A Quantitative Study of True-Prairie Vegetation after Three Years of Extreme Drought

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A QUANTITATIVE STUDY OF TRUE-PRAIRIE VEGETATION AFTER THREE YEARS OF EXTREME DROUGHT

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A QUANTITATIVE STUDY OF TRUE-PRAIRIE VEGETATION AFTER THREE YEARS OF EXTREME DROUGHT[1]

INTRODUCTION

Current opinion and activity toward revegetating exploited and submarginal grasslands justify the expenditure of considerable time in improving our knowledge of the behavior of native species under the stress of drought. The drought of 1936 equaled or surpassed in severity the great drought of 1934. This study is intended as another link in the chain of investigations concerning the composition, structure, and behavior of the rapidly disappearing remnants of true prairie. Attention is focused upon the relative capacity for survival and reproduction shown during drought by prairie species. That even a single species may well merit close and continued study is shown in such investigations as those of Savage (1934), Savage and Jacobson (1935), and Humphrey (1937).

A number of papers emanating from various parts of the grassland area have set forth the results of the drought of 1934. Pechanec *et al.* (1937) found that perennial herbs were reduced 25 percent on the upper Snake River plains of Idaho. The injury was not permanent as shown by the fact that in 1935 the number was higher than before the drought. However, the principal forage grasses recovered only slightly. In southeastern Montana, forage grasses were injured far beyond their ability to recover during the favorable season of 1935. Blue grama *(Bouteloua gracilis),* western wheat grass *(Agropyron smithii),* and buffalo grass *(Buchloe dactyloides)* were reduced to 25 percent, but Sandberg bluegrass *(Poa secunda)* nearly trebled its holdings (Ellison and Woolfolk 1937). In the same state, overgrazed prairie pastures showed recovery during drought under correct utilization (Bell 1935). Beath (1935) reported the ranges of eastern Wyoming to be in good condition in June, 1935. However, Allred (1935) states that in eastern Colorado blue grama and buffalo grass had been greatly injured and that 40 percent of the forage grasses had been killed.

The present study is most closely related to the work of Weaver and Albertson (1936) and Weaver, Stoddart, and Noll (1935). They found that among native grasses the worst killing was correlated with shortest root systems. Western wheat grass and aster *(Aster multiflorus)* had increased. That soil moisture was the critical factor was shown by the normal activity of watered plants during the period of greatest stress. The investigations of Weaver (1919, 1920) and of Nedrow (1937) on the root development and depth of efficient absorption by prairie plants have made possible the inter-

[1] Contribution from the Department of Botany, University of Nebraska, No. 109. The writer was aided in this research by a grant from the Nebraska Academy of Sciences.

pretation of drought behavior of most native plants in terms of available soil moisture. The effects of any disturbance can be well known only in so far as the original or normal condition is understood. The bases of comparison for this study have been provided by the extensive survey of Weaver and Fitzpatrick (1934) and the intensive work of Steiger (1930).

It is a pleasure to acknowledge the assistance given the writer by Dr. J. E. Weaver. It was he who suggested the problem and whose thorough familiarity with the vegetation made possible the identification of species in all stages of development.

PROCEDURE

In order to obtain an average of conditions and to study behavior of various species under different local conditions of soil and climate, selection was made of nine prairies. Eight of these had been previously described. The most distant is 110 miles southwest of Lincoln and the two nearest each other are 10 miles apart but on quite different soil types (Fig. 1).

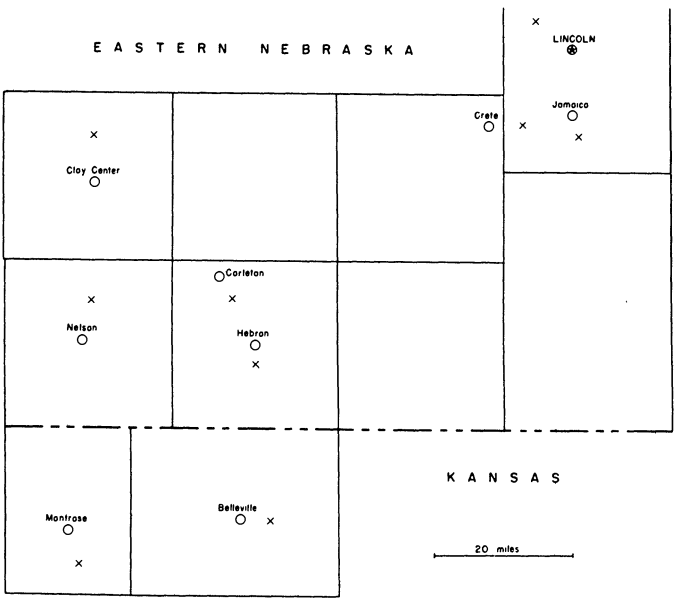

FIG. 1. Map showing location of prairies studied (x) and the towns near which they lie (o).

Field work was carried on during the summers of 1936 and 1937. Studies were made at three periods each season, always with the assistance of one or two competent helpers. After careful reconnaissance, enough permanent plots were established to sample each of the principal types of vegetation. The plots were usually placed on the tension line between alternes and thus included two types. The size and shape of the plots varied with the kind and

density of the vegetation, but the meter quadrat proved most satisfactory. The list or census method was employed, owing to the dominance of the sod form and to the belief that this is the most accurate method and the only one which can be used by subsequent workers with equal accuracy. In a few instances where stolons were present or short grasses were especially dense, estimated percent of cover instead of number of stems was recorded. In such cases the number of stems required to form one percent basal cover was determined. Where short-lived annuals were unusually dense, they were ordinarily not counted; instead the number of square decimeter units occupied by them was recorded. The plots were marked at diagonally opposite corners by a square oak stake and a round iron one, each 15 inches long, and driven even with the soil surface in order not to interfere with mowing. A conspicuous piece of red rubber was embedded with an end exposed just outside the wooden stake and the position of the latter established by angle and distance from a land mark and when practicable from one other plot.

Under the stimulus of such work as that of Cain (1931), Emmett and Ashby (1934) and others, an effort was made to correlate vegetation type with chemical and physical factors of the soil. Soil samples were taken from different types of vegetation on prairies where alternes were the sharpest, and tests were made for the amount of chlorides by the method described by Weaver and Clements (1938).

Determinations of available moisture were made from samples from depths of 3 to 4 feet twice each season, and on three prairies to depths of 8 to 15 feet once each August. Only water in excess of the hygroscopic coefficient was considered available. Tests for the presence of carbonates and for the degree of acidity by using the colorimetric method were also made on numerous samples from different alternes.

The species were recorded on five prairies each year in 25 to 100 semicircular temporary plots .8 sq. m. in area and spaced at fixed intervals along predetermined lines. The interval and number of plots were governed by the size of the tract and general uniformity of the vegetation. This was done in order to determine whether drought causes changes in distribution of dominants concomitant with changes in abundance.

Notes were taken concerning the condition of the important species, and an estimate of the abundance of each species observed was recorded on a 5-point scale. A prepared form containing the names of 120 species most important on upland prairies (Weaver and Fitzpatrick 1934) was used. The figure 1 placed after the name of a species indicated that it was very abundant; 2 indicated abundant; 3, common; 4, infrequent; and 5, rare.

Meteorological data were obtained from United States Weather Bureau records for the station nearest the prairie under discussion, and behavior of the vegetation was interpreted in the light of these data and conditions of soil.

Under normal precipitation, very pervious soils would be expected to

contain more moisture than less pervious ones. Experiments were performed to ascertain differences, if any, in the degree to which different types of prairie vegetation influence the absorption of water. This was done on seven prairies in a total of twelve types of vegetation. Well developed bunches of grass, stems of forbs, sodded areas or bare areas only a few feet distant were selected. Cylinders were made from 15-inch sections of seamless steel tubing 4 inches in diameter and sharpened at one end. These were forced into the soil vertically to depth of 14 inches. A coating of light motor oil inside and

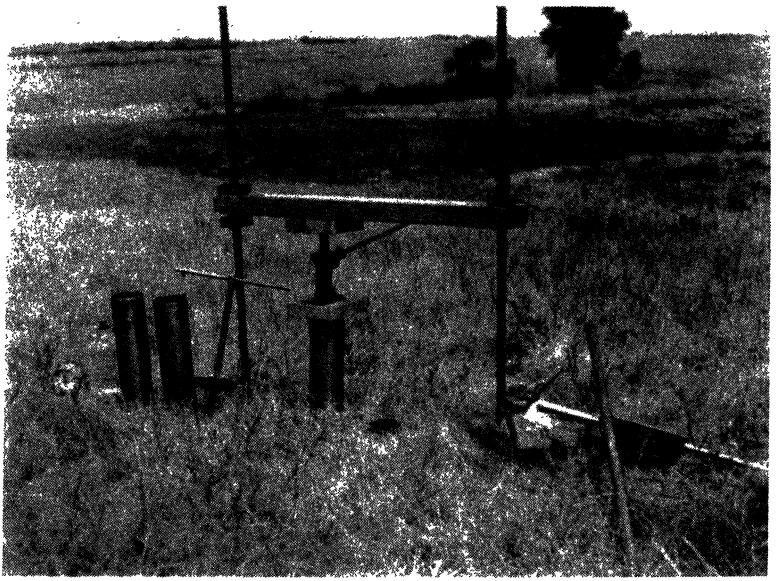

FIG. 2. Equipment for measuring the rate of infiltration of water into the soil pictured in use on the Belleville, Kansas, prairie. One cylinder is ready to receive the first of 4 inches of water, and another is in position to be forced into the soil.

out, combined with the sharpness of the cutting edge and the thinness (.1 inch) of the wall of the cylinder reduced to a minimum the possibility of altering the structure of the enclosed soil. Two heavy steel augers anchored in the soil were employed to support a heavy, steel-faced oak beam under which the jack was set as described by Weaver, Hougen, and Weldon (1935) (Fig. 2). The cylinders were usually paired at each setting of the augers. Each surface inch of water was added separately and a record kept of the time of watering and of the disappearance of the water into the soil. All tests were made in replications of four cylinders. On completion, the cylinders were removed without disturbing the sod by means of an especially designed jack. It consisted of a metal disk at the end of a strong screw which pressed downward on the soil within the cylinder while a cross-bar fitting into the holes in the cylinder wall pulled the latter out of the ground.

