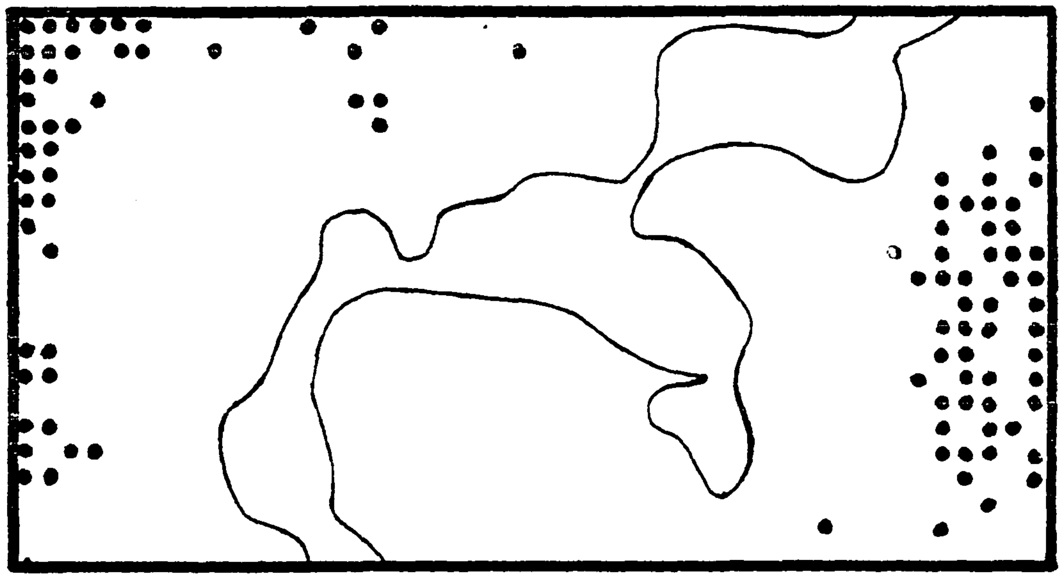


Figure 61. Distribution pattern of Liatris aspera in the 20-acre intensive study plot

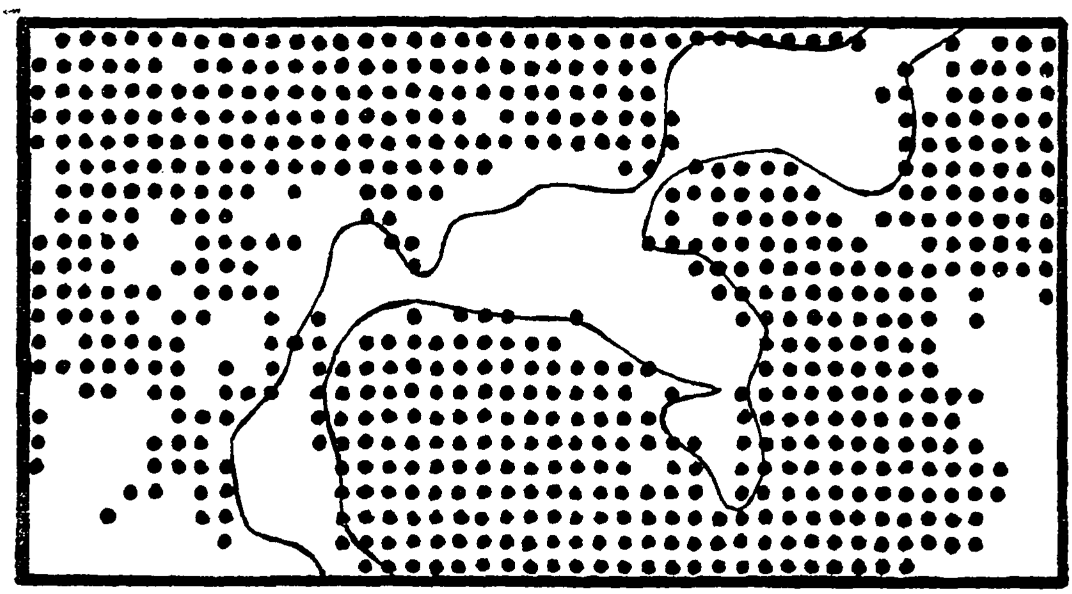


Figure 62. Distribution pattern of Liatris pycnostachya in the 20-acre intensive study plot

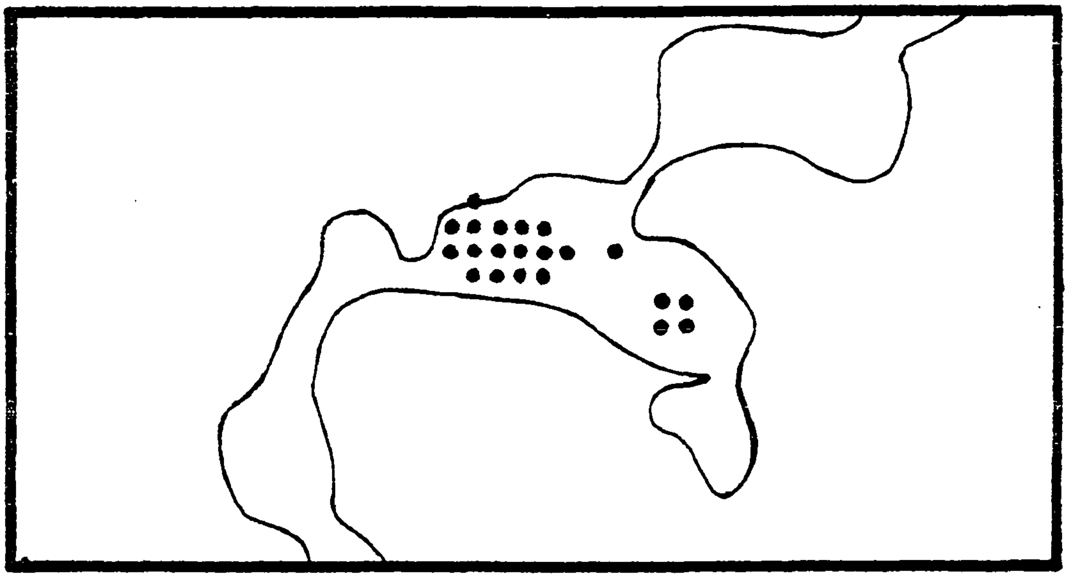


Figure 63. Distribution pattern of *Lysimachia hybrida* in the 20-acre intensive study plot

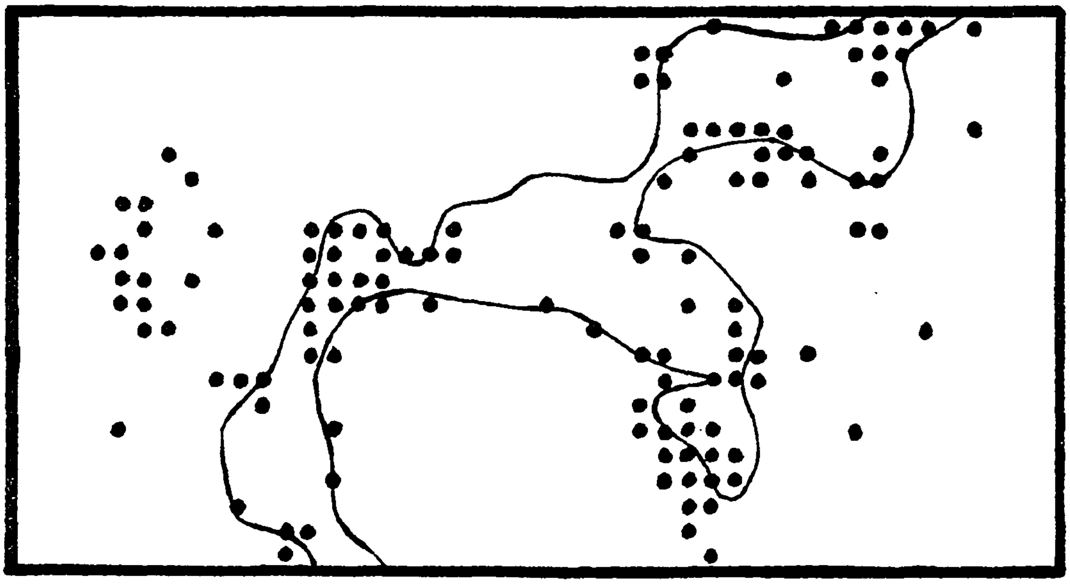


Figure 64. Distribution pattern of *Lycopus americanus* in the 20-acre intensive study plot

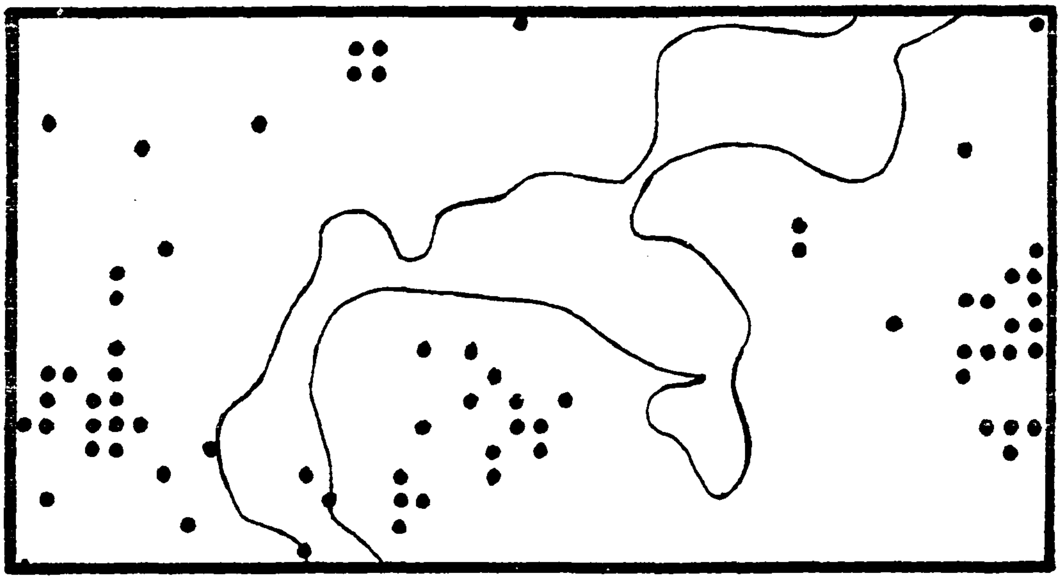


Figure 65. Distribution pattern of Oxalis stricta in the 20-acre intensive study plot

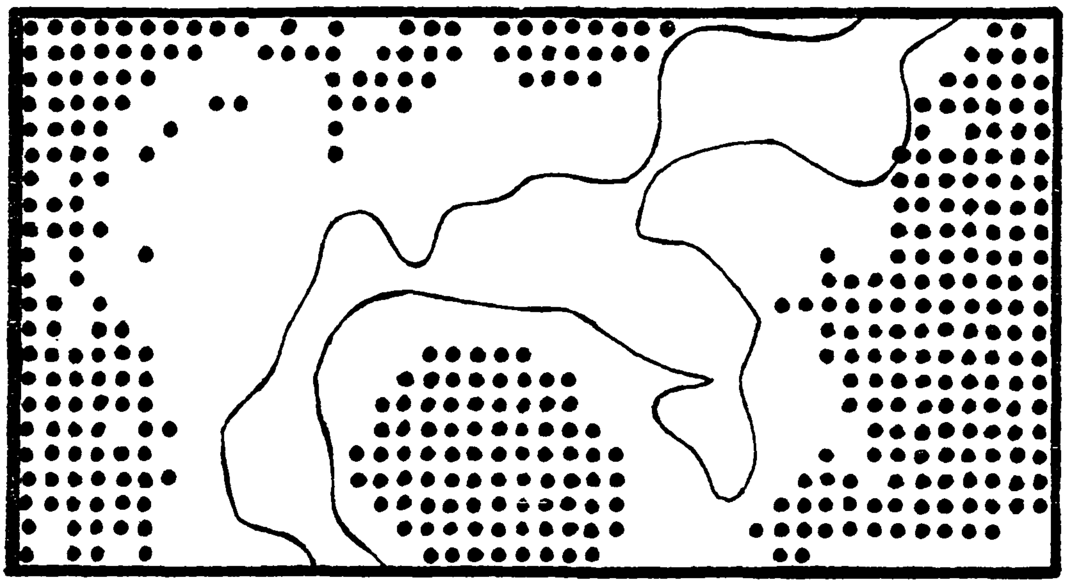


Figure 66. Distribution pattern of Panicum leibergii in the 20-acre intensive study plot

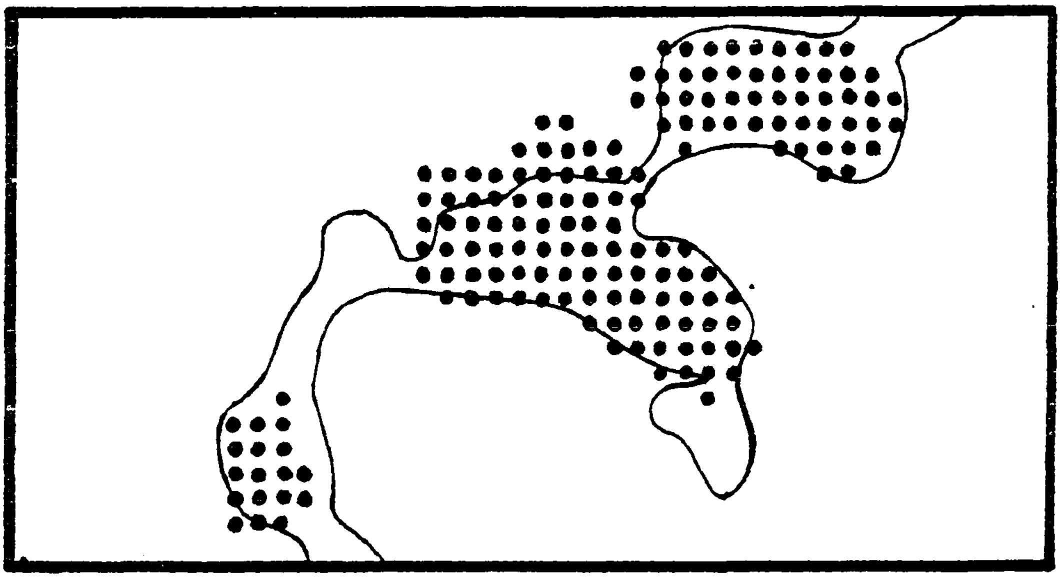


Figure 67. Distribution pattern of Polygonum coccineum in the 20-acre intensive study plot

