

Structure of Prairie Vegetation

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STRUCTURE OF PRAIRIE VEGETATION ¹

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INTRODUCTION

The prairies have furnished a fascinating field for study since the days of the early botanical explorations. Notwithstanding numerous studies, however, most of which have been merely descriptive, few quantitative investigations have been made. With the rapid breaking of the prairie as a result of agricultural progress, it seemed that it might entirely disappear before a detailed record of its structure had been made. This fact was clearly brought by Dr. J. E. Weaver to the attention of the writer, who is a native of Switzerland and upon whom the grasslands have made a deep impression. After two years of preliminary studies, intensive work was pursued during 1927 and 1928.

The literature on prairies is concerned primarily with their origin, floristic composition, and seasonal aspects. An extensive bibliography is given by Shimek ('25) which includes the work of Pound and Clements (1898, '00), Harvey ('08), and Schaffner ('13). Quantitative investigations on habitat and flora have been summarized by Weaver and Thiel ('17). More recently studies on the composition of grasslands have been made by Sarvis ('20) and Schaffner ('26). Extensive work on root relations of prairie plants has been carried on by Weaver ('19, '20, '22). "Experimental Vegetation" by Clements and Weaver ('24), and "Plant Competition" by Clements, Weaver, and Hanson ('29) have appeared. All of these quantitative investigations definitely aid in an understanding of the structure of the prairie, the work of Sarvis in North Dakota ('20) and that of Thornber in southeastern Nebraska ('00) being especially concerned with the composition and density of the vegetation.

LOCATION AND EXTENT OF AREA

A continuous tract of approximately 800 acres of climatic true prairie, and one of the few large remaining areas of unbroken land in eastern Nebraska, was selected for study. It is located 3 miles north and 5.5 miles west of the public square in Lincoln, Nebraska. This tract is in a primeval condition except that it has been ungrazed for at least a quarter century, the vegetation being mowed annually in early fall for hay. The presence of coyotes,

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rattlesnakes, etc., gives evidence of the slight disturbance caused by man, the annual removal of the matured vegetation being comparable in some respects to its former removal by prairie fires.

Topography

The topography is distinctly rolling, consisting of a series of drift hills, often with broad, flat tops, and long, gentle slopes, level lowlands, and ravines of moderate depth. The general elevation is approximately 1,200 feet, and the highest hill 140 feet. Plate II, figure 1, shows the rounding or flat-topped hill crests, the characteristic long, gentle slopes, and the nature of the ravines. Nowhere are there outward signs of erosion, and the draws appear as mere folds in a continuous carpet of vegetation. Where the plant cover is partially removed by close grazing, as in adjoining pastures, the gently curving profile of the landscape is soon replaced by the abrupt margins of bare gullies, as shown in Plate II, figure 2.

A thorough study was made of the entire tract. The most intensive investigations were carried on from the crest of a large, flat-topped hill, down its long northern slope of 5 per cent inclination, and on the almost level space at its base, *i.e.*, throughout a distance of approximately 1/3 mile.

The Environment

Extensive studies on the environmental factors of prairies have been made by Weaver and his students throughout a period of many years ('24). Hence only a brief statement need be given here with special emphasis upon the differences in the environment of the less dense vegetation of hilltops and upper slopes as compared with that of the denser sod of their lower slopes and bases.

Precipitation

The mean annual precipitation at Lincoln for a period of 50 years is 27.9 inches. During 1927 the annual precipitation fell to 21.4 inches, but in 1928 it was approximately normal (27.8 inches). The rainfall for the growing season (April to September inclusive) was 6 inches below normal in 1927, and normal in 1928. The precipitation is of the Great Plains type, 70 per cent occurring during the spring and summer months, a distribution that is especially favorable to the growth of grasses.

Soils

The water falls upon a fine-textured, silt loam soil of glacial origin. That of both the upland and lowland is a Carrington silt loam, although much deeper and richer at the base of the hills. Mechanical analyses of these soils to a depth of 6 feet are given in Table I. The fine texture and high water retaining capacity of the soil is at once indicated by the large proportion of very fine sand, silt, and clay.

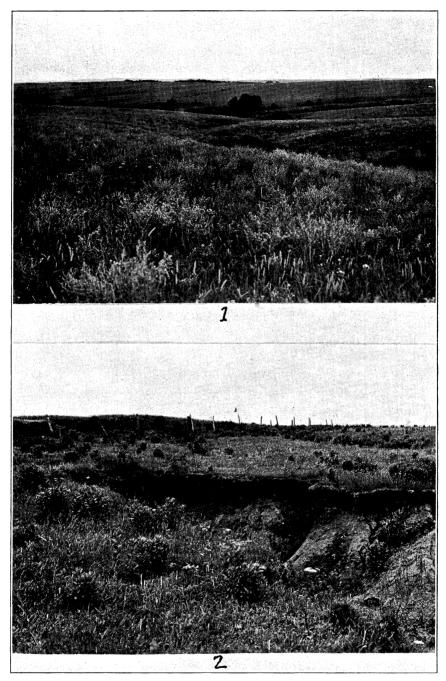


FIG. I. General view of prairie showing the rolling topography and sparselywooded ravines. The most abundant dicotyledon of this early summer aspect (June 10) is *Psoralea floribunda*.

FIG. 2. Gulley at the head of a ravine showing erosion resulting from overgrazing. The low shrub, *Ceanothus ovatus*, has increased in abundance as a result of decreased competition with the grasses.

January, 1930 STRUCTURE OF PRAIRIE VEGETATION

The physical and chemical properties of the soil have a profound effect upon the growth of vegetation, especially through their water and nutrient relations. Hence, detailed studies were made of a typical profile in both upland and lowland.

Depth, inches	Coarse gravel	Fine gravel	Coarse sand	Medium sand	Fine sand	Very fine sand	Total sand	Silt	Clay
				Upland	Prairie				
$\begin{array}{c} 0-3\\ 3-5\\ 5-8\\ 8-12\\ 12-17\\ 17-31\\ 31-38\\ 38-46\\ 46-72 \end{array}$	0.6 4.0 5.6 8.0 6.6 1.0 1.7 2.1 3.0	2.5 2.8 3.3 3.7 4.0 1.7 1.1 1.6 1.3	7.6 6.3 7.1 5.7 4.8 4.5 4.2 4.4 4.2	8.5 8.3 8.7 6.4 4.5 4.6 5.0 5.0 4.9	13.6 13.2 12.8 9.4 8.7 9.6 10.2 10.5 10.1	26.0 25.6 22.6 21.6 17.5 17.5 18.3 18.2 18.0	58.2 56.2 54.5 47.5 39.5 37.9 38.8 39.7 38.5	20.6 18.9 18.1 18.0 18.5 18.8 19.6 20.0 20.3	21.2 24.9 27.4 34.5 42.0 43.3 41.6 40.3 41.2
			Ŀ	Lowland	Prairie				
0-2 2-12 12-27 27-36 36-50 50-72	0.0 0.0 0.0 0.0 0.0 0.0	0.7 0.1 0.0 0.3 0.2	0.8 0.4 0.3 0.2 0.3 0.3	I.2 I.0 0.4 0.2 0.2 0.3	4.5 3.2 1.5 1.2 0.6 1.8	32.0 31.7 25.9 32.4 34.4 27.9	39.2 36.4 28.2 34.0 35.8 30.5	31.2 29.9 34.0 30.4 30.1 32.9	29.6 33.7 37.8 35.6 34.1 36.6

TABLE I. Mechanical analyses of virgin prairie soils near Lincoln, Nebraska.

In the upland, the A horizon, or zone of extraction, from which the carbonates have been leached and much of the clay alluviated, extends to a depth of 17 inches. The B horizon, or zone of concentration, where much clay has accumulated, is 21 inches thick, reaching a depth of 38 inches. Zone C, where neither extraction nor accumulation of materials have occurred as a result of soil forming processes, extends far beyond the depth to which even the most deeply rooted species grow.

The structure profile is diagrammatically shown in figure 3. As a result of the alluviation of colloidal clay, alternate wetting and drying, freezing and thawing, and the clutching action of myriads of roots, the surface 17 inches have an excellent granular structure. From 17 to 38 inches, where much of the lime has been leached and the clay accumulated, the structure is distinctly columnar. This results from the shrinking of the soil in drying and its cleavage into long, perpendicular columns. At greater depths, the soil has a massive structure. Here the carbonate content is high, streaks and pockets of chalky material being much in evidence. The soil is friable, easily penetrated by roots, and prismatic cleavage becomes imperfectly developed. The color likewise changes with depth (Fig. 3). The surface 8 inches of grayishbrown intergrades into a ferruginous brown, which changes to buff at about 31 inches. In Table II, the hygroscopic coefficients, moisture equivalents, plastic limits, per cent of nitrogen, carbon dioxide, and hydrogen ion concentration are given at the several depths to 6 feet. The high hygroscopic coefficients between 8 and 38 inches indicate a layer of high clay content. The low nitro-

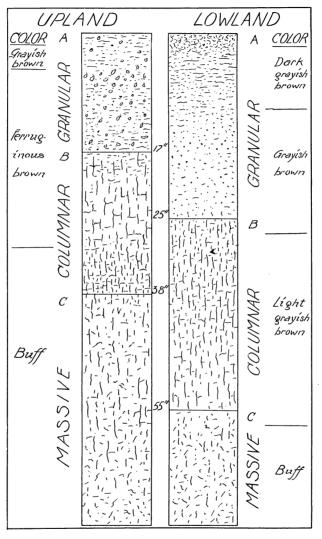


FIG. 3. Structure profiles of virgin prairie soils.

gen content at all depths is indicative of the conditions prevailing throughout the growing season. Soil analyses of the surface foot at 8 different periods during the growing season showed that only a trace of nitric nitrogen occurred. The plants were using the nitrogen as rapidly as it was being elab-

January, 1930 STRUCTURE OF PRAIRIE VEGETATION

orated by the soil organisms. Even in quadrats that were closely clipped. only a very small amount of nitrates was shown by the tests at any time. The last column in Table II shows the effect of the leaching of the lime from the surface soil, and its abundance in the lower portion of the zone of concentration and in the massive zone. In general, lime occurs at a depth of 35 inches.

Depth.	Hygro.	Moist.	Mecha	anical an	alysis	Pl	astic lim	its	Percent	Percent	
inches		equiv.			nitrogen	CO ₂	pН				
				τ	Jpland	Prairie	;				
0-3 3-5 5-8 8-12 12-17 17-31 31-38 38-46 46-72	8.5 9.0 8.7 10.4 11.7 12.5 12.9 11.6 11.2	20.6 22.1 22.2 24.8 27.6 28.6 28.5 28.4 27.1	58.2 56.2 54.5 47.5 39.5 37.9 38.8 39.7 38.5	20.6 18.9 18.1 18.0 18.5 18.8 19.6 20.0 20.3	21.2 24.9 27.4 34.5 42.0 43.3 41.6 40.3 41.2	30.6 32.2 32.3 34.9 40.1 38.4 36.5 32.8 38.1	29.5 29.4 25.1 23.4 23.1 21.8 20.3 18.9 20.6	1.1 2.8 7.2 11.5 17.0 16.6 16.3 13.9 13.5	0.184 0.155 0.128 0.104 0.077 0.062 0.022 0.020	0.04 0.03 0.03 0.04 0.06 0.31 1.30 1.80 5.44	5.85 5.73 6.11 6.12 6.45 7.44 8.5 8.5 8.5
				L	owland	l Prairi	e				
0-2 2-12 12-27 27-36 36-50 50-72	10.7 10.9 11.0 11.1 12.4 11.2	31.6 25.3 25.5 30.9 29.7 32.9	39.2 36.4 28.2 34.0 25.8 30.5	31.2 29.9 34.0 30.4 30.1 32.9	29.6 33.7 37.8 35.6 34.1 36.6	39.1 31.8 36.1 34.9 36.0 34.1	37.6 25.4 23.0 21.8 22.4 21.9	1.5 6.4 13.1 13.1 13.6 12.2	0.265 0.180 0.070 0.058 0.039 0.030	 0.04 0.01 0.00 0.01 0.03	6.83 6.45 6.60 7.07 7.24 8.05

$T_{1} = T_{1}$, (1	· · ·	,,	T • 7	377 1
I ABLE II.	ijata on treo	profiles o	t inrain	prairie soils	near Lincoln,	Nehraska
		110,000 0	<i>j c i g i i</i>	prante botto	near Lineoni	2100100100.

The zone of extraction in the lowland soil extends to a depth of about 25 inches, and the zone of concentration to 55 inches (Fig. 3). The surface 2-inch layer consists of vegetable mold, thickly matted with roots, and lacks definite structure. Even to a depth of 7 inches the soil is only laminated to structureless. At greater depths, to 25 inches, a distinctly granular structure prevails. In the zone of concentration, the structure varies from prismatic to columnar, but fissuring and cracking is much less pronounced than in the upland, and roots penetrate with only slightly more difficulty than that encountered in the structureless, massive zone below.

The color is darker, and the dark brown color extends to greater depths than in the uplands. The surface II inches are dark grayish-brown; from II to 27 inches it is grayish brown; and light grayish brown soil extends throughout the columnar layer (to 58 inches), below which a buff color prevails.

An examination of Table I shows that the lowland soil contains more silt and less sand at all depths than that of the upland. Likewise, the hygroscopic

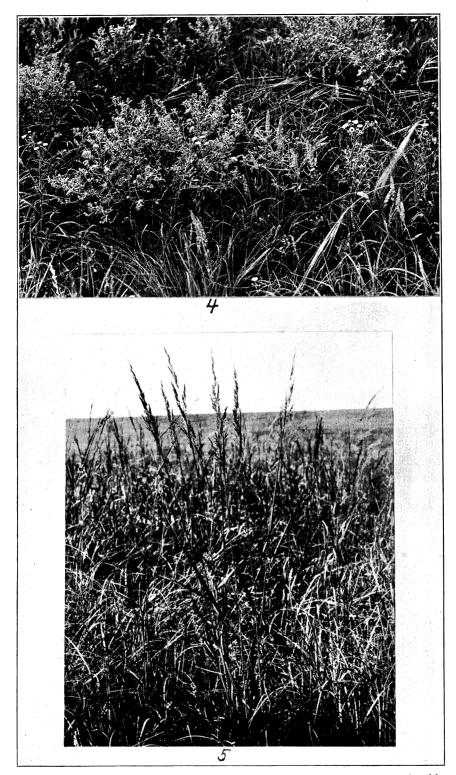


FIG. 4. June grass (Koeleria cristata) and needle grass (Stipa spartea) with some Erigeron ramosus and an abundance of Psoralea floribunda on high prairie, June 10.

