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Vegetational Pattern on a Sand Area Dominated by Prairie Species in Southwestern Michigan

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VEGETATIONAL PATTERN ON A SAND AREA DOMINATED BY PRAIRIE SPECIES IN SOUTHWESTERN MICHIGAN

by

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INTRODUCTION

Although Michigan is not especially noted for its prairie vegetation, grassland was an important vegetation type at the time the state was settled. Reporting on Michigan dry prairies, Veatch (1928) stated that they occurred as small, separate bodies of about 80 acres to a maximum of about 25 square miles and were restricted to the southwestern part of the state; collectively, they occupied about 80,000 acres. Veatch (1928) listed about 40 prairies, the locations of which he determined mainly by soil characteristics. This list was expanded by the use of historical records to 58 (Butler 1947, 1948, 1949). Counties containing prairie were Newaygo, Barry, Eaton, Kalamazoo, Calhoun, Berrien, Cass, St. Joseph, Van Buren and Branch.

There have been few actual studies done on the vegetation of Michigan prairies (Gleason 1917, Transeau 1935, Butler 1947, 1948, 1949, Hauser 1953, Benninghoff 1964, Brewer 1965). Michigan settlers quickly recognized the potential of the prairie lands for agriculture, and so the prairie disappeared before any extensive study could be made. Little, if any, virgin prairie now exists.

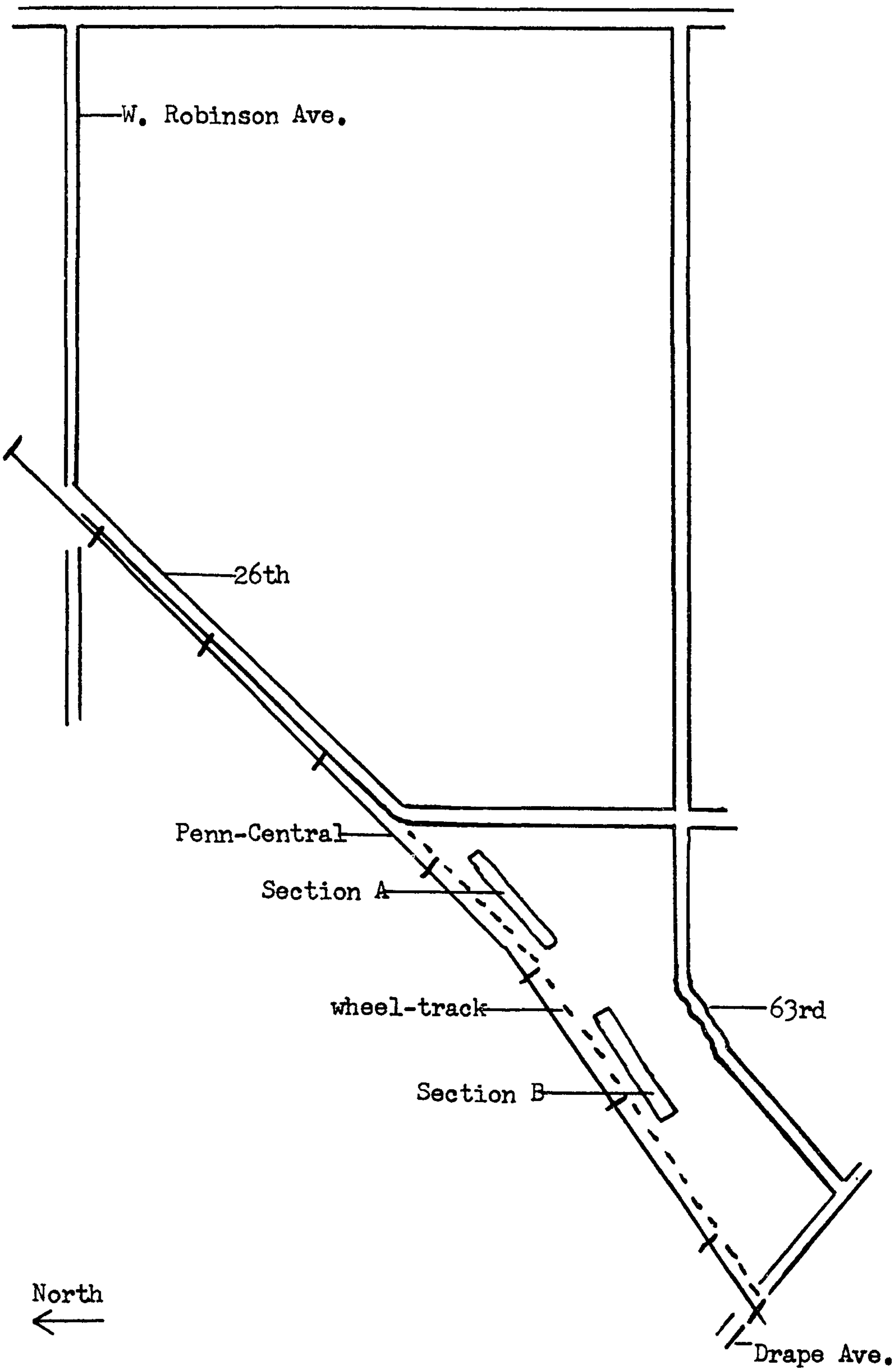
The purpose of this investigation was to study the composition of vegetation in a sandy area dominated by prairie plants in Van Buren County, Michigan, and also to detect the presence of pattern and interspecific association in the more common species. Species lists of other regions in Michigan and other states were compared with lists of the study area.

STUDY AREA

The study area lies about two miles southwest of Mattawan, Van Buren County, Michigan, in the SE ¼ of Sect. 22, R 13 W, T 3 S. It consists of a narrow strip lying southeast of the Penn-Central Railroad, between Drape Ave. and West Robinson Ave. (Fig. 1). Total length of the area is about 4,000 feet and the width is about 150 feet. Elevation is mostly 820-840 feet above mean sea level. The area can be subdivided into two smaller areas based on soil differences. One section (A) consists of a sand base covered with cinders; the other section (B) is sand that may have been exposed in construction of the levee on which the railroad is located. The study area is bounded for 2,112 feet along the southwest by a forest of black and white oak (*Quercus velutina* and *Quercus alba*) and along the remaining 1,118 ft. to the south by cultivated fields. (Plant names follow Gleason, 1952.)

An area about 0.2 mile long where the forest and prairie meet has been made into a fire lane; however, no major disturbance has occurred in the sampled area during the three-year period that the area was studied. Southeast of the study area there are char markings on an old wooden railroad post and in the forest adjacent to the southwest part of the prairie there is a burned oak stump. But residents of the area cannot remember when a fire occurred or if it had any effect on the study area itself. It should be noted, however, that in past times many areas along railroad rights-of-way were subjected to

Figure 1 Sketch showing location of prairie in relation to roads of the area. Scale: 1.3 cm. equals .1 mile.


W. Robinson Ave.
26th
Penn-Central
Section A
wheel-track
63rd
Section B
North
Drape Ave.

frequent fires set by sparks from locomotives and other sources. Bordering the north side of the study area is the Penn-Central Railroad Line. On the other side of the railroad is another forest. Sometime between three to ten years ago this forest was burned over but it is not known if this fire passed over the railroad bed and disturbed the area.