Musgrave (1935) used similar equipment to study the relation of infiltration to runoff and erosion. He states that the method gave results "in substantial agreement" with those obtained by the use of lysimeters which measure percolation and runoff. Auten (1933) also used cylinders to learn that overgrazing and surface fires reduce absorption. Smith *et al.* (1937) found that manuring increased the rate of infiltration in cultivated fields. Great differences between cylinders were explained by the presence of wormholes and decayed stalks of corn.

Finally, in order to learn what potential invaders were present in droughtbared areas, 20 to 25 random samples of bare soil to a depth of two inches were taken with a trowel on each of five prairies. The samples from each prairie were thoroughly mixed and placed in five flats in the greenhouse. A record was made of the number and species of all seedlings appearing during a period of five months.

RESULTS

JAMAICA PRAIRIE

This prairie has been described (Weaver and Albertson) as "65 acres of rather low, level land lying north of a stream bordered by postclimax woodland 12 miles south of Lincoln." The 20- to 30-foot trees along the stream, Salt Creek, shelter the lower part of the prairie from the desiccating south winds (Fig. 3). The soil of the lowland is Wabash silt loam. That

FIG. 3. Jamaica prairie in 1937 showing a broad alterne of wheat grass (dark) occupying most of the low ground of the prairie. The wheat grass was interrupted by smaller alternes of big bluestem (Fig. 7).

of the south-facing slope on the north, which forms about 10 percent of the area and ascends 20 feet above the general level, is Waukesha silt loam.

Prior to 1934 big bluestem *(Andropogon furcatus)*[1] furnished "60 to 90 percent" and little bluestem *(A. scoparius)* on the upland "as much as 25 percent of the cover." Considerable prairie dropseed *(Sporobolus heterolepis)* was present in alternes, and Kentucky bluegrass *(Poa pratensis)* was of general distribution. Wheat grass, blue grama, and buffalo grass were restricted

[1] The nomenclature here is that employed by Weaver and Fitzpatrick (1934).

to a few small alternes. Among the forbs, aster, Missouri goldenrod *(Solidago glaberrima),* and prairie rose *(Rosa arkansana)* were most abundant, with prairie sage *(Artemisia gnaphalodes)* and rough pennyroyal *(Hedeoma hispida)* being less abundant.[2]

The present study of this prairie was begun in June, 1936. Big bluestem was found to be greatly injured, being represented more by dead crowns and exposed rhizomes than by living shoots. It no longer ranked first in abundance, but was replaced in this respect by wheat grass. The latter formed a broad belt diagonally across the prairie (shown by the darker area in the middle of Fig. 3). It had its best development on poorly drained areas and formed an open stand over most of the former area of little bluestem. It also had many other foci of dissemination established over the low ground, even to within 40 yards of the wooded creek bank, but was fruiting only on the ground invaded during previous years.

Little bluestem was almost entirely absent where it formerly made up 25 percent of the cover. Prairie dropseed was widely distributed and commonly represented by large half- or more than half-dead bunches. June grass *(Koeleria cristata)* and needle grass *(Stipa spartea)* were both abundant and conspicuous.

The small interstitial panic grasses *(Panicum scribnerianum* and *P. wilcoxianum),* though not abundant, were so uniformly distributed that nearly every square meter contained at least a few plants. The same was true of Kentucky bluegrass and seedlings of goat's-beard *(Tragopogon pratense).* Canada bluegrass *(Poa compressa)* was scattered over most of the prairie, except the upper slope, but seemed most closely associated with *Agropyron smithii.* Six-weeks fescue *(Festuca octoflora)* was not seen and side-oats grama *(Bouteloua curtipendula)* was rare.

Aster multiflorus was the most abundant perennial forb. Individuals of all heights up to 20 inches formed open to dense stands, both pure and mixed, everywhere except in the best *Andropogon furcatus* along the creek and in alternes of pure *Agropyron smithii, Buchloe dactyloides,* and *Bouteloua gracilis.* It was not difficult to find square meter areas containing 250 to 300 stems. Daisy fleabane *(Erigeron ramosus)* ranked next to aster in abundance and was even more conspicuous on higher ground where the severest drought injury had occurred.

Solidago glaberrima was common and widely distributed although largely defoliated by grasshoppers. The same was true of upland prairie sunflower *(Helianthus rigidus)* and Tragopogon seedlings, the former being less abundant. Withered seedlings of wild lettuce *(Lactuca scariola)* were very abundant but larger plants were uncommon.

As on most prairies, the major grasses as well as some of the forbs were largely aggregated into distinct minor communities of relatively pure popula-

[2] Information as to condition of prairies before 1934 is drawn from Weaver and Albertson (1936) and from Dr. Weaver's original prairie notes.

tion. This marked alternation is attributable either to local soil differences or to chance priority followed by effective aggregation and successful competition with neighbors and would-be invaders.

Chemical and moisture analyses of soil samples from within wheat-grass alternes and adjacent areas of big bluestem showed only a few minor differences. Assuming the chlorides present to be in the form of NaCl, the highest salt content (540 parts per million) was in the densest, poorest drained wheat-grass alterne, and an average of all series down to 2 feet showed Agropyron soil twice as salty (210 p.p.m) as that underlying *Andropogon furcatus* (110 p.p.m). However, a younger Agropyron alterne yielded at the 0-6-inch depth the smallest amount of salt (30 p.p.m.). The soil varied in acidity from pH 4.7 at the surface to pH 6.6 at a depth of 2 feet. An average of all samples from wheat-grass soil equaled pH 5.1 as compared with pH 4.9 in the big bluestem type, a difference which may easily have resulted from errors in determination.

No positive test for carbonates was obtained. Available soil moisture ranged from a negative amount in the surface six inches to about 12 percent at the three-foot level. In two series for which hygroscopic coefficients were determined, more available moisture was present under big bluestem than under wheat grass at each depth except in the surface six inches where none was available in 1936. This difference increased downward at least to 3 feet. In late August of the following year, however, more moisture was present in the Agropyron area because the grass had lain dormant since being mowed two months earlier (Table 1). At a depth of two feet under wheat-grass sod, the soil was lighter in color, harder when dry, less pervious when pinched under water, and stickier when wet than under that of big bluestem.

In the vicinity of Lincoln in 1936, the rainfall deficiency was nearly one-third greater than in 1934 (Fig. 4). Extremes of temperature and humidity also deviated widely from normal in 1936. February and July were the coldest and hottest, respectively, ever recorded in Nebraska. July was also the driest, and August the hottest on record. As shown in Figs. 4 and 5, July (7) was 10 degrees warmer than normal with the average percentage relative humidity 22 lower and rainfall more than 3.5 inches below normal.

TABLE 1. PERCENTAGE OF AVAILABLE SOIL MOISTURE IN ALTERNES OF BIG BLUESTEM AND WESTERN WHEAT GRASS SIX FEET APART

Depth in feet	ANDROPOGON				AGROPYRON			
	Hygroscopic coefficient	1936	1937		Hygroscopic coefficient	1936	1937	
		June 25	June 19	Aug. 23		June 25	June 19	Aug. 23
0-.5.....	13.7	—3.4	14.8	2.7	12.0	—2.5	13.0	4.5
.5-1.....	10.7	1.2	15.8	4.0	10.2	0.2	7.7	7.9
1-2.....	13.0	5.6	5.9	3.0	14.5	2.5	4.2	3.1
2-3.....	12.7	7.7	11.0	3.4	11.3	7.1	3.8	4.6

Rainfall for the three summer months was 73 percent of normal in 1937 but only 24 percent in 1936. The maximum temperature in 1936, 115° F., was 3 degrees higher than in 1934. Evaporation at Lincoln from an open pan from April to October was 78.1 inches in 1934, or 9 inches more than in 1936. The mean vapor pressure deficit was higher than normal in 1936 but, except for July, lower than that of 1934 (Fig. 5). That summer humidity was far below normal in 1936 may be seen by comparing the positions of numbers 6 to 8 in Figure 5.