FIG. 5. A sod of bluestems on low prairie: *Sorghastrum nutans*, also called Indian grass and goldstem, is the conspicuous plant in the foreground. Photograph taken on August 30.

STRUCTURE OF PRAIRIE VEGETATION

coefficients are higher in the surface soils, indicating a greater water-holding capacity. The pH values, as on the upland, are higher in the deeper layers. As a whole, the lowland soils contain more humus, are mellower, and more fertile than those of the upland. Differences in water content of lowland and upland soil are so marked as to deserve special consideration.

Water Content

Water-content determinations were made at both the upland and lowland stations, as were also measurement of temperatures, humidity, wind, and evaporation. The upland station was located on a nearly level hilltop, fully exposed to the wind from all quarters. The xeric conditions were indicated by the abundance of needle grass (*Stipa spartea*), June grass (*Koeleria cristata*), and alternes or layers of blue grama (*Bouteloua oligostachya*) (Fig. 4).

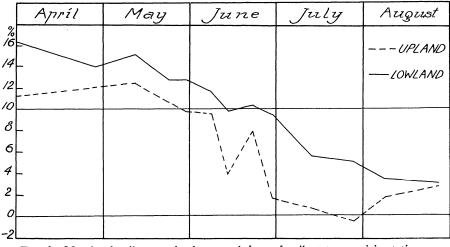


FIG. 6. March of soil water in the second foot of soil at two prairie stations during 1927.

That on the low prairie was on a broad, nearly level expanse at the foot of the north slope, where the abundance of bluestems (*Andropogon*), etc., indicated more mesic conditions for growth (Fig. 5).

The approximate amount of water available for growth (*i.e.*, that above the hygroscopic coefficient) is given for the several depths at both stations in Table III. Although the precipitation was 6 inches below normal, at no time was there a deficiency of water at any depth in the lowland soil. But in the high prairie little water was available to a depth of 3 feet late in June, and similar conditions again prevailed late in July. The constantly greater supply of available water at the lowland station is clearly revealed in figure 6. Water-content determinations during 1928 showed that there was no deficiency at any depth, a condition which is usual in the grasslands at Lincoln (Weaver '20).

			High Pr	airie					Low I	Prairie		
	0–6 in.	6–12 in.	1-2 ft.	2-3 ft.	3-4 ft.	4-5 ft.	06 in.	6–12 in.	1–2 ft.	2-3 ft.	3-4 ft.	4−5 ft.
March 26. April 28. May 12. May 21. May 28. June 6. June 14. June 27. July 11. July 26. Aug. 9. Aug. 25.	20.5 14.0 5.5 6.9 5.7 7.6 11.1 1.1 .3 -1.1	I 3.8 I 3.8 I 4.2 I 1.5 5.8 7.3 3.1 4.9 2.1 I.5 .4 3.1 3.6	III.I I2.0 I2.4 I0.7 9.8 9.6 3.8 7.9 I.5 .3 7 I.8 2.9	8.3 8.6 8.7 6.4 7.0 7.6 3.6 6.8 0.0 1.1 -1.1 .6 1.4	$\begin{array}{c} 6.5\\ 6.4\\ 5.3\\ 5.3\\ 4.4\\ 5.1\\ 4.0\\ 7.7\\ 3.5\\ 2.0\\ .9\\ 2.8\\ 4.6\\ \end{array}$	3.4 5.2 1.6 2.5 2.8 5.9 6.1 3.5 3.1 2.3 4.0	27.0 19.3 10.5 14.8 9.3 13.7 16.5 4.2	18.2 17.1 12.9 11.5 9.0 6.7	14.0 15.1 12.9 12.9 11.8 9.9 10.4 9.3 5.9 5.1 3.4	13.4 12.7 12.0 12.5 11.9 11.5 11.6 10.5 6.4 6.4	10.1 9.4 9.6 9.8 9.5 10.1 9.0 3.1 4.0 6.9	10.1 10.8 11.1 10.0 12.0 9.9 10.4 10.5 6.1 4.9 8.9
Hygroscopic coef- 8.7 9.8 12.2 12.7 11.8 11.2 10.8 10.9 11.0 11.1 12.4 11.4												

TABLE III. Water content in excess of the hygroscopic coefficient during 1927.

Temperature and Humidity

Continuous records of temperature and humidity were obtained at both stations during two growing seasons by means of hygrothermographs. To conserve space, however, a single representative week during midsummer will be used to illustrate the differences in these factors in high and low prairie.

Humidity, per cent	Mean day	Mean night	Minimum	Maximum
Upland	47.2	80.3	38.9	90.4
Lowland	47.2	90.8	38.1	98.0
Temperature, degrees F.	Mean day	Mean night	Minimum	Maximum
Upland	85.5	61.7	60.0	93.I
	85.3	69.7	63.7	92.I

TABLE IV. Humidity and temperature during the first week in July, 1927.

It may be seen that there is little or no difference in the average day humidity or temperature at the two stations. The mean night temperature, however, is 8° F. higher in the low prairie, and the mean humidity 10.5 per cent greater. The high prairie also has a wider range of extremes of mean temperature (23.8°). Differences in temperature are so small, however, that they probably have little influence upon the differences in the development of the vegetation, the controlling factor being water content of soil, and humidity as affecting transpiration.

Soil Temperature

Continuous records of soil temperature at a depth of 6 inches were secured by thermographs. Figure 7 shows the average daily maximum and minimum temperatures and the differences between the averages of these at the two stations. The higher temperatures and greater fluctuations in temperature at

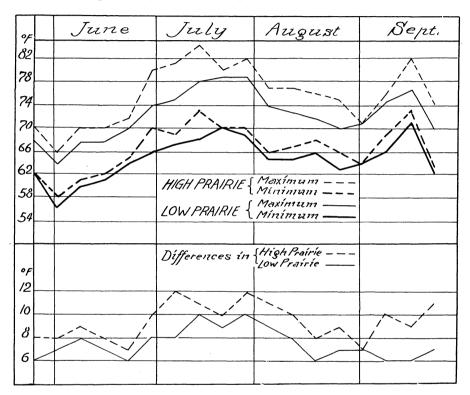


FIG. 7. Average daily maximum and minimum soil temperatures by weeks at depth of 6 inches, and average differences in their sums on high and low prairie, respectively.

the upland station are due to the greater insolation resulting from the sparser plant cover and also greater wind movement, resulting in part from topography. Even if these differences in temperatures have only a slight effect upon physiological activities, the effect upon water loss from the surface soil by direct evaporation is marked. Moreover, soil temperature exerts a profound effect upon the time of resumption of growth in spring, and it is at this time that the greatest differences in temperature (often 10° to 15° F.) are found.

Wind and Evaporation

The average hourly wind movement at the two stations was ascertained by means of the weather bureau type of anemometers which were continuously operated at a height of 0.5 meter during the three summer months. In the low prairie, the average rate per hour was 5.8 miles, and this increased 33 per cent, *i.e.*, to 7.7 miles, on the upland where the anemometer was exposed to wind movement from all directions.



FIG. 8. A dense sod consisting mostly of *Andropogon furcatus*, with *Amorpha* canescens; showing the development of vegetation on low prairie by midsummer (July 12).

The relative rate of evaporation was measured by Livingston's white, cylindrical, porous cup atmometers, each equipped with a non-absorbing device. During the period of July 11 to August 4, for example, the average daily water loss at the level of vegetation was 16.7 cc. in low prairie and 28.4 cc. on the upland. Thus, because of greater wind movement and higher rates of evaporation, the vegetation of the upland is subjected to greater desiccation than that of the lower slopes and valleys.

FLORISTIC COMPOSITION AND ASPECTS

Duplicate specimens of every plant occurring in the prairie were secured, and one lot placed in the herbarium of the University of Nebraska. The total flora, exclusive of cryptogams, but including plants of ravines and wet meadows, and such ruderals as had migrated along trails into the prairie, consisted of 345 species of flowering plants.

The transition between high prairie and low prairie is gradual except on

ECOLOGY

VOL. XI, PLATE IV

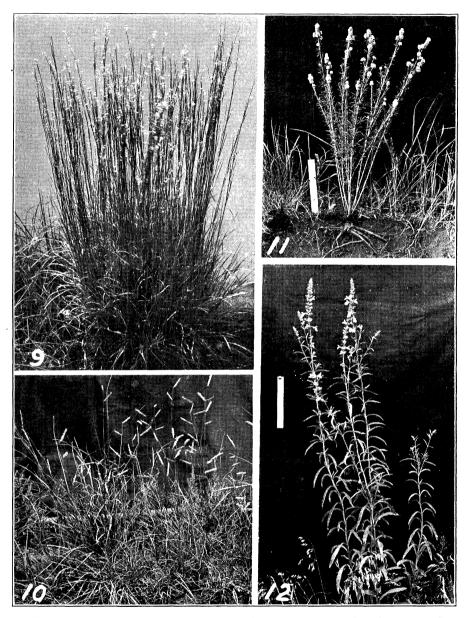


FIG. 9. A large bunch of little bluestem (Andropogon scoparius) in seed on September 7.

FIG. 10. Grama grass (Bouteloua hirsuta) in blossom on high prairie, July 23.

FIG. II. *Petalostemon candidum*, a prairie clover characteristic of the estival aspect; the roots penetrate to depths of 5 to 8 feet.

FIG. 12. A blue sage (Salvia pitcheri) characteristic of the autumnal aspect.

steeper slopes where the water content markedly varies within a distance of a few meters. One familiar with the vegetation, however, can determine within rather narrow limits the transition from the low prairie to that of the uplands. The former is characterized by a continuous, dense sod, predominantly composed of big bluestem (*Andropogon furcatus*) (Fig. 8), the latter by more

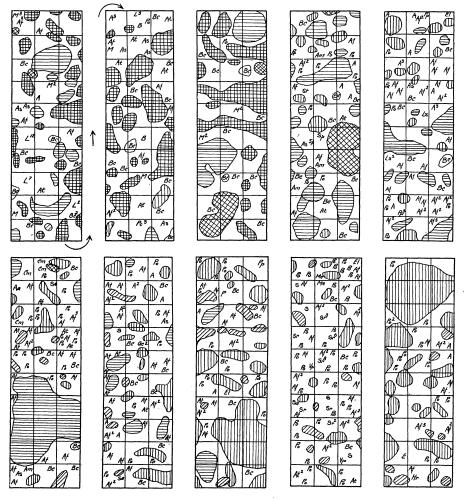


FIG. 13. Portions of a transect 30 cm. wide and 100 meters long extending from a hilltop to a ravine at its base. Horizontal lines, Andropogon scoparius; vertical lines, Andropogon furcatus; diagonal lines, Poa pratensis; diagonal cross-hatch, Sporobolus heterolepis; vertical-horizontal cross-hatch, Bouteloua hirsuta; other symbols as in Table VI.

open ground and a varied pattern of little bluestem (A. scoparius), needle grass (Stipa spartea), June grass (Koeleria cristata), dropseeds (Sporobo-

lus), grama grass (*Bouteloua*), and a profuse growth of non-grassy subdominants (Pl. III, Figs. 9, 10, 11, and 12).

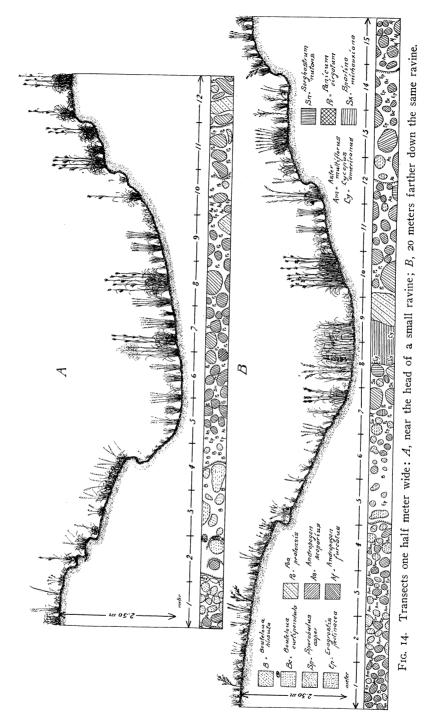
Typical high and low prairie and the transition between them is shown in a transect which extends from the top of a ridge down a south slope and includes the vegetation at its base (Fig. 13). Differences in water content and soil temperature, as well as the height of the vegetation, and yield are shown in Table V.

August 16, 1928	Knoll	Upper slope	Lower slope	Base of hill near ravine	
Dominant grasses	Bouteloua gracilis and Sporobolus heterolepis	Andropogon scoparius	Andropogon furcatus and Andropogon scoparius	Andropogon furcatus	
Height of vegetation, centimeters	20	30	35	65	
	Available w	ater content, per	cent		
Depth					
o-6 in	0.2	1.3	1.3	3.8	
6-12 in	0.2	2.5	3.7	Ğ.2	
1-2 ft 2-3 ft	0.1	1.6	4.3	$5.5 \\ 5.6$	
2-3 ft 3-4 ft	1.5 3.6	2.5 4.8	4.4 3.0	5.0 4.7	
	Soil te	emperature, °F.	·		
Depth					
6 in	86.0	83.0	80.0	73.0	
12 in	85.0	81.0	79.0 70.0	72.0	
4 ft	75.0	70.0	70.0	69.0	
	Yield in gra	ams per square m	leter		
Green weight	336	551	887	964	
Dry weight	199	199	389	390	

 TABLE V. Dominant grasses, available water, soil temperature, and yield along a transect

 30 cm. wide and 100 meters long extending from a hilltop to a ravine at its base.