METHODS

In the summer of 1965 16 permanent plots (four meters on a side) were placed randomly in the study area. Each plot was divided into 16 one-square-meter quadrats, thus giving a total of 256 one-square-meter quadrats. For the density studies half of the plots were picked randomly from the above sixteen. Eight square-meter quadrats were then selected from each of these eight plots giving a total of 64 square-meter quadrats. The eight quadrats from each plot to be used were determined by alternating three arrangements: in every arrangement the four middle quadrats were used; in arrangement A the two north quadrats and the two south quadrats were added, in arrangement B the two east quadrats and the two west quadrats were added, and in arrangement C the four corner quadrats were added. For the pattern studies, the same four middle quadrats of the eight random plots picked in the density study were used. Each of these four was divided into 100 10-square-cm. plots, in which stems of all vascular plants except bunch-grasses were counted. The results were then compared with random expectations as indicated by a Poisson series having the same mean. The variance mean ratio test (Greig-

Smith 1964) also known as the coefficient of dispersion (Blackman 1942) or relative variance (Clapham 1936) was used to test for pattern. This test makes use of the equality of mean and variance of the Poisson distribution. If the ratio of variance to mean is less than one, a tendency toward a uniform distribution is indicated; if the ratio of variance to mean is greater than one a contagious or aggregated distribution is indicated. The difference may then be compared with its standard error by means of a t test. For the variance/mean ratio test each meter quadrat was broken up into four 2500-square-cm. quadrats, thus giving a total of 96 2500-square-cm. quadrats for section A and 32 2500-square-cm. quadrats for section B.

The area sampled was placed into the prairie vegetational continuum (series of communities whose floristic composition gradually changes along an environmental gradient) developed by Curtis (1959). In his study on the vegetation of Wisconsin he divided the Wisconsin prairies into five units based mainly on soil moisture content. The five units were wet, wet-mesic, mesic, dry-mesic, and dry. In addition Curtis made a list of ten characteristic species in each section of the continuum and called them indicator species. The position of a given stand of vegetation on the continuum can be determined by taking one's data and expressing the number of indicator species as a percentage of the total number of indicators present and then weighting the values by multiplying the percentage of wet indicators by one, by multiplying the percentage of wet-mesic indicators by two, etc. By adding the resulting values an index value

is obtained and thus the given stand of vegetation can be classified as to its position on the continuum. Curtis' continuum ranged from 100 to 500, 100 equalling wet prairie and 500 equalling dry prairie.

The vegetation was analyzed according to Raunkiaer's life form system. Assignment of species to life forms was based on the lists of Ennis (1928) and McDonald (1937).

The species area relation, often expressed as the species:area curve was next considered. Kilburn (1963) describes the species area relations for plant species with the following equation: $y=kx^z$. In this equation y represents the number of species, x represents the area, k is a constant selected as the mean number of species in one square meter, and z is an exponent relating the increase of number of species to increase in area. The same plots and quadrats used in the frequency and pattern studies were used to construct the species area curves. This resulted in the following areas being used: for section A 2,400 .01-square-meter quadrats, 96 .25-square-meter quadrats, 144 one-square-meter quadrats, and one 144-square-meter quadrat; for section B 800 .01-square-meter quadrats, 32 .25-square-meter quadrats, 112 one-square-meter quadrats, and one 112-square-meter quadrat. The data were fitted to the equation given above using a linear regression and correlation program developed by Zar (1968).

Greig-Smith (1964) states that if species in a community exhibit pattern this would indicate a control by influencing factors and the study of interspecific association between species would provide evidence of any grouping of species or competitive relations from a like response. Interspecific association was studied using two different

sized quadrats to assess the effects of scale. The quadrat sizes used were one square meter (144 for section A and 112 for section B) and .01 square meters. For the .01 square meter quadrat two plots from each section were randomly chosen to see if any associations could be detected. The plots chosen were plot one and plot six for section A and plots 11 and 12 for section B. This gave a total of 800 .01-square-meter plots for each section. Species with an 11 per cent or higher frequency were tested from section A and species with a 14 per cent or higher frequency were tested from section B. The data were tested to see if the species occurred together more or less frequently than would be expected on the basis of chance by the use of chi-square calculated from a 2 x 2 contingency table. (For a more complete description of the method used, see Greig-Smith, 1964.)

RESULTS

Composition of Vegetation

Section A

Of the 43 species of plants found in the section, Andropogon scoparius, Helianthus occidentalis, Poa compressa, Panicum oligosanthes, Rumex acetosella, and Rubus sp. had a frequency of 50 per cent or higher (Table 1). (Frequencies were determined from 144 one-square-meter quadrats.) Three species had a frequency between 40 per cent and 50 per cent. They were Euphorbia corollata, Tradescantia ohiensis, and Poa pratensis.

Density was the next quantitative aspect of the area to be considered. Of the 29 species of plants used in the density study Heli-

Table 1

Percentage frequency (based on 144 one-square-meter quadrats) and density (based on 48 one-square-meter quadrats) of vascular plants occurring in quadrats of section A of a sand area dominated by prairie plants in Van Buren County, Michigan.

Species	Per cent frequency	Stems per one square meter quadrat
Helianthus occidentalis	95.0	32.6
Andropogon scoparius	92.0	
Rumex acetosella	82.0	30.9
Panicum oligosanthes	71.0	6.1
Poa compressa	61.0	21.4
Rubus sp.	50.0	1.3
Euphorbia corollata	46.0	1.7
Tradescantia ohiensis	43.0	1.1
Poa pratensis	40.0	2.3
Rosa carolina	39.0	5.3
Hypericum perforatum	35.0	1.85
Oenothera rhombipetala	23.0	.62
Aster azureus	18.0	1.6
Andropogon Gerardi	13.0	
Solidago nemoralis	11.0	
Artemisia caudata	11.0	1.1
Cyperus Schweinitzii	10.4	8.1
Fragaria virginiana	7.0	1.2
Erigeron strigosus	6.9	.06
Solidago sp.	6.9	.22
Rudbeckia hirta	6.2	.20
Krigia virginica	5.5	.27
Liatris aspera	4.8	.08
Rhus Copallinum	4.8	.08
Hieracium longipilum	4.8	.04
Ambrosia artemisiifolia	4.1	.04
Physalis grandiflora	4.1	.04
Potentilla recta	4.1	.29
Sisymbrium altissimum	4.1	
Helianthemum canadense	3.4	
Antennaria neglecta	3.4	.39
Viola pedata	2.0	
Quercus velutina	2.0	
Phlox pilosa	1.3	
Anemone cylindrica	1.3	

Table 1--Continued

Species	Per cent frequency	Stems per one square meter quadrat
Coreopsis tripteris	1.3	
Cyperus filiculmis	1.3	.11
Carex sp.	1.3	
Aster sp.	1.3	
Melilotus officinalis	1.3	
Aster concinnus	.6	.06
Tragopogon pratensis	.6	
Lactuca sp.	.6	.02

anthus occidentalis, Poa compressa, and Rumex acetosella had densities above 20 individuals per one square meter quadrat. (Note that although the stems of Andropogon Gerardi and Andropogon scoparius were not counted, they had densities of at least 60 individuals per one square meter quadrat.) Four species had densities between two and 20 individuals per one meter quadrat. They were Cyperus Schweinitzii, Panicum oligosanthes, Rosa carolina, and Poa pratensis. The other 22 species and their densities can be found in Table 1.