Careful counts of rooted shoots of all species in 13 plots were made during the last week in June, 1936 and 1937, and the principal data are shown in Table 2.

The generally vigorous condition of the vegetation in June, 1937, as well as the nearly normal moisture conditions of soil and air (Figs. 4 and 5, and Table 1) lead to the conclusion that losses in number of stems were due to death of their underground parts, rather than to mere inhibition of growth. In May, many species of the vernal aspect appeared highly vigorous. Several carices were in flower, wheat grass had definitely extended its territory, aster was more abundant, and the yellow flowers of goat's-beard were beginning to appear on nearly every square meter (Fig. 6). Most of the bunches of prairie dropseed were dead, especially in the dense new alterne of *Agropyron smithii*. Rhizomes of the latter had penetrated many of the bunches and pierced the dead crowns with their sharp new spears. It was possible to proceed in one general direction for 79 paces through this area stepping only upon these totally dead crowns.

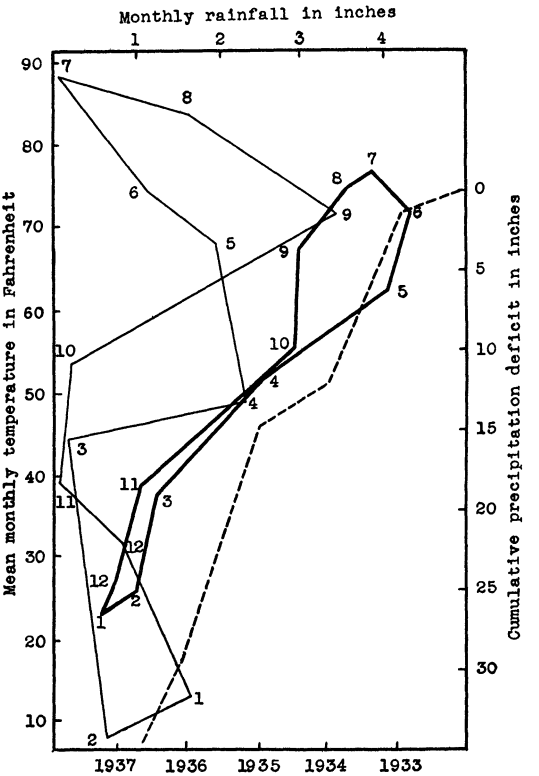

FIG. 4. Hythergraph showing mean monthly temperature and rainfall for 1936 (light line) and for the 50-year period (heavy line). Numbers 1 to 12 represent months. Broken line shows cumulative precipitation deficit (in inches on right) from January 1, 1933, to August 31, 1937.

The part of this prairie containing most of the plots was mowed early (June 13) in order to improve the palatability of the wheat-grass hay. This

naturally increased the difficulty of identification in quadrating and made necessary the exclusion of data on a few of the rarer species. Accuracy in listing of others was not prevented.

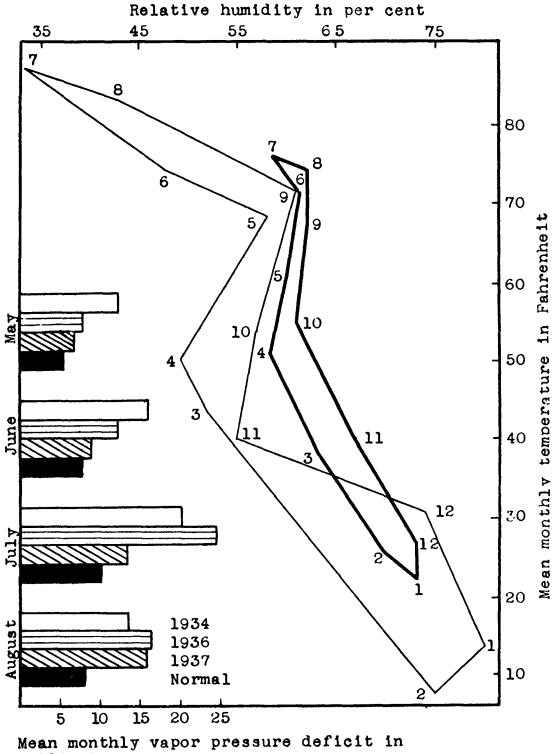

FIG. 5. Climograph of mean monthly relative humidity and temperature for 1936 (light line) and for a 50-year period (heavy line) at the Jamaica prairie. Numbers 1 to 12 represent months. Bar graph shows mean monthly vapor pressure deficits for 4 summer months in 1934, 1936, 1937, and the 50-year period. Humidity and vapor pressure calculations are based on averages of 7:00 A.M., 12:00 Noon, and 7:00 P.M. readings.

Two weeks after mowing, the generally distributed bunches of Stipa had produced about 13 inches of new growth, *Andropogon furcatus* 8 inches, *Sporobolus heterolepis* 5.5 inches, but Agropyron none. By August 15, only *Sporobolus asper* had recovered enough to fruit. The flower stalks in the widely spaced bunches were well over a meter tall.

Within the plots Agropyron and downy brome *(Bromus tectorum)* were the only grasses able to take advantage of the lessened competition correlated with the huge losses suffered by little bluestem, Koeleria, and Kentucky bluegrass and to a smaller degree by big bluestem, Canada bluegrass, *Panicum scribnerianum,* Stipa, and prairie dropseed. The large gain in number of plots occupied by Oxalis was less impressive than that of Lepidium because of the relative numbers of plants involved. Very large increases by the only annual grass, downy brome, failed to offset the smaller percentage decreases by perennials. Both annual and perennial forbs made distinct increases, the former gaining by about the same percentage as the ruderals[1] (Table 2).

Each meter quadrat was divided into 100 units, each one decimeter square, in order to permit accuracy in listing. In eight of the plots, one or more of the square decimeter units of observation were bare the first year. The total number of these bare units decreased from 78 to 57 in spite of the creation

[1] The term *ruderal* (weed) is used to mean an herb not originally a component of prairie vegetation.

of many new ones. The principal invaders of these areas were, in order of decreasing importance, catchfly *(Silene antirrhina)*, peppergrass *(Lepidium virginicum)*, seedlings of daisy fleabane, goat's-beard, and downy brome.

FIG. 6. Goat's-beard, an introduced weed, on the part of the low prairie dominated by needle grass and big bluestem.

TABLE 2. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, TOTAL NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937, AT JAMAICA, NEBRASKA

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
GRASSES						
Agropyron smithii	1,334	1,869	+ 40.0	11	2	0
Andropogon furcatus	1,094	569	— 48.0	10	0	1
Andropogon scoparius	908	21	— 97.6	8	0	7
Bromus tectorum	244	863	+253.7	4	2	1
Carex	533	145	— 72.8	9	0	1
Koeleria cristata	830	5	— 99.4	4	0	3
Panicum scribnerianum	75	39	— 48.0	8	2	1
Poa compressa	216	133	— 38.4	4	0	0
Poa pratensis	6,412	2,428	— 62.1	10	1	2
Sporobolus heterolepis	72	50	— 30.5	2	0	0
Stipa spartea	574	300	— 47.7	4	0	1
NON-GRASSES						
Artemisia gnaphalodes	253	131	— 48.2	6	0	2
Aster multiflorus	334	685	+105.1	10	1	1
Erigeron ramosus	198	359	+ 81.3	6	2	1
Hedeoma hispida	76	129	+ 69.7	7	2	0
Lepidium virginicum	108	635	+487.9	9	3	0
Oxalis	24	37	+ 54.2	7	6	0
Rosa arkansana	13	9	— 30.8	4	0	1
Solidago glaberrima	102	113	+ 10.8	8	1	3
Tragopogon pratensis	177	287	+ 62.1	10	3	0

Only 16 unit areas were devoid of plants both years. The 41 newly bared areas were made so by the disappearance of 16 species, chief among which were bluegrass, daisy fleabane, aster, and little bluestem.

When the behavior of different ecological groups of species was studied, it was again seen that grasses suffered more than forbs, and perennials more than annuals (Table 3).

TABLE 3. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT JAMAICA, NEBRASKA

	Number of species	Number of Stems		Percentage of change	Number of plots	Species Per Plot	
		1936	1937			Average 1936	Percentage of change 1937
Grasses.....	19	15,564	9,103	— 41.5	13	5.92	— 15.5
Annual.....	1	244	863	+253.7	3	.15	+ 50.0
Perennial.....	18	15,320	8,240	— 46.2	13	5.77	— 17.3
Forbs.....	29	1,107	2,016	+ 82.1	12	4.46	+ 19.0
Annual.....	6	302	944	+212.5	8	.85	+100.0
Perennial.....	23	805	1,072	+ 33.1	12	3.62	0
Ruderals.....	5	570	1,824	+220.0	12	1.77	+ 21.4
Total....	52	16,997	12,080	— 28.9	13	12.0	+ 2.5

On a per-plot basis, the number of kinds of annual forbs doubled but perennials made no change, while perennial grasses lost 17 percent and weeds gained 21 percent.