Vegetation of the ravines or draws is more mesic than that of low prairie, the flora varying greatly with their depth and exposure to insolation and wind. Trees and shrubs may extend to the heads of ravines on sheltered north slopes, but in the exposed south-facing ones they usually occupy only the lower portions. Boxelder (*Acer negundo*), western cottonwood (*Populus deltoides*), and several species of willows (*Salix cordata, S. amygdaloides, and S. nigra*) are the only trees. They are all of relatively small stature and occur in small groups or, more usually, as isolated individuals. Small thickets and isolated



clumps of shrubs accompany them, often extending farther up the ravines; and some of these, especially *Toxicodendron radicans* and *Rhus glabra*, extend into the low prairie. The following also occur: *Prunus americana, Cornus stolonifera, Sambucus canadensis, Salix interior, and Symphoricarpos occidentalis.*

The absence of prairie grasses, resulting from the partial shade, affords a suitable habitat for a few mesic woodland herbs, although frequently the ground layer consists mostly of *Poa pratensis*. The transition from the shrubs to grassland is abrupt and follows the line determined by the annual

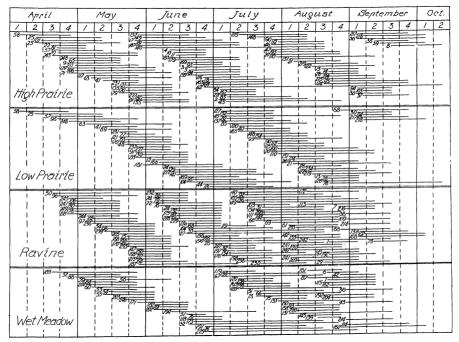


FIG. 15. Aspect chart showing the period of anthesis for each species of the several prairie habitats.

mowing. The nature of the vegetation near the head of a grass-covered draw is shown by transects in figure 14. The more xeric vegetation of the steep banks, where run-off is high, is in striking contrast to that of the moist bottom of the ravine.

An early stage in the development of prairie is represented by the wet meadow. Here aeration is deficient, and upland species cannot grow (Clements and Weaver '24). A general background of several species of sedges and rushes is varied by patches of *Eleocharis palustris* and relict plants of *Typha latifolia* and *Scirpus validus*. The dominant carices are *Carex stipata* and *C. nodosus*; the rushes are chiefly *Scirpus paludosus* and *S. atrovirens*. The transition to prairie is through *Spartina cynosuroides* and *Poa pratensis*.

Extensive data were secured on the time of flowering of each species in the several habitats, and on the length of the period of anthesis. Little difference was found during the two years. Owing to the extensive area and the large number of species involved, further studies may result in slight modifications in the time sequence. A summary of the results of these studies is given for each of the four communities in figure 15, where each species is numbered as in Table VI. The duration of the period of blossoming is indicated by the length of the line under the month or months respectively.

TABLE VI.	List of specie	es of (H) high prairie	(L) low prairi	ie, (R) ravine,	(W) wet meadow,
and (D) dist	urbed areas.	The letters following	the names are	those used in	the quadrats and
		trans	ects		

Key No. fo Fig. 15	or Species	Habitat	Months of anthesis
rig. 15	-		anthesis
-	Abutilon abutilon (L) Rusby		8
I 	Acalypha virginica L		8–9
	Acer negundo L.		- 0
2	Acerates angustifolia (Nutt.) Dec. (Aa)		7-8
3	Acerates auriculata Engelm.		6-7 6
4	Acerates lanuginosa (Nutt.) Dec. (Al) Acerates viridiflora (Raf.) Eaton		6-7
5	Achillea millefolia L		0-7
6	Acnida tuberculata Mog.	Ŵ	8-9
7	Acuan illinoensis (Michx.) Kuntze	Ř	8-9
8	Agalinis aspera (Dougl.) Britton		9-10
9	Agoseris cuspidata (Pursh.) D. Dietr.	Ĥ	4-5
10	Agropyrum smithii Rydb.		- 6 - 6
II	Agropyrum tenerum Vasey	D, H	6
12	Agrostis alba L		6
13	Allionia hirsuta Pursh	Ĥ	8-9
14	Allionia linearis Pursh	Н	8-9
15	Allionia nyctaginea Michx	R, D	5-6
16	Allium canadense L	Ŕ	Ğ-7
17	Allium mutabile Michx	Н	5-7
	Amaranthus hybridus L		
	Amaranthus retroflexus L		
	Ambrosia elatior L. (Ab)		
	Ambrosia trifida L.		
18	Amorpha canescens Pursh (A)	H, L	6-7
19	Amorpha fruticosa L	R	6
20	Andropogon furcatus Muhl. (Af)	L, H	7-9
2 I	Andropogon scoparius Michx. (As)		8-9
22	Androsace occidentalis Pursh.	H H	4-5
23	Anemone caroliniana Walt.		4-5
24	Anemone cylindrica A. Gray (Ae) Antennaria campestris Rydb. (At)	L, R H. L	6-7
25	Alopecurus aristulatus Michx	W	4-5
26	Apocynum cannabinum L.	R.W	6-8
20	Apocynum sibiricum Jacq	R	6-8
28	Aristida oligantha Michx.		89
29	Artemisia dracunculoides Pursh.	R .	89
30	Artemisia gnaphalodes Nutt. (Ag)		9
31	Asclepias incarnata L.		7-9
	Asclepias sullivantii Engelm	R, W	. ,
32	Asclepias syriaca L	W, D	6-8
33	Asclepias tuberosa L.	Ŕ	6-8
34	Asclepias verticillata L.	D, H	7
35	Aster fendleri A. Gray	H	9
36	Aster multiflorus Ait (Am)	Η, D	9-10
37	Aster oblongifolius Nutt	H	9
38	Aster paniculatus Lam	R, W	8–9

186

	TABLE VI.—Continued		
Key No. fo	or		Months of
Fig. 15	Species	Habitat	anthesis
	*		
39	Aster sericius Vent. (Ast)	ĹΗ	9-10
40	Astragalus carolinensis L.	R, L	7^{-8}
	0		
41	Baptisia bracteata Ell. (Ba)	H, L	5
42	Bidens frondosa L.	Ŵ	5 8–9
	Bidens vulgata Greene	Ŵ	8-9
43	Blephariglottis leucophaea (Nutt.) Farwell	••	6-7
44	Diepinangiottis ieucopinaea (Nutt.) Fai weil \ldots	D	0-7
	Boebera papposa (Vent.) Rydb	D	. 0
45	Bouteloua curtipendula Michx. (Bc)	H, L	7-8
46	Bouteloua hirsuta Lag	Н	7 - 8
47	Bouteloua hirsuta Lag Bouteloua oligostachya (Nutt.) Torr	Н	7-8
	Brassica napus L.	D	
	Bromus hordeacus L		
	Bromus tostorum I		
	Bromus tectorum L Bulbilis dactyloides (Nutt.) Raf	Ď	
	Building dactyloides (Nutt.) Rai	D	
	Bursa bursa-pastoris (L.) Britton		
		-	
48	Callirrhoe alceoides (Michx.) A. Gray	L	5–6
	Camelina sativa (L.) Crantz	D	
49	Campanula americana L	R	7-8
	Cannabis sativa L	D, R	•
50	Capnoides montanum (Engelm.) Britton	Ŕ	4-5
	Carex atherodes Spreng.	ŵ	⁺ ⁵
51	Carex festucacea Schkuhr	ŵ	4-5
52			
53	Carex haydeni Dewey		5
	Carex heliophila Mackenzie	H	4
. 54	Carex interior Bailey	W <u>,</u> R	5-6
55	Carex lanuginosa Michx	w	5-6
56	Carex lurida Wahl.	W	5-6
57	Carex meadii Dewey (Cm) Carex pennsylvanica Lam. (Cp)	H, L	4-5
<u>5</u> 8	Carex pennsylvanica Lam. (Cp)	H, L	4
59	Carex stipata Muhl	Ŵ	5
60	Carex stricta Lam.	Ŵ	Š
61	Cassia marylandica L	Ř	58
62	Cathartolinum sulcatum (Riddell) Small	H.L	6-10
	Cathartonnum suicatum (Kiuden) Sman	H, L	
63	Ceanothus ovatus Desf. (Ce)		5-6
64	Celastrus scandens L		5-6
	Cenchrus carolinianus Walt	D	
65	Cerastium brachypodum (Engelm.)	H	4-5
	Chaetochloa glauca (L.) Scribn	D	
	Chaetochloa viridis (L.) Scribn	D	
66	Chamaecrista fasciculata (Michx.) Greene	F,DW	7-8
	Chamaesice geyeri (Englm. & Gray) Small	D	
	Chamaesice preslii (Guss.) Arthur	D, R	
	Chenopodium album L.		
	Chenopodium hybridum L.		
67	Cicuta maculata L	Ŵ	7-8
68	Cinna arundinacea L		8-9
00	Cinita al unumacea L	R, D	09
	Cirsium altissimum (L.) Spreng	K, D	
	Cirsium ochrocentrum A. Gray	. D	_ 0
69	Clematis virginiana L.	. <u>R</u>	7-8
70	Cogswellia foeniculacea (Nutt.) Coult. & Rose	. <u>H</u>	4-5
71	Comandra umbellata (L.) Nutt. (Co)	. н	4–6
	Convolvulus arvensis L	. D	
72	Cornus stolonifera Michx.	R	6-7
	Cuscuta arvensis.	Ŕ	
73	Cuscuta paradoxa Raf		9 6
74	Cyperus erythrorhizos Muhlb.	. N, W	7-8
75	Cyperus erythrormzos Munib	· · · · · · · · · · · · · · · · · · ·	
76	Cyperus filiculmis Vahl	. W	6-7
77	Cypripedium candidum Willd	. L	5-6
		т	0
78	Dasystephana puberula (Michx.) Schmall	. L	8-10

	TABLE VI.—Continued		
Key No. fo	or		Months of
Fig. 15	Species	Habitat	anthesis
	-		antificata
79	Delphinium virescens Nutt.	Н	5-6
	Dichrophyllum marginatum (Pursh.)	D	
80	Diplachne acuminata	W	8
81	Draba caroliniana Walt		4-5
82	Drymocallis agrimonioides (Pursh.) Rydb. (Da)	L, R	7
			•
83	Echinacea pallida (Nutt.) Britton (Ech.)	н	6-7
	Echinochloa crus-galli (L.) Beauv.	R, D	•
84	Eleocharis palustris (L.) R. & S	Ŵ	4-5
	Eleusine indica (L.) Gaertn	Ď	+ J
85	Elymus canadensis L. (El)	H. Ī. D	7-8
	Elymus jejunus (Ramaley) Rydb	Ŕ, Ĺ	, -
86	Elymus striatus Willd.	Ŕ	6
	Elymus virginicus L	R	-
87	Epilobium coloratum Muhl	W	8-9
88	Equisetum arvense L	RW	4-5
	Equisetum kansanum	R	+ 5
89	Equisetum kansanum Equisetum laevigatum A. Br. (Es)	Ē	5-6
	Equisetum robustum A. Br	R	5 5
	Eragrostis hypnoides (Lan.) B.S.P	Î.	
	Eragrostis major Host	$\tilde{\mathbf{D}}$	
90	Eragrostis pectinacea (Michx.) Steud. (Ep)	H. Ď. W	7-8
	Eragrostis pilosa (L.) Beauv	,,	1 °
	Eragrostis purshii Schrad.	$\tilde{\mathbf{D}}$	
91	Eragrostis purshii Schrad. Erigeron ramosus (Walt.) B.S.P (E)	H, L	5-6
92	Eupatorium urticaefolium Richard	Ŕ	7-8
93	Eupatorium perfoliatum L	Ŵ	' 8 8
94	Euthamia graminifolia (L.) Nutt	L, H	9
			,
95	Festuca octoflora Walt	H. D. L	6-7
-96	Fragaria virginiana Duchesne (F)	R. L	4-6
-		, =	T ³
97	Galium aparine L	R	5
98	Galium lanceolatum Torr	R	5-6
	Galium trifidum L.	Ŵ	0 •
99	Gaura biennis L	L, D	7-8
100	Gaura parviflora Dougl	Ľ.	7-9
, 101	Geoprumnon crassicarpum (Nutt.) (Gc)	Ĥ	7-9
102	Geum canadense Jaco	R	15
103	Glycine apios L.	R	7-8
104	Glycyrrhiza lepidota Pursh	L, R	6-7
105	Grindelia squarrosa (Pursh.) Dunal	D, H	- /
106	Grossularia missouriensis (Nutt.) Cov. & Britt.	Ŕ	4-5
	Hedeoma hispida Pursh	D	
	Helianthus annuus L	D	
107	Helianthus grosse-serratus Martens	R	9
108	Helianthus maximiliani Schrad	R	ģ
109	Helianthus petiolaris Nutt	R, D	8-9
110	Helianthus scaberrimus Ell. (H)	H, L	7-8
III	Helionsis scabra Dunal	Ŕ	7-8
II2	Hieracium longipilum Torr. (Hi)	L, H	7-8
113	meracium scabra Michx	Ŕ	8-9
114	Homalocenchrus virginicus (Willd.) Britt	W	8-9
115	Homalocenchrus oryzoides (L.) Poll	W .	8-9
	Hordeum jubatum Nutt	D	-
	Hordeum pusillum L	D	
116	Houstonia angustifolia Michx.	Н	6-7
	Humulus lupulus L	R, D	•
		_	
117	Ionoxalis violacea (L.) Small	Н	5