Although the Wisconsin continuum for prairies (Curtis 1959) clearly cannot be simply transferred to Michigan, calculation of a continuum index value should give a rough idea of the relative mesicness of the prairie. Out of the total 43 species found in section A, nine were indicator species: Fragaria virginiana, Phlox pilosa, and Rudbeckia hirta for wet mesic (30 x 2); Liatris aspera for mesic (10 x 3); Anemone cylindrica, Helianthus occidentalis, and Panicum oligosanthes for dry mesic (30 x 4) and Andropogon scoparius, Artemisia caudata, and Solidago nemoralis for dry (30 x 5). Calculation indicated an index value of 360, suggesting a mesic or dry-mesic prairie.

A floristic analysis of the total flora showed that the Compositae comprised 41.8 per cent of all species followed next by Gramineae with 11.6 per cent and Rosaceae with 9.3 per cent. A list of the 14 other families and their percentages can be found in Table 2.

When the vegetation sampled was analyzed using Raunkiaer's life forms, it was found that the area was dominated by hemicryptophytes

Table 2

Sections A and B: list of families, number of species found in each family, and total percentage of flora family composes.

Family	Section A		Section B	
	No. of Species	Percentage	No. of Species	Percentage
Gramineae	5	11.6	6	18.7
Compositae	18	41.8	12	37.5
Rosaceae	4	9.3	2	6.2
Polygonaceae	1	2.3		
Commelinaceae	1	2.3	1	3.1
Euphorbiaceae	1	2.3	1	3.1
Hypericaceae	1	2.3	1	3.1
Onagraceae	1	2.3		
Leguminosae	1	2.3	3	9.3
Cyperaceae	3	6.9		
Polemoniaceae	1	2.3	1	3.1
Cruciferae		2.3	1	3.1
Anacardiaceae	1	2.3		
Solanaceae	1	2.3		
Violaceae	1	2.3		
Fagaceae	1	2.3		
Ranunculaceae	1	2.3		
Cistaceae	1	2.3		
Companulaceae			1	3.1
Polypodiaceae			1	3.1
Rhamnaceae			1	3.1
Santalaceae			1	3.1

(67.4 per cent) followed by cryptophytes (13.9 per cent), phanerophytes (9.3 per cent), therophytes (4.6 per cent), chamaephytes and geophytes (2.3 per cent).

Section B

Of the 32 species of plants found in section B, Panicum perlongum, Andropogon scoparius, Rosa carolina, and Poa compressa had a frequency of 50 per cent or higher (Table 3). (Frequencies were determined from 112 one-square-meter quadrats.) Four species had a frequency between 30 per cent and 50 per cent. They were Tradescantia ohiensis, Euphorbia corollata, Specularia perfoliata, and Helianthus occidentalis. All other species had a per cent frequency between 0.8 and 30. Only four species out of 15 in this section had a density of two individuals per quadrat or higher (Table 3). They were Poa compressa, Rosa carolina, Melilotus alba, and Specularia perfoliata.

Out of the 32 species found in section B, nine were indicator species: Phlox pilosa for wet mesic (10 x 2); Ceanothus americanus and Liatris aspera for mesic (20 x 3); Helianthus occidentalis and Panicum oligosanthes for dry mesic (20 x 4); and Andropogon scoparius, Artemisia caudata, Panicum perlongum and Solidago nemoralis for dry (40 x 5). Calculation indicated an index value of 360, suggesting a mesic prairie. This is the same index value calculated for section A even though some of the indicator species were different.

Analysis of the total flora of section B shows that there was a total of 13 families present (Table 2). The family Compositae had the

Table 3

Percentage frequency (based on 112 one-square-meter quadrats) and density (based on 16 one-square-meter quadrats) of vascular plants occurring in quadrats of section B of a sand area dominated by prairie plants in Van Buren County, Michigan.

Species	Per cent frequency	Stems per one square meter quadrat
Panicum perlongum	92.0	
Andropogon scoparius	82.0	
Rosa carolina	65.0	3.06
Poa compressa	54.0	17.1
Tradescantia ohiensis	39.0	.43
Specularia perfoliata	33.0	2.8
Helianthus occidentalis	31.0	1.94
Euphorbia corollata	30.0	.81
Andropogon Gerardi	20.5	
Melilotus alba	19.0	2.4
Hypericum perforatum	16.0	.10
Panicum oligosanthes	15.0	.18
Erigeron strigosus	14.0	.50
Pteridium aquilinum	14.0	
Solidago nemoralis	9.9	
Lupinus perennis	8.9	.06
Artemisia caudata	8.9	.37
Phlox pilosa	8.0	
Ceanothus americanus	8.0	
Arabis lyrata	6.2	
Vicia americana	6.2	
Poa pratensis	5.3	
Rubus sp.	3.5	
Tragopogon pratensis	3.5	
Ambrosia artemisiifolia	2.6	
Comandra Richardsiana	2.6	
Aster concinnus	1.7	
Antennaria neglecta	1.7	.06
Aster azureus	.8	
Krigia virginica	.8	
Liatris aspera	.8	
Lactuca sp.	.8	.18
Solidago sp.	.8	.18

highest percentage with 37.5 per cent followed by the Gramineae with 18.7 per cent.

When the vegetation sampled for section B was analyzed using Raunkiaer's life forms, it was found that the area was dominated by hemicryptophytes (68.7 per cent), followed by cryptophytes (9.3 per cent), therophytes (9.3 per cent), phanerophytes (6.2 per cent), chamaephytes and geophytes (3.1 per cent).

Distribution of Species: Pattern

Aggregation predominated in most species which were well enough represented to test, except at the smallest quadrat size. Of 13 species tested for the largest quadrat size (one square meter), all were significantly aggregated (Table 4). For the middle quadrat size (2500 square cm.) in 35 tests involving 10 species, only four cases of random distribution were detected (Table 5). These were *Tradescantia ohiensis* in plot six (the same species was aggregated in plot three); *Hypericum perforatum* in plot six (testing was not possible in other plots); and *Helianthus occidentalis* in plots seven and 11 (this species was aggregated in four other plots). At the smallest scale (10 square cm. quadrats), only four species could be tested. Of these, *Rumex acetosella* was significantly aggregated in all of four tests; *Poa compressa* was significantly aggregated in four of five tests; *Helianthus occidentalis* was significantly aggregated in only one of five tests; and *Rosa carolina* was randomly distributed in the single test possible (Table 6).

Based on these four species which were testable at all three

Table 4

Calculated data (based on 48 one-square-meter quadrats) showing the variance, mean, variance/mean, *t* values, and probabilities for fit to a Poisson distribution of vascular plants on a sand area dominated by prairie plants in Van Buren County, Michigan. *t* values marked with an asterisk are significant at the .001 per cent level. Based on plots 1, 3, 4, 6, 7, and 9. Standard error is .206.