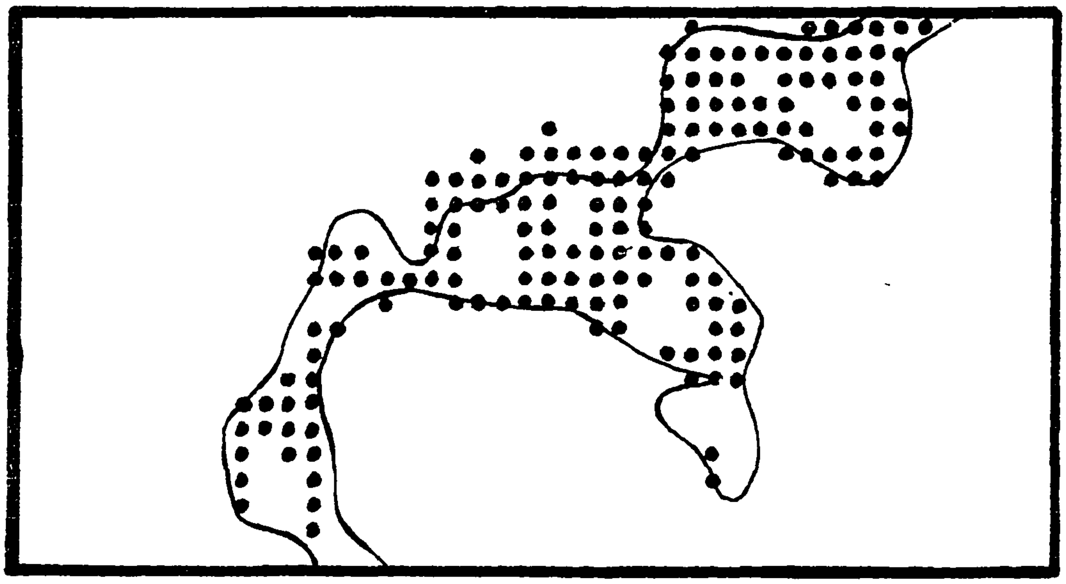


Figure 68. Distribution pattern of Phalaris arundinacea in the 20-acre intensive study plot

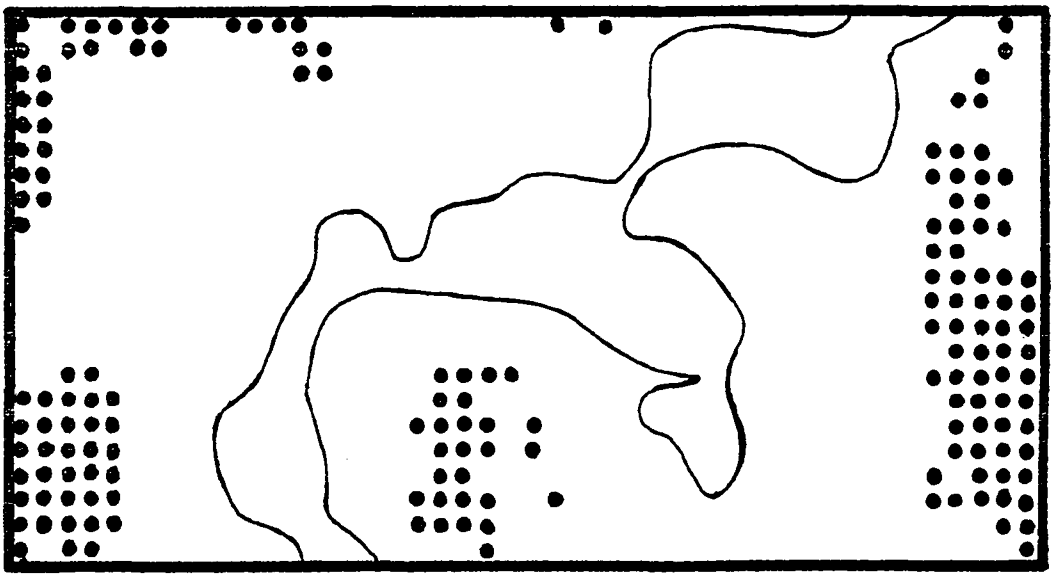


Figure 69. Distribution pattern of Psoralea argophylla in the 20-acre intensive study plot

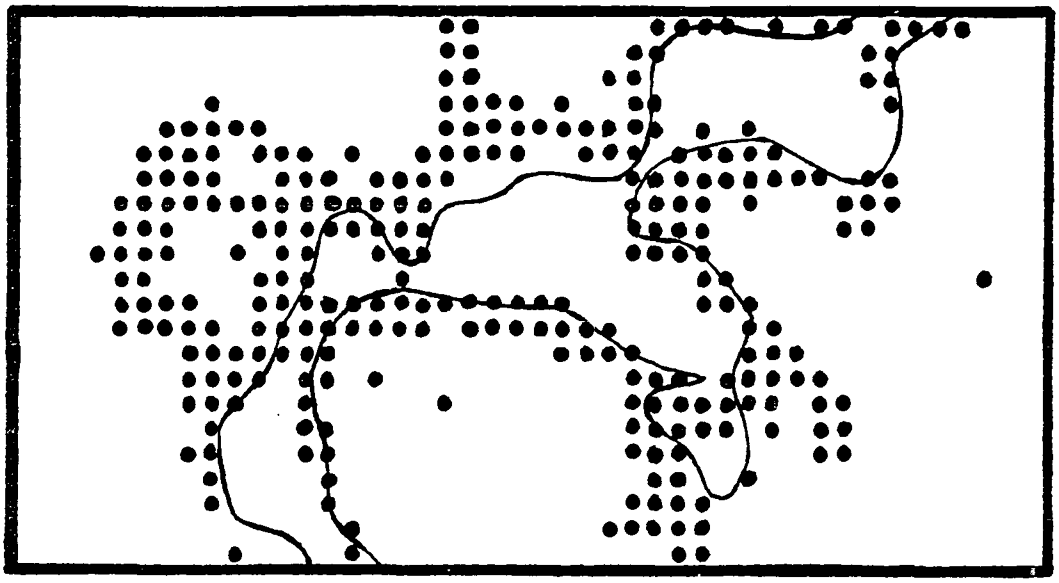


Figure 70. Distribution pattern of Senecio aurens in the 20-acre intensive study plot

Figure 71. Distribution pattern of Spartina pectinata in the 20-acre intensive study plot

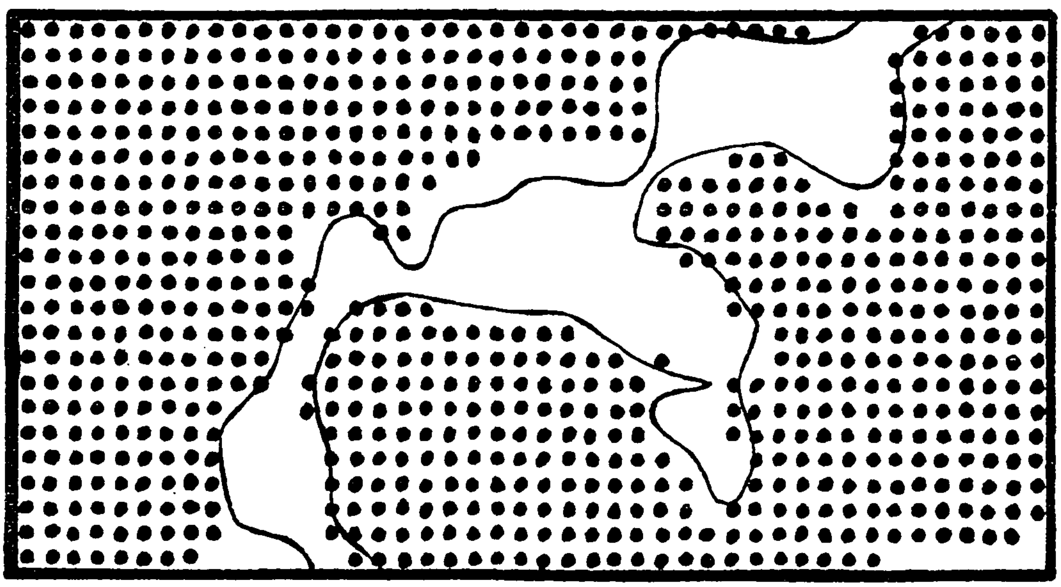


Figure 72. Distribution pattern of Sporobolus heterolepis in the 20-acre intensive study plot

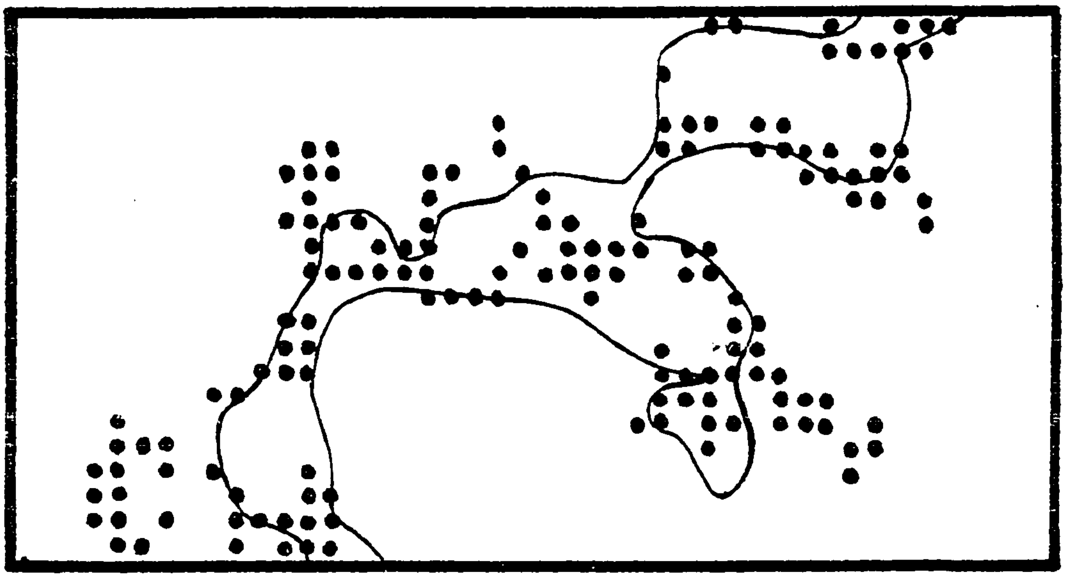


Figure 73. Distribution pattern of Teucrium canadense in the 20-acre intensive study plot

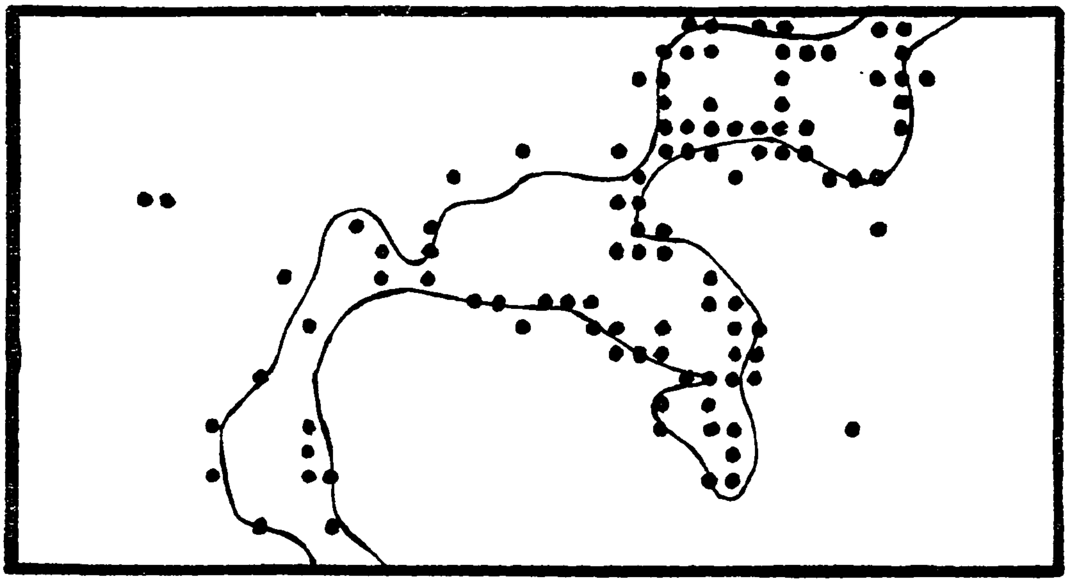


Figure 74. Distribution pattern of Vernonia fasiculata in the 20-acre intensive study plot

of reproduction, seed dispersal, immigration rates, etc.), or one to several edaphic factors (soil and water regimes, macronutrients, micronutrients, texture, organic matter, etc.) (Curtis, 1959; Greig-Smith, 1964; Kershaw, 1964). From this we can conclude that species showing similar patterns of distribution may be equally well adapted in their response to one or more environmental stimuli and yet differ greatly in their basic ecological amplitudes. The response of individuals to the environmental complex is measured in a species distribution pattern as well as in its importance within the community.