Selection was made of an area on low, level ground having a well developed wheat-grass sod surrounding an "island" of big bluestem. Dead and living bunches of prairie dropseed showed by their abundance that it had once been codominant here with big bluestem. Aster was present and prairie rose abundant, all within four square rods (Fig. 7). A moderately hard claypan was present at depths ranging from 14 to 21 inches in wheat grass territory but not in the big bluestem nor prairie dropseed. The results of infiltration experiments are shown in Figure 8 and soil moisture conditions in Table 1. The first inch of water required 23 minutes to enter the soil covered with wheat grass, but disappeared in the other types in 8 minutes or less, requiring only 1.1 minutes in bunches of prairie dropseed. The addition of each successive inch resulted in a lag in infiltration rate for at least one type. The soil in which aster was rooted absorbed the 4 inches in 1.6, 2.9, 3.3, and 4.4 minutes respectively, while the rate for big bluestem was 8.0 and 20.5 for the third and fourth inches. Soil occupied by Agropyron did not absorb the first half of the third inch even after 16.5 hours.

The composite of shallow random soil samples obtained in August, 1937, yielded seedlings of 22 species during 5 months in the greenhouse. Annuals comprised 82 percent of the species and 86 percent of the plants. The 10

ruderals present provided 0.4 of the seedlings. Catchfly was the most abundant species.

CRETE AND LINCOLN PRAIRIES

These prairies are treated together because of their proximity and similarity as to vegetation, soil, and topography. The Crete prairie of 60 acres

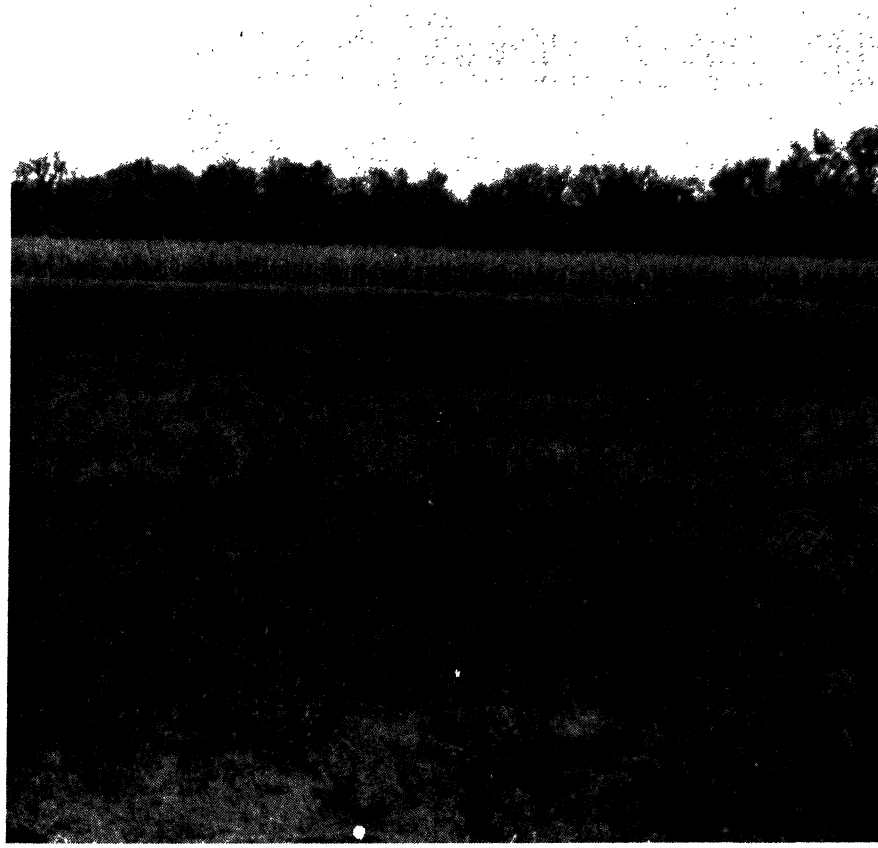

FIG. 7. The areas of wheat grass and bluestem where infiltration rates were measured 2 months after mowing. The dark area is big bluestem, the light area, wheat grass.

is eight miles northeast of Crete, Nebraska, and is one mile west of the prairie of the same name described by Weaver and Albertson (1936). The Lincoln prairie lies 8.5 miles northwest of the University of Nebraska. It includes nearly a section (640 acres) but this study was restricted to approximately 200 acres in the southeast corner.

Both tracts consist of flat-topped hills separated by grassy swales and wooded ravines. The soil is Carrington silt loam of glacial derivation. It is dark, granular, friable, and without lime in the first foot but harder, yellow, and speckled with grains of lime at a depth of three feet. Pure veins of lime

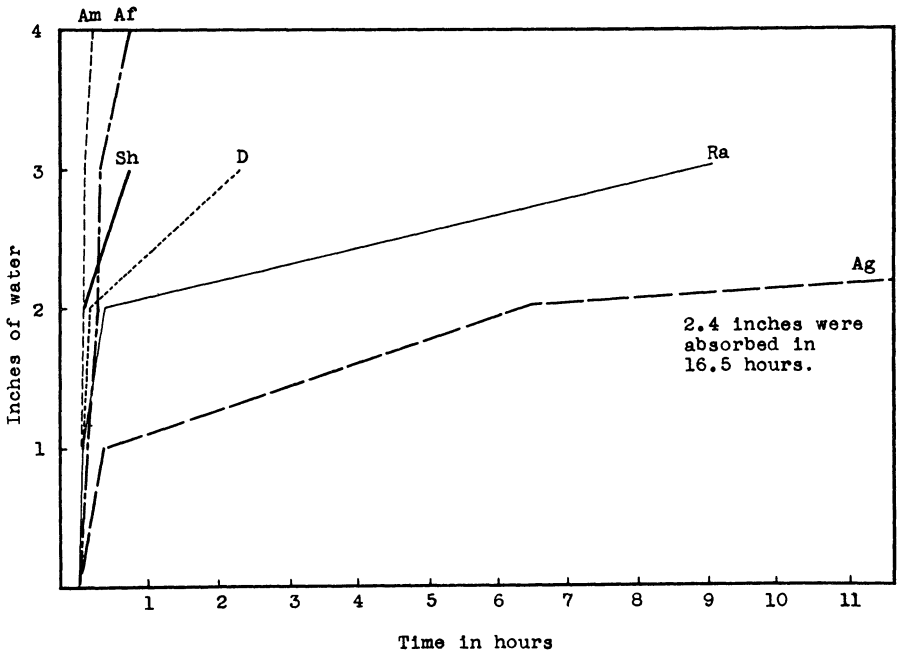

FIG. 8. Rate of infiltration of water into the soil in 6 types of vegetation at Jamaica, Nebraska; aster (Am), big bluestem (Af), prairie dropseed (Sh), dead crowns of prairie dropseed (D), prairie rose (Ra), and western wheat grass (Ag).

are occasionally encountered at four feet and glacial pebbles at all depths. High uniformity in texture is suggested by the narrow range in hygroscopic coefficients to a depth of 15 feet (Table 4). However, very sandy areas are

TABLE 4. PERCENTAGE OF AVAILABLE SOIL MOISTURE OF NEARLY LEVEL UPLAND (ANDROPOGONS), LOWLAND (SPARTINA), AND A XERIC SLOPE (BOUTELOUA-SPOROBOLUS)

	CRETE PRAIRIE						LINCOLN PRAIRIE			
	UPLAND			LOWLAND			SOUTHWEST EXPOSURE			
Depth in feet	Hygroscopic coefficient	August 10 1936	August 10 1937	Hygroscopic coefficient	August 10 1936	August 10 1937	Hygroscopic coefficient	July 30 1936	June 7 1937	August 5 1937
0-.5 ..	10.8	1.7	0.0	11.2	0.7	0.7	7.3	—2.4	—0.4	0.2
.5-1 ..	12.2	1.6	0.3	11.0	0.1	1.5	7.6	—0.8	5.8	1.5
1-2 ..	13.3	0.7	0.9	9.6	3.0	3.8	7.4	—1.5	4.0	0.0
2-3 ..	11.5	0.8	2.7	11.0	3.6	2.5	5.2	0.0	1.6	0.1
3-4 ..	10.6	3.6	2.3	11.4	4.6	3.6	4.6	0.1	0.4	—0.1
4-5 ..	11.9	3.2	1.2	10.9	5.5	4.8				
5-6 ..	11.8	4.2	3.5	11.1	7.7	5.8				
6-7 ..	11.3	6.4	5.1	11.7	10.8	4.8				
7-8 ..	11.4	7.1	3.9	11.8	12.3	9.4				
8-9 ..	11.8	8.3	3.3	11.4	12.2	13.1				
9-10 ..	11.8	9.5	8.0	13.8	13.0	10.8				
10-11 ..	10.0	8.6	...	10.5	13.7					
11-12 ..	9.7	8.2	...	11.7	13.6					
12-13 ..	10.8	9.8	...	11.9	12.9					
13-14 ..	12.2	9.8	...	12.0	12.9					
14-15 ..	12.8	9.7	...	11.9	12.7					

not infrequent. Enough fine material is present to give this soil a high water-holding capacity, but it is easily permeable to both water and roots.