Species	Variance	Mean	Variance/Mean	*t*
Oenothera rhombipetala	1.867	.583	3.202	10.674*
Aster azureus	4.269	1.16	3.680	13.00*
Hypericum perforatum	21.38	1.81	11.812	52.48*
Euphorbia corollata	3.040	1.54	1.974	4.728
Tradescantia ohiensis	1.986	.895	2.218	5.912*
Rosa carolina	78.371	5.39	14.540	65.72*
Poa compressa	1774.56	22.16	80.07	383.8*
Helianthus occidentalis	446.48	32.64	13.67	61.50*
Rumex acetosella	826.67	31.08	26.59	124.22*
Poa pratensis	85.02	2.31	36.80	169.90*
Rubus sp.	6.36	1.31	4.85	18.68*
Fragaria virginiana	10.79	1.22	8.84	38.05*
Artemisia caudata	26.90	1.10	24.45	108.98*

Table 5

Calculated data (based on 16 2500 cm. quadrats) showing the variance, mean, variance/mean, t values, and probabilities for fit to a Poisson distribution of vascular plants on a sand area dominated by prairie plants in Van Buren County, Michigan. t values marked with a single asterisk are significant at the one per cent level and those marked with two asterisks are significant at the .1 per cent level. Standard error is .365.

Species	Plot	Variance	Mean	Variance/Mean	t
Rosa carolina	1	17.47	6.0	2.912	5.238**
	6	1.19	.562	2.11	3.04*
	7	182.2	3.37	54.06	145.37**
	9	1.98	.875	2.65	3.5*
	12	5.16	1.81	2.85	5.13**
Tradescantia ohiensis	3	1.85	.625	2.96	5.44**
	6	.400	.500	.8	.55
Euphorbia corollata	1	7.75	.875	8.85	21.8**
	4	1.69	.687	2.45	4.02*
	12	2.362	.687	3.438	6.77**
Hypericum perforatum	6	.929	.562	1.653	1.813
	9	15.729	3.43	4.585	9.958**
Rubus sp.	6	1.06	.500	2.120	3.11*
	9	4.516	1.375	3.824	6.257**
Fragaria virginiana	1	2.783	1.87	1.488	1.35
Helianthus occidentalis	1	5.165	2.31	2.235	3.430*
	3	17.57	7.1	2.474	4.094**
	4	377.44	9.312	40.53	109.8**
	6	31.45	11.1	2.833	5.09**
	7	29.45	16.2	1.817	2.269
	9	12.22	3.6	3.39	6.63**
	11	1.06	.562	1.886	2.46

Table 5--Continued

Species	Plot	Variance	Mean	Variance/Mean	t
Rumex acetosella	1	22.46	5.000	4.492	9.700**
	3	156.51	18.12	8.637	21.21**
	6	44.60	12.25	3.640	7.33**
	7	18.60	4.70	3.957	8.213**
	9	66.132	10.00	6.613	18.36**
Poa pratensis	3	67.05	5.625	11.92	30.33**
Poa compressa	1	33.86	8.937	3.788	7.744**
	3	441.09	38.187	11.55	29.3**
	4	143.89	17.1	8.41	20.58**
	6	2.39	.562	4.25	9.027**
	7	17.31	5.87	2.948	5.411**
	11	13.76	5.18	2.65	4.60**
	12	64.36	13.00	4.950	10.97**

Table 6

Calculated data (based on 400 10-square-cm. quadrats) showing the variance, mean, variance/mean, t values, and probabilities for fit to a Poisson distribution of vascular plants on a sand area dominated by prairie plants in Van Buren County, Michigan. t values marked with a single asterisk are significant at the one per cent level and those marked with two asterisks are significant at the .1 per cent level. Standard error is .005.

Species	Plot	Variance	Mean	Variance / Mean	t
Helianthus occidentalis	3	.273	.272	1.022	.311
	4	.328	.372	.12	1.695
	6	.588	.445	1.321	4.534**
	7	.612	.670	.913	1.229
Rumex acetosella	1	.367	.202	1.816	11.52**
	3	.964	.717	1.344	4.859**
	6	.601	.490	1.226	3.192*
	9	.662	.405	1.634	8.95**
Rosa carolina	1	.243	.240	1.012	.169
Poa compressa	1	.636	,357	1.781	11.031**
	3	4.439	1.285	3.516	35.537**
	4	1.899	.687	2.764	24.92**
	7	.195	.235	.829	2.42
	11	1.176	.520	2.261	17.81**

scales, there appears to be a trend for reduced pattern at the lowest scale. No species tested showed uniform distribution.

Analysis of the Species-Area Relation

The species area-relation or species area curve was next calculated. The calculated number per unit area of each section is shown in Table 7 along with the expected data which was determined through a linear regression and correlation program. The expected data and calculated data were then plotted on semi-log paper (Figs. 2 and 3). The exponential equation or power function as described by the formula $y=kx^z$ was next calculated. The equation forming the best fit for the data is $y=9.38x^{.421}$ (section A) and $y=6.22x^{.352}$ (section B). Kilburn (1966) found for a hill prairie in Illinois that the equation was $y=12x^{0.26}$; therefore, k, the number of species in one square meter quadrat, was 12, whereas in the Mattawan study area it was 9.38 and 6.22. Also his exponent--z--was lower--.26 as compared to .421 and .352. It is plain to see from the data that as additional increments of area are sampled, additional species are found, but at a decreasing rate. Kilburn (1966) found that the number of species in his prairie plot was fewer than that expected from the exponential equation. This is also true for the Mattawan study area except in both sections at the .25 square meter quadrat size the calculated data was higher than the expected data (Figs. 2 and 3). Therefore it can be seen that if one were, for example, to combine the flora of a total county and see how its numbers would compare to the expected number from the exponential equation it would be found that the total number

Table 7

Expected and calculated data for mean number of species for various quadrat sizes on two sand areas: Mattawan sand area, Van Buren County, Michigan and Wisconsin hill prairie (after Kilburn 1966).

Quadrat size	Mattawan sand area				Wisconsin hill prairie
	Section A		Section B		
	Cal.	Ex.	Cal.	Ex.	Cal.
PT	—	—	—	—	0.1
$.001m^2$	—	—	—	—	0.1
$.01m^2$	1.48	1.34	1.23	1.22	2.1
$.25m^2$	7.27	5.23	4.17	3.81	—
$(m/2)^2$	—	—	—	—	7.2
$1m^2$	8.93	9.38	6.33	6.22	11.9
$4m^2$					18.1
$16m^2$	20.19	30.16	15.71	16.5	—
$25m^2$	—	—	—	—	28.0
$100m^2$	—	—	—	—	39.2
$112m^2$	—	—	32.0	32.76	—
$144m^2$	—	—	—	—	—
$900m^2$	43.0	76.14	—	—	66.0

Figure 2 Species-log area data from a sandy area dominated by prairie species (section B) compared with equation $y=6.22x^{.352}$ shown by solid line curves. Note: for area $.01m^2$ and $1m^2$ the data for expected and calculated are so close that their points are almost on top of each other. ⊙ represents field data.