STRUCTURE OF PRAIRIE VEGETATION

	ABLE VI.—Continued		
Key No. fo			Months of
Fig. 15	Species	Habitat	anthesis
118	Juncus dudleyi Wiegand	W	6-7
119	Juncus interior Wiegand		7
120	Juncus nodosus L	W, L	7
		n	
	Kochia scoparia (L.) Rothb	D	- 6
121	Koeleria cristata (L.) Pers. (K)	H, L	5-6
122	Kuhnia glutinosa Ell. (Kg)	L, H L	89
		Ľ	
123	Lacinaria punctata (Hook.) Kuntze (L)	Η	8-9
124	Lacinaria scariosa (L.) Hill	н	89
125	Lactuca canadensis L	L, R	7-8
126	Lactuca ludoviciana (Nutt.) DC. (La)	_L_	8
127	Lactuca pulchella (Pursh.) DC		7
	Lactuca virosa L.		
	Lappula lappula (L.) Karst.	D	
	Lepidium apetalum Willd. (Lp)	D, H D	
	Lepidium draba L Lepidium virginicum L. (Lv)	D	
	Leptilon canadensis (L.) Britton	Ď	
	Leptilon divaricatum (Michx.)Raf		
128	Lespedeza capitata Michx. (Le)		8-9
·	Lithospermum arvense L		
129	Lithospermum canescens (Michx.) Lehm	Н	4–6
130	Lithospermum carolinense (Walt.) MacM	L	5-6
131	Lobelia syphilitica L	W	8-9
132	Lychnis drummondi (Hook.) S. Wats		6-7
133	Lycopus americanus Muhl Lygodesmia juncea (Pursh.) D. Don	W D	7-8
134	Lygodesinia Juncea (1 disil.) D. Don	R, W	7-8
134		11, 11	7 0
	Medicago sativa L	D	
135	Meibomia canadensis (L.) Kuntze	R	8
136	Meibomia dillenii (Darl.) Kuntze		7-9
137	Meibomia illinoensis (A. Gray) Kuntze (Me)		7 - 8
	Melilotus alba Deav.	D D	
1.09	Melilotus officinalis (L.) Lam	R	0
138 139	Mentha canadensis L	***	9 8
139	Meriolix serrulata (Nutt.) Walp. (M)		5-8
141	Mesadenia tuberosa (Nutt.) Britton	. L	6-7
142	Micrampelis lobata (Michx.) Greene	. R	8
143	Mimulus ringens L	. <u>W</u>	8
144	Monarda mollis L	R	7-8
145	Muhlenbergia mexicana (L.) Trin	D, R	8-9
	Muhlenbergia racemosa (Michx.) B.S.P	W, D D	
	Muhlenbergia schreberi Gmel	, D	
146	Nepeta cataria L	R	6-7
	Norta altissima (L.) Britton	. D	•
147	Nyctelea nyctelea (L.) Britton	. R	5-6
			- 0
148	Oenothera biennis L.		7-8
149	Onosmodium occidentale Mackenzie	. н	5-6
150	Padus virginiana (L.) Mill	. R	4-5
150	Panicum capillare L	D. H. L	4-5 8
	Panicum dichotomiflorum Michx.	. D	
152	Panicum praecocius Hitch, & Chase	. L	7
153	Panicum scribnerianum Nash (Pa)	.H, L, D	7 5-6
154	Panicum virgatum L. (Pv)	. L, R	7-8
155	Panicum wilcoxianum Vasey (Pa)	.н, L, D	5-6

	TABLE VI.—Continued		
Key No. fo	r .		Months of
Fig. 15	Species	Habitat	anthesis
	-		
156	Parietaria pennsylvanica Muhl.	D, R	6–7
	Parthenocissus quinquefolia (L.) Planch	R	- (
157	Pentstemon cobaea Nutt.	H	5-6
	Pentstemon grandiflorus Nutt	H	0
158	Persicaria hydropiperoides (Michx.) Small	W	8
159	Persicaria lapathifolia (L.) S. F. Gray Persicaria muhlenbergii (S. Wats.) Small	W	7-8
160	Persicaria muhlenbergii (S. Wats.) Small.	W	8-10
161	Persicaria opelousiana (Riddell) Small	W	8
162	Persicaria portoricensis (Bertero) Small.		8–9
163	Petalostemum candidum (Willd.) Michx. (Pc)	H	6-7
164	Petalostemum purpurea (Vent.) Rydb. (Pp)	H	6-7
165	Phalaris arundinacea L.	L, W	7-8
166	Physalis heterophylla Mes. (Ph)		6
	Physalis lanceolata Michx		
167	Physalis longifolia Nutt		7
	Plantago aristata Mich	D	
	Plantago major L.	D	
	Plantago purshii R. & S.	D	
168	Plantago rugelii Deere	R	6-7
169	Poa compressa L	D, H, L	6-7
170	Poa pratensis L. (Po)	all	5-6
171	Poa pseudopratensis Scribn. & Rydb	W	5-6
172	Poinsettia cuphosperme (Englm.) Small	D, R	5-6 8-9
173	Poinsettia dentata (Michx.) Small	D, W	6-8
174	Polygala verticillata L. (Py)	D, W L	8
175	Polygonatum commutatum (R. & S.) Dietr		6-7
	Polygonum aviculare	D	
	Populus sargentii Dode		
176	Potentilla monspeliensis L. (Pt)	L, R	7-8
177	Potentilla pentandra Engelm		6–8
178	Prunus americana Marsh.		4-5
179	Psoralea argophylla Pursh. (Pr)		6-7
180	Psoralea esculenta Pursh. (Pe)		5-6
181	Psoralea floribunda Nutt. (P)		5-7
101		, =	57
* 9a	Dedivels released (L) Meansh	W	6
182	Radicula palustris (L.) Moench		
183	Ranunculus abortivus L.		4-5
184	Ratibida columnaris (Sims.) D. Don	H, D	6–7 7–8
185	Ratibida pinnata (Vent.) Barnhart		
186	Rhus glabra L.	R	6-7
187	Rosa pratincola Greene (R)		5-7
188	Rubus alleghaniensis Porter		5-6
190	Rubus occidentalis L		5-6
191	Rudbeckia hirta L.		6-8
192	Rudbeckia laciniata L		8–9
	Ruellia ciliosa Pursh		
	Rumex acetosella L.		- (
193	Rumex altissimus Wood.		5-6
	Rumex crispus L	D	
		***	6 -
194	Sagittaria cuneata Sheldon		6–7
	Salix amygdaloides Anders	R	
	Salix cordata Muhl		
	Salix interior Rowlee		
	Salix nigra Marsh		
	Salsola pestifer A. Nelson		
	Salvia lanceifolia Poir		_
195	Salvia pitcheri Rorr (Sa)	<u>H</u>	7-8
196	Sambucus canadensis L		6-8
197	Sanicula canadensis L	. R	7
198	Sanicula gregaria Bicknell.	. R	7
199	Schedonnardus paniculatus (Nutt.) Trelease	. D, H	6-7
	10		

Structure of Prairie Vegetation

	I ABLE VIContinued		35
Key No. fo Fig. 15	or Species	Habitat	Months of anthesis
200	Scirpus americanus Pers.	W W	5 6
201	Scirpus atrovirens Muhl.		6-7
202	Scirpus paludosus A. Nelson		5-6
203	Scirpus validus VahlScrophularia leporella Bicknell		50
	Scutellaria laterifolia L.	Ŵ	8-9
204	Scutellaria parvula Michx.	Ď	•)
205	Senecio integerrimus Nutt.	ñ	5-6
205	Senecio plattensis Nutt.	Ĥ	<u>4</u> –6
207	Silene stellata (L.) Ait.	R	. 7
208	Silphium integrifolium Michx	R	7-8
209	Silphium perfoliatum L	R	8-9
210	Silphium laciniatum L	• , W	8
	Sinapis arvense L	Ð	
211	Sisyrinchium campestre Bicknell (Si)	H	4-5 5-6
212	Smilax herbacea L	R	5-6
213	Smilax hispida Muhl	R	5–6
	Solanum rostratum Dumal	D	8 0
214	Solidago canadensis L.	R, W	8–9 7–8
215	Solidago glaberrima Martens (S)	R, L, D	7-8 8-9
216	Solidago nemoralis Ait.		9
217 218	Solidago rigida L Solidago rigidiuscula (T. & G.) Porter	L, H	9-10
210	Sorghastrum nutans (L) Nash (Sn)	Ľ, H	8
219	Spartina michauxiana (L.) Roth	Ř, W	8
220	Specularia leptocarpa (Nutt.) A. Gray.	D, H	7
	Specularia perfoliata (L.) A. DC		•
. 222	Sphenopholis obtusata (Michx.) Scribn.	L	6-7
223	Sporobulus asper (Michx.) Kunth. (Spa)	. H, D	8-9
224	Sporobulus heterolepis A. Gray (Sp)	. Ĥ	8-9
225	Stachys palustris L	W	6-9
226	Steironema ciliatum (L.) Raf	R, W	6-7
227	Stipa spartea Trin. (St)	.H, L, D	5-6
228	Symphoricarpos occidentalis Hook	. <u>R</u> , D	6-7
229	Symphoricarpos symphoricarpos (L) MacM	R, D D	6-7
	Syntherisma sanguinale (L.) Dulac	. D	
230	Teucrium canadense L.	W, R	7-8
230	Thalesia uniflora (L.) Britton	L, H	5
232	Thalictrum dasycarpum Fisch. & Lall	R	Ğ
	Thlaspi arvense L.	. D	
	Thlaspi arvense L Tiniaria convolvulus (L.) Wels. & Mog	. L, R	
233	Tiniaria scandens (L.) Small	, К	8
234	Tithymalopsis corallata (L) Kl. & Garcke	. <u>L</u>	8-9
235	Toxicodendron radicans (L.) Kantze		5-6
236	Tradescantia bracteata Small		5-6
237	Tragopogon pratensis L		5-6
	Tribulus terrestris L	. D	
-	Trifolium pratense L.	. D . W	
	Typha angustifolia L.		7
238	Typha latifolia L	. w, K	7
	Ulmus americana L		
	Urtica dioica L	. R, D	
239	Vagnera stellata (L.) Morong	. R	5-6
	Verbena bracteosa Michx.		~
	Verbena hastata L	. D	
240	Verbena stricta Vent.	. D. R	8-9
241	Verbena urticifolia L.	.L, R, D	8-9
242	Vernonia baldwinii Torr. (V)	. R, D	8–9
	Veronica arvensis L.	. D	

Key No. fe Fig. 15		Habitat	Months of anthesis
243 244 245 246 247 248 249 250	Veronica peregrina L Vicia sparsifolia var. linearis Nutt Viola eriocarpa Schwein Viola palmata L Viola palustris L Viola papilionacea Pursh Viola petadifida Don. (Vp) Viola rafinesquii Greene Vitis vulpina L	H R W R H, L R	4 5 5- 56 45 4-5 4-5 5-6
	Xanthium commune Britton Xanthoxalis stricta (L.) Small (Xs)		

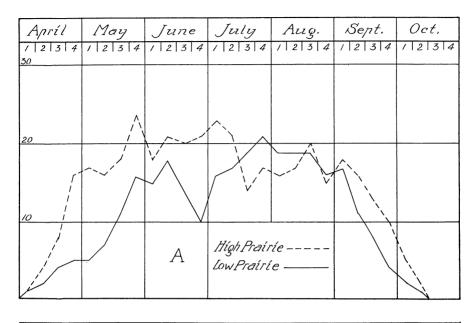
TABLE VI.—Continued

A comparison of the periods of anthesis in the several habitats reveals that the high prairie has the greatest number of species flowering in June. The low prairie reaches its maximum in July, the ravines still later, and the maximum flower production in wet meadow occurs in August. This sequence is in accordance with the soil temperature and water relations. The high prairie soils warm more quickly, and the water content is frequently lower in late June when the low prairie soil is still moist. The much more moist ravines afford an ample water supply in August, and the formerly cold, wet meadow even in late summer.

The prevernal, vernal, estival, and autumnal aspects are somewhat more distinctly marked in high than in low prairie. A conspicuous decline in the number of species flowering in all four habitats occurs toward the end of June, but this is most marked in low prairie when the estival aspect replaces the vernal. A somewhat similar decline occurs on upland prairie when the autumnal aspect replaces that of summer (Fig. 16).

Among the total of 345 species, 237 are regular elements of the prairie, 70 being characteristic of high prairie; 45 are most commonly found in low prairie, 77 in ravines, and 45 inhabit wet meadows. Since many species grow in more than one habitat, the total number of high prairie species, exclusive of ruderals, is 81 and that of low prairie 75; 132 are common to ravines and 58 to wet meadow. Among the 106 species of rather regular occurrence in disturbed areas, such as gopher mounds, roadsides, areas formerly covered with haystacks, etc., 40 are regular elements of the prairie and 66 are characteristic ruderals. The ruderal population was somewhat increased by including species of adjacent overgrazed pastures, as well as those from a small area of grassland that had been broken several years previously and abandoned.

Among the 237 regular species of the prairie, 38 are grasses and 18 are sedges. Thus, the Graminales contribute only 24 per cent to the flora, but these 56 species constitute at least 90 per cent of the vegetation. Composites and legumes rank next to the grasses and grass-like plants (Figs. 17 and 18). There are 46 species of the former and 20 of the latter. Other families of



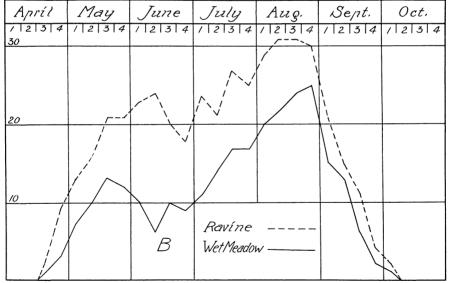


FIG. 16. Graphs showing the number of species flowering at different times during the growing season; A, on high and low prairie; B, in ravine and wet meadow.

importance are the *Asclepiadaceae* (II species), the *Rosaceae* (IO species), the *Labiatae* (7 species), and the *Polygonaceae* and *Violaceae* with 6 species each. The remainder of the vegetation is produced by 50 families, each of which is represented by I to 4 species.