Attempts were made to access the response of the species included in this study to the factors of soil and topography. Soil and elevation readings were recorded at all 968 points of the grid. From these readings a soils map (Figure 75) and contour and elevation maps (Figures 76 and 77) were constructed for the 20-acre plot. This made it possible to group all plant samples according to 0.5-foot changes in elevation or according to soil series. Once grouped, average cover values were computed for all participating species and recorded in Tables 14 (elevation data) and 15 (soils data). As can be seen from these tables all species showed response to these factors. Several species, Andropogon gerardi, Amorpha canescens, Aster ericoides, Elymus canadensis, Panicum leibergii, Poa pratensis, Solidago canadensis, Sporobolus heterolepis, and Zizia aurea, showed wide tolerance in relation to both soil and elevation, but all exhibited peaks or plateaus of occurrence. These peaks or plateaus are interpreted to represent the optimum conditions under which a particular species can reach its highest importance within the community in relation to the entire species complex.

Figure 75. Soil series map of 20-acre intensive study area, abbreviations described in Methods section; A = Clarion, $\bar{A}$ = Clarion-Nicollet, N = Nicollet, Na = calcareous Nicollet, $\bar{N}$ = Nicollet-Webster, $N\bar{a}$ = calcareous Nicollet-Webster, W = Webster, Wh = heavy Webster, Wa = calcareous Webster, C = Canisteo, H = Harps, $\bar{H}$ = Harps-Canisteo, $\bar{C}$ = inverted Canisteo-heavy Webster, G = Glenco, Ga = calcareous Glenco, GO = Glenco-Okoboji, O = Okoboji

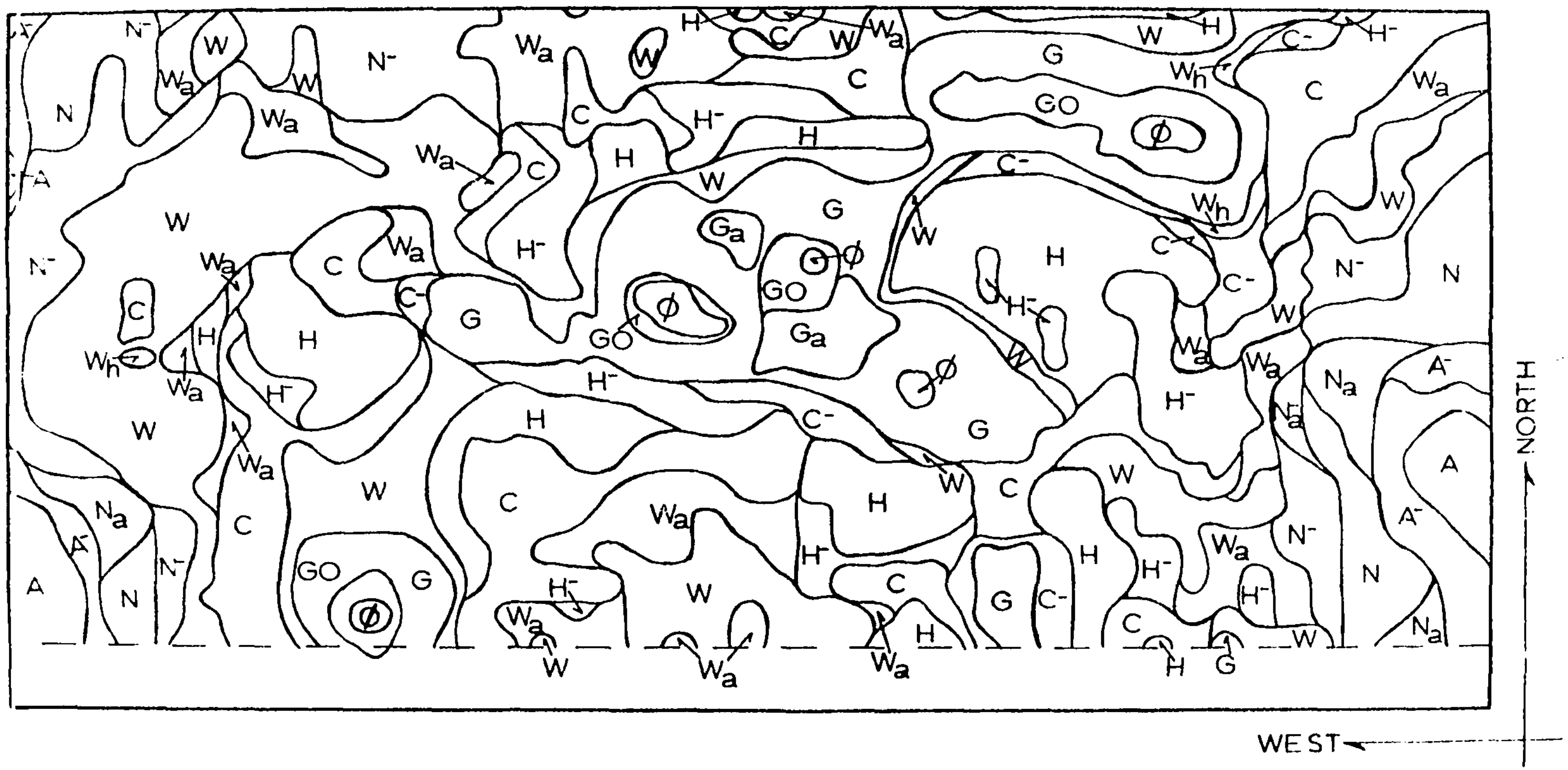

NORTH
WEST

Figure 76. Topographic map of 20-acre intensive study area

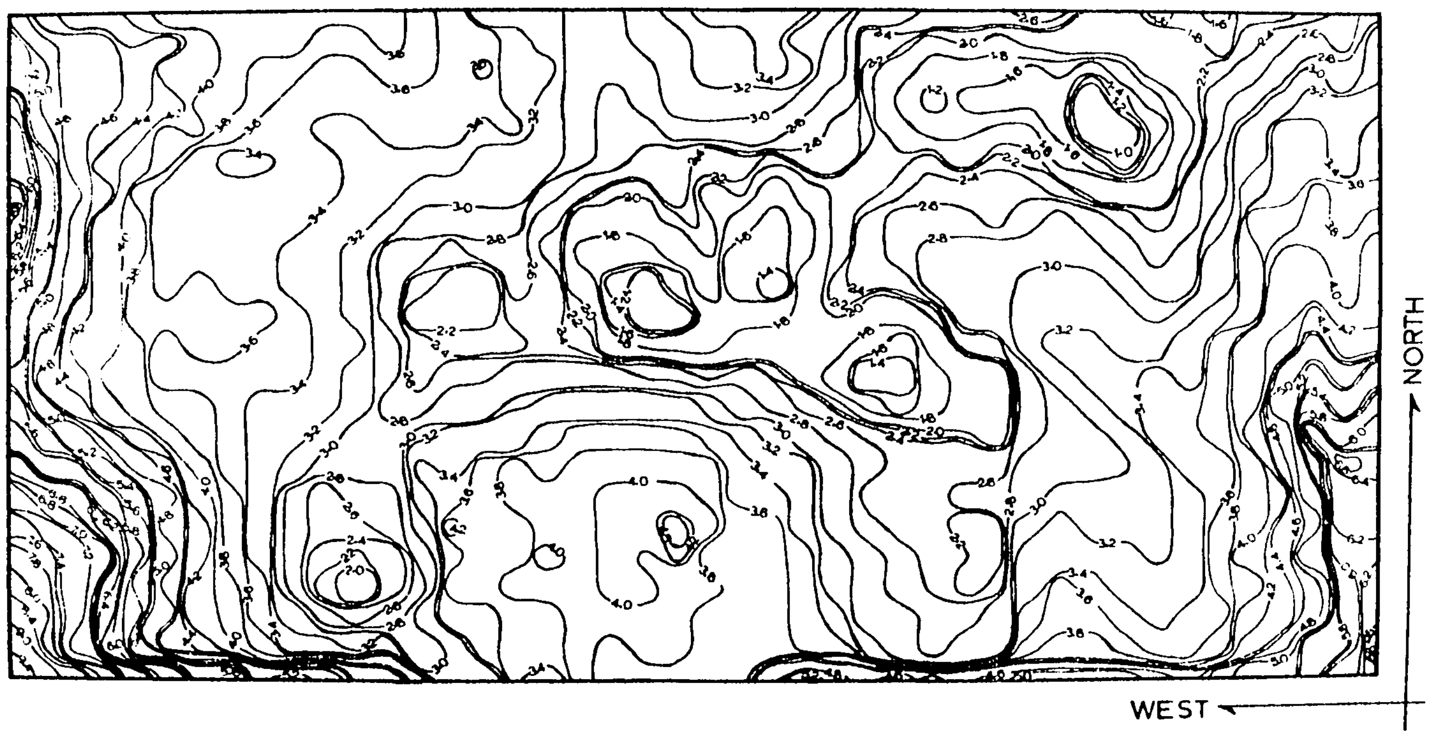
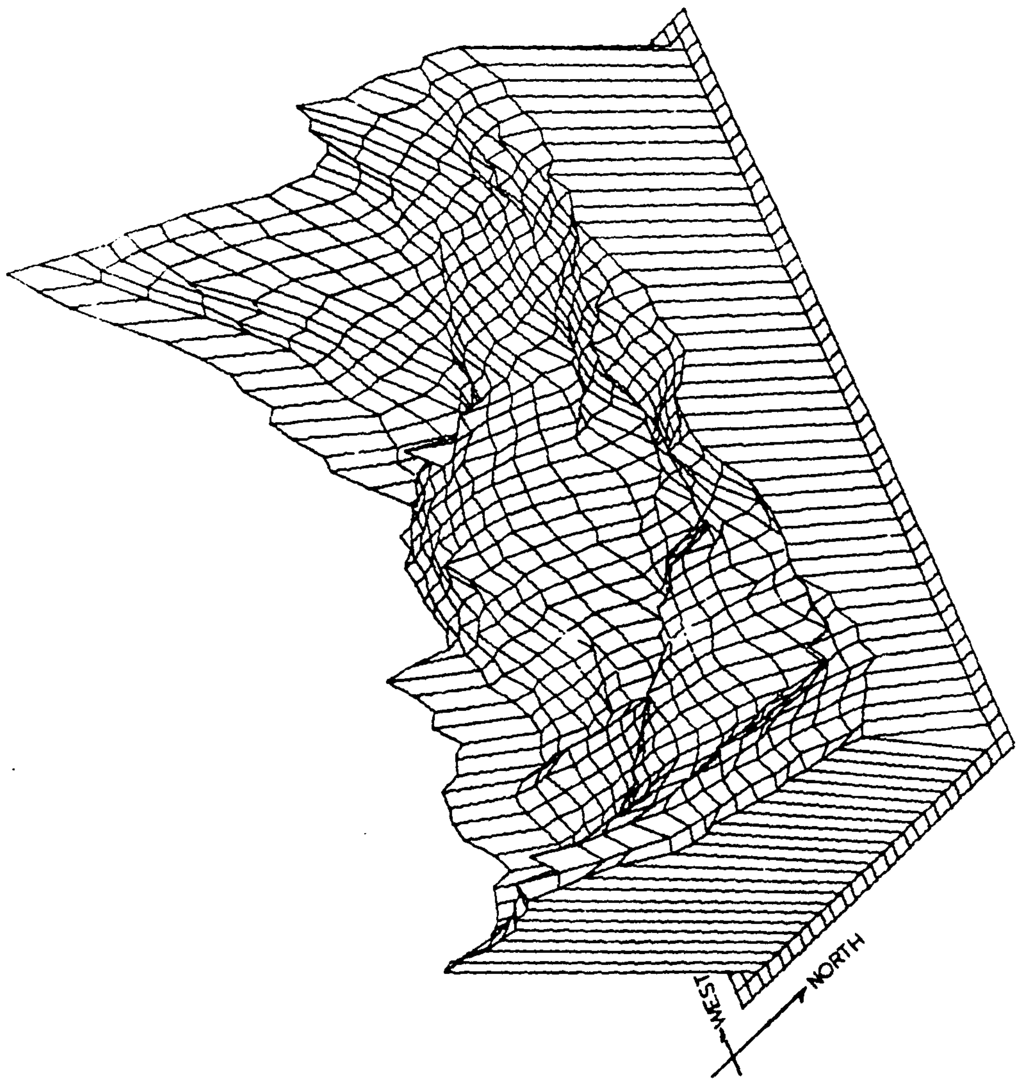

NORTH
WEST

Figure 77. Topographic map of 20-acre intensive study area plotted by computer


WEST
NORTH

Other species showed rather narrow ranges of tolerance. Some of these were Andropogon scoparius, Apocynum sibiricum, Asclepias sullivantii, Calamagrostis canadensis, Carex atherodes, Eryngium yuccifolium, Lysimachia hybrida, Physalis heterophylla, Viola pedatifida and Ceanothus americanus. Those exhibiting narrow ranges also showed peaks of occurrence. For species exhibiting narrow tolerances, four basic types of distribution patterns as related to elevation (Table 14) are recognizable: (1) pothole and drainage, (2) lower slopes, (3) mid and upper slopes, and (4) ridges.

For species showing response to the soil factor (Table 15) three basic classes are recognizable: (1) Glenco, Glenco-Okoboji, and Okoboji, (2) calcareous, and (3) non-calcareous and ridge. Species indicating preference for class 1 were Calamagrostis canadensis, Carex atherodes, Carex aquatilis, Carex lasiocarpa, Carex retrorsa, Lysimachia hybrida, Polygonum coccineum, and Scirpus fluviatilis. Species showing preference for the calcareous soils (class 2) were Agropyron smithii, Desmodium canadense, Galium obtusum, Helenium autumnale, Petalostemum purpureum, Senecio pauperculus, Silphium laciniatum, Solidago canadensis, Solidago nemoralis, and Solidago riddellii. Examples of species preferring class 3 are Amorpha canescens, Artemisia ludoviciana, Asclepias tuberosa, Baptisia leucophaea, Eryngium yuccifolium, Lathyrus palustris, Panicum leibergii, Poa pratensis, Solidago missouriensis, Vicia americana, and Ceanothus americanus.