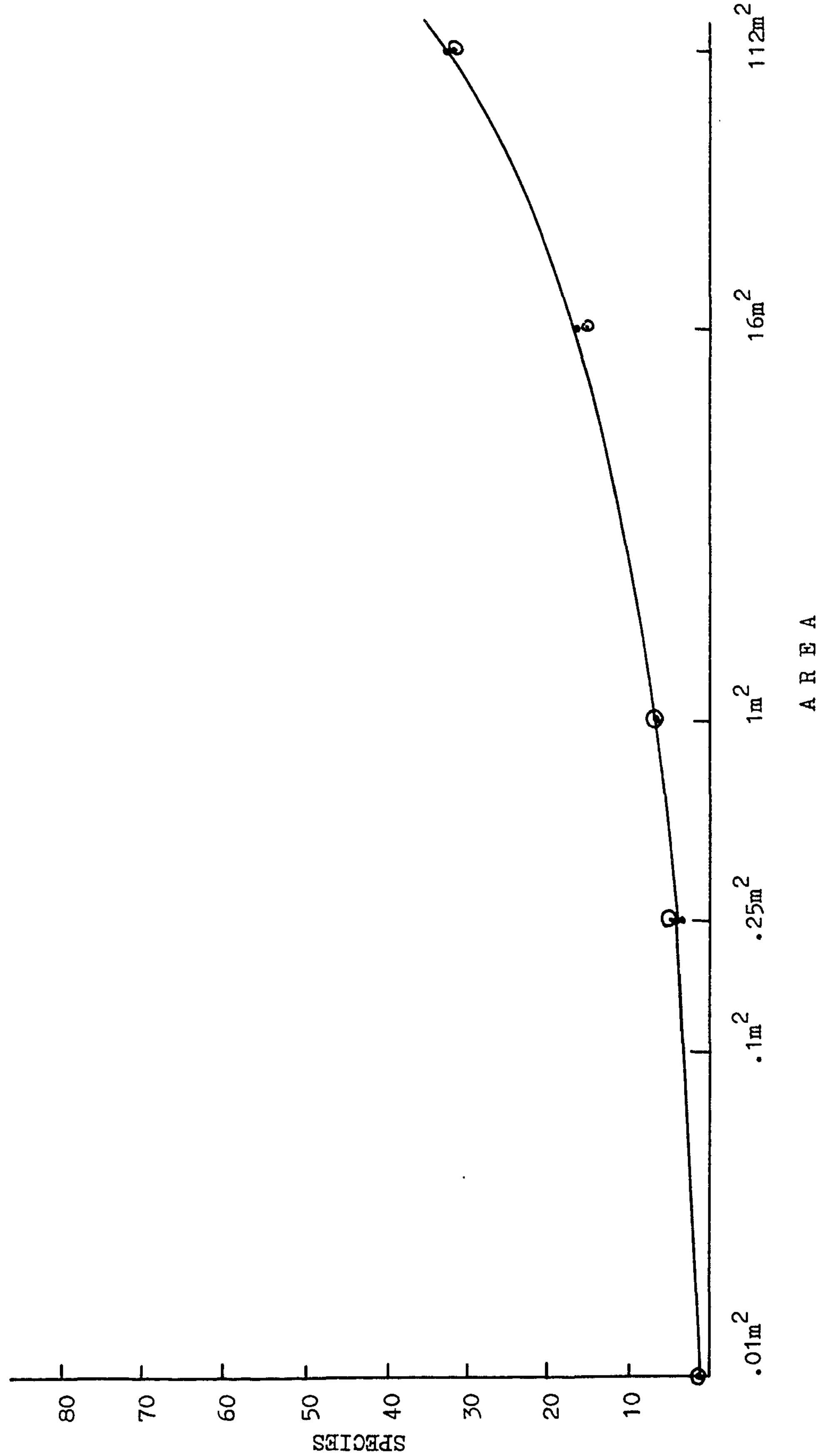
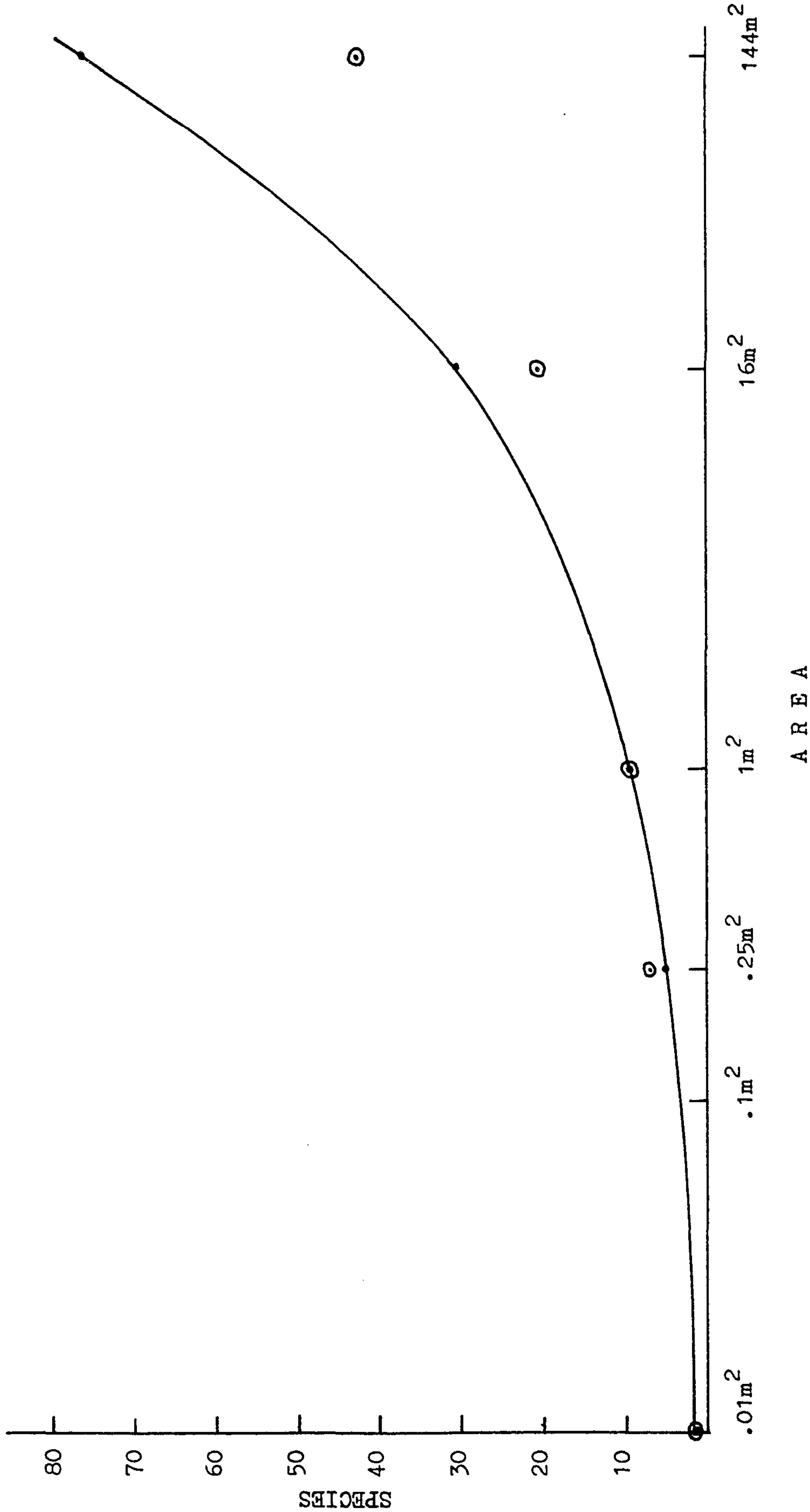

SPECIES
10
20
30
40
50
60
70
80
AREA
.01m²
.1m²
.25m²
1m²
16m²
112m²

Figure 3 Species-log area data from a sandy area dominated by prairie species (section A) compared with equation $y=9.38x^{.421}$ shown by solid line curve. ⊙ represents field data.