Quadrat Studies

Extended studies were made by means of chart quadrats in order to determine the exact structure of the vegetation. Although laborious, this method gives exact, quantitative results, and, when used extensively, furnishes a complete picture of the structure of vegetation above ground. Each quadrat was one meter square, the area being definitely marked off by a rigid iron framework which was subdivided into square decimeters by metal cross strips. The quadrats were made between June 15 and August 20, and hence at a time when at least the vegetative parts of all of the species were present. Thus it was possible, after thorough acquaintance with the plants, to identify each with a high degree of certainty. Exceptions were those of Panicum scribnerianum and P. wilcoxianum, which were both charted as Pa, and Bouteloua oligostachya and B. hirsuta, charted as B. Grasses and sedges were mapped according to the actual surface area covered by the base of the bunch or sodded area except in the case of small, isolated individuals which were designated by a symbol. Other species were also designated by means of a symbol, and the number of basal stems indicated by an exponent (e.q., Am³ indicates an Aster multiflorus with three stems).

The charts were of heavy bristol board ruled to such a scale that I decimeter of the quadrat was represented on 1.5 centimeters on the chart, thus affording ample room for exact charting. After charting, the lines were retraced in India ink, thus making a permanent record for study. A series of fine lines was drawn on tracing paper in such a manner that each minor division of the chart (2.25 sq. cm.) could be divided into 100 unit areas. Thus, by placing the tracing paper successively over each of the 100 subdivisions of the chart, the areas occupied by the various bunches, mats, etc., were accurately obtained.

The 40 quadrats on low prairie were selected at regular intervals along four parallel lines. A similar number were selected on the upland with the express purpose of including various portions of the tract upon which the vegetation was much more diversified.

The charting of the 80 quadrats required many days, even with the aid of an efficient helper. Those on the upland contained a total of 44 species, 14 of which were grasses. Eight of these 44 species do not occur in low prairie quadrats. On the low prairie, 55 species are included, 20 of which were not in the quadrats of the high prairie. A larger number of quadrats would have increased the number of species encountered, but such species are of far less importance in the vegetational complex than those that occur regularly and abundantly.

For convenience in analyzing the data, the plants are divided into two groups, the first including grasses and sedges and the second other herbs. The grasses and sedges of low prairie are listed according to their relative abundance (Table VII). An examination of the table reveals the fact that

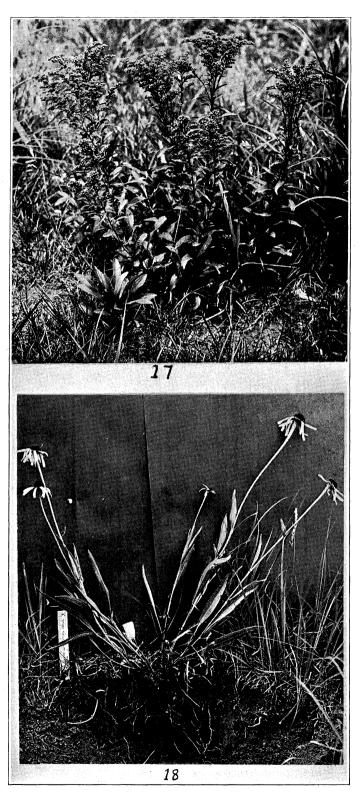


FIG. 17. A cluster of goldenrod (*Solidago glaberrima*) from high prairie. This plant propagates by rhizomes; note the new rosette in the foreground.

FIG. 18. Nigger heads (*Echinacea pallida*); a coarse, deeply-rooted species of the estival aspect. Photo. taken July 5.

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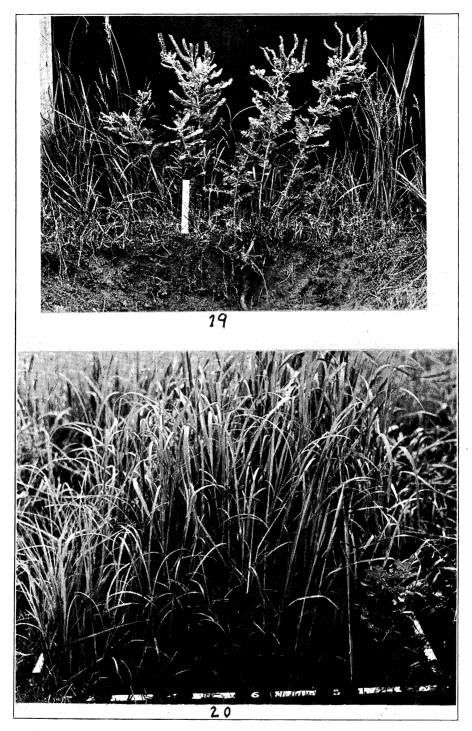


FIG. 19. Lead plant (Amorpha canescens) in flower, July 13. This cosmopolitan prairie species has a very deep tap root and is well adapted to endure drought.

FIG. 20. A quadrat of Andropogon furcatus from the low prairie on July 24. It gave a yield of 706 grams of air dry material.

Quadrat	1 Af	2 Po	3 Bc	4 As	5 Cm	6 Pa	7 St	8 K	9 E1	10 Sn	11 Ep	12 Sp	13 Cp	14 Pv
6	76	47	120	30		15	9	<u>+ </u>	3	1011	1.10	top.		1.
7	105	109	+	32		17	5	2	Ť	12				1
8	96	96	3	13	5	27	4	$\frac{\tilde{3}}{3}$	8	<u>+~</u>	+		4	+
12	109	106	+		+	4	+	+	1 2		+	+	<u> </u> -	
15	132	126	+	16	9	5	3	6	<u>† </u>	2	+	t_1	<u>} </u>	
16	$+\overline{111}$	79		- 9	1 8	$+\tilde{4}$	6	3	11	+~	+			† – –
17	156	94	1	12	13	$1\bar{4}$	5	4	2	-	-			<u> </u>
18	111	87	2	25	5	$\frac{1}{14}$	$\frac{1}{4}$		1	+	1	11	1	1
19	135	85	5		6	23	3	2	<u> </u>	+		+-	<u> </u>	
22	139	89	7	2	2	5	3	$+\tilde{4}$	1	2		1		
23	98	91	6	118	<u>+</u>	12	± 11	<u>–</u>	1	+~	+	+		
24	114	107	+	112	1 1	$\frac{1}{4}$	12	4		3	1			
25	137	123	+		$+\overline{1}$	<u> </u>		<u>+ </u>	6	<u> </u>	-			
51	81	71	22	50	$+\frac{-}{4}$	3	+	2	Ť	4	1	+		<u> </u>
52	96	61	47	75	5	2	3	$\frac{\tilde{2}}{2}$		+	1	t		<u> </u>
55	102	79	55	20	<u> </u>	8	6	3		<u>+</u>	$\pm \overline{1}$	1		
56	102	80	107	28	18	2	5	7			tī	<u> </u>	1	
57	111	70	59	21	19	5	17	$+1\dot{4}$	7		+ī			
58	151	1117	35	119	37	6	<u>+</u>	-9	·		2			
59	143	109	78	19	8	4	11	7		1	Ĩ			
60	146	118	24	9	5	± 11	$\frac{1}{2}$	4		<u>+ -</u>	Ī			
61	192	110	7	9	17	${4}$	5	$+\bar{1}$			<u> </u>			9
62	147	98	5	5	6	6	6	8	5		<u> </u>			⊢∸-
63	158	105	29	18	9	6	3				1			
64	127	108	61	12	14	5	8	5				<u> </u>		
65	107	87	61	41	8	32	19	11						
66	99	77	63	93	8	7	7	5						
67	106	139	32	55	10	3	8	7	<u> </u>	<u> </u>	<u> </u>			
68	125	89	3	2	18	14	24	<u> </u>	25		2			
69	56	3	5	2	10	2	13		28					
70	41		16		6	2	1	1	12					
72	31	65	1	3			1							
73	134	59	29	31	6	3	1	10	1		1	3	1	
74	76	91	62	31	5	4		9			1		1	
75	107	102	37	14	1	1	12	1						
76	16	53	20	47	4	12	3	1						
78	64	75	66	46	1	1	8							
79	87	82	15	57	11	5	11	4				7		
80	119	108	19	13	6	8	3	5	3			Í		
81	218	61		11	5		6							
Total		h		<u> </u>	<u> </u>	<u> </u>	<u> </u>							
for		1		1										
Species	4439	3456	980	891	277	269	215	132	105	14	14	13	8	9
er cent				<u> </u>										
f total	41	32	9	8	3	3	2	1	1					

TABLE VII. Grasses and sedges of low prairie listed in order of their relative abundance.

Legend:

Af—Andropogon furcatus As—Andropogon scoparius Bc—Bouteloua curtipendula

- Cm—Carex meadii Cp—C. pennsylvanica El—Elymus canadensis Ep—Eragrostis pectinacea K—Koeleria cristata

- Pa—Panicum scribnerianum P. wilcoxianum Po—Poa pratensis Pv—Panicum virgatum Sn—Sorghastrum nutans Sp—Sporobolus heterolepis St—Stipa spartea

Quadrat	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
•••••	Af	Bc	As	Po	В	Cm	St	Sp	Pa	K	Cp	El	Sn	Ep	Spa
1	47	26	2	4	86	15	1	25	5	3	1			1	
2	52	7	20	3	3	13	5	1	18	8	3			4	
3	1	55	59	2	2	3	1		19	7	1			1	
4	9	28	1	41		1	4	1	2	1		1			
5	1	62	64	37	1	5	10	1	2	7	1	2	1		9
9	41	89	62	47	1		21	3	16	23	4	T		1	
10	17	59	26	6	8	110	2	19	1	5	1			1	
11	97	55	37	54	1	11	21		15	32	5				
13	47	10	21	2	6	3	39		15	1			1		
14	35	12	46	24	53	3	5	2	11	13	1				
20	53	79	5	2	3	33	23	8	8	9	4			2	
21	80	27	11	4	3	54		12	14	17	10			1	
26	79	47	10	27	1	37	4	12	12	18	17			1	
27	63	26	45	31	7	34	5	1	11	13	19				
28	41	10	46	18	2	30	2	24	2	13	13			1	
29	9	19	55	17		28	4	5	7	8	16				
30	27	13	26	1		33		26	2	14	7			2	
31	69	5 8	47	12		49		9	15	9	12				
32	77	91	38	15	4	57	1	14	15	16	20			1	
33	78	45	27	117		11		8	11	3	5		20		
34	82	56	24	14	17	42		27	8	12	6		8	10	
35	60	5	16	6	54	-9		42	12	15	6			4	
36	111	41	7	132	2	5	6	15	14		14	1			
37	24	101	82	12	2	4	17	29	30	19	3			2	
38	3	76	75	4	4		11	10	31	19	7				
39	16	18	58	2	89	3	3	23	8	9	7				
40	13	11	17	1	98	35	8	16	6	11	8				
41	24	46	6	1	2	20	66	2	1	15	2	L	1		
42	8	27	18	9	2	24	44	7		13	1	1	4		
43	8	24	12	26	31	7	-58	6	1	20	11	<u> </u>			
44	36	21	2	38	93	3	5	34	1-1-	7	2	8	I		
45	39	15	1	33		28	16	25	12	4	·····		 		
46	18	13	3	73	31	2	24	22	1	9	1				
47	23	22	37	19	3	1	33		34	4		<u> </u>		1	
48	8	20	22	28	20	13	26	1	11	3			<u> </u>		
49	5	71	50	20	8	25	24		2	1		24			
50	23	31	25	29	5	1	1-10	7	16	10	<u> </u>		<u> </u>		
53	57	45	8	93	27	2	16	20	19	10	<u> </u>		<u> </u>		
54	75				AF	$\frac{1}{2}$	5	29	10	6	1	110			
77 00+01	2	14	3	2	45	2	1	59	12	23	1	14			
Total	1								ł						
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Species Per cent	μοο/	1220	1135	1019	713	047	1977	458	421	405	201	51	32	31	9
of total	18	18	13	12	8	7	6	5	5						
or cocar	10	10	10	27	9	17	0	ð	3	4	2				

TABLE VIII. Grasses and, sedges of high prairie listed in order of their abundance.

Legend:

- gend: Af—Andropogon furcatus As—Andropogon scoparius B—Bouteloua hirsuta B. oligostachya Bc—B. curtipendula Cm—Carex meadii Cp—C. pennsylvanica El—Elymus canadensis Ep—Eragrostis pectinacea

K—Koeleria cristata

Pa—Panicum scribnerianum P. wilcoxianum

P. wucoxianum Po—Poa pratensis Sn—Sorghastrum nutans Sp—Sporobolus heterolepis Spa—Sporobolus asper St—Stipa spartea

Andropogon furcatus and Poa pratensis are represented by far the largest numbers, and that Bouteloua curtipendula and Andropogon scoparius are next in order. The first two species are excellent sod formers, Andropogon furcatus being in control throughout the area. Poa is favored by annual mowing, the removal of the taller grasses furnishing sufficient light for early growth in spring which is followed by seed production before this species is greatly shaded by the taller grasses. The 10 remaining species constitute only 10 per cent of the total as regards numbers.

An examination of the grasses and sedges of high prairie (Table VIII) shows that the same four species are most important, constituting 61 per cent of those listed. The sequence, however, is somewhat different, *Andropogon furcatus* again ranking first, and the others as before except that *Poa* is reduced from second to fourth place. Moreover, each of these species is represented by smaller numbers than on the lowland. The average numbers per square meter are as follows:

	Low Prairie	High Prairie
Andropogon furcatus	111	3 9
Poa pratensis	86	25
Bouteloua curtipendula	25	38
Andropogon scoparius	22	33
Average	61	33

The II remaining species of upland furnish only 39 per cent of the total number of grasses and sedges.