These groups of recognizable patterns, each involving several species, suggest the existence of sub-communities within the prairie area. To ascertain the existence of such communities the data from Tables 14 and 15

Table 14. Average cover values for species in relation to elevation in

Species	1 .7-1.2	2 1.3-1.8	3 1.9-2.4	4 2.5-3.0	5 3.1-3.6	6 3.7-4.2
Achillea lanulosa				.23	.23	.28
Agropyron smithii			.02	.12	.09	
Ambrosia artemisifolia				.01	.01	.55
Amorpha canescens				.20	1.49	4.27
Andropogon gerardi		.52	5.57	9.06	9.49	10.10
Andropogon scoparius			.25	.92	.75	.55
Anemone canadensis					.02	.03
Anemone cylindrica						
Apocynum sibiricum	1.36	1.98	1.15	.65	.04	.19
Arabis hirsuta					.01	
Artemisia ludoviciana					.06	.02
Asclepias incarnata		.52				
Asclepias sullivantii				.08	.02	
Asclepias syriaca			.13		.07	.28
Asclepias tuberosa			.02	.02	.44	.71
Aster ericoides			.41	1.87	2.09	1.72
Aster laevis				.10	.77	1.84
Aster simplex		.56	2.72	2.55	1.66	.82
Baptisia leucantha						
Baptisia leucophaea					.13	
Calamagrostis canadensis	1.59	33.65	36.13	9.52	1.09	
Carex atherodes	34.55	16.35	4.28	.23		
Carex aquatilis		2.05	3.22	1.33	.19	.02
Carex gravida					.01	
Carex lasiocarpa		1.63	1.91	.53	.08	
Carex retrorsa		4.51	7.24	2.67	.57	.02
Chenopodium album			.02		.14	
Cicuta maculata						
Cirsium altissimum			.54	.55	.67	.44
Comandra umbellata		.03	.02	.14	.38	.32
Convolvulus sepium					.09	.03
Desmodium canadense			.72	2.37	3.49	2.96
Elymus canadensis			.11	.49	1.05	.85
Equisetum kansanum			.04	.14	.21	.24
Eryngium yuccifolium					.05	.91
Fragaria virginiana			.89	.92	1.91	1.11
Galium obtusum		.90	1.91	1.69	1.84	.93
Gentiana andrewsii		.21		.01	.06	.13
Helenium autumnale		.03	.28	.19	.18	.02
Helianthus grosseserratus		2.95	8.89	8.88	7.46	4.59
Helianthus laetiflorus				.01	.43	1.39
Helianthus maximiliani					.01	
Heliopsis helianthoides				.28	.22	.24

20-acre intensive study area

7	8	9	10	11	12	13	14	15
4.3-4.8	4.9-5.4	5.5-6.0	6.1-6.6	6.7-7.2	7.3-7.8	7.9-8.4	8.5-9.0	9.1-9.6
.71	1.00	1.07	.13			8.00		
.05		.71						
2.03	4.50	1.79	1.71	7.86	.83	7.50	1.25	
11.70	14.67	10.95	26.21	14.29	57.92	40.00	20.00	
1.42								
.33	.08	.71	2.50	4.29		3.00		
		.71						
1.46	.25	.71						
3.35	3.08	2.02	7.89	2.50		3.50	1.25	
1.37	2.42	4.76	7.37	2.50	5.83	1.00		
.09								
.28								
.33	1.08							
		.12						
.33				2.14				
.24		.12						
			.79	2.14	2.92	3.00	7.50	
2.36	2.08	2.50	.26	2.14				
.71	.25	.48	.26	.71	.42		1.25	
.09	.08			.36		.50		
.09	.08	.71						
.99	.08		.13					
.52	.25	.12	.13	.71				
3.82	.83	.24						
3.16	2.67	2.50	8.16	5.71				
.14			.79					

Table 14. (Continued)

Species	1 .7-1.2	2 1.3-1.8	3 1.9-2.4	4 2.5-3.0	5 3.1-3.6	6 3.7-4.2
Lactuca scariola				.02	.06	.03
Lathyrus palustris		.03	.02	.08	.06	
Lathyrus venosus						.06
Lespedeza capitata				.01	.01	.11
Liatris pycnostachya			.20	.80	.63	.65
Lithospermum canescens			.07	.26	.34	.33
Lycopus americanus			.24	.13		.03
Lysimachia chiliata					.01	
Lysimachia hybrida	21.50	1.42				
Lysimachia quadriflora			.07	.04	.03	.03
Lythrum alatum		.24	.20	.12		
Mentha arvensis		.28		.08		
Muhlenbergia racemosa			.52	.78	.25	.22
Oxalis stricta				.18		
Panicum capillare					.01	
Panicum leibergii			.02	.51	1.19	2.31
Panicum virgatum			.26	.66	.86	.60
Pedicularis canadensis				.47	.09	.13
Petalostemum candidum			.02		.02	.02
Petalostemum purpureum		.03	.13	.59	.40	.35
Phalaris arundinacea	7.05	5.49	3.98	.49		
Phlox pilosa			.04	.05	.13	.13
Physalis heterophylla						
Physalis virginiana				.01	.04	.03
Poa pratensis			1.24	2.82	3.57	4.24
Polygonum coccineum	27.27	16.81	4.02	1.52	.01	
Potentilla arguta						.02
Psoralea argophylla					.02	.09
Pycnanthemum virginianum			.37	1.83	.77	.35
Ratibida columnifera		.21	.30	1.65	1.93	1.50
Rosa suffulta				.24	.46	.91
Rudbeckia hirta				.10	.01	.03
Scirpus atrovirens		.52				
Scirpus fluviatilis	2.05	6.22	1.41	.08		
Scutellaria leonardii			.07	.04	.13	.08
Senecio pauperculus		.42	3.15	3.92	.59	.35
Setaria lutescens			.13		.01	.09
Setaria viridis				.01	.03	.24
Silphium laciniatum			2.09	4.84	2.75	2.10
Solidago canadensis		.66	3.98	6.02	5.68	2.12
Solidago gymnospermoides				.01	.31	.11
Solidago missouriensis				.01		.09
Solidago rigida				1.81	3.20	5.44

7	8	9	10	11	12	13	14	15
4.3-4.8	4.9-5.4	5.5-6.0	6.1-6.6	6.7-7.2	7.3-7.8	7.9-8.4	8.5-9.0	9.1-9.6
.33	.17	.12	.39					
.28	.08							
.24	.08							
.47	.25	.24	.53		.42			
	.50	.71						
.05		.71						
.05								
2.64	2.16	2.62	9.74	2.50	2.92	.50		
.24	.67		.13					
	.17		.13					
.09	.58							
		.12						
			4.87	2.14	5.00			
.09		.12	.13		2.50			
7.36	9.25	26.55	22.50	27.86	26.67	38.50	61.25	
		.71	.13					
.05	1.00	.83	.13	.71	2.92	.50		
.24	.17							
1.46	2.75		2.11					
2.03	1.50	2.62	1.18				1.25	
.09				.36				
.57								
		2.50	.79					
2.41		4.88	.13					
.61								
2.22	3.50	2.38	4.34	11.43	2.92		7.50	
			1.58		2.50			
5.66	3.17	2.74	.79					

Table 14. (Continued)

Species	1 .7-1.2	2 1.3-1.8	3 1.9-2.4	4 2.5-3.0	5 3.1-3.6	6 3.7-4.2
Sorghastrum nutans			.09	.17	.42	.08
Spartina pectinata	1.36	4.27	3.74	1.79	.84	.30
Sporobolus heterolepis		.52	7.76	23.83	40.98	49.78
Stipa spartea						.05
Teucrium canadense		.03	1.07	.31	.01	
Thalictrum dasycarpum				.04	.44	.33
Vernonia fasiculata			.59			
Veronicastrum virginicum						.02
Viola pedatifida					.04	.08
Viola sp.			.07	.12	.12	.08
Vicia americana					.05	.05
Zizia aurea		.21	1.43	3.28	4.18	2.74
Allium sp.					.02	
Aster novae-angliae				.23	.02	
Cacalia tuberosa						.02
Ceanothus americana					.01	
Panicum implicatum					.06	.09
Prenanthes racemosa				.08		
Solidago nemoralis			.02	.13	.45	1.69
Solidago riddellii		.03	.13	.69	.18	.03
Taraxacum officinale						.09
Echinacea pallida						.02

7	8	9	10	11	12	13	14	15
4.3-4.8	4.9-5.4	5.5-6.0	6.1-6.6	6.7-7.2	7.3-7.8	7.9-8.4	8.5-9.0	9.1-9.6
.09			.26					
.05								
42.74	43.08	26.90	17.63	33.21	8.75	8.00		
.09	.08	.95	.26			.50	1.25	
			.13					
.42								
.09	.08							
.05								
.09			.26		.42			
2.36	.25	1.31	.13		.42			
	.50		1.97	2.14	2.50	24.50		
.05								
.05								

Table 15. Average cover values for species in relation to soil series in

Species	A	A^-	N	Na	N^-	$N\bar{a}$	W
Achillea lanulosa	.14	.19	.57		.44	.21	.37
Agropyron smithii							.01
Ambrosia artemisifolia		.56					
Amorpha canescens	3.47	2.87	4.16	4.06	6.57		2.56
Andropogon gerardi	39.72	19.25	12.26	21.56	10.04	10.63	6.70
Andropogon scoparius					.08		.80
Anemone canadensis							.03
Apocynum sibiricum							.09
Arabis hirsuta							
Artemisia ludoviciana	3.19	.56	.38	1.88	.12		
Asclepias incarnata							
Asclepias sullivantii							
Asclepias syriaca			.28				.01
Asclepias tuberosa		.65	.61	1.88	.73		.19
Aster ericoides	3.89	1.94	3.58	2.19		.42	1.50
Aster laevis	3.47	4.44	1.56	9.68	1.29	2.50	.46
Aster simplex					.08		2.12
Baptisia leucophaea	.14		.85	1.88	.24		.03
Calamagrostis canadensis							10.48
Carex atherodes							.75
Carex aquatilis							1.11
Carex gravida							.01
Carex lasiocarpa							.28
Carex retrorsa							2.07
Chenopodium album							.01
Cirsium altissimum			.33		.48		.60
Comandra umbellata	.14	.19	.19		.08	.21	.05
Convolvulus sepium	.97		.28		.04		
Desmodium canadense		.65	1.88	2.19		2.71	1.64
Elymus canadensis	.28	.19	.24	2.19	.44	1.04	.60
Equisetum kansanum	.14		.05	.31	.44	.42	.12
Eryngium yuccifolium			.61		.65		.38
Fragaria virginiana	.14	.19	.24		.16		2.15
Galium obtusum			.14		.65	.42	1.83
Gentiana andrewsii							.01
Helenium autumnale							.03
Helianthus grosseserratus			1.65	.31	2.58	1.25	9.26
Helianthus laetiflorus	3.19	6.20	3.87	6.87	2.18	4.79	.18
Helianthus maximiliani							
Heliopsis helianthoides			.28				.03
Lactuca scariola					.24		.01
Lathyrus palustris							.08
Lathyrus venosus	.56	.09	.24	1.88			
Lespedeza capitata		.65				.21	
Liatris pycnostachya			.14	.31	1.21		.40

20-acre intensive study area

Wh	Wa	C	H	H⁻	C⁻	G	Ga	GO	O
.42	.40	.07	.02	.09	.65				
.10		.09	.22	.17					
					.09				
.73	1.93	.33	.33	.04		.02			
12.19	9.09	10.87	14.42	11.57	14.25	.05	.13		
.63	.77	.46	1.74	1.31		.02			
			.02						
.73		.09	.25		.74	2.06	3.50	2.63	
			.02						
	.17								
								1.88	
	.03	.02	.16						
		.18							
	.71	.64	.07	.81					
2.81	1.22	2.81	2.59	2.42	1.76				
	1.70	1.18	.31	.55					
3.54	1.02	1.36	1.63	1.18	3.98	1.80	2.38		
	.17								
11.15		2.46	1.41	.81	13.61	45.26	56.88	1.50	
.63				.25		7.73	8.25	32.38	21.50
1.88		.20	.11	.64	1.48	3.90	3.00		
1.04		.04	.16	.25	.39	2.48	3.88	.25	
6.88		.37	.58	1.23	1.38	8.27	10.63	6.00	
.10	.77	.50	.67	.68	.19	.35			
	.45	.64	.16	.30	.09				
.10	.48					.14			
1.35	4.66	3.53	2.79	4.15	2.69	.14			
.31	1.08	1.10	.56	1.10	.37	.07			
.10	.31	.15	.11	.17					
	.26	.02							
.52	2.24	1.62	.96	.98	1.57	.07	.13		
2.08	1.42	2.43	1.52	2.16	1.85		.13		
		.18				.14			
		.31	.58	.30	.09				
13.85	5.17	9.96	7.86	6.31	12.41	3.36	4.63		
.10	.20			.04					
			.02						
	.34	.31	.18	.34	.65				
	.06		.02						
.10	.06		.05	.09		.02			
.10									
	.23								
.63	1.02	.72	.67	.42	.28				

Table 15. (Continued)