SPECIES
80
70
60
50
40
30
20
10
A R E A
.01m²
.1m²
.25m²
1m²
16m²
144m²

of species in the county would be fewer than that expected by the use of the exponential equation.

Interspecific Association

Interspecific association among the frequent species in both areas was next studied. Two different quadrat sizes were used (800 .01-square-meter--sections A and B; 144 one-square-meter--section A; 112 one-square-meter--section B). Any species that did not occur in at least five quadrats was not used. A total of 111 tests was possible. To test if the species occurred together in quadrats by chance, chi-square was calculated from a 2 x 2 contingency table (Greig-Smith, 1964). Unadjusted values and those values using Yates' correction for continuity were both calculated (see Simpson, Roe, and Lewontin, 1960). Of the 111 associations tested 21 showed significance at the .05 level in both adjusted and unadjusted values (Tables 8 and 9). There were 11 more that showed significance at the .05 level only in the unadjusted value. The number of associations found in section A was 17; the remaining four associations were in section B. Of the 21 associations showing significance only 13 species were involved with *Poa compressa* showing association with six different species and *Helianthus occidentalis* and *Andropogon scoparius* showing associations with five different species each. Two associations of the 21 were positive; the remaining 19 showed negative associations. The two associations showing positive association are *Poa compressa*-*Panicum oligosanthes* and *Tradescantia ohiensis*-*Rubus* sp.

Table 8

Species showing positive or negative association, and chi-square for section A of a sand area dominated by prairie plants, Van Buren County, Michigan. Note: * indicates the corrected chi-square values.

Species Association	Chi-square		Association
	.01m^2	1m^2	
Poa compressa Panicum oligosanthes		6.37 5.48*	+
Poa pratensis Panicum oligosanthes		4.66 3.90	-
Poa compressa Rubus sp.		7.48 6.57*	-
Poa compressa Poa pratensis		15.48 14.13*	-
Rubus sp. Tradescantia ohiensis		4.80 4.09*	+
Euphorbia corollata Poa pratensis		4.72 4.00*	-
Helianthus occidentalis Andropogon scoparius	16.38 15.68*		-
Helianthus occidentalis Rumex acetosella	7.41 7.41*		-
Helianthus occidentalis Poa compressa	8.13 7.38*		-
Helianthus occidentalis Rosa carolina	9.24 8.43*		-
Andropogon scoparius Rumex acetosella	8.08 7.62*		-
Andropogon scoparius Rosa carolina	12.36 11.60*		-

Table 8--Continued

Species Association	Chi-square		Association
	$.01m^2$	$1m^2$	
Rumex acetosella Rosa carolina	13.66 12.75*		-
Panicum oligosanthes Tradescantia ohiensis	9.93 4.94*		-
Panicum oligosanthes Solidago nemoralis	9.93 4.94*		-
Poa compressa Rosa carolina	15.68 14.37*		-
Poa compressa Artemisia caudata	5.66 4.30*		-

Table 9

Species showing positive or negative association, and chi-square for section B of a sand area dominated by prairie plants, Van Buren County, Michigan. Note: * indicates the corrected chi-square values.

Species Association	Chi-square		Association
	.01m^2	1m^2	
Poa compressa Rosa carolina		23.25 21.37*	-
Panicum perlongum Andropogon scoparius	103.94 101.26*		-
Panicum perlongum Helianthus occidentalis	6.86 4.86*		-
Andropogon scoparius Euphorbia corollata	18.027 14.34*		-

DISCUSSION

The area studied in this presentation is not believed to be a relict prairie. According to Kenoyer (1934) at the time of the original land survey (1826-1832) the area was probably an oak-hickory forest. There probably existed in these oak forests small isolated open areas that contained prairie species. Local inclusions of prairie within forests were found in Illinois by Vestal (1918a) and in Colorado by Livingston (1952). Also, according to Cole (1901) and Livingston (1902) many of the species present in prairie were also present in oak forests, at least in the driest, most open parts. Thus when the forest was cleared for cultivation or the laying down of a railroad bed these prairie species could migrate into the open areas and become established. Such areas sometimes proved to be favorable for the development of prairie. Vestal (1918b) gives four factors that would favor the growth of prairie in a new area. They are first, coarse, well-drained soil; second, considerable exposure to wind and sun; third, deficiency of rainfall during one critical or several successive growing seasons; and fourth, the destructive effects of burning or mowing, both of which are common on railroad rights-of-way. Possibly the most important factors involved in maintaining the area under study is the destructive effects on woody vegetation of burning or mowing, and, in modern times, the use of herbicides to control the growth of trees and shrubs that may seed in the community. Because of this, the study area is an open sandy area that is dominated by prairie species that presumably migrated into

the region from oak forest openings.

Comparisons with Prairies of Other Regions

Many authors (Gleason 1923, Transeau 1935, Braun 1950, Benninghoff 1964) had discussed the prairie peninsula as a means of explaining the occurrence of prairie in Illinois, Indiana, southern Michigan and southern Wisconsin. The term prairie peninsula was originated by C. C. Adams (1905) because of the occurrence of prairie plants in a peninsula-like projection from the Mississippi valley through Illinois, western Indiana, central Ohio, and southern Michigan. It is difficult to make quantitative comparisons between different areas because of differences in objectives of the investigators. But it might be beneficial to compare species list of the area under study with other areas in the state and other states. The most northern extension of Michigan prairie is that in Newaygo County which lies in the west-central part of the lower peninsula of Michigan. The prairies are located within four adjoining townships of Newaygo County: Everett, Big Prairie, Brooks and Croton (Hauser 1953). The Newaygo prairies are about 85 to 99 miles north of the Mattawan study area. Hauser describes the Newaygo prairie as dry prairie or sand prairie because of the excessive drainage and sandy nature of the soil. Following this description the Mattawan area would also be considered as dry prairie or sand prairie. Of the 144 species found on the Newaygo prairies 29, or 24 per cent, were found on the Mattawan study area (Table 10). That is to say that 55 per cent of the total plants that compose the vegetation of the Mattawan sand area are also found in

Table 10

List of vascular plants* found on the Newaygo, Michigan dry prairie, Illinois sand prairie, Wisconsin dry prairie and Nebraska sand hills that are also found on a sand area dominated by prairie plants in Mattawan, Michigan.