The soil and vegetation of the Lincoln prairie were fully described before the drought (Steiger 1930). *Andropogon scoparius* was dominant on the upland and occurred most constantly in random upland plots, followed by *Bouteloua gracilis, Sporobolus heterolepis, Poa pratensis, Andropogon furcatus,* and *Boutelou curtipendula.* The most abundant upland forbs, in order of decreasing importance, were *Amorpha canescens,* prairie cat's foot *(Antennaria campestris), Solidago glaberrima,* and wild alfalfa *(Psoralea floribunda). Aster multiflorus* ranked eighth in 1928. The exact structure of the Crete prairie before the drought is not known.

FIG. 9. One of the many upland areas left bare by the death of *Sporobolus heterolepis* following the drought of 1936.

Meteorological data presented for the Jamaica prairie may be considered as approximate, also, for these prairies (Figs. 4 and 5).

These areas were studied each year in late July and early August. The vegetation was extremely dry in 1936. The more mesic grasses were so brittle that stems readily broke off underfoot. Many large cracks were present, especially in bluegrass sod, and excessive disturbance by rodents was apparent. Drought injury in 1934, as judged from the number of dead crowns present, was less than on prairies farther south and west. Invasion by wheat grass and downy brome, and increase in abundance of aster were also comparatively less. The most abundant grasses were big bluestem, little bluestem, and prairie dropseed. The last appeared to have come through the

drought of 1934 nearly unscathed. Needle grass and side-oats grama were common and of general distribution. Many well established patches of smooth brome grass *(Bromus inermis)* were present at Crete where the yield in 1936 was scarcely one-half ton of hay per acre.

FIG. 10. A slough-grass ravine at Crete in 1936 (above) and 1937 (below). Two crops of hay were produced by Spartina the first year but the ravines were too weedy for mowing in 1937. Note the progressive injury to the willow.

Only the most deeply rooted upland forbs, for example Amorpha and Aster, were not badly dried. The behavior of Amorpha in folding it leaves daily indicated that the moisture-supplying capacity of the subsoil was quite low (Table 4). Scarcely any moisture was available in the Lincoln prairie to root systems penetrating less than four feet. Antennaria, which failed to recover when watered at a depth of 2.5 feet (Weaver *et al.* 1935), was infrequent on these prairies and absent on others. Aster had advanced from eighth position to replace Amorpha as the most important forb.

Abundance of other important forbs in 1936 and 1937 was as follows: Amorpha, 3-3; Erigeron, 2-2; Hedeoma, 4-3; *Helianthus rigidus,* 2-3; and *Solidago glaberrima* 3-3.

Seven plots containing 40 species were established at the Lincoln prairie and eleven containing 52 species at Crete. A census was taken each year. In 1937 certain vegetational changes were obvious owing to the drought of the previous year. Much prairie dropseed and Kentucky bluegrass had been killed, leaving numerous areas protected from erosion only by dead crowns and rhizomes (Fig. 9). These and other areas were rapidly being invaded by Agropyron and Aster, in some instances nearly to the bottoms of ravines. The rank growth of Aster and other weedy species, coupled with the sparseness of perennial grasses, reduced the value of the hay so that most of each prairie was left unmowed (Fig. 10). The 75 percent foliage cover of the hilltops consisted largely of seedlings of Erigeron, Senecio, and Tragopogon.

Big bluestem had merely grown less dense in the 16 plots it occupied, but little bluestem had disappeared from four plots while appearing in two new ones in 1937 (Table 5). The loss by bluegrass was due in part to severe injury by grasshoppers. Other perennial grasses which lost ground were sideoats grama, June grass, and the carices. Needle grass and switch grass showed small gains, but wheat grass increased over 40 percent. Comparable increases were shown only by aster, daisy fleabane, and peppergrass. These three species are representative of perennial forbs, annual forbs, and ruderals, the abundance of which is shown in Table 6. Perennial grasses alone, of the five groups, were reduced by the drought.

The number of species per plot (13.7) was the same on both prairies in 1936.

TABLE 5. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937. CRETE AND LINCOLN PRAIRIES

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
GRASSES						
Agropyron smithii	705	997	+ 41.4	7	0	1
Andropogon furcatus	1,536	1,057	— 31.2	16	0	0
Andropogon scoparius	1,383	131	— 90.5	13	2	4
Bouteloua curtipendula	913	789	— 13.6	11	1	0
Carex	949	346	— 63.5	14	0	4
Koeleria cristata	578	177	— 69.4	11	0	3
Panicum virgatum	288	300	+ 4.2	8	2	4
Poa pratensis	2,066	1,940	— 6.1	14	0	5
Sporobolus heterolepis	1,291	460	— 64.4	12	0	4
Stipa spartea	148	163	+ 10.1	11	0	3
NON-GRASSES						
Amorpha canescens	50	44	— 12.0	8	0	1
Aster multiflorus	717	875	+ 22.0	15	1	0
Erigeron ramosus	164	361	+120.1	14	3	1
Helianthus rigidus	69	40	— 42.0	7	0	2
Lepidium virginicum	68	1,084	+1,494.1	10	2	1
Silphium integrifolium	462	392	— 15.1	1	0	0
Solidago glaberrima	30	26	— 13.3	10	4	1

TABLE 6. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT CRETE AND LINCOLN PRAIRIES

	Number of species	Number of Stems		Percentage of change	Number of plots
		1936	1937		
Grasses	24	10,457	7,750	− 25.8	17
Annual	4	53	82	+ 54.7	8
Perennial	20	10,404	7,668	− 26.3	17
Forbs	26	1,687	2,008	+ 19.0	18
Annual	6	173	437	+152.6	15
Perennial	20	1,514	1,571	+ 3.8	18
Ruderals	11	179	1,217	+579.9	14
Total	59	12,301	10,915	− 11.3	18

Study of the 88 units of observation that were bare the first year showed that 74 were invaded in 1937, chiefly by Erigeron and Lepidium. Death of Poa, *Andropogon furcatus, Sporobolus heterolepis,* and Erigeron resulted in most of the 106 new bare units.

Big bluestem ranked first and aster third in percentage frequency in 85 random plots in both 1936 and 1937. The first year bluegrass was second with needle grass and lead plant fourth and fifth. Side-oats grama was second in frequency, peppergrass fourth, and daisy fleabane fifth in 1937. Little bluestem, which was most frequent in 1928, occurred in 30 and 9 percent of the plots during the two years, respectively.

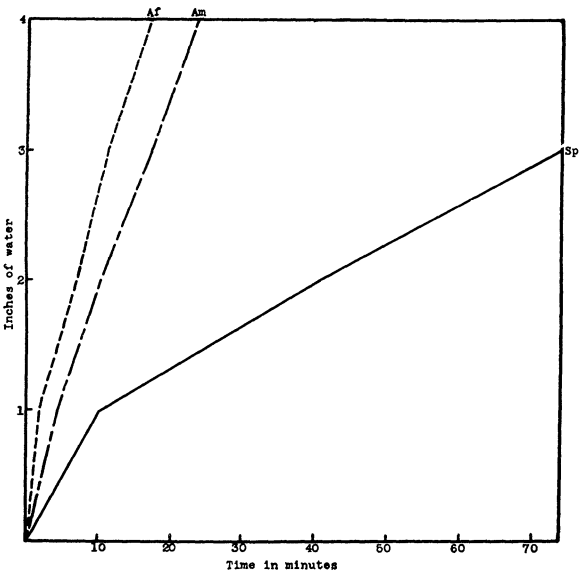

FIG. 11. Rate of infiltration of water into the soil in 3 types of vegetation at Crete, Nebraska; big bluestem (Af), aster (Am), and slough grass (Sp).

Perennial forbs were slightly shorter in 1937, in spite of higher precipitation than in 1936, but perennial grasses were 40 to 50 percent higher.

The rates of infiltration of water in three types of vegetation were measured at the end of the growing season in 1937. As usual, sod of big bluestem absorbed most readily. The time required increased from 2 minutes for the first inch of water to 5.4 for the fourth. Seven minutes longer were required in aster sod, and in slough grass only 3 inches were

absorbed in 74 minutes (Fig. 11). Range in rate of absorption in the 4 cylinders was rather large, especially in bluestem. For the three types of vegetation the average rate of infiltration was 2.8 times as rapid in the fastest as in the slowest cylinder.

A composite of random samples of surface soil was made up in August, 1937, from the Crete prairie. Under greenhouse care during 5 months, this sample yielded seedlings of 24 species. Only one fifth of the species and 4 percent of the plants were perennials. Ruderals constituted one fourth of the seedlings, but Kentucky bluegrass was the most abundant species.