A similar study of non-grassy species or forbs of the lowland shows that *Antennaria campestris* is by far the most abundant, averaging 15 plants per quadrat (Table IX). *Equisetum laevigatum* and *Solidago glaberrima* rank next in order with 9 and 6 representatives in each quadrat respectively. Only 6 other species are represented by more than I plant per square meter. Not only do the first 9 species listed hold first rank in number per quadrat, but their distribution is very general, ranging from 85 per cent for *Amorpha canescens* to 48 per cent for *Psoralea argophylla*. Certain species, although few in number of individuals, are widely distributed. Thus, *Petalostemon candidum* (*Pc*) is represented by less than I plant per quadrat, but occurs in 42 per cent of the quadrats studied.

The number of most abundant herbs exceeds or equals that of the grasses (exclusive of the 4 most abundant) and they are sufficiently conspicuous during their periods of anthesis to determine the character of the seasonal aspect.

A similar study of the species of high prairie (Table X) shows that *Amorpha canescens* is most abundant with an average of 9 plants per quadrat, and that it is represented in every quadrat studied (Fig. 19). Next in order is *Antennaria campestris* with an average of 6, but only 7 other species occur at a rate exceeding a single plant per square meter. All of these are widely distributed, 6 occurring in at least 50 per cent of the quadrats. The very local occurrence of *Psoralea esculenta* in abundance is shown by its presence in

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TABLE IX.

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For other symbols see Table VI.

At—Antennaria campestris

Es-Equisetum laevigatum

S-Solidago glaberrima

only 7 per cent of the quadrats but with an average of 1.2 plants. Of the 9 species in each list that have a frequency of 1 or more per quadrat, 8 occur at both stations; *Psoralea esculenta* occurred only on high prairie while *Equise-tum laevigatum* and *Psoralea argophylla* were found in low prairie quadrats exclusively.

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Legend:

A—Amorpha canescens Am—Aster multiflorus At—Antennaria campestris Cs—Cathartolinum sulcatum E—Erigeron ramosus For other symbols see Table VI. H—Helianthus scaberrimus P—Psoralea floribunda Pe—Psoralea esculenta S—Solidago glaberrima

The relative areas occupied by the grasses and sedges were determined for both lowland and upland prairie. From the total amount of this cover, *i.e.*, 100 per cent, the relative percentage was calculated for each species. In calculating this area, the base of the bunch, clump, or mat of sod was used rather than the spreading tops. A quadrat consisting of *Andropogon furcatus*, for example, owing to the spreading tops, may have an apparent density of 100 per cent, while actually only one-fourth of the soil surface is occupied (Fig. 20). The apparent density of a sod of *Bouteloua hirsuta*, on the other hand, may exceed only slightly its basal area (Sarvis '20).

T. L. Steiger

Table XI shows that the basal density of grasses and sedges in the low prairie varies from 13 to 37 per cent, with an average of 24 per cent, although in all but 5 quadrats the entire area was apparently occupied by tops. Even casual examination of the table shows that *Andropogon furcatus*, *Poa pratensis*, and *Andropogon scoparius* are by far the most important species, the three

TABLE XI.	Total basal area occupied by grasses and sedges in each quadrat of low
	prairie, and the relative proportion occupied by each species.

Number of	Total		_													Apparent	Number	Number	Total no.
quadrat	basal	1 1	2	3	4	5	6	7	8	9	10	11	12	13	14	density	of	of	of
quuuruv	area	Af	Po	As	Bc	St	ĸ	Pa	EI	Cm						per cent			species
6	26.5		10.4	5.6	20	.6		.1	.1	0.00		H PP-	<u> </u>	00		100	6	5	11
7	23.5		11.6	3.9		.5	.1-			<u> </u>			.1			100	ž	10	17
8	25.5		13.7	3.4	.2	.2	.1	.5		1.1	-		••	.1		100	10	- 10	18
12	28.4		12.0					1.1	1					••		100	4		11
15	20.6	8.7	7.4	3.6		.2	.3	1.1		.1	.1	<u> </u>	1.1			100	9	- 11	20
16	28.3		4.9	11.8		.5	.ï	1.1	.1	1.1	• •	<u> </u>	• 1			100	- 9	10	18
17	18.7		6.9	.1		.5	1:1	1.2		1.1	-					100	8	10	18
18	23.0	6.6	7.7	6.8	.1	.2	•1	1.2	1.1	1.1				.1		100	10	10	22
19	18.2		6.2	0.0	1	2	1.1	.5	•1	1.1	.1			• -		100	10	12	18
22			7.4		.2	.2				1.1									17
	19.6			.1		.5	.4			•1			.1			100	9	8	
23	21.5	7.9	10.5	2.4	.1			.1					<u> </u>	-		100	6	12	18
24	25.0	8.8	9.2	6.4		.1	•1	.1		1.1		.1	•1			100	9	13	10
25	35.6		26.3	124 0	-	l		<u>⊢</u>	.1	.1			-	-		100	4	6	
51	30.4	5.5		14.6	.7		.1	-1		11		-	.1			100	8	11	19
52	29.4	4.0		19.6	1.7	.3	.2			.1		1.1	-			100	9	10	19
55	19.0	4.9	7.0		2.2	1	.1	.2	.1	-		.1		_		90	9	13	22
56	20.0	5.1	5.4	3.9	4.6	.1	.4	.1		.2		.1		.1		100	10	11	21
57	22.3	5.7	5.3	6.9	2.4	•5	1.0	•1	•1	.2		.1				100	10	9	19
58	*19.7	7.6	7.4		1.3		•8			.4		.1				100	8	17	25
59	16.1	6.0	5.0	1.4	2.7	.1	.7	.1		.1		.1	.1			90	10	12	82
60	19.2	9.1	7.1	1.7	.4	1.	.3			.1		.1			_	100	9	16	25
61	18.4	7.7	8.9	.7	.2	.2	.4	•1		.1		Ľ.			.1	90	8	12	20
62	22.3	8.0	10.8	1.2	•3	.7	•5		.1	.1						100	9	11	20
63	22.9	10.1	8.3	2.0	1.4	•5		.4		.1		.1		_		100	8	11	19
64	22.3	7.3	7.7	4.3	1.6	•8	.2	•2		.2						100	8	16	24
65	24.3	4.9	4.9	11.5	1.4	1.1	.1	•3		.1						100	8	12	20
66	25.5	2.6		16.6	2.0	.2	.4	•3		.1						100	8	10	18
67	27.7	3.3		13.3	1.2	.4	.6	.1		.1						100	8	11	19
68	13.1	4.1	4.3	.5		2.9		•3	•3	•3		.1				80	9	9	18
69	15.5	2.4	.1	3.8		8.0		.1	•9	.1						90	8	10	18
70	33.9	23.9	1.1	2.4	5.1			.1	2.3	.1						100	6	5	11
72	36.5	29.2	3.5	3.8												100	3	1	4
73	27.0	9.2	2.5	12.2	1.1	.2	1.0	.1	.1	.1	.3	.1		.1		100	12	8	20
74	25.1	4.3	5.8	11.5	2.1		.9	.2		.1		.1		.1		100	9	10	19
75	26.0	10.8	7.6	5.5	1.7	.3		.1								100	6	5	11
76	37.2	1.1	3.3	30.8	1.4	.1	.1	.3		.1						100	8	8	16
78	28.7	3.2		14.9	2.2	.8		<u> </u>								100	5	8	13
79	22.8	5.5	4.8	9.1	.4	.8	.3	.1		.1	1.7					100	9	10	19
80	26.1		15.6	2.3	.7	.1	.3	.2	.1	.1	.2					100	10	10	20
81	21.0		.9	.9		.3		- ···		.1						100	5	5	10
Per cent			<u> </u>							-				-					
of total		34.9	30.3	25.6	4.2	2.3	1.0	.7	•4	.4	.2					98			
Occurrence in quadrats																			
per cent		100	98	92	75	82	68	00	38		72	30	- E	1 2	2)	,	

Legend:

Af—Andropogon furcatus As—Andropogon scoparius Bc—Bouteloua curtipendula Cm—Carex meadii Cp—Carex pennsylvanica El—Elymus canadensis Ep—Eragrostis pectinacea K—Koeleria cristata Pa—Panicum scribnerianum P. wilcoxianum Po—Poa pratensis Pv—Panicum virgatum Sn—Sorghastrum nutans Sp—Sporobolus heterolepis St—Stipa spartea

making up 91 per cent of the total area and occurring in 92 to 100 per cent of the quadrats.

Conditions on the high prairie are shown in Table XII. Here the vegetation is less dense and also less luxuriant. The apparent density varies from 30 to 100 per cent and the basal area, which shows a wider range than in the lowland, from 9 to 43 with an average of 20 per cent. Andropogon scoparius

is the chief grass, occupying 26 per cent of the area. The short Boutelouas and *Sporobolus heterolepis* occupy 17 and 13 per cent respectively. Four other species each occupy 7 or more per cent of the area and another group of 3 take up 2 to 5 per cent. Thus the major portion of the total area is divided among many more species than in the lowland.

Number of quadrat	Total basal	1	2	3	4	5	6	7	8	9		11			14	15	Apparent density per cent	of	of	Total no. of species
	area	As	В	Sp			Bc	K	St	Pa				ET.	Sn	Spa		12	5	17
1	43.1		29.6	7.4		1.3	.9	.6	.01	.2	.4	.01	.1				100	12	6	17
2	28.3	7.1	.4		.3	8.5		2.5	.7	1.7			1.9				70	10	6	16
3		16.6	.2		•1			1.2	.01	.8	.1	.04	<u> </u>				80	9	4	13
4	28.2	.01			23.7				.2	.02				.01		.14		· 10		19
5	14.5	8.5	.2		2.3		2.6	.2	.4	.1	.1	.01		.1			50 30	- 10	11	19
9	10.0	4.8		.2	.8		2.0	.7	.5	.2			<u> </u>		<u> </u>			8	6	14
10	20.8	6.3	.3	8.7	.2		3.3	.8				<u> </u>					70 50	10	5	15
11	14.3	4.8	.1			2.9		1.9	.4	•5		.1					60	9	9	18
13	17.8	8.5	1.0			1.8			4.2		•03	-	<u> </u>				70	11		17
14	20.8	7.6	6.7	.4	1.7			1.5	.3		•03	.01	<u> </u>					11		- 17
20	14.1	.4	.3	3.6			3.2		1.7	.4	.4	-1	-1				40 40	12	5	19
21	13.0	1.3	.3	1.8		2.9				1.3		.2	.1		···		40	11		19
26	12.4	1.5	.2	1.0	1.0				.2	.7	.8	.3	.1	-			40 50	12	9	20
27	15.7	7.1	.4	.1	1.5				.2	.4	1.5	.4	.1				60	11	2	14
28	20.8	5.3	.2	3.9		2.5		$\frac{5.3}{1.6}$	-1	.6		1.5	•+				70	10	· 6	16
29		12.0		1.1	.9	.3			.7		1.5	1.1	.2				80	10	<u> </u>	12
30	23.4	4.7		11.6		1.9		2.5			1.1	1.2						9	8	17
31	16.8	6.6		2.7	1.7	$\frac{2.0}{2.7}$					1.7		.04				60 70	11	- ů	20
32	18.2	3.7	.9	4.0									.04		.3		70	10	8	18
33	18.0	6.2		.6	5.5			.3		.5		11	.5		.2		70	10	- ñ	21
34	15.5	2.6	1.8	1.7		3.6				.6	-8	1.			•2		50	12	6	17
35	14.5	1.1	5.5	4.4		1.0		1.1	·	.6	-1	.1	•3	.01			60	11	- 11	22
36	17.1	.4	.1	.9	9.3		2.8	0.0	.3	.6 1.3	-1			•01			60	12	9	21
37	18.9	6.8							.7	1.2	.1	.1	.1				60	10	9	19
38	17.5	9.0	.8	1.6	.1			2.0	.1		.03	1.1					70	10	6	17
39	24.8		12.9	2.3	.1	.3		1.9	1	.5		1.2					80		6	17
40	25.5		14.9	4.4	.01						.6 .3	.02					30		3	14
41	10.3	.5	.1	.1	.01		2.4	$\frac{1.4}{1.3}$.04		.02		.01	- 1		30		2	13
42	9.4	1.2	5.1	.7	1.3	•3 •5			3.3		.4	.03		+01	•*		70		3	14
43	15.2		14.6	3.5		2.1	.7	.4	.2	.04	.03	1.03		.1			80	11	4	15
44	23.2		14.0	3.4		2.0	.6		2.5	.7	9	••					50	9	4	13
45 46	13.8		5.9	6.8	4.7	2.0	.7			.02		.01				4	70	11	5	16
46	22.3		5.0	0.0	1.8				2.3		.03	1.01	.1				80	10	4	14
49	22.7		4.1	.04	1:1		1.4		1.8	1.2	1.2						80	10	6	16
48	23.5	9.7	2.1	.04	2.5		5.1		2.6	1.2	.4			.6			80	10	- ĕ	18
50	23.9		2.4	.7	1.3		1.6		2.00		.04				-		80	9	- 8	17
53	26.6	2.8	7.6	4.7		3.7			1.8	1.0		.01					80	11	5	16
54	18.0		1		5.4			.5	1.0	1.0		.01					70		5	14
77	29.9		00	12.0	1	.02		4.6	.01	1.4		.02		.2			90	12	5	17
	29.9	2.1	0.0	12.10	· · ·			1.0				1.22							I	
Per cent of total		26.4	16.5	12.6	9.6	8.8	8.0	7.3	4.8	2.8	1.9	.6	.5	1	.1		66			
Occurrence			1								-									
		1	1		1					1	1	1							. 1	
in quadrat	8	100	80	78	98		100			.95	93	78	30	17	7	2				

Table XII.	Total basal area occupied by grasses and sedges in each quadrat of high
	prairie, and relative proportion occupied, by each species.