Species	A	$\bar{A}$	N	Na	$\bar{N}$	$\overline{Na}$	W
Lithospermum canescens	.28	.56	.52	.31	.56	1.04	.17
Lycopus americanus					.04		.11
Lysimachia chiliata							
Lysimachia hybrida							
Lysimachia quadriflora							.03
Lythrum alatum							.01
Mentha arvensis							.12
Muhlenbergia racemosa						.21	.23
Oxalis stricta		.09		1.88			
Panicum capillare						.21	.01
Panicum leibergii	6.67	7.50	2.64	4.06	.77	3.33	1.20
Panicum virgatum		1.20	.14		.44	2.71	.49
Pedicularis canadensis					.04		
Petalostemum candidum		.19	.09				
Petalostemum purpureum		.65			.12		.21
Phalaris arundinacea							1.09
Phlox pilosa		.19			.16		.03
Physalis heterophylla		2.31	.28	1.88			
Physalis virginiana	.14	.09	.28		.08		.03
Poa pratensis	16.53	31.09	5.99	32.81		5.21	3.22
Polygonum coccineum							.44
Potentilla arguta	.14	.56	.05				
Psoralea argophylla	1.81	1.30	.15	.31	.08	.21	
Pycnanthemum virginianum		.28					.43
Ratibida columnifera	2.92	3.24	.05		.32	1.46	1.29
Rosa suffulta	.14	3.06	1.56	2.19		1.67	.29
Rudbeckia hirta					.04		
Scirpus atrovirens							
Scirpus fluviatilis							.01
Scutellaria leonardii		.09	.05		.08		.14
Senecio pauperculus							1.24
Setaria lutescens		.56					
Setaria viridis		.56		.31			
Silphium laciniatum			.38			1.25	2.15
Solidago canadensis	.14	2.41	3.21	.31	2.86	1.25	3.16
Solidago gymnospermoides			.09		.69	1.88	
Solidago missouriensis	1.67	.56	.28				
Solidago rigida		.56	3.25	.31	4.27	2.50	3.79
Sorghastrum nutans				.31	.20		.11
Spartina pectinata					.04		.83
Sporobolus heterolepis	12.08	21.76	62.69	37.19	58.95	27.92	37.41
Stipa spartea	.97	.09	.14		.08	.21	.05
Teucrium canadense			.05			.21	.23
Tahlictrum dasycarpum							.05
Vernonia fasiculata							.09

Wh	Wa	C	H	H^-	C^-	G	Ga	GO	O
.10	.48	.33	.22	.21	.09				
.10	.03	.02	.18	.04	.09	.05	.13		
		.02							
						.28			17.25
	.03	.02	.11	.04	.09				
						.19	.25		
						.02	1.31		
.10	.20	.42	1.47		.93	.05	.75		
	.43								
	2.70	1.57	.05	.68					
.31	.80	1.03	.51	.30	.83				
	.20	.46	.45	.25					
	.06		.02						
.31	.60	.50	.87	.42	.28				
1.56						6.24	6.63	.75	
.63	.20	.09	.07	.17	.09				
	.06	.02	.05						
1.35	2.81	3.86	3.15	3.18	5.74	.05			
				.25		8.74	2.88	40.50	36.75
.10	.06								
.10	.45	.99	2.17	1.99	.83				
.10	1.73	3.05	1.94	1.91	.09				
	.68	.42	.20	.25					
		.09	.16						
						.35			
						1.87		13.63	17.50
.21	.11	.04	.09	.09	.09				
3.65	.48	2.45	3.59	2.84	9.17		.13		
						.14			
				.25					
7.40	2.95	3.84	4.69	4.79	3.61	.28	.75		
2.50	4.12	7.30	7.39	5.30	13.43	.05			
	.26			.09					
			.05						
.63	5.34	3.77	1.36		1.20				
.10	.17	.35	.63	.34	.09				
1.88	.28	.15	.54	.85	.56	7.22	6.88	3.38	
29.38	44.40	25.42	24.08	32.80	9.44	.79	.13		
.73	.28	.15	.38	.25	.09	.30		.13	
		.20	.38	.17	.09				
						.49			

Table 15. (Continued)

Species	A	A$^-$	N	Na	N$^-$	Na$^-$	W
Veronicastrum virginicum							.01
Viola pedatifida			.09		.12		.05
Viola sp.							.03
Vicia americana	.28	.09	.05	.31	.04		.03
Zizia aurea	.14	.93	4.58	4.06	1.73	3.33	1.52
Allium sp.							
Aster novae-angliae							.09
Cacalia tuberosa							.01
Ceanothus americana	10.56	.56			.04		
Panicum implicatum					.04		.15
Prenanthes racemosa							.09
Solidago nemoralis			.28		.93		.75
Solidago riddellii							.01
Taraxacum officinale							

Wh	Wa	C	H	H^-	C^-	G	Ga	GO	O
.21				.04					
	.09	.31	.09	.25	.09				
	.09	.02	.02						
.31	3.41	5.31	4.64	5.13	3.52				
.10			.02						
		.13	.05	.04	.56				
		.04							
.73	1.02	.31	.47	.17					
2.92	.09	.50	.45	.03	.19				

were treated using Orloci's (1966) method of ordination. When the results from the soils analysis were plotted (Figure 78) four basic groups were recognizable. These groups are labeled A, B, C, and D, group A corresponding to the non-calcareous and ridge entity described previously and made up of plants showing preference for Nicollet and Nicollet-Webster soils. Group B includes all but one of the calcareous soil types plus four non-calcareous types. The non-calcareous types are found at the periphery of the group and include Clarion, Clarion-Nicollet, Webster and heavy Webster soil types. Group C includes the Glenco-Okoboji and Okoboji soils while group D includes Glenco and calcareous-Glenco soils. These last two groups correspond to group 1 for species showing response to the soil factor described above.

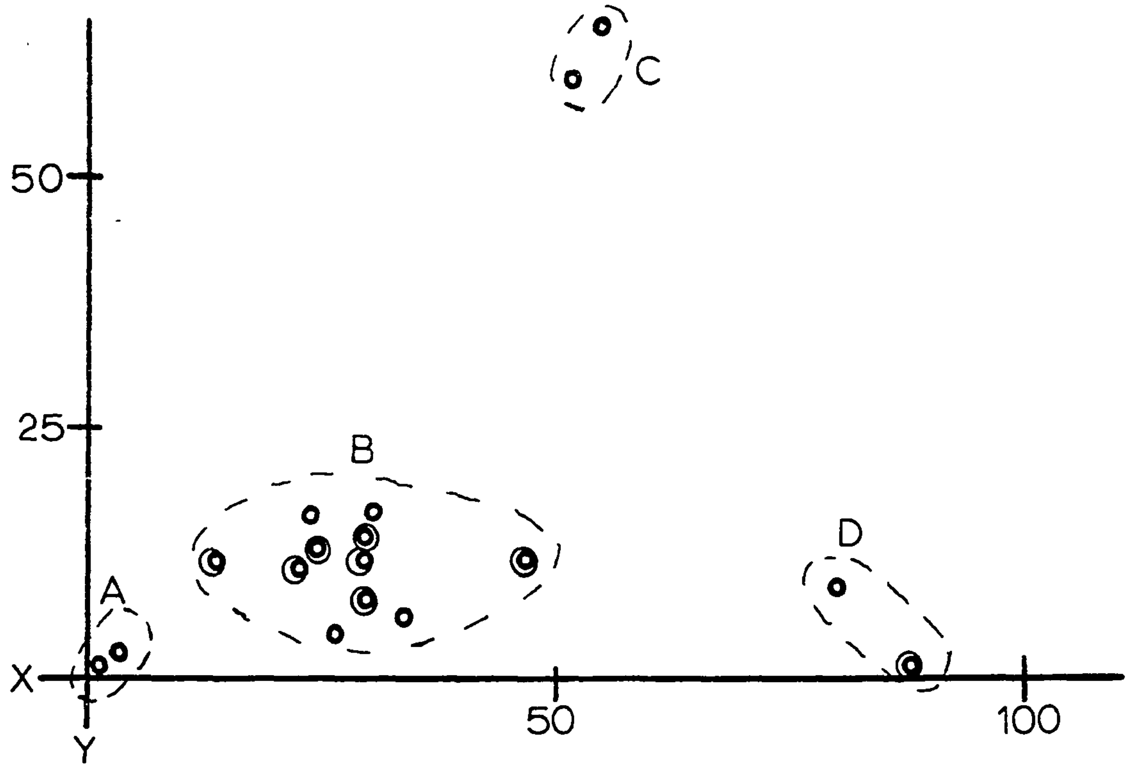
Ordination of elevation data (Figure 79) showed no recognizable groupings. Instead it separated the different elevation classes (Table 14) along a curve, point 14 representing the ridge tops and point 1 representing the bottom of the potholes. This would tend to support statements made earlier that the vegetation of Kalsow Prairie is best represented by the continuum concept of Curtis and McIntosh (1951).

The definable sub-communities or groups (Figure 78) as based on soils data represent the response of the different taxa in the vegetation to an environmental stimulus (i.e., carbonate soils) which is not distributed along gradients (i.e., at 30 x 30-foot sampling levels) but in mappable units with fairly discrete boundaries. This would tend to cause vegetation sensitive to carbonate influence to group accordingly.

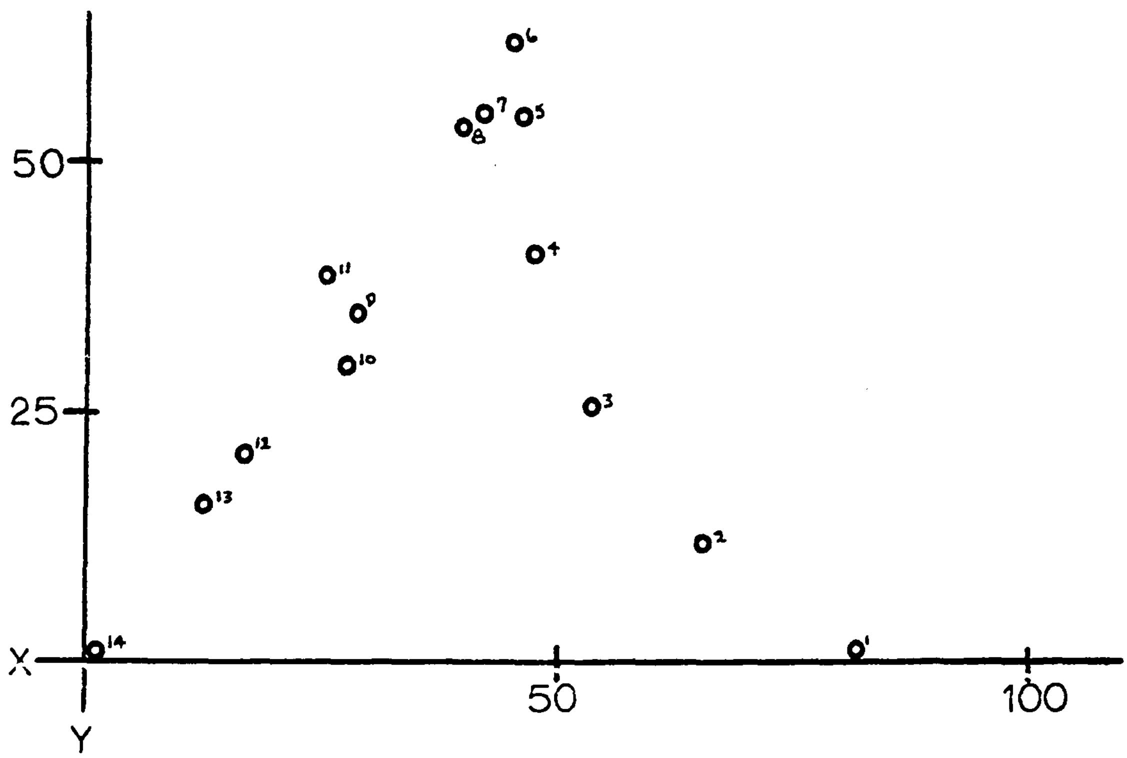
An ordination of species, utilizing the data from Tables 14 and 15, isolated taxa having distinct distribution patterns. These species are

Figure 78. Two-dimensional ordination of vegetation found on the different soil types in the 20-acre study area; cluster A indicates vegetation on Nicollet and Nicollet-Webster soil types; B indicates vegetation on Clarion, Clarion-Nicollet, Webster, heavy Webster, calcareous Nicollet, calcareous Nicollet-Webster, calcareous Webster, Canisteo, Harps, Harps-Canisteo, and inverted Canisteo-heavy Webster soil types; C indicates vegetation on Glenco-Okoboji and Okoboji soil types; D indicates vegetation on Glenco and calcareous Glenco

Figure 79. Two-dimensional ordination of vegetation found at different elevations in the 20-acre study area; 1 = .7-1.2 feet elevation, 2 = 1.3-1.8 feet elevation, 3 = 1.9-2.4 feet elevation, 4 = 2.5-3.0 feet elevation, 5 = 3.1-3.6 feet elevation, 6 = 3.7-4.2 feet elevation, 7 = 4.3-4.8 feet elevation, 8 = 4.9-5.4 feet elevation, 9 = 5.5-6.0 feet elevation, 10 = 6.1-6.6 feet elevation, 11 = 6.7-7.2 feet elevation, 12 = 7.3-7.8 feet elevation, 13 = 7.9-8.4 feet elevation, 14 = 8.5-9.0 feet elevation