Species	Newaygo, Michigan dry prairie	Illinois sand prairie	Wisconsin dry prairie	Nebraska sand hills
Andropogon Gerardi	x	x	x	x
Andropogon scoparius	x	x	x	x
Poa compressa	x	x		
Poa pratensis	x	x		
Cyperus filiculmis	x	x		
Ambrosia artemisiifolia	x	x	x	
Anemone cylindrica	x	x	x	
Artemisia caudata	x	x	x	
Asclepias tuberosa	x	x		
Aster azureus	x	x	x	
Erigeron strigosus	x	x	x	
Euphorbia corollata	x	x	x	
Fragaria virginiana	x	x		
Helianthus occidentalis	x	x		
Hieracium longipilum	x	x		
Hypericum perforatum	x			
Krigia virginica	x	x		
Liatris aspera	x			
Lupinus perennis	x	x		
Melilotus alba	x			
Oenothera rhombipetala	x	x		
Quercus velutina	x	x		
Rosa carolina	x			
Rumex acetosella	x	x		
Saponaria officinalis	x	x		
Solidago nemoralis	x	x		
Specularia perfoliata	x	x		
Viola pedata	x	x		
Pteridium aquilinum		x		
Panicum perlongum		x	x	
Cyperus Schweinitzii		x		x
Tradescantia ohiensis		x		
Arabis lyrata		x	x	
Ceanothus americanus		x		

Table 10--Continued

Species	Newaygo, Michigan dry prairie	Illinois sand prairie	Wisconsin dry prairie	Nebraska sand hills
Phlox pilosa		x		
Rudbeckia hirta		x		
Antennaria neglecta			x	
Comandra Richardsiana			x	
Helianthemum canadense	x			

*Sources for plant lists:

Newaygo, Michigan dry prairie (Hauser 1910: 159-161)
Illinois sand prairie (Gleason 1910: 146-170; Vestal 1911: 55-56)
Wisconsin dry prairie (Curtis 1959: 553-554)
Nebraska sand hills (Weaver and Albertson 1956: 163-192)

the Newaygo prairie. Of the 47 species listed as prevalent species of dry Wisconsin prairie by Curtis (1959) 13, or 27 per cent, were found on the Mattawan study area (Table 10). The major dominant species of the Wisconsin prairie were Andropogon scoparius, Andropogon Gerardi, Panicum perlongum, Euphorbia corollata, and Solidago nemoralis. In 1917 Gleason studied a prairie in Ann Arbor, Michigan. Curtis compared the species list from this Ann Arbor prairie with the species list of a Wisconsin prairie and found that the Ann Arbor prairie contained 26 species of which 92.3 per cent were found in the Wisconsin stands.

Gleason (1910) and Vestal (1911), writing on the inland sand deposits of Illinois and the Illinois sand prairie, state that the sand of the Illinois prairie is fine grained, yellowish-brown in color and free from organic matter except in the upper layer. This fits the description of the sand area in Mattawan.

Gleason describes four distinct formations or types of vegetation which consist of several associations characterized by distinct groups of plants, a distinct habitat, or both. It would seem that the Mattawan sand area would particularly fall closely to the Panicum pseudopubescens association and the bunch-grass association as described by him. In the Hanover area Gleason found the greatest portion of the sand prairie was originally occupied by a mixed community in which several species of bunch-grasses were well represented. Gleason states that two-thirds of the surface area of sand prairies in Illinois was occupied by the mixed community. The more prominent bunch grasses were Andropogon scoparius, Andropogon Gerardi, Panicum

perlongum, Poa pratensis and Cyperus Schweinitzii; more prominent perennials were Anemone cylindrica, Euphorbia corollata, Ceanothus americanus, Viola pedata, Solidago nemoralis, Helianthus occidentalis and Artemisia caudata; more prominent interstitials were Cyperus filiculmis, Arabis lyrata, Oenothera rhombipetala, Specularia perfoliata, and Erigeron strigosus. Altogether Gleason found 89 species in the mixed community of which 31 species, or 35 per cent, were found on the Mattawan sand area.

Other states such as Nebraska (Weaver and Albertson 1956), Kansas, South Dakota, Colorado and Missouri (Weaver and Fitzpatrick 1934, Albertson 1937, Livingston 1952, Weaver and Albertson 1956, Weaver 1954) contain large expanses of prairie or grasslands. Some of the species found in these areas are also found on the Mattawan study area. They are Andropogon scoparius, Andropogon Gerardi, Poa pratensis, Erigeron strigosus, Euphorbia corollata, Liatris aspera, Anemone cylindrica, Hieracium longipilum, Aster azureus, Solidago nemoralis, Fragaria virginiana, Phlox pilosa and Comandra Richardsiana. Curtis (1959) found that when he compared Wisconsin prairies with those of other areas there was a decreasing similarity with increasing distance. He found that the prairies of Illinois, Iowa, and Minnesota had 75 per cent or more of their species in common with those on the Wisconsin lists, whereas these values drop to 30 or 40 per cent in the true prairie states and below 20 per cent in the high plains and the Palouse region of Washington and Idaho. This same trend can be observed as one goes south from Michigan toward the Mississippi Valley. A small number of the species that are found in the

areas closer to the true prairie regions are found also in Michigan.

Section A and Section B Compared

In sections A and B combined there occur 52 species. Of the 52 species Andropogon scoparius (87 per cent), Helianthus occidentalis (67 per cent), Poa compressa (59 per cent), and Rosa carolina (51 per cent) had frequencies of 50 per cent or higher (based on 256 one-square-meter quadrats). Five species had a frequency between 30 per cent and 50 per cent. They were Panicum oligosanthes (46 per cent), Rumex acetosella (46 per cent), Tradescantia ohiensis (41 per cent), Panicum perlongum (40 per cent), and Euphorbia corollata (39 per cent).

Of the 43 species found in section A 20 species, or 46 per cent, were not found in section B. Of the 32 species which were present in section B, nine species, or 28 per cent, were not found in section A. The predominant species in section B is Panicum perlongum whereas in section A the predominant species is Helianthus occidentalis (Fig. 4). One obvious difference between the two areas is that although there are more species in section A there are more areas of bare ground. Section B is more densely covered even though it has fewer species because of the mats of Andropogon scoparius and Panicum perlongum (Fig. 5).

Several other comparisons can be made between the two areas. First, there is a more mature soil profile in section B than in section A. This would seem to follow because of the more dense clumps of Andropogon scoparius and Panicum perlongum which would tend to

Figure 4 *Helianthus occidentalis* (section A) showing predominance of species.

Figure 5 Densely covered mats of *Andropogon scoparius* (section B).

hold the soil together and prevent leaching and the loss of decaying vegetation. With the holding of decaying vegetation and the accumulation of the grasses year after year, the soil tends to build up, becoming more mature. Second, the vegetation of section B, although containing fewer species, seems to be more stable than section A. In other words the invasion of new species into section B would be much more difficult than an invasion into section A because of the lack of area open to new plants. It is difficult for a new species to become established with the ground covered with bunches of Andropogon scoparius, Panicum perlongum and Andropogon Gerardi (Fig. 6). No two species can occupy the area at the same time. In section A bare ground exists where new species (weeds) can become established. Therefore, section A is not as advanced as section B. Of the two areas, it is obvious (although it has not been tested) that there is a larger biomass per area in section B than in section A. This shows that there is greater total utilization of sunlight in section B than in section A, and thus it is probably a more mature area. The denseness of vegetation in section B would also make it difficult for invading plants not only because of their utilization of space but also because of their use of other physical factors such as water, minerals, and sunlight. Third, the closer an area comes to being a climax association the fewer negative associations there should be among its species (Greig-Smith 1964, Brewer 1965). Section B shows only four negative associations, whereas section A shows 17 negative associations among its species. Therefore, on the basis of negative associations, section B would tend to be a more mature area than section A.

Figure 6 Ground cover in section B showing bunches of Andropogon Gerardi.