HEBRON PRAIRIE

The Hebron prairie occupies most of a rolling upland tract of 30 acres two miles south of that city (Fig. 1). It consists of a low divide and parts of 3 shallow ravines, the broader of which is in cultivation and contains the only level land on the tract. Soils of two series are represented. The northeast one fourth is Shelby fine sandy loam. Although gravel is to be seen on the surface, the first foot is a fine sandy loam which gives way at a depth of 1 to 2 feet to light colored, gravelly subsoil. The remainder of the prairie is Nuckolls silt loam, a soil of much greater water-holding capacity. No carbonates occur to a depth of 4 feet.

In 1931, this prairie was dominated by *Andropogon scoparius* of the xeric bunch type intermingling with *A. furcatus* on the upland, and on dry slopes with a high percentage of *Bouteloua curtipendula* and *B. gracilis*. Koeleria was abundant, Stipa and Buchloe rare. Abundance of forbs in 1931 is shown in Table 7.

TABLE 7. RELATIVE ABUNDANCE OF THE CHIEF FORBS AT HEBRON, NEBRASKA. THE FIGURE 1 MEANS VERY ABUNDANT, 2 ABUNDANT, 3 COMMON, 4 INFREQUENT, 5 RARE, AND 0 NOT SEEN.

Species	1931	1936	1937
Amorpha canescens	1	3	3
Artemisia gnaphalodes	3	3	4
Aster multiflorus	1	1	2
Erigeron ramosus	1	1	3
Hedeoma hispida	4	0	3
Liatris punctata	4	4	3
Linum sulcatum	5	5	3
Opuntia humifusa	0	3	4
Plantago purshii	5	4	2
Psoralea argophylla	3	5	0
Senecio plattensis	3	0	0
Solidago glaberrima	3	3	3

The summer of 1936 at Hebron was characterized by maximum temperatures of 108°, 111°, and 109° F. for June, July, and August, respectively. From May to August, inclusive, the greatest rainfall in one day for each of the consecutive months was 0.95, 1.3, 1.1, and 0.9 inches. During that time two drought periods occurred. None of the 39 days from June 18 to July 26 received more than 0.08 inch of rain, and in August, 20 consecutive days

passed with no effective rain. Precipitation for the year was 12.87 inches. All except two months, January and September, received less than normal rainfall while mean monthly temperatures were much higher in summer and lower than normal in winter. The year 1935 had 10.5 inches above normal precipitation, while 1934 and 1936 each had about equally low rainfall (Fig. 12). That available moisture was largely depleted in the upper 3 feet is shown in Table 8.

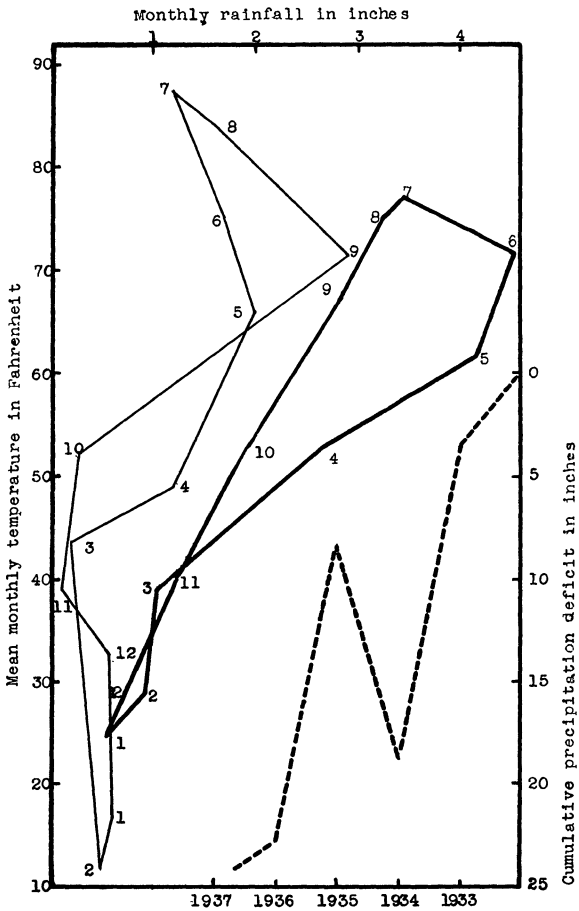

FIG. 12. Hythergraph of mean monthly temperature and rainfall for 1936 (light line) and for a 35-year period (heavy line) at Hebron, Nebraska. Broken line shows cumulative precipitation deficit from January, 1933, to August, 1937.

Burning had been used here as a method of weed control. June grass was usually abundant over most of the prairie, both as mature plants fruiting at heights of 4 to 18 inches, and as seedlings. Locally it provided a basal cover of 5 to 10 percent but was most conspicuous along cracks on poorly covered ridges.

Wheat grass was limited to two sharply defined alternes, both coinciding with recent deposits of dust from cultivated fields on the north and south (Fig. 13). The dust varied in depth from over an inch at the center to one-fourth inch at the edge where the wheat grass bordered bluestems and grama grasses. The scattered tufts of little bluestem were nearly always sheltered by big bluestem and appeared to be much more vigorous than the latter.

Where the heat had been the greatest on burned spots, only blue grama had survived.

Thirteen permanent plots, enclosing 11 square meters and including 48 of the 63 species observed on the prairie, were located in different types of

TABLE 8. PERCENTAGE OF AVAILABLE SOIL MOISTURE OF UPLAND ON GENTLE NORTHWEST SLOPE AT HEBRON, NEBRASKA

Depth in feet	Hygroscopic coefficient	1936	1937	
		July 22	June 7	July 22
0-.5	7.0	-2.7	22.0	5.0
.5-1	7.4	-0.5	10.7	2.9
1-2	12.6	0.2	7.9	0.0
2-3	12.0	-2.6	3.1	1.9

vegetation. A census was taken in 1936 and again in 1937 and heights of species in each plot were recorded. In addition, a record was made of the species found in each of 33 temporary plots.

On August 4, 8 days after a 1.1-inch rain, each tuft of little bluestem had new leaves among the dead ones while the 9 inches of new growth of big bluestem upheld dead tips 3 to 5 inches long.

FIG. 13. Wheat-grass alternes established on wind-deposited dust (white). Agropyron was reduced in density but not in extent in 1937.

During the first 6 months of 1937, the mean monthly rainfall was normal while temperatures averaged 2.6° F. below normal. The longest drought period, 17 days, ended with an inch of rain on July 3. Six more showers totaling 2 inches occurred before the date of study. This precipitation was reflected by the soil moisture content (Table 8) and especially by the condition of the vegetation, which was obviously taller and weedier. Downy

brome was distributed over the whole prairie, whereas Agropyron had spread but little, becoming less dense in its former territory. Elymus had invaded the upland and was established in many small patches. Koeleria and sand dropseed were abundant, but Poa and Eragrostis were rare (Fig. 14). Among the forbs yellow flax *(Linum sulcatum)* and Hedeoma were much more abundant (Table 7).

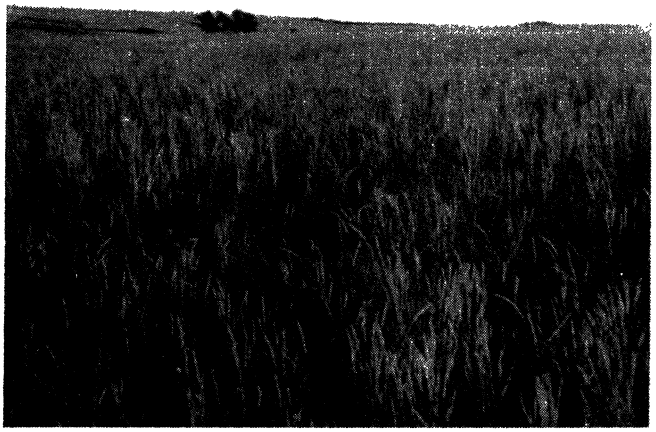

FIG. 14. June grass *(Koeleria cristata)* in the Hebron prairie where burning was practiced.

Analysis of data from the permanent plots, summarized in Tables 9 and 10, shows that some of the perennial grasses, big bluestem, Poa, Koeleria, *Panicum scribnerianum,* and *P. wilcoxianum* lost 11 to 93 percent of the number of stems present in 1936. Others, such as Agropyron, little bluestem, species of Carex, blue grama, and side-oats grama made gains of 1 to 65 percent, but the net loss in abundance of perennial grasses was 20 percent.

Annual grasses, that is Hordeum, Bromus, and Festuca, were abundant in 1937 but not in 1936. Stems of the last were so numerous that increase was calculated on the basis of the number of square decimeters occupied. Annual forbs, for example Plantago and Linum, were consistent in making enormous gains which for the 7 species averaged 674 percent. Perennial forbs, on the other hand, were inconsistent. Amorpha made a small gain in abundance, Aster decreased 25 percent, and Solidago increased 1.5 times, largely due to the presence of seedlings. The average gain of 14 species of these deep-rooted forbs was 19 percent.