50
25
A
B
C
D
X
Y
50
100

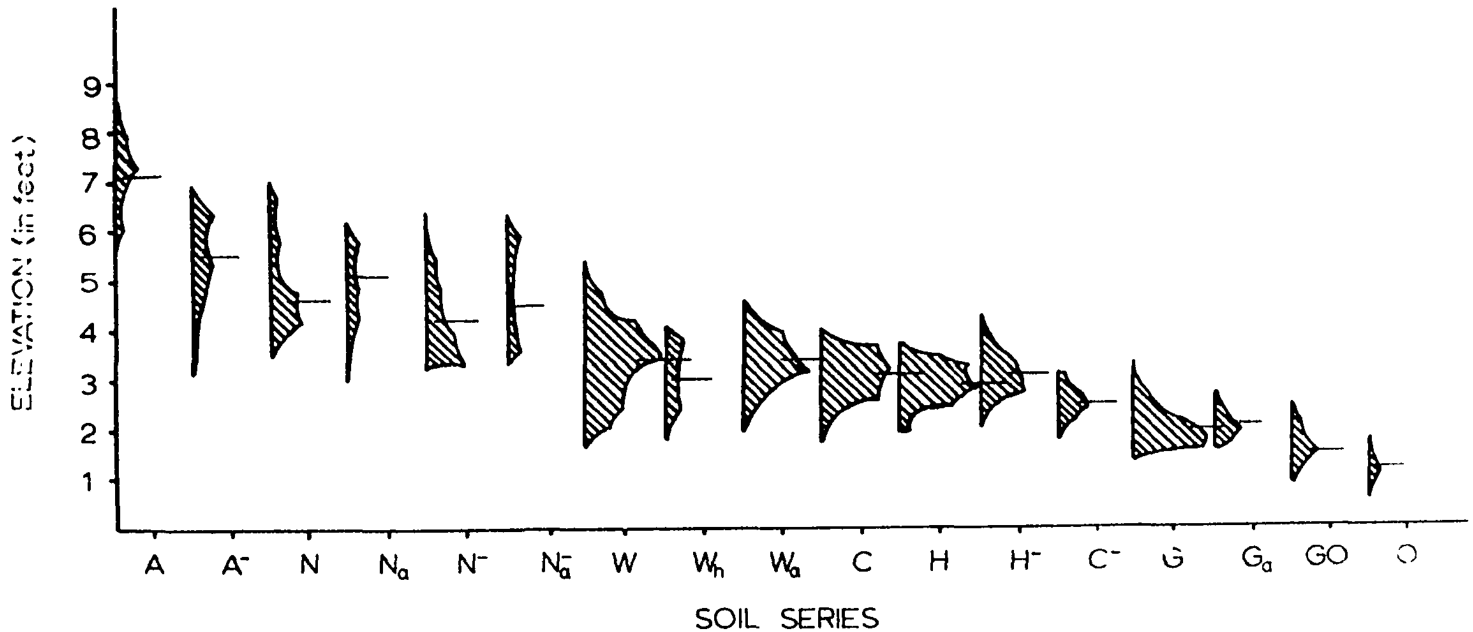


50
25
X
Y
50
100
1
2
3
4
5
6
7
8
9
10
11
12
13
14

Amorpha canescens, Andropogon gerardi, Aster ericoides, Aster laevis, Calamagrostis canadensis, Carex atherodes, Carex aquatilis, Desmodium canadense, Helianthus grosseserratus, Helianthus laetiflorus, Panicum leibergii, Phalaris arundinacea, Poa pratensis, Polygonum coccineum, Ratibida columnifera, Scirpus fluviatilis, Silphium laciniatum, Solidago canadensis, Solidago rigida, Spartina pectinata, Sporobolus heterolepis, Zizia aurea, and Ceanothus americanus, all of which show distinct distribution patterns and in many cases high preference for certain soil groups or elevations.

The relationships between elevation and soil series are shown in Figure 80. The soil types are positioned along the base line as they appeared in the field. In all cases where the non-calcareous soils had adjacent calcareous varients the calcareous varients showed higher average elevations.

Figure 80. Relationships between elevation and soil series as found in 20-acre intensive study area; mean value indicated for each soil by short horizontal line


ELEVATION (in feet)
9
8
7
6
5
4
3
2
1
A
A⁻
N
Nₐ
N⁻
Nₐ⁻
W
Wₕ
Wₐ
C
H
H⁻
C⁻
G
Gₐ
GO
O
SOIL SERIES

SUMMARY AND CONCLUSIONS

Studies emphasizing species composition, distribution and phyto-sociology of an original tall-grass prairie in central Iowa (Kalsow Prairie) are summarized below:

1. Five plant communities identified on the prairie are upland prairie, potholes and drainage, Mima mounds, grazed prairie, and weed borders.

2. Species lists, average percentage cover, species distributional patterns, and community structure including sub-communities are presented for all five vegetation types.

3. Data were analyzed using Orloci's (1966) R and Q-techniques of three-dimensional ordination and Cole's (1949) Index of interspecific association. Both techniques were useful in defining the phyto-sociological structures of the communities.

4. Sporobolus heterolepis is the dominant plant of the upland prairie which places Kalsow Prairie within the "Consociation" designated by Weaver and Fitzpatrick (1934) as the Prairie-Dropseed type.

5. The vegetation of the upland prairie communities is best described and represented by the continuum concept as described by Curtis (1955).

6. The vegetation of the upland prairie has changed since Moyer's 1953 study. Species showing increased importance in my study are Solidago canadonsis, Solidago rigida, Panicum leibergii, Helianthus grosseserratus, and Fragaria virginiana. Species decreasing in importance were Phleum pratense, Poa pratensis, Zizia aurea, Andropogon scoparius, Panicum virgatum, Sorghastrum nutans, and Sporobolus heterolepis.

7. The vegetation of the potholes and drainage of Kalsow Prairie is a series of five zones each exhibiting distinct spatial and floristic properties.

8. The zones of pothole and drainage vegetation represent a successional sequence controlled by the degree of fill and corresponding moisture regimes. The following successional sequence is proposed beginning at the pothole center:

I *Polygonum coccineum-Lysimachia hybrida* zone

II *Polygonum coccineum-Scirpus fluviatilis* zone

III *Carex atherodes-Polygonum coccineum* zone

IV *Spartina pectinata-Carex aquatilis-Calamagrostis canadensis* zone

V *Calamagrostis canadensis* zone

VI Upland prairie edge

9. Mima mounds of unknown origin in the upland prairie affect the structure and stability of the adjacent vegetation. Many species respond to the new microenvironment of the mound. Microrelief and disturbance by burrowing animals appear to be influential factors on these microhabitats in the prairie vegetation which retard succession and cause changes to earlier stages.

10. The mound vegetation is composed of a mixture of prairie plants and pioneer weed species. *Poa pratensis* and *Solidago canadensis* are the two most important species on the mounds. The mound vegetation as a unit is described as a continuum with succession occurring but with interruptions. Controlling environmental influences are age of the mound, degree of disturbance, and floristic composition of the adjacent prairie vegetation.

11. Prairie species are becoming reestablished within the boundaries of an old pasture, now the NW 1/5 of the prairie. Andropogon gerardi comprises 90% of the prairie species cover and shows a decreasing pattern of average percentage cover extending into the pasture from the prairie-pasture border. In ten years the pasture is expected to be completely dominated by Andropogon gerardi, but a return to the original prairie vegetation now represented by the rest of Kalsow Prairie is not expected in 100 years.

12. Five weed communities are described along the south and west borders of the prairie. This vegetation is the result of several factors, the most important being the fall-plowing of adjacent cultivated fields with the subsequent deposition of wind-blown soil. Different weed communities appeared with soil blown in from land in corn and from land in soybeans the previous year.

13. Soil series, elevations, and species distribution patterns were mapped on a 20-acre intensive study plot. Elevation and soils data are correlated with species distribution patterns. All species show a response. Nine general patterns of distribution are described with the following species as examples:

a. Andropogon gerardi--species of wide distribution, limited only by conditions peculiar to the drainage areas of the prairie.

b. Silphium laciniatum--a pattern closely resembling that of Andropogon gerardi but showing limited distribution on the higher and drier ridges.

c. Ambrosia artemisifolia--species limited to the border weed communities.

d. Amorpha canescens--a pattern common to species limited to the ridges and lower slopes.

e. Solidago nemoralis--species limited to mid and upland slopes of the prairie.

f. Ceanothus americanus--a pattern limited to the ridges and drier sites of the prairie.

g. Helenium autumnale--limited to growth on soils which are highly calcareous to the surface.

h. Calamagrostis canadensis--limited to growth along the shallower areas of the pothole and drainage system.

i. Scirpus fluviatilis--growth corresponds to deeper areas within the drainage system.

14. Species occurring in the intensive study were ordinated using Orloci's (1966) method. In all cases the technique did not delineate associated groups of species yet it pointed out species exhibiting peculiar distribution patterns. Such species are useful as indicator species.

15. Indices of interspecific association were computed for all participating species (Cole, 1949) and found to be extremely useful in identifying clusters or groups of species having similar ecological amplitudes.

LITERATURE CITED

Aikman, J. M. 1959. Prairie research in Iowa. The American Biology Teacher 21: 7-8.

Aikman, J. M and R. F. Thorne. 1956. The Cayler Prairie: An ecologic and taxonomic study of a Northwest Iowa Prairie. Iowa Acad. of Sci. 63: 177-200.

Austin, M. P. and L. Orloci. 1966. Geometric models in ecology. II. An evaluation of some ordination techniques. Jour. of Ecology 54: 217-227.

Beals, E. 1960. Forest bird communities in Apostle Islands of Wisconsin. Wilson Bull. 72: 156-181.

Berry, W. J. 1927. The influence of natural environment in North-Central Iowa. Iowa Jour. of History and Politics 25: 277-298.

Bray, J. R. 1956. A study of mutual occurrence of plant species. Ecology 37: 21-28.

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

Brennan, K. M. 1969. Vertebrate fauna of Kalsow Prairie. Unpublished master's thesis. Ames, Iowa, Library, Iowa State University.

Brotherson, J. D. 1967. A study of certain community relationships of Eriogonum corymbosum Benth. in DC in the Uintah Basin, Utah. Unpublished master's thesis. Provo, Utah, Library, Brigham Young University.

Cain, S. A. and F. C. Evans. 1952. The distribution patterns of three plant species in an old-field community in southeastern Michigan. Contributions from the Laboratory of Vertebrate Biology No. 52.

Calvert, P. P. 1922. Methods for expressing the associations of different species. Ecology 3: 163-165.

Christensen, E. M. 1963. The foothill bunchgrass vegetation of central Utah. Ecology 44: 156-158.

Clausen, J. J. 1957. A phytosociology ordination of the conifer swamps of Wisconsin. Ecology 38: 638-646.

Cole, L. C. 1949. The measurement of interspecific association. Ecology 30: 411-424.

Cole, L. C. 1957. The measurement of partial interspecific association. Ecology 38: 226-233.

Collins, G. B. 1968. Implications of diatom succession in postglacial sediments from two sites in northern Iowa. Unpublished Ph.D. thesis. Ames, Iowa, Library, Iowa State University.

Cratty, R. I. 1933. The Iowa flora. Iowa State Coll. Jour. Sci. 7: 177-252.

Crawford, R. M. M. and D. Wishart. 1966. A multivariate analysis of the development of dune slack vegetation in relation to costal accretion at Tentsmuir, Fife. Jour. of Ecology 54: 729-743.

Crawford, R. M. M. and D. Wishart. 1967. A rapid multivariate method for the detection and classification of groups of ecologically related species. Jour. of Ecology 55: 505-524.

Crawford, R. M. M. and D. Wishart. 1968. A rapid classification and ordination method and its application to vegetation mapping. Jour. of Ecology 56: 385-404.

Curtis, J. T. 1955. A prairie continuum in Wisconsin. Ecology 36: 558-566.

Curtis, J. T. 1959. The vegetation of Wisconsin. Madison, Wisconsin, University of Wisconsin Press. 657 pp.

Curtis, J. T. and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476-496.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. orthwest Science 33: 43-66.

Davids, R. C. 1967. The mystery of Mima mounds. Farm Journal 91: 17-19.

DeVries, D. M. 1953. Objective combinations of species. Acta Bot. Neerl. 1: 497-499.

Dice, L. R. 1945. Measures of the amount of ecological association between species. Ecology 26: 297-302.

Dick-Peddie, W. A. 1955. Presettlement forest types in Iowa. Unpublished master's thesis. Ames, Iowa, Library, Iowa State University.

Dix, R. L. and J. E. Butler. 1960. A phytosociological study of a small prairie in Wisconsin. Ecology 41: 316-327.

Dondore, D. A. 1926. The prairie and the making of middle America: four centuries of description. Cedar Rapids, Iowa, The Torch Press. 472 pp.

Edwards, A. W. F. and L. L. Cavalli-Sforza. 1965. A method for cluster analysis. Biometrics 21: 363-375.

Ehrenreich, J. H. 1957. Management practices for maintenance of native prairies in Iowa. Unpublished Ph.D. thesis. Ames, Iowa, Library, Iowa State University.

Ellsworth, E. W. 1924. Parry's catalog of Iowa plants of 1848. Proc. Iowa Acad. Sci. 29 (1922): 339-344.

Esau, K. L. 1968. Carabidae (Coleoptera) and other arthropods collected in pitfall traps in Iowa cornfields, fencerows and prairies. Unpublished Ph.D. thesis. Ames, Iowa, Library, Iowa State University.

Fager, E. W. 1957. Determination and analysis of recurrent groups. Ecology 38: 586-595.

Forbes, S. A. 1925. Method of determining and measuring the associative relations of species. Science, New Series, 61: 524.

Freckmann, R. W. 1966. The prairie remnants of the Ames area. Proc. Iowa Acad. Sci. 73: 126-136.

Gilly, C. L. 1946. The Cyperacae of Iowa. Iowa State Coll. Jour. of Sci. 21: 55-151.

Gilly, C. L. 1948. The flora of Iowa--a progress report based on past contributions. Proc. Iowa Acad. Sci. 54: 99-106.

Gittins, R. 1965a. Multivariate approaches to a limestone grassland community. I. A stand ordination. Jour. of Ecology 53: 385-401.

Gittins, R. 1965b. Multivariate approaches to a limestone grassland community. II. A direct species ordination. Jour. of Ecology 53: 403-409.

Gittins, R. 1965c. Multivariate approaches to a limestone grassland community. III. A comparative study of ordination and association analysis. Jour. of Ecology 53: 411-425.

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

Gleason, H. A. 1922. The vegetational history of the Middle West. Annals Assoc. Amer. Geog. 12: 39-85.

Gleason, H. A. 1925. Species and area. Ecology 6: 66-74.

Gleason, H. A. 1952. The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada. 3 vol. Lancaster, Pennsylvania, Lancaster Press, Inc.