Fourth, the closeness of the calculated data and the expected data in the species area curve (Figs. 2 and 3) would tend to indicate a more stable area, whereas the deviation of the calculated and expected data in section A would tend to indicate an area that fluctuates in numbers per area. Therefore, for the reasons given above, section B seems to be more stable than section A.

Section B is sand and section A consists of a sand base covered with cinders. Cinders are an important factor in vegetation. They tend to increase the intensity of the xerophytic conditions (Gleason 1910). Due to their dark color there is greater heat absorption and Gleason feels that this factor favors perennials while it reduces annuals. Gleason also states that the general effect of both fire and cinders increases the amount of open space and restricts vegetation in an area. Although not tested, section A would tend to be more xerophytic than section B because of the cinders and also because there would be more water loss from open areas. The large percentage of Rumex acetosella (which grows in a highly acidic soil) in section A and the lack of it in section B would tend to indicate that the pH of section A is more acidic than that of section B (Smith 1961, Gleason 1952).

Pattern

A number of authors have tested data from randomly thrown quadrats for fit to the Poisson expectation. Blackman (1942, 1935), in examining various grasslands, has found some of its species to have a random distribution. However, Ashby (1948), representing the more

popular view, found species to be generally overdispersed or aggregated. In 1936 Clapham examined data for prairie vegetation compiled by Steiger and pointed out that of 25 species in low prairie only four were randomly distributed and of the 19 species in high prairie none was randomly distributed (Greig-Smith 1952). In 1948 Ashby showed that in large areas where there is a uniformity of soil and microclimate the tendency of the species would be toward non-random distribution but he also noted that in smaller areas that seem to be uniform the plants tend to be distributed non-randomly also. Curtis (1959) also showed extreme aggregation of some mesic prairie plants in Wisconsin. Thus the field work done in the area of distribution indicates that species, in general, will tend to show aggregation or non-randomness. In 1966 Kershaw stated that most authors conclude that vegetative spread and heavy seeds were the two most likely factors which cause aggregation. Curtis (1959), in writing about the aggregated species of the Wisconsin prairie, stated "It is of interest that all but one of the extremely aggregated species are characterized by the possession of active vegetative reproduction by means of short rhizomes. The exception is Phlox pilosa which has no known means of vegetative increase. On the other hand, the nearly random species are annuals, biennials, or non-spreading taprooted perennials." Thus the evidence would lead one to believe that aggregation is the result of vegetative reproduction and seed dispersal. Of the species in the study that indicate aggregation the following reproduce vegetatively by means of rhizomes: Helianthus occidentalis, Rosa carolina, Euphorbia corollata, Rubus sp., Fragaria virginiana, Poa pratensis, and Poa

compressa. Rumex acetosella, because of its seed habit, tends to form clumps or aggregations. It has also been discovered that some plants that show aggregation are known or suspected to produce anti-biotic chemicals which repress growth of other species. For example, Helianthus occidentalis has been shown to produce autotoxic substances (Curtis 1959). How many of the other plants produce substances that can repress the growth of other species is not known. This would make an interesting topic for a further study. Also if the physical factors of an environment are aggregated because of specific reasons, the plants that depend on these physical factors will also be distributed in an aggregated or non-random manner. Therefore, a more detailed study of the physical factors that affect the area is needed before a total examination of pattern in the area can be made.

All species tested tended to show aggregation with only slight differences with quadrat size. The exceptions were Helianthus occidentalis which showed randomness in one plot at the 10-square-cm. quadrat size but aggregation in the one square meter and 2500 square cm. quadrat sizes, Poa compressa which showed randomness in one plot at the 10-square-cm. quadrat size with all the rest showing aggregation and Tradescantia ohiensis which showed randomness at the 2500 square cm. quadrat size. It seems possible that these three scales are measuring three things. First, the one square meter quadrats measure distribution due to physical factors and the existence of large clumps. Second, the 2500 square cm. quadrat size measures the existence of smaller clumps. And, third, the 10 square cm. quad-

rats measure the spacing of individuals in clumps. It should be kept in mind that differences will exist among species due to their size. For example, Ceanothus clumps might be larger than one square meter and thus one square meter for that species might correspond with 2500 square cm. for another species. It is interesting to note that Poa and Rumex, both very small plants, tended to be clumped at the 10 square cm. level, suggesting small clumps in a small plant whereas two larger species, Helianthus and Rosa, tended to be random at the 10 square cm. size, suggesting that at the 10 square cm. quadrat size the detection of the distribution of individual stems of clumps is indicated.

Species Area Relation

Kilburn (1966) found that the exponential equation of the species-area-relation would tend to overestimate species number in areas larger than those he sampled (Table 7). This is also true of the Mattawan study area. For example, the area of Kalamazoo County is 576 square miles or 1.48×10^9 square meters. If this area is put into the equation for sections A and B it is discovered that the number of species that should be present in that large an area is much larger than that found in 1947 by Hanes and Hanes for Kalamazoo County. The calculated number of species using the exponential equation for section A shows that in an area of 1.48×10^9 square meters there should be 71,326 species and for the same area using an exponential equation for section B there should be 10,372 species. In reality there are about 1,555 species in Kalamazoo County.

It is hoped that through further study of the species-area-relation it may be possible to compare communities by the use of the equation $y=kx^z$. For example, it appears that in a given area as the amount of stress increases in the area the exponent becomes smaller. The exponent is the measure of a community's species richness which is affected by several factors. This view appears to contrast with that of MacArthur and Wilson (1967). Once the exponent z can be calculated the stress on the community and factors involved can be studied. There is need for work in this area especially from other prairie areas so that comparisons can be made. Kilburn (1966) in his paper suggests other aspects of the species-area-relation such as a means for understanding and unravelling past floristic histories. Greig-Smith (1964) states that if observed species curves can be fit to equation constants the equations will represent characteristic features of the stands investigated and it might be possible to use the values to group stands into classes characterized by similarities of structure, regardless of difference in composition.

Interspecific Association

Association between species is an important aspect of the organization of communities. If the presence of an individual means the absence or presence of another species the distribution of plants in the community will be affected by that individual. If there is an influencing factor working in an environment it may affect not one species but several. Therefore, if several species are shown to be associated it may be because they are responding to the same influencing factors

and thus this factor can be isolated (Greig-Smith 1964).

Associations between species can result from similar responses of two or more species to the physical environment, producing positive association, and differing responses of two or more species to the physical environment, producing negative association. They may also result from interspecific effects. Of these, competition, which would tend to produce negative associations among the competing species is probably most important. Positive associations could result from relationships in which the presence of one species enhanced the growth or survival of another. Extreme cases of this sort of relationship would be parasitism and mutualism. Nearly all of the associations detected here were negative, suggesting either competitive interactions or an organization in which each species was responding individually to the physical factors of the area.

Another reason may exist for the large number of negative associations which were detected using the smallest quadrats. Greig-Smith (1964) and Kershaw (1966) show that small quadrats on the order of the size of individual plants may tend to produce results indicating negative associations simply because of the impossibility of two individuals occupying the same space.

It is peculiar, and unaccountable without further study, that almost no species showed significant associations on both scales studied.

Thus it can be seen from the study of pattern, species area-curve, and association between species a better understanding of community organization can be found with a better understanding of the

physical factors and individual interactions that take place in a community. Through further study communities may be better compared with a more thorough understanding of community dynamics.

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