Other ruderals than downy brome made large gains as well. Peppergrass led this group of six species with its gain of nearly 90 fold. The average gain of all species in the 13 plots was 26 percent. Moreover, the prairie as a whole appeared to have a much denser cover.

The average number of species per plot was 15.7 in 1937, or 17 percent greater than the previous year. Considered similarly, species of perennial grasses were 22 percent fewer, annual grasses 42 percent more numerous, annual forbs and ruderals each 150 percent more abundant, but perennial forbs were unchanged.

TABLE 9. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES IN PERMANENT PLOTS AT HEBRON, NEBRASKA, NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937; ALSO THE PERCENTAGE OF TEMPORARY PLOTS IN WHICH SPECIES OCCURRED IN 1936 AND 1937

Species	Number of Stems		Percentage of change	Number of Plots			Percentage Occurrence In Temporary Plots	
	1936	1937		Total	Invaded	Vacated	1936	1937
GRASSES								
Agropyron smithii	900	908	+ 0.9	4	0	1	16	9
Andropogon furcatus	2,035	1,806	— 11.2	10	0	0	82	81
Andropogon scoparius	574	660	+ 15.0	7	0	1	26	27
Bouteloua curtipendula	364	600	+ 64.8	9	0	2	24	45
Bouteloua gracilis	703	785	+ 11.7	6	0	0	44	57
Bromus tectorum	63	872	+1,284.1	7	3	0	2	30
Carex	318	353	+ 11.0	9	0	2	36	39
Festuca octoflora	(485)*	(833)*	+ 71.8	11	2	0	36	87
Koeleria cristata	2,082	940	— 54.9	10	0	1	66	54
Panicum scribnerianum	61	35	— 42.6	8	1	2	12	18
Panicum wilcoxianum	39	3	— 92.3	7	1	5	6	3
Poa pratensis	745	52	— 93.0	5	0	3	12	3
NON-GRASSES								
Amorpha canescens	85	94	+ 10.6	8	0	1	66	57
Aster multiflorus	273	205	— 24.9	8	0	1	48	48
Erigeron ramosus	380	945	+152.1	11	0	1	72	78
Hedeoma hispida	0	851	+	11	11	0	0	75
Lepidium virginicum	3	271	+8,933.3	8	6	0	4	33
Linum sulcatum	0	320	+	7	7	0	2	57
Plantago purshii	45	1,144	+2,442.2	5	1	0	22	45
Solidago glaberrima	20	50	+150.0	6	1	1	28	21

*Number of square decimeter units in which species occurred.

TABLE 10. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT HEBRON, NEBRASKA

	Number of species	Number of Stems		Percentage of change	Number of plots
		1936	1937		
Grasses	22	8,192	7,410	— 9.5	13
Annual	2	100	914	+814.0	8
	1	(488)*	(849)*	+ 74.0	11
Perennial	19	8,092	6,496	— 19.7	13
Forbs	21	989	3,958	+300.2	11
Annual	7	425	3,289	+673.9	11
Perennial	14	564	670	+ 18.8	10
Ruderals	6	112	1,164	+939.3	10
Total	48	9,230	11,661	+ 26.3	13

*Number of square decimeter units in which species occurred.

When first quadrated, 35 of the square decimeter areas were bare but not one in 1937. This increase in general density was due to invasion by 21 species, of which 7 were perennial and 3 annual grasses; 4 were perennial forbs, and the rest annual forbs and weeds. Festuca, Hedeoma, Erigeron, and Plantago were the chief invaders.

The vegetation was much taller (58 percent) in 1937, the average height being 11 inches. Perennial grasses were 73 percent and annual grasses 214 percent taller. Perennial forbs were 33 percent and ruderals 125 percent taller. These increases in stature were related to the difference in available moisture (Table 8).

Since percentage occurrence in temporary, random plots may be considered as indicative of the distribution of individual species, data are given in Table 9 for the 20 species that were also most prominent in the permanent plots. Gains and losses in the latter are in agreement with increased and restricted distribution as found in the temporary plots for all but 4 species. For these the disagreement is small or explainable by the fact that the species are restricted to a few alternes.

BELLEVILLE PRAIRIE

Four miles east of Belleville, Kansas, there is a well-drained, north-sloping, upland prairie of about 15 acres.

The pervious, black loam soil is derived from soft limestone parent material which occasionally lies within 3 feet of the surface on both high and low ground. Below one foot, the black topsoil gives way to light brown, then to yellow, less pervious, clayey subsoil. Lime content varies from zero in the first 6 inches to nearly pure limestone at 4 feet. Soil reaction in the first 6 inches varied from pH 5.4 on the upland to pH 7.3 in a wheat-grass hollow, and to pH 7.8 at a depth of 2 to 3 feet. Salt content at this depth ranged from 4 to 388 p.p.m., being less at shallow depths, and highest where wheat grass was dominant.

The vegetation in 1931 was characterized by co-dominance of big bluestem with both sod and bunch types of little bluestem on the upland, and with nodding wild rye in the ravines. Wheat grass was limited to a steep-sided hollow on the east. Numerous alternes of buffalo grass and blue grama, both pure and mixed, occurred on the upland as did the generally distributed side-oats grama, June grass, and prairie dropseed. Cactus, plantain, and rough pennyroyal were present.

Although 1936 was the driest year on record for Kansas, the rainfall deficiency in the vicinity of Belleville was only 48 percent as great as in 1934. The maximum temperature attained in 1936 (114° F.) was 1 degree less than the 1934 maximum. Only 3 months of 1936 had adequate rainfall, while winter temperatures were below and summer temperatures above normal (Fig. 15).

On June 29, available soil moisture was present to a depth of 4 feet in the blue-grama alternes but was exhausted between 2 and 4 feet in the big-bluestem type a few feet distant. However, more water was available in the first foot in the latter (Table 11).

Late in June, the vegetation of ravines and protected slopes was thriving, but that of the upland was dwarfed and the cover quite open. The dominants were wheat grass and big bluestem, the former being densest on deposits of dust from adjacent fields. Little bluestem was represented by generally distributed wisps of 2 to 6 stems on the edges of otherwise dead bunches. It was exceeded in abundance by both side-oats grama and six-weeks fescue. Both buffalo grass and blue grama formed nearly pure alternes on ridges and exposed slopes. June grass and *Panicum scribnerianum* were common, but Kentucky bluegrass was rare. Downy brome and plantain were locally abundant as colonists in bared areas. Abundance of other forbs was as follows, the rankings being for 1936 and 1937, respectively: Amorpha, 2-2; Artemisia, 2-4; Aster, 1-3; Erigeron, 3-2; Hedeoma, 3-1; Liatris, 3-4; sensitive-brier *(Morongia uncinata)*, 3-3; Opuntia, 4-3; and Solidago, 4-4.

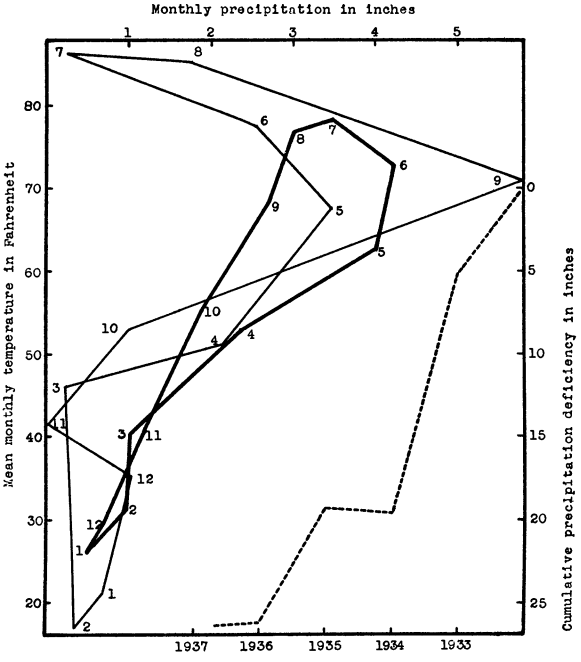

FIG. 15. Hythergraph of mean monthly temperature and rainfall for 1936 (light line) and for a 33-year period (heavy line) at Belleville, Kansas. Numbers 1 to 12 represent months. Broken line shows cumulative precipitation deficit from January 1, 1933, to August 31, 1937.

TABLE 11. PERCENTAGE OF AVAILABLE SOIL MOISTURE IN TWO UPLAND TYPES OF VEGETATION AT BELLEVILLE, KANSAS

Depth in feet	Hygroscopic coefficient	*Bouteloua gracilis*		*Andropogon furcatus*
		June 29 1936	June 7 1937	June 29 1936
0-1	12.1	6.5	8.6	16.3
1-2	13.6	0.3	3.9	0.3
2-3	13.2	1.6	0.3	— 0.9
3-4	13.0	0.5	0.8	— 0.3

A census taken in the 11 permanent plots the last week in June in both 1936 and 1937 revealed that they contained 54 of the 78 species observed.