Legend:

Af—Andropogon furcatus
As—Andropogon scoparius
B–Bouteloua hirsuta
B. oligostachya
Bc—B. curtipendula
Cm—Carex meadii
Cp—C. pennsylvanica
El—Elymus canadensis
Ep—Eragrostis pectinacea

K—Koeleria cristata Pa—Panicum scribnerianum P. wilcoxianum Po—Poa pratensis Sn—Sorghastrum nutans Sp—Sporobolus heterolepis Spa—Sporobolus asper St—Stipa spartea

Table XIII shows the relative area that each species of grass or sedge occupies in low and high prairie, respectively. Andropogon scoparius has regularly the largest average area per plant owing to its bunch habit. Sporobolus ranks second, and is followed by Bouteloua, Koeleria, and Stipa. Several species, notably Koeleria cristata, Panicum spp., Carex meadii, Sporobolus heterolepis, and Eragrostis pectinacea show a decided increase in size of individuals in the high prairie where they meet less competition with the bluestems. In low prairie they are more scattered and suppressed. Conversely, Andro-

Hab1tat		Ar Ar		Po H	A 1	As	a 1	Вс н	·	St =	-	×	84	-	E -	╞┼╻	8		r S		E E	m	r Su			8	Cp H	CP P4	Cp H	Cp Pv C	CP PV B
Rank in habitat	-	2	n 🗠	4	a 10		4	9	a n	: 0	a o	-	1 1	- o	1 00	1 12			1 01	+			+				:	11 14	11 14 - 1	11 14 - 15	11 14 - 15
Total area in sq. dm.	335.2 68.5	68.5		74.7	291.5 74.7 245.6 205.7 39.9 62.2 22.1 37.5 9.3 57.2 6.2 21.5 4.2 1.0 3.8 15.2	205.7	39.9	62.2	22.1	37.5	9.3	57.2	2.5	21.5	1.2	.03	.8 15		2.2	98.5	6.	3.6	4.	0.		2 4	.2 4.3	7	•	•	7
Percentage of total	34.9	8.8	30.3	9.6	25.6	26.4	4.2	8.0	2.3	4.8 1.0	1.0	7.3		2.8	.4		.4	1.9	.2 12.6 tr.	6 t	÷	.5 tr.		.1 tr.				.6 tr.		.6 tr	.6 tr
Percentage occurrence 1n quadrats	100	86	98	86	8	100	75	100	88	80	68	95	6	95	38	17	8	92	13	78	30	30	15		13	78	78 2	78 2	78	78 2 -	78 2
Average number per quadrat		111.0 39.0		61.4 25.4	22.3		28.4 24.5	38.4		12.8	3.3	5.4 12.8 3.3 10.1 6.7	5.7	10.5 2.6 1.3 6.9	2.6 J		.9 16	16.2	.3 11.4		• 4	80	.4	60	°.	5.	5.0	5.0 .2	5.0	5.0 .2 -	5.0 .2
Average area occupied, sq. cm.	7.6	4.4	8.4	7.4	27.6		4.07	18.1 4.07 4.05 10.3	10.3		7.0	7.3 7.0 14.1 2.3	5.3	5.1	1.0	0.1	4.	5.1 4.0 2.0 1.4 2.4 16.9 21.5 6.4 11.6 2.4 2.8 2.5 2.1	N 0	5	4.		4	N 00	ده در	•		•		•	•
Legend: A A	: Af—Andropo As—Anàropo	idroj viroj	pogon furcatus bogon scobarius	fur	catus barius							Cp—Carex pennsylvanica F]—Flymus canadensis	d x	enns	ylvc uden	mic. sis						ੂ ਮੁੱਧੂ		00	prat um		ensi	ensis anvaat	ensis viraatum	ensis viraatum	Po—Poa pratensis Pv—Pancum miraatum

TABLE XIII. Comparison of species of grasses and sedges in low and high prairie.

As—Anåropogon scoparius B—Bouteloua hirsuta B. oligostachya Bc—Bouteloua curtipendula Cm—Carex meadii

Ep—Eragrostis pectinacea K—Koeleria cristata Pa—Panicum wilcoxianum P. scribnerianum El—Elymus canadensis

204

T. L. Steiger

Sn—Sorghastrum nutans Sp—Sporobolus heterolepis Spa—Sporobolus asper St—Stipa spartea

pogon furcatus, A. scoparius, and Elymus canadensis develop into larger clumps in the lowland. Sorghastrum nutans and Panicum virgatum occur in very small amounts and affect the total composition but little.

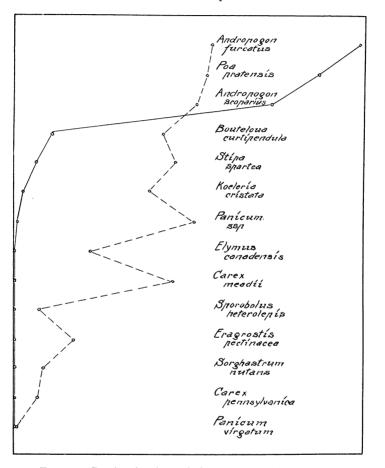


FIG. 21. Graphs showing relative areas occupied by low-prairie grasses and sedges (solid line) and the frequency of their occurrence (broken line). Actual values are given in Table XI.

Figure 21 shows graphically the total area occupied by each lowland species and the constancy with which it appears in the quadrats. There are three rather distinct groups : the three dominants occupy a large area and show great constancy; the members of the second group of species occupy a relatively small area, but also show a high constancy; and the species of lower rank, which occur only occasionally and occupy an insignificant area. Figure 22 shows similar graphs for the upland. Here the species do not readily fall into distinct groups. While on the lowland 3 species (*Andropogon furcatus, Poa* pratensis, and Andropogon scoparius) make up 91 per cent of the total, 7 upland species are included in 89 per cent of the vegetation.

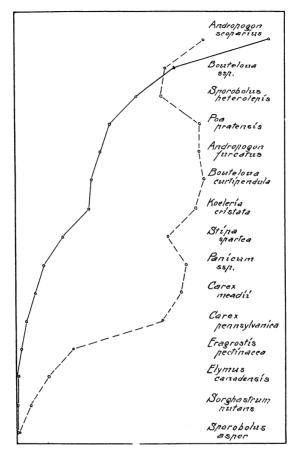


FIG. 22. Graphs showing relative areas occupied by high-prairie grasses and sedges (solid line) and the frequency of their occurrence (broken line). Actual values are given in Table XII.

CHARACTERISTICS OF THE MORE IMPORTANT GRASSES

The most important prairie grass is *Andropogon furcatus*. The foliage of this species reaches a greater height, approximately 65 cm. in low prairie, than any other grass. Its rank growth and widely spreading tops exert a controlling effect, yet only 20 per cent of the ground is occupied. The total leaf area of a square meter of this bluestem from low prairie was measured, as was also that from a quadrat where other grasses were intermixed (Table XIV). Measurements of height of plants, dry weight, basal area, and total leaf length were also obtained. For comparison, similar data

January, 1930

from a square meter of *Bouteloua oligostachya* was secured, the grama grass representing the most xeric conditions of the upland.

Vegetation	Height, cm.	Dry weight, grams	Basal area, sq. dm.	Total length of leaves, m.	Total leaf surface (2 sides), sq. m.
Pure Andropogon furcatus	65	365	15.5	1038	6.05
Andropogon furcatus in mixture.	50	211	20.8	937	3.37
Pure Bouteloua oligostachya	10	158	42.4	1378	2.55

TABLE XIV. Relative development of prairie grasses per square meter.

Kiesselbach ('16) has calculated the leaf surface of corn where 3 stalks were grown per hill, and the hills were spaced 42 inches apart. This was found to be 4 times as great as the surface of the soil occupied by the plants. Thus, while the leaf area of the short grama grass is 63 per cent as great as that of corn, the area of a pure stand of the big bluestem exceeds that of corn by 50 per cent.

Table XIV clearly shows that there is no direct correlation between basal area and development of the above-ground parts; the xeric short grass has nearly 3 times the basal area of the bluestem. The dry weight, however, is closely related to the leaf surface, and it is the best criterion to be used in expressing the response of the vegetation to the sum of the environmental factors. This has been clearly demonstrated by Weaver ('24), who measured the several grassland environments in terms of plant production.

Andropogon scoparius is the grass ranking second in importance (Fig. 9). On the low prairie, it occurs only in small tufts intermixed with its larger competitor. Here it is a sod and bunch former, usually 40–50 cm. tall. It increases in importance on the slopes, largely because A. furcatus requires more water and can not thrive, and is the chief dominant of the upland prairie. Under the intense competition of the prairie sod, neither species of bluestem blossoms regularly nor abundantly, except during very wet years, A. scoparius showing a greater tendency toward blossoming on the slopes than at their foot where competition is more severe. This is in striking contrast to their behavior along roadsides and other places where more water is available. Great differences in height-growth also occur, the usual stature sometimes being doubled where an extra supply of water is available.

Poa pratensis is a relatively low-growing, early, shade-tolerant species. Its abundance has been greatly increased as a result of the removal of the taller grasses by annual mowing. Although occupying much ground area, it is really subordinate to the taller bluestems. During May and June, before the late-blooming Andropogons have made much growth, *Poa* is very conspicuous and flowers abundantly.

Bouteloua curtipendula regularly occurs in small amounts throughout the prairie. The inflorescence reaches a height of 30 to 45 centimeters and is

especially characteristic where competition of other grasses is not too severe (Fig. 23).

Stipa spartca is typically a species of upland, although it is also found at the foot of slopes and even on their flat bases (Fig. 24). The characteristic small bunches are the first to resume growth in spring, and, in fact, many of the leaves remain green all winter, especially under a cover of snow. It resumes growth very early in spring. *Stipa* is also often the first species to colonize small disturbed or denuded areas. This is probably due to its method of planting the seed by means of a twisting awn. Gopher mounds are readily colonized by this species, and the fruits may be blown a considerable distance by strong winds, especially when they twist together in clumps.

June grass, *Koeleria cristata*, forms small tufts, in this manner resembling *Stipa*. Flower stalks occur abundantly in late May and early June; these usually reach a height of 20 to 30 cm. Seed is produced in great quantity.

The vegetative parts of *Panicum scribnerianum*, *P. praecocius*, and *P. wilcoxianum* are so similar that no attempt was made to separate them in quadrating. They are interstitial species of small stature and are of rather minor importance. The first is found in low prairie, but all do best and are most abundant in the upland. They are very similar in their demands to *Eragrostis pectinacea*.

Carex pennsylvanica and *C. meadii* are the most important sedges. The latter occurs in greatest abundance and is also most widely distributed. The former is slightly more xeric, but both blossom and fruit early throughout the prairie.

Panicum virgatum and Sorghastrum nutans are of relatively little importance, notwithstanding their stature, which is about equal to that of Andropogon furcatus. They are more often found in low prairie, and are of greatest abundance in the ecotones between prairie and thickets on the one hand and in slightly disturbed places on the other. In such places Sorghastrum flourishes, and Panicum to a lesser extent, even on the upland.

Elymus canadensis is a tall-growing, coarse grass, characteristic of moist ravines and of disturbed areas which afford slightly more water. Under the latter condition it frequents uplands.

Sporobolus asper, a common species of disturbed grasslands is scattered sparingly throughout the stabilized prairie. Its occurrence is most obvious during years of extreme drought when its tall flower stalks and partially sheathed inflorescence make it a conspicuous feature of the landscape. Sporobolus heterolepis, a species with finer leaves and shorter, finer flower stalks, forms bunches which are often very abundant on the dry crests of ridges. The shining, gracefully curved foliage is in striking contrast to the coarser, duller foliage of Andropogon scoparius.

A study of the quadrats (Fig. 25) makes clear the variation in the components of the plant cover. Quadrats 51 to 59 and 65 to 67 inclusive (Table XI) are near the foot of a north slope where the little bluestem (*Andropogon*

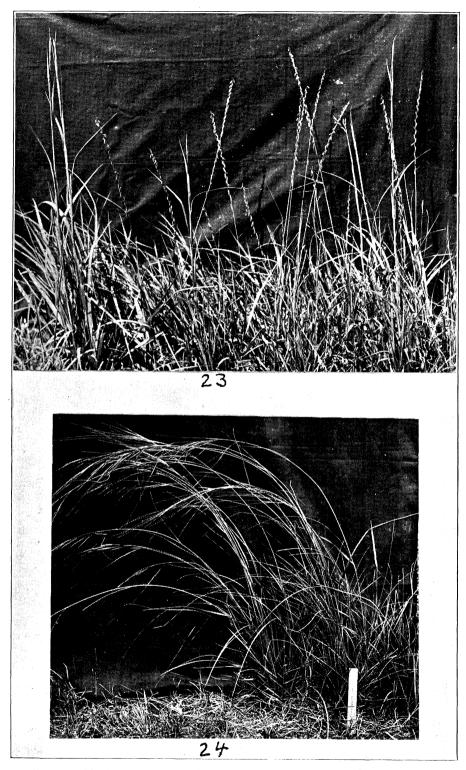


FIG. 23. Slender grama grass (Bouteloua curtipendula) with flower stalks 80 cm.
high, and a small clump of big bluestem (left) on high prairie. Photographed July 23.
FIG. 24. A few plants of needle grass (Stipa spartea) in fruit on high prairie, June 20. The stems curve gracefully under the weight of the heavy fruits.

scoparius) is dominant. Quadrats 70 and 72 are adjacent to the wooded draws where *Andropogon furcatus* makes a rank growth. Numbers 68 and 69 were made on a steep, dry slope where *Stipa* was especially abundant.

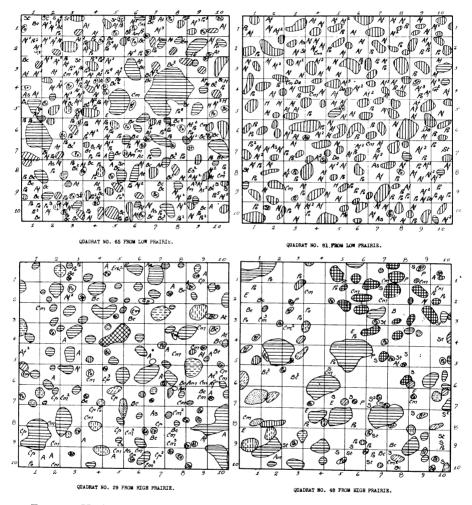


FIG. 25. Horizontal lines, Andropogon scoparius; vertical lines, Andropogon furcatus; diagonal cross-hatch, Sporobolus heterolepis; vertical-horizontal cross-hatch, Bouteloua hirsuta; broken vertical lines, Stipa spartea; broken horizontal lines, Koeleria cristata; broken diagonal lines, Bouteloua curtipendula; dotted, Panicum scribnerianum; for other symbols see Table VI.