Goodall, D. W. 1952. Objective methods for the classification of vegetation. I. The use of positive interspecific correlation. Australian Jour. Bot. 1: 434-456.

Goodall, D. W. 1954. Objective methods for the classification of vegetation. III. An essay in the use of factor analysis. Australian Jour. Bot. 2: 304-324.

Greig-Smith, P. 1964. Quantitative plant ecology. Washington, D. C., Butterworth's.

Hale, M. E., Jr. 1955. Phytosociology of corticolous cryptograms in the upland forests of southern Wisconsin. Ecology 36: 45-62.

Hansen, R. M. 1962. Movements and survival of Thomomys talpoides in a Mima mound habitat. Ecology 43: 151-154.

Harberd, D. J. 1960. Association analysis in plant communities. Nature, London 185: 53-54.

Harvey, L. H. 1908. Floral succession in the prairie-grass formation of southeastern South Dakota. Bot. Gaz. 46: 81-108, 272-298.

Hayden, Ada. 1943. A botanical survey in the Iowa lake region of Clay and Palo Alto Counties. Iowa State Coll. Jour. of Sci. 17: 277-416.

Hayden, Ada. 1945. The selection of prairie areas in Iowa which should be preserved. Proc. Iowa Acad. Sci. 52: 127-148.

Hayden, Ada. 1946. A progress report on the preservation of prairie. Proc. Iowa Acad. of Sci. 53: 45-82.

Hewes, L. 1950. Some features of early woodland and prairie settlement in a central Iowa county. Annals Assoc. Amer. Geog. 40: 40-57.

Hewes, L. 1951. The northern wet prairie of the United States: nature, sources of information, and extent. Annals Assoc. Amer. Geog. 41: 307-323.

Hewes, L. and P. E. Frandson. 1952. Occupying the wet prairie: the role of artificial drainage in Story County, Iowa. Annals Assoc. Amer. Geog. 42: 24-50.

Hurlbert, S. H. 1969. A coefficient of interspecific association. Ecology 50: 1-9.

Jaccard, P. 1902. Lois de distribution florale dans la zone alpine. Bull. de la Soc. Vaud. des Sciences Naturelles 38: 69-130.

Jaccard, P. 1908. Nouvelle recharches sur la distribution florale. Bull. Soc. Vaud. Sciences Naturelles 44: 223-270.

Kennedy, R. K. 1969. An analysis of tall-grass prairie vegetation relative to slope position, Sheeder Prairie, Iowa. Unpublished master's thesis. Ames, Iowa, Library, Iowa State University.

Kershaw, K. A. 1964. Quantitative and dynamic ecology. London, England, Edward Arnold Ltd.

Kershaw, K. A. 1968. Classification and ordination of Nigerian savanna vegetation. Jour. of Ecology 56: 467-482.

Lambert, J. M. and W. T. Williams. 1962. Multivariate methods in plant ecology. IV. Nodal analysis. Jour. of Ecology 50: 775-802.

Lance, G. N. and W. T. Williams. 1965. Computer programs for monothetic classification ("Association analysis"). Computer Jour. 8: 246-249.

Lance, G. N. and W. T. Williams. 1966. Computer programs for hiearchical polythetic classification ("Similarity analysis"). Brit. Comp. Jour. 9: 60-64.

Landers, R. Q. 1966. Visit the virgin prairie. Iowa Farm Science 21: 418-419.

Looman, J. and J. B. Campbell. 1960. Adaptation of Sorensen's K (1948) for estimating unit affinities in prairie vegetation. Ecology 41: 409-416.

Marean, H. W. and G. B. Jones. 1903. Soil survey of Story County, Iowa. Field Operations of the Bureau of Soils 836.

McGinnies, William J. 1960. Effect of Mima type microrelief on herbage production of five seeded grasses in western Colorado. Jour. of Range Management 13: 231-239.

McIntosh, R. P. 1957. The York Woods, a case history of forest succession in southern Wisconsin. Ecology 38: 29-37.

McIntosh, R. P. 1962. Pattern in a forest community. Ecology 43: 25-33.

McIntosh, R. P. 1967. The continuum concept of vegetation. The Botanical Review 33: 130-187.

Monson, P. H. 1959. Spermatophytes of the Des Moines lobe in Iowa. Unpublished Ph.D. thesis. Ames, Iowa, Library, Iowa State University.

Moyer, John F. 1953. Ecology of native prairie in Iowa. Unpublished Ph.D. thesis. Ames, Iowa, Library, Iowa State University.

Nash, C. B. 1950. Association between fish species in tributaries and shore waters of western Lake Erie. Ecology 31: 36-45.

Nicollet, J. N. 1845. Report intended to illustrate a map of the hydrographic basin of the Upper Mississippi River. (House of Representatives) 26th Congress, 2nd Session. Published in 1845.

Norton, D. C. and P. E. Ponchillia. 1968. Stylet-bearing nematodes associated with plants in Iowa prairies. Jour. Iowa Acad. Sci. 75: 32-35.

Odum, H. T., Cantlon, J. E., and L. S. Kornicker. 1960. An organizational hierarchy postulate for the interpretation of species-individual distributions, species entropy, ecosystem evolution, and the meaning of a species-variety index. Ecology 41: 395-399.

Orloci, L. 1966. Geometric models in ecology. I. The theory and application of some ordination methods. Jour. of Ecology 54: 193-215.

Orloci, L. 1967. An agglomerative method for classification of plant communities. Jour. of Ecology 55: 193-206.

Oschwald, W. R. et al. 1965. Principal soils of Iowa. Special Report No. 42. Ames, Iowa, Department of Agronomy, Iowa State University.

Palmblad, I. G. 1968. Competition in experimental populations of weeds with emphasis on the regulation of population size. Ecology 49: 26-34.

Phillips, E. A. 1959. Methods of Vegetation Study. New York, New York, Henry Holt and Company, Inc.

Pohl, R. W. 1966. The grasses of Iowa. Iowa. Iowa State Jour. of Science 40: 341-566.

Pound, R. and F. L. Clements. 1898. The vegetation regions of the prairie province. Bot. Gaz. 25: 381-394.

Richards, M. S. 1969. Observations on responses of prairie vegetation to an April fire in central Iowa. Unpublished master's thesis. Ames, Iowa, Library, Iowa State University.

Ross, B. A., Tester, J. R., and W. J. Breckenridge. 1968. Ecology of Mima-type mounds in northwestern Minnesota. Ecology 49: 172-177.

Ruhe, R. V. 1969. Quaternary landscapes in Iowa. Ames, Iowa, Iowa State University Press. 249 pp.

Rydberg, P. A. 1931. A short phytogeography of the prairies and great plaints of Central North America. Brittonia 1: 57-66.

Sampson, H. C. 1921. An ecological survey of the prairie vegetation of Illinois. State Dept. of Registration and Education, Division of Natural History Survey Bull. 13: 523-577.

Sanders, D. R. 1969. Structure and pattern of the herbaceous understory of deciduous forests in central Iowa. Unpublished Ph.D. thesis. Ames, Iowa, Library, Iowa State University.

Schaffner, J. H. 1926. Grasslands of the Central United States. Ohio State Univ. Studies Contr. Bot. 178: 5-56.

Scheffer, V. B. 1947. The mystery of the Mima mounds. Science Monthly 65: 283-294.

Scheffer, V. B. 1958. Do fossorial rodents originate Mima-type microrelief? American Midland Naturalist 59: 505-510.

Schmitt, D. P. 1969. Plant parasitic nematodes and nematode populations in the Kalsow Prairie. Unpublished master's thesis. Ames, Iowa, Library, Iowa State University.

Shanks, R. E. 1953. Forest composition and species association in the beech-maple forest region of western Ohio. Ecology 34: 455-466.

Shantz, H. L. 1923. The natural vegetation of the great plains region. Annals Assoc. Amer. Geog. 13: 81-107.

Sherff, E. E. 1912. The vegetation of Skokie marsh, with special reference to subterranean organs and their interrelationships. Bot. Gaz. 53: 415-435.

Shimek, B. 1911. The prairies. Bull. Lab. Nat. Hist., State Univ. Iowa 6: 169-240.

Shimek, B. 1915. The plant geography of the Lake Okoboji region. Bull. Lab. Nat. Hist., State Univ. Iowa 7: 1-90.

Shimek, B. 1925. The persistence of the prairie. Univ. of Iowa Studies 11: 3-24.

Sorensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. Biol. Rev. 23: 411-488.

Sorensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analysis of the vegetation on Danish commons. Biol. Skr. 5: 1-34.

State Conservation Commission. 1968. Letters, reports, data. Unpublished material. Kalsow Prairie file, State Conservation Commission, Des Moines, Iowa.

Steiger, T. L. 1930. Structure of prairie vegetation. Ecology 11: 170-217.

Tester, J. R. and W. H. Marshall. 1961. A study of certain plant and animal interrelations on a native prairie in northwestern Minnesota. Minnesota Museum of Natural History. Occasional Papers No. 8: 1-50.

Thorp, James. 1949. Effects of certain animals that live in the soil. Sci. Monthly 68: 180-191.

Trauger, D. L. 1967. Habitat factors influencing duck brood use of semi-permanent and permanent prairie potholes in North Dakota. Unpublished master's thesis. Ames, Iowa, Library, Iowa State University.

U. S. Government. 1868. First survey of the State of Iowa. Plats deposited in the State House, Des Moines.

Weaver, J. E. 1930. Underground plant development in its relation to grazing. Ecology 11: 543-557.

Weaver, J. E. 1954. North American Prairie. Lincoln, Nebraska, Johnsen Publishing Company. 348 pp.

Weaver, J. E. and F. E. Clements. 1938. Plant Ecology. New York, New York, 2nd ed. McGraw-Hill Book Co.

Weaver, J. E. and T. J. Fitzpatrick. 1932. Ecology and relative importance of the dominants of the tall-grass prairie. Bot. Gaz. 93: 113-50.

Weaver, J. E. and T. J. Fitzpatrick. 1934. The prairie. Ecol. Monogr. 4: 109-295.

Whitford, D. B. and P. J. Salamun. 1954. An upland forest survey of the Milwaukee area. Ecology 35: 533-540.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26: 1-80.

Williams, C. B. 1954. The statistical outlook in relation to ecology. Jour. of Ecology 42: 1-13.

Williams, W. T. and J. M. Lambert. 1960. Multivariate methods in plant ecology. II. The use of an electronic digital computer for association-analysis. Jour. of Ecology 48: 689-710.

Williams, W. T. and J. M. Lambert. 1961a. Nodal analysis of associated populations. Nature, London 191: 202-229.

Williams, W. T. and J. M. Lambert. 1961b. Multivariate methods in plant ecology. III. Inverse association-analysis. Jour. of Ecology 49: 717-729.

Williams, W. T. and J. M. Lambert. 1962. Multivariate methods in taxonomy. Taxon. 10: 205-211.

Yapp, R. H. 1909. On stratification in the vegetation of a marsh, and its relations to evaporation and temperature. Ann. Bot. 23: 275-320.

ACKNOWLEDGEMENTS

The author wishes to express appreciation and gratitude to Dr. R. Q. Landers, Jr. for his guidance and suggestions throughout the investigation of this problem and for his cooperation and constructive criticism of the manuscript during its writing. Special thanks is given to Dr. Don C. Norton in the direction of my graduate program; to Dr. David Jowett, Roger Mrachek, and Charles Graham for aid and assistance in data handling; and to the Department of Botany and Plant Pathology, Iowa State University for their aid in supplying laboratory space, equipment, and partial funding in the completion of this study.

The cooperation of the Iowa State Conservation Commission and especially their area supervisor, Mr. Jack Galliart, is greatly appreciated, for without their permission and funding it would not have been possible to carry out this study.

Acknowledgement is also given to Mrs. Susan Atwell of Fort Dodge, Iowa, for her generous offer of a home away from home.

The author wishes to express his love and gratitude to his wife, Karen, who has supported him in this work in every possible way. Assistance in field work, data analysis, and in the preparation and typing of the manuscript are recognized and appreciated, but the value of her love and moral support are beyond means of expression.

APPENDIX

APPENDIX

Plant List Kalsow Prairie

NOTE:

1. Cyperaceae nomenclature after:

   Gilly, Charles L. 1946. The Cyperaceae of Iowa. Iowa State College Journal of Science 21: 55-151.

2. Gramineae nomenclature after:

   Pohl, Richard W. 1966. The Grasses of Iowa. Iowa State Journal of Science 40: 341-566.

3. All other nomenclature after:

   Gleason, Henry A. 1952. The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada. 3 Vol. Lancaster Press, Inc., Lancaster, Pennsylvania.

4. Original plant list for Kalsow Prairie determined by John F. Moyer. 1953. Ecology of Native Prairie in Iowa. Unpublished Ph. D. dissertation. Library, Iowa State University, Ames, Iowa.

   *Species added to Moyer's list as collected and determined by Jack D. Brotherson.

   +Species included in Moyer's list and recollected by Jack D. Brotherson.

   -Species included in Moyer's list and not collected by Jack D. Brotherson.