Owing to the annual mowing, the short grasses (*Bouteloua oligostachya* and *B. hirsuta*) occur more or less abundantly on hilltops. Both form dense mats of sod where they are locally controlling, but grow in isolated, small tufts among the taller, upland species. They produce flower stalks in great

abundance. Quadrats 1, 39, 40, and 44 were made in areas largely dominated by these grasses (Table XII).

The great variation in the structure of high prairie vegetation may be seen by comparing quadrats 3, 29, and 47 to 50 inclusive, where *Andropogon scoparius* dominates, with the preceding and numbers 30 and 77. The latter is dominated by *Sporobolus heterolepis*.

Number of quadrats in which it held:	Andropogon scoparius	Bouteloua spp.	S porobolus heterolepis	Poa pratensis	Andropogon furcatus	Bouteloua curtipendula	Koeleria cristata	Stipa spartea
First place. Second place. Third place.	17 7 1	7 	7 7 4	2 2 5	3 5 10		2 3 10	2 4 2
Total No.	25	12	18	9	18	15	15	8

TABLE XV. Relative ranking of the several species in the different quadrats. High Prairie

Low Prairie								
Number of quadrats in which it held:	Andropogon furcatus	Poa pratensis	Andropogon scoparius	Bonteloua curti pendula	Stipa spartea	Other species		
First place Second place Third place	13 19 7	14 16 8	12 4 16	I		Once each		
Total No.	39	38	32	I	3	7		

Low Prairie

Table XV gives the relative importance of the several species of the upland and lowland, respectively, by indicating how many times each held first, second, or third place, on the basis of area occupied, in the various quadrats. It may be seen that on the upland 7 species hold the rank of first place; on the lowland this place is confined (with one exception) to 3. The great importance of the Andropogons is again emphasized.

Relative Growth and Plant Production

Differences in the upland and lowland habitats are clearly shown in the relative growth and total dry weight of the different species making up the vegetation. Table XVI shows the development of several important species in the two habitats.

The vegetation from 10 square meters of typical upland prairie was cut close to the ground during June and July of the 2 years respectively, air dried, and the dry weight determined. The yield from 10 sq. m. of lowland

prairie was ascertained at the same time and in a similar manner. The average yield on high prairie was 215 grams per sq. m., as compared with 301 grams on the lowland. The smallest yield was from an upland quadrat of *Boutcloua* (193 grams) and the largest from a rank growth of Andropogon on low prairie (488 grams).

TABLE XVI. Relative growth of species in lowland and upland prairie during 1927.

		Average length of 100 in cm.		
Date Species		Low prairie	High prairie	
July 5	Stipa spartea, flower stalks Stipa spartea, leaves Koeleria cristata, flower stalks	93.2 62.3 52.0	80.2 50.5 40.8	
July 22 July 23	Andropogon furcatus, leaves after 10 days growth in clipped quadrat Andropogon furcatus, leaves Amorpha canescens, stems Bouteloua curtipendula, flower stalks	13.8 40.8 58.5 66.8	7.533.845.337.4	

REACTIONS OF THE VEGETATION

The presence of a cover of vegetation reacts upon the habitat in many ways. Studies have been made of its effect upon water content, temperature, evaporation, and light.

Reactions on Water Content

The vegetation of areas 4 meters square, and located in both high and low prairie was clipped 4 times during the growing season, and measurements were made therein to determine the effect of the plant cover upon the several factors. As a result of greater insolation, the surface soil to a depth of 8 to 12 inches was usually drier than that of adjacent prairie, but at greater depths an excess of 1 to 3 per cent of moisture was found in the clipped areas.

In similar denuded areas where all of the vegetation was kept out and a loose surface mulch established, a marked difference in water content was found (Table XVII). Similar results were obtained on low prairie where the water content was regularly 5 to 10 per cent higher in the bare area.

TABLE XVII. Effect of plant cover on soil water content in high prairie, August 25, 1927.Total soil moisture in per cent

Habitat	0-6 in.	6-12 in.	1-2 ft.	2–3 ft.	3-4 ft.	4-5 ft.			
With plant cover	10.0 13.5	3.6 10.9	2.9 12.2	1.4 9.4	4.6 9·4	5.2 11.3			

The removal of the vegetation by burning or mowing promotes water loss from the upper layers of the soil. In 1927 the plant cover about each station was left unmowed, although later a fire swept over a portion of this area. Water content determinations on February 3 of the following spring showed that there was 3 per cent more moisture in the surface 6 inches of the unmowed area, due to decreased surface evaporation. On June 21, the water content on low prairie to a depth of 4 feet was as follows:

Condition	0-6 in.	6-12 in.	τ−2 ft.	2-3 ft.	3-4 ft.
MowedUnmowed		6.8 9.3	5.8 6.8	5.4 5.8	4.1 4.6

Thus, water content was 1 to 4.6 per cent greater in the unmowed area to a depth of 2 feet.

One cause of lower water content on the upland is the smaller amount of vegetable debris. Where the prairie is annually mowed, the soil between the bunches and mats of grass is often bare. For example, the average amount of debris from a square meter of upland weighed only 76 grams as compared with 1,098 grams from an equal area of low prairie. On an unmowed low-land area the mulch of compacted litter covered the soil to a depth of 4 centimeters, and this was covered by looser materials 10 centimeters thick. A large quantity of fallen leaves, etc., is carried by the wind from the upland to the lower areas. The dried plants of *Psoralca floribunda* and other species sometimes accumulate in ravines to a depth of 60 to 120 cm., and regularly there is an accumulation of debris to a depth of 20 to 40 centimeters. Such large amounts, of course, are distinctly unfavorable to the development of low-growing plants.

Reaction on Temperature

The effect of a cover of vegetation on soil temperature is marked. Under a sod of *Bouteloua oligostachya* the temperature at a depth of 3 inches was 4° F. lower than in the bare area between the mats. The temperature at a depth of 6 inches in midsummer was 87.5° F. in a clipped, upland quadrat and 79° under the cover of low prairie grasses. The effect of cover on soil temperature is especially important in early spring. Temperatures at depths of 1, 3, and 6 inches, respectively, in level high prairie and low prairie from which the vegetation of the preceding year had not been removed, and in mowed, burned, and denuded low prairie are shown in figure 26. The wet meadow is also included for the purpose of comparison. This shows a direct relation between soil temperature and different degrees of plant cover.

Reaction on Evaporation

The effect of a plant cover on evaporation is clearly illustrated by the following experiment: During midsummer (July 11 to August 4) evaporation rates were determined at a height of 3 inches among upland and lowland

vegetation and in clipped quadrats in each. The average daily losses, in the above sequence, were 28.4 and 16.7 cc. as against 34.7 and 28.9 cc., respectively. Thus, a cover of vegetation greatly reduces evaporation, and the amount of reduction is in proportion to the density of cover.

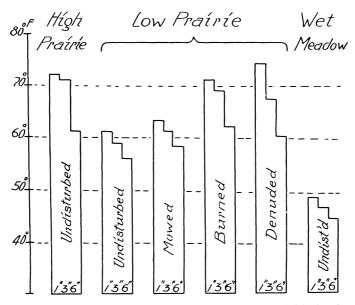


FIG. 26. Soil temperatures at 1 inch, 3 inches, and 6 inches in various communities in early spring (March 28), showing effect of cover.

Reaction upon Light

Layering in prairie is less pronounced than in forest, but there is nearly always severe competition for light. The absence of upland species from low prairie is not due to excessive water content, but in the main to a deficiency of light. Here the light is frequently reduced as low as 5 to 10 per cent at the soil surface, as measured by the Clements' photometer, and a light intensity of only 1 to 2 per cent occurs in dense vegetation.

The early flowering habit of certain low-growing species, such as Antennaria campestris, Carcx pennsylvanica, C. meadii, Fragaria virginiana, and Viola pedatifida, is possibly a seasonal adaptation to the amount of light. At any rate, the seedling development of prairie species must be regulated, at least to a large degree, by their light requirements. That certain species, such as Amorpha canescens and Lacinaria punctata are more tolerant of shade than Helianthus scaberrimus and Kuhnia glutinosa is shown by the yellowing and dropping of the lower leaves of the latter species and their development quite to the base of the plant in the former. Meibomia is one of the most tolerant of the dicotyledons, its basal leaves persist in the densest shade, where also seedling plants are not infrequent. The broad, deep green, lower, shaded

January, 1930

STRUCTURE OF PRAIRIE VEGETATION

leaves of Andropogon furcatus are quite in contrast to the more brownish, narrower, upper ones that are exposed directly to the sun.

The general cover of vegetation in the high prairie reduces the light at the soil surface to about 20 per cent, although greater reduction occurs under some of the larger forbs. *Psoralea floribunda*, for example, reduces the light to 8 to 12 per cent, and a single large plant sometimes exerts an influence over nearly a square meter. One bush with 33 stems was 90 cm. tall, and had a spread of 60 by 150 cm. Only 6 per cent of light reached the sparse, grassy cover beneath it. Under a good growth of Amorpha canescens the light is reduced sometimes to 4 per cent or less, and where clumps of the prairie shrub, Ceanothus ovatus, occur only the most tolerant grasses, such as Poa pratensis. are found.

PROPAGATION OF PRAIRIE PLANTS

A careful study was made of 100 areas of 1 square foot each, located at random in various parts of the prairie, for the purpose of determining the amount of reproduction from seed. This investigation was continued throughout spring and early summer; the following seedlings were found:

- 4 Onagra biennis 29 grass seedlings
- 17 Psoralea floribunda
- 11 Solidago glaberrima
- 9 Meibomia illinoensis
- 6 Antennaria campestris
- 5 Senecio plattensis
- 4 Viola pedatifida
- 3 Physalis sp.
- 2 Vicia americana
- 2 Helianthus scaberrimus
- I Psoralea argophylla

Germination of seed in the high prairie is made difficult by the rapid drying of the surface soil after rains. In the lowland the seedlings are almost certain to succumb in the deep shade produced by plants already established. Thus, it seems clear that the usual method of propagation is by vegetative parts. Stabilized prairie is a closed community. As shown by Clements, Weaver, and Hanson ('29), in their studies on competition, every individual is dwarfed for lack of enough of the necessary factors. Water may be in excess immediately after a rain, but it soon evaporates from the soil surface and is quickly absorbed by the network of roots that occupies all but the surface half-inch of soil. Thus a seedling starting in an apparently bare area is growing in territory already occupied by roots, and, except early in the season, the light is utilized by overhanging leafy shoots. Once established, however, prairie plants endure for a long time.

Of the 237 species of the prairie, only 10 are annuals. Propagation by rhizomes is the usual method among grasses, the size of the bunch or mat being largely determined by the severity of competition. Older mats of sod may become broken by the death and decay of certain parts, and in these areas, as well as between the clumps, new plants of the same or of different species

may gain a foothold. Many dicotyledons, such as species of *Helianthus*, *Aster, Salvia, Rosa,* etc., also employ the rhizome habit with a marked degree of success, their occupation of any new area being rapid and certain.

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SUMMARY

Investigations of the vegetation of virgin prairie were carried on during 1927 and 1928 near Lincoln, Nebraska.

Extensive measurements of the edaphic and aerial factors of the environment were made on both upland and lowland prairie. The water content of soil showed the greatest and most consistent variation, and is the most important factor determining the differences in the structure of the vegetation. Available water for growth is sometimes deficient in the surface layers of the upland soil.

There are 237 species in the grassland studied; and they are distributed as follows: high prairie, 70; low prairie, 45; ravines, 77; and wet meadow, 45. Grasses and sedges make up 24 per cent of the flora, composites and legumes ranking next in importance.

Prevernal, vernal, estival, and autumnal aspects are pronounced in both high and low prairie, the high prairie reaching its climax of flowering earlier in the summer, due to limited soil moisture. Ravine and wet meadow show a maximum in August.

Quadrat studies were made to determine the rank and relative importance of the various species with regard to the area occupied as well as their number and frequency.

Andropogon scoparius is dominant in the high prairie, covering 26 per cent of the area occupied by grasses and sedges. Six other grasses are of secondary importance, covering 7 to 17 per cent, respectively. These are the Boutelouas (*B. oligostachya* and *B. hirsuta*), Sporobolus heterolepis, Poa pratensis, Andropogon furcatus, Bouteloua curtipendula, and Koeleria cristata. Six other grasses and 2 sedges are of minor or local importance. In the low prairie, Andropogon furcatus, Poa pratensis, and Andropogon scoparius take first rank, covering 34, 30, and 25 per cent of the area, respectively. Eleven other species are of minor importance. A discussion of the autecology of the more important prairie plants is given.

Plant growth in the 2 habitats is expressed in terms of dry weight and

measurement of plant parts, that on the high prairie being 14 to 47 per cent less in all cases, due to more xeric conditions.

The reactions of vegetation on the habitat have been measured for each of the various factors of the environment. The loss of water from the soil by direct evaporation is greatly reduced by a cover of vegetation. This is pronounced in the surface foot in the lowland, and even more so in upland, which is much more exposed due to the sparser cover.

The soil temperature is much lower under a heavy cover of plants; thus, burning results in earlier resumption of growth in spring. Evaporation is reduced 6 to 8 per cent at the base of vegetation compared with that in bare areas. Light values range from I to 5 per cent under dense cover, and I0 to 20 per cent in an open one. Light is of great importance in the development of seedlings of prairie plants.

A detailed study of numerous small areas showed that the propagation of prairie species is largely vegetative.

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