5. Species listed alphabetically by genera.

Species	Common Name
*Acer negundo L.	Box Elder
+Achillea lanulosa Nutt.	Yarrow
+Agropyron repens (L.) Beauv.	Quack Grass
*Agropyron smithii Rydb.	Western Wheatgrass
+Agropyron trachycaulum (Link) Malte.	Slender Wheatgrass
+Agrostis alba L.	Redtop
*Agrostis hiemalis (Walt.) B.S.P.	Ticklegrass
*Agrostis scabra Willd.	Ticklegrass
+Allium canadense L.	Wild Onion
-Allium schoenoprasum L.	Wild Onion
*Amaranthus albus L.	Tumble-weed

Species	Common Name
*Amaranthus retroflexus L.	Pigweed
*Amaranthus tamariscinus Nutt.	Pigweed
+Ambrosia artemisifolia L.	Common Ragweed
*Ambrosia trifida L.	Giant Ragweed
+Amorpha canescens Pursh	Lead-plant
*Amphicarpa bracteata (L.) Fern.	Hog Peanut
+Andropogon gerardi Vitman	Big Bluestem
+Andropogon scoparius Michx.	Little Bluestem
+Anemone canadensis L.	Anemone
+Anemone cylindrica Gray	Long-headed Anemone
+Antennaria neglecta Greene	Pussy-toes
*Apocynum sibiricum Jacq.	Indian Hemp
-Aquilegia canadensis L.	Wild Columbine
-Arabis divaricarpa Nels.	Rock Cress
*Arabis hirsuta (L.) Scop.	Rock Cress
+Artemisia ludoviciana Nutt.	Mugwort
+Asclepias incarnata L.	Swamp Milkweed
*Asclepias purpurascens L.	Purple Milkweed
+Asclepias sullivantii Engelm.	Prairie Milkweed
+Asclepias syriaca L.	Common Milkweed
+Asclepias tuberosa L.	Butterfly-weed
*Asclepias viridiflora Raf.	Green Milkweed
+Asclepias verticillata L.	Whorled Milkweed
+Aster Ericoides L.	Many Flowered Aster
+Aster laevis L.	Smooth Aster
*Aster novae-angliae L.	New England Aster
*Aster sericeus Vent.	Silky Aster
*Aster simplex Willd.	Simple Aster
+Astragalus canadensis L.	Milk-vetch
-Astragalus caryocarpus Ker.	Ground Plum
*Astragalus crassicarpus Nutt.	Ground Plum
+Baptisia leucantha T. & G.	Prairie False Indigo
+Baptisia leucophaea Nutt.	Cream colored False Indigo
*Bidens vulgata Greene	Beggar-ticks
+Bouteloua curtipendula (Michx.) Torr.	Side-oats Grama
*Brassica nigra (L.) Koch.	Black Mustard
*Bromus inermis Leyss.	Smooth Brome
-Bromus purgans L.	Purging Brome
+Cacalia tuberosa Nutt.	Tuberous Indian-plantain
+Calamagrostis canadensis (Michx.) Beauv.	Bluejoint
*Calamagrostis inexpansa A. Gray	Unexpanded Bent-grass
*Cannabis sativa L.	Hemp
*Carex aquatilis Wahl. var. altior (Rydb.) Fern.	Carex
*Carex atherodes Spreng.	Carex
+Carex brevoir (Dew.) Mackenz.	Shorter Carex
*Carex gravida Bailey	Heavy Carex
*Carex lasiocarpa Ehrh. var. latifolia (Böekl.) Gilley	Carex

Species	Common Name
*Carex meadii Dewey	Carex
-Carex retrorsa Schw.	Carex
*Carex sartwellii Dewey	Carex
+Carex stipata Muhl.	Carex
*Carex stricta Lam.	Carex
*Ceanothus americanus L.	New Jersey Tea
*Chenopodium album L.	Lamb's Quarters
*Chenopodium berlandieri Moq.	Goosefoot
+Cicuta maculata L.	Spotted Cowbane
*Cirsium altissimum (L.) Spreng.	Thistle
*Cirsium arvense (L.) Scop.	Canada Thistle
-Cirsium discolor (Muhl.) Spreng.	Two-colored Thistle
-Cirsium hillii (Canby.) Fern.	Thistle
-Cirsium iowense (Pammel) Fern.	Iowa Thistle
+Comandra umbellata (L.) Nutt.	Bastard Toad-flax
+Convolvulus sepium L.	Hedge Bindweed
+Coreopsis palmata Nutt.	Tickseed
*Cornus racemosa Lam.	Dogwood
*Delphinium virescens Nutt.	Larkspur
+Desmodium canadense (L.) DC	Tick-trefoil
-Dodecatheon media L.	Shooting Star
+Echinacea pallida Nutt.	Purple Coneflower
*Echinochloa crusgalli (L.) Beauv.	Barnyard Grass
*Eleocharis compressa Sull.	Spike Rush
*Eleocharis macrostachya Britt. in Small	Spike Rush
+Elymus canadensis L.	Canadian Wild Rye
*Elymus virginicus L.	Terrell Grass
*Equisetum arvense	Common Horsetail
-Equisetum fluviatile L.	Scouring Rush
*Equisetum hiemale L.	Scouring Rush
+Equisetum kansanum Schaffn.	Horsetail
+Erigeron strigosus Muhl.	Daisy Fleabane
+Eryngium yuccifolium Michx.	Rattlesnake-master
-Euphorbia corollata L.	Flowering Spurge
*Eurphorbia obtusata Pursh	Spurge
*Eurphoabia serpyllifolia Pers.	Spurge
-Fragaria vesca L.	Woodland Strawberry
*Fragaria virginiana Duchesne	Wild Strawberry
*Fraxinus americana L.	White Ash
*Fraximus pennsylvanica Marsh	Green Ash
+Galium obtusum Bigel.	Bedstraw
*Gentiana andrewsii Griseb.	Closed Gentian
-Gentiana crinita Forel.	Fringed Gentian
+Gentiana puberula Michx.	Gentian
*Gerardia tenuifolia Vahl.	Gerardia
-Geum triflorum Pursh	Avens
*Glychorriza lepidota Pursh	Licorice
+Helenium autumnale L.	Sneezeweed
+Helianthus grosseserratus Martens	Sunflower

Species	Common Name
*Helianthus maximiliani Schrad.	Sunflower
-Helianthus rigidus (Cass.) Fern.	Sunflower
+Heliopsis helianthoides (L.) Sweet.	Ox-eye
*Heuchera richardsonii R. Br.	Alum Root
*Hierchloë odorata (L.) Beauv.	Holy Grass
+Hordeum jubatum L.	Squirreltail
+Hypoxis hirsuta (L.) Coville	Star Grass
-Ipomoea purpurea (L.) Roth.	Morning Glory
*Iris virginica L.	Blue Flag
*Juncus tenuis Willd.	Wire Rush
*Kochia scoparia (L.) Schrad.	Summer Cypress
+Koeleria cristata (L.) Pers.	June Grass
+Lactuca ludoviciana (Nutt.) Riddell	Wild Lettuce
*Lactuca pulchella (Pursh) DC	Blue Lettuce
*Lactuca scariola L.	Prickly Lettuce
*Lappula echinata Gilib.	Stickseed
+Lathyrus palustris L.	Vetchling
+Lathyrus venosus Muhl.	Vetching
-Leptoloma cognatum (Schult.) Chase	Fall Witch Grass
*Lespedeza capitata Michx.	Bush Clover
*Liatris aspera Michx.	Blazing-star
+Liatris pycnostachya Michx.	Blazing-star
-Liatris scariosa (L.) Willd.	Blazing-star
-Lilium canadense L.	Wild Yellow Lily
+Lilium philadelphicum L.	Wood Lily
+Lithospermum canescens (Michx.) Lehm.	Orange Puccoon
*Lobelia siphilitica L.	Blue Cardinal Flower
+Lobelia spicata Lam.	Highbelia
-Lobularia martima (L.) Desv.	Sweet Alyssum
+Lycopus americanus Muhl.	Water Horehound
-Lycopus rubellus Moench.	Water Horehound
+Lysimachia chiliata L.	Loosestrife
+Lysimachia hybrida Michx.	Loosestrife
+Lysimachia quadriflora Sims	Loosestrife
+Lythrum alatum Pursh	Loosestrife
*Malus pumila Mill.	Apple
-Medicago lupulina L.	Black Medick
+Melilotus alba Desr.	Sweet Clover
-Melilotus officinalis (L.) Lam.	Yellow Sweet Clover
*Mentha arvensis L.	Mint
-Mirabilis hirsuta (Pursh) MacM.	Four-o'clock
*Mirabilis nyctaginea (Michx.) MacM.	Four-o'clock
*Monarda fistulosa L.	Horse Mint
-Monarda punctata L.	Wild Bergamot
*Morus alba L.	Mulberry
*Muhlenbergia mexicana (L.) Trin.	Muhly Grass
*Muhlenbergia racemosa (Michx.) B.S.P.	Muhly Grass
+Oenothera biennis L.	Evening Primrose
+Oxalis stricta L.	Wood-sorrel

Species	Common Name
+Oxalis violaceae L.	Violet Wood-sorrel
*Panicum implicatum Scribn.	Panicum
*Panicum capillare L.	Witchgrass
-Panicum praecocius Hitchc. & Chase	Panicum
*Panicum leibergii (Vasey) Scribn.	Panicum
+Panicum scribnerianum Nash.	Panicum
+Panicum virgatum L.	Switchgrass
*Parietaria pennsylvanica Muhl.	Pellitory
+Pedicularis canadensis L.	Lousewort
-Pedicularis lanceolata Michx.	Lousewort
+Petalostemum candidum (Willd.) Michx.	White Prairie-clover
+Petalostemum purpureum (Vent.) Rydb.	Purple Prairie-clover
+Phalaris arundinacea L.	Reed Canary Grass
+Phleum pratense L.	Timothy
-Phlox maculata L.	Sweet William
+Phlox pilosa L.	Prairie Phlox
+Physalis heterophylla Nees.	Ground Cherry
-Physalis longifolia Nutt.	Ground Cherry
*Physalis virginiana Mill.	Ground Cherry
+Poa compressa L.	Canada Bluegrass
*Poa palustris L.	Bluegrass
+Poa pratensis L.	Kentucky Bluegrass
*Polygonum aviculare L.	Knotweed
*Polygonum coccineum Muhl.	Smartweed
*Polygonum convolvulus L.	Black Bindweed
*Polygonum pennsylvanicum L.	Pinkweed
*Polygonum persicaria L.	Lady's Thumb
*Polygonum ramosissimum Michx.	Bushy Knotweed
*Populus deltoides Marsh	Eastern Cottonwood
*Portulaca oleracea L.	Purslane
+Potentilla arguta Pursh	Tall Cinquefoil
-Potentilla canadensis L.	Cinquefoil
+Potentilla norvegica L.	Cinquefoil
*Prenanthes racemosa Michx.	Rattlesnake Root
*Prunus americana L.	American Plum
+Psoralea argophylla Pursh	Scurf-pea
+Pycnanthemum virginianum (L.) Durand & Jackson	Mountain Mint
*Ranunculus fascicularis Muhl.	Buttercup
*Ratibida columnifera (Nutt.) Wooton & Standl.	Prairie Coneflower
-Ratibida pinnata (Vent.) Barnh.	Prairie Coneflower
*Rhamnus catharticus L.	Buckthorn
-Rosa arkansana Porter	Wild Rose
*Rosa blanda Ait.	Wild Rose
*Rosa suffulta Greene	Prairie Rose
*Rudbeckia hirta L.	Black-eyed Susan
-Rudbeckia serotina Nutt.	Black-eyed Susan
*Rumex crispus L.	Sour Dock
*Rumex patientia L.	Patience Dock

Species	Common Name
*Sagittaria latifolia Willd.	Arrow-head
+Salix humilis Marsh.	Upland Willow
*Salix nigra Marsh.	Black Willow
*Salix petiolaris	Willow
*Scirpus atrovirens Willd.	Bulrush
+Scirpus fluviatilis (Torr.) Gray	River Bulrush
*Scutellaria leonardii Epl.	Skullcap
-Scutellaria parvula Michx.	Skullcap
*Senecio aurens L.	Golden Ragwort
-Senecio integerrimus Nutt.	Ragwort
*Senecio pauperculus Michx.	Ragwort
+Setaria lutescens (Weigel.) Hubb.	Yellow Foxtail
*Setaria viridis (L.) Beauv.	Green Foxtail
+Silphium laciniatum L.	Compass Plant
+Sisyrinchium campestre Bickn.	Blue-eyed Grass
*Solanum nigrum L.	Black Nightshade
-Solidago altissima L.	Goldenrod
*Solidago canadensis L.	Goldenrod
+Solidago gigantea Ait.	Goldenrod
-Solidago graminifolia (L.) Salisb.	Goldenrod
+Solidago gymnospermoides (Greene) Fern.	Goldenrod
+Solidago missouriensis Nutt.	Missouri Goldenrod
+Solidago nemoralis Ait.	Goldenrod
*Solidago riddellii Frank	Goldenrod
+Solidago rigida L.	Rigid Goldenrod
-Solidago rugosa Ait.	Goldenrod
*Sorghastrum nutans (L.) Nash	Indian Grass
+Spartina pectinata Link	Slough Grass
*Sphenopholis obtusata (Michx.) Scribn. var. obtusata	Wedgegrass
*Spiranthes cernua (L.) Rich.	Ladies' Tresses
-Sporobolus heterolepis (A. Gray) A. Gray	Prairie Dropseed
+Stipa spartea Trin.	Porcupine Grass
*Taraxacum officinale Weber.	Dandelion
*Teucrium canadense L.	Wood Sage
+Thalictrum dasycarpum Fisch. & Lall.	Meadow Rue
+Tradescantia bracteata Small	Spiderwort
*Tragopogon dubius Scop.	Goat's Beard
-Tragopogon pratensis L.	Goat's Beard
-Trifolium agarium L.	Hop Clover
-Trifolium hybridum L.	Alsike Clover
+Trifolium pratense L.	Red Clover
*Ulmus pumila L.	Siberian Elm
+Verbena hastata L.	Simpler's-joy
+Verbena stricta Vent.	Hoary Vervain
+Vernonia fasiculata Michx.	Ironweed
+Veronicastrum virginicum (L.) Farw.	Culver's Root
*Viola papilionacea Pursh	Violet

Species	Common Name
+Viola pedatifida G. Don	Prairie Violet
+Vicia americana Muhl.	Vetch
-Zizia aptera (Gray) Fern.	Golden Alexanders
+Zizia aurea (L.) W.D.J. Koch	Golden Alexanders
+Helianthus laetiflorus	Sunflower