Precipitation for the first 6 months of 1937 was 0.3 inch below normal, and soil moisture below 2 feet had not been increased (Table 11). Temperature during the summer averaged 4° F. above normal. In spite of apparently better growing conditions in 1937, the vegetation was again badly dwarfed. Perennial grasses were slightly taller but the average height of the vegetation (10 inches) was the same as the previous year. Because of the abundance of annuals, the cover appeared denser than the year before.

Other obvious changes were a further large reduction in density of little bluestem and such an increase in wheat grass that the dominance of the depleted big bluestem was challenged.

Switch grass *(Panicum virgatum),* blue grama, June grass, and the bluestems sustained losses ranging from 12 to 95 percent. Despite moderate gains by side-oats grama, wheat grass, nodding wild rye, and dropseed, the net result was a reduction of 17 percent in perennial grasses (Tables 12 and 13).

Big bluestem formed numerous large, dense bunches in the ravine in 1936. The following year these were open and invaded by bluegrass, dropseed, and nodding wild rye. This apparently represents the first step in changing from the bunch to the sod form which is prevalent in drier habitats. Perennial forbs, with such losses as 70 percent for Aster and 90 percent for Artemisia,

TABLE 12. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, WITH TOTAL NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937, AT BELLEVILLE, KANSAS

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
GRASSES						
Agropyron smithii	887	1,047	+ 18.0	7	1	0
Andropogon furcatus	1,822	1,037	— 43.1	10	0	0
Andropogon scoparius	178	9	— 94.9	4	0	3
Bouteloua curtipendula	1,146	1,300	+ 13.4	10	0	1
Bouteloua gracilis	7.62*	5.90*	— 22.6	8	1	0
Buchloe dactyloides	0.53*	0.53*	0	2	1	0
Carex	182	181	— 0.5	7	1	1
Elymus canadensis	23	31	+ 34.8	3	0	0
Koeleria cristata	394	279	— 29.2	9	0	2
Panicum virgatum	132	116	— 12.1	3	0	0
Sporobolus asper	362	585	+ 61.6	7	0	1
NON-GRASSES						
Amorpha canescens	33	43	+ 30.3	4	1	0
Androsace occidentalis	0	472	+	7	7	0
Artemisia gnaphalodes	178	18	— 89.9	4	0	1
Aster multiflorus	390	125	— 67.9	6	1	1
Erigeron ramosus	59	543	+820.3	10	4	0
Hedeoma hispida	62	1,862	+2,903.2	9	0	0
Lepidium virginicum	31	1,165	+3,658.1	9	4	0
Plantago purshii	355	4,121	+1,060.8	7	0	0
Spermolepis patens	0	163	+	5	5	0

*Estimated cover in percent.

showed an average decrease of 67 per cent, but annual grasses, forbs and weeds became 8 to 36 times more abundant (Fig. 16).

The total number of species per plot increased from 13.5 to 16.9, which was the highest number and largest increase recorded for any prairie. This was due to invasion by annuals. While there were 4 percent fewer species of perennial grasses and 7 percent fewer species of perennial forbs, annual grasses had increased 24 percent, weeds and annual forbs 100 percent.

FIG. 16. *Plantago purshii* at Belleville. This early annual overtopped the short grasses in June, 1937.

Dissemination of annuals was such that bare units of observation were rare in 1937, although 29 were present in 1936. The chief invaders were Festuca, Lepidium, Hedeoma, Erigeron, and Spermolepis (all annuals).

The many clearly defined alternes afforded an opportunity to study the influence of different vegetation on absorption. The rate of infiltration of 4 inches of water was measured in 5 types. The time required for absorption ranged from 34.5 minutes in big bluestem on the upland to 47.4 minutes in the wheat-grass hollow. Soil permeated by the fine, fibrous roots of buffalo grass absorbed the water in 35 minutes, which was 6 minutes less than re-

TABLE 13. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT BELLEVILLE, KANSAS

	Number of species	Number of Stems		Percentage of change	Number of plots
		1936	1937		
Grasses	23	10,497	10,422	— 0.7	11
Annual	3	361	1,992	+ 451.8	10
Perennial	20	10,136	8,430	— 16.8	11
Forbs	27	1,152	7,452	+ 546.9	10
Annual	9	476	7,228	+ 1,418.1	10
Perennial	18	676	224	— 66.9	10
Ruderals	5	237	2,112	+ 791.1	10
Total	54	11,683	19,074	+ 63.3	11

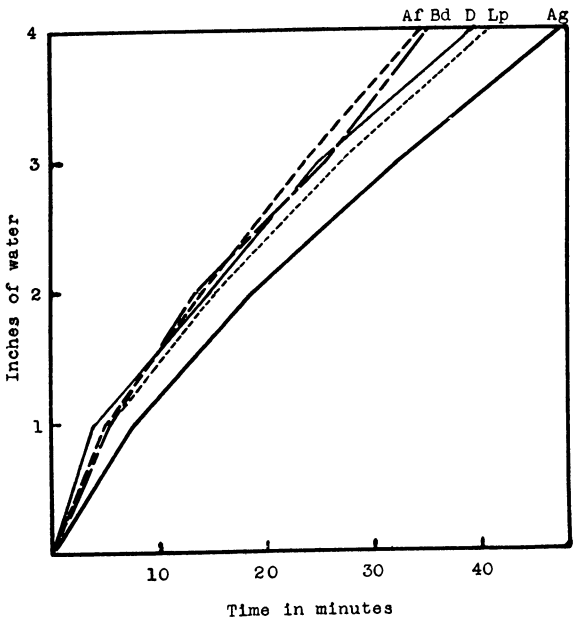

FIG. 17. Rate of infiltration of water into the soil in 5 types of vegetation at Belleville, Kansas; big bluestem (Af), buffalo grass (Bd), dead crowns of grass (D), blazing star (Lp), and wheat grass (Ag).

quired by soil occupied by a large taproot of blazing star. Soil covered only by crowns of dead grass absorbed the first inch in 4 minutes, but the total time was only a minute less than for blazing star (Fig. 17).

CARLETON PRAIRIE

A slightly rolling, typical upland bluestem prairie of 35 acres lies three miles southeast of Carleton, Nebraska. Its surface gives the impression of being slightly warped as the north part slopes to the east and the south to the west with a shallow swale draining diagonally eastward across the center. An old road, now seldom used, crosses the prairie from northwest to southeast and acts as a source of migrules of weedy annuals. The soil is all Crete silt loam. The topsoil is dark brown to black and coarsely granular. Lime is generally present at a depth of 2 to 3 feet and the soil is brown to light brown, hard and rather impervious at this depth. In the swale in the wheatgrass type a definite claypan is present, beginning at 9 to 12 inches and extending to depths of 26 to 30 inches. Over the remainder of the prairie this layer is present but more pervious and less superficial. Greater differences in acidity occurred between the depths of 6 inches and 3 feet (pH 4.5 to 7.4) than between samples from the upper 6 inches on different parts of the prairie (pH 4.5 to 5.7). No correlation was found between vegetation type and pH number.

Before the drought this prairie was dominated by the sod form of little bluestem except in the swales where this dominance was shared with big bluestem and wheat grass. That these swales once supported a more mesic vegetation is shown by the presence of relict switch grass, spike-rush *(Eleocharis acuminata),* and clover fern *(Marsilia vestita).* Several small alternes of blue grama and buffalo grass and one of needle grass were found. June grass was frequent but not abundant, and Kentucky bluegrass was locally abundant. Daisy fleabane, aster, poppy mallow, and lead plant were the most

abundant forbs. The relative abundance of these and other species is shown in Table 14.

Four days spent on this prairie in the middle of July, 1936, served to impress one with the severity of physical and biotic factors so extreme that even native vegetation could not endure them uninjured. Daily maximum temperatures ranging from 104 to 111° F. accompanied by relative humidities of 19 to 24 percent, continuous strong winds, glaring sunlight, and subnormal precipitation combined to make the grasses crackle underfoot like wheat stubble. Only prairie false boneset *(Kuhnia glutinosa)* and blazing star appeared unhampered by drought, and they were borne down and partly eaten by hordes of grasshoppers. Amorpha folded its leaves during the day and opened them only slightly by sunrise although the nights were cool and relatively calm. Foliage of all other plants was partly or entirely dead. Both bluestems appeared in all stages of perishing. Buffalo-grass foliage, including stolons as much as 16 inches long, was bleached and apparently lifeless. Bunches of blue grama, some a foot in diameter, seemed entirely dead.

Despite the excess supply of moisture in 1935, which resulted in a fair crop of hay, the subsoil moisture supply was greatly depleted (Table 17). The eastern half of the prairie was mowed in July, 1935, a month earlier than the western half. An economy of soil moisture was thus effected during a period which was too rigorous to permit growth. This, coupled with

TABLE 14. VARIATION IN ABUNDANCE AND FREQUENCY OF MOST IMPORTANT SPECIES AT CARLETON, NEBRASKA

Species	Relative Abundance			Temporary Plots Percentage Occurrence	
	1931	1936	1937	1936	1937
GRASSES					
Agropyron smithii	3	1	1	76	93
Andropogon furcatus	2	2	2	61	42
Andropogon scoparius	1	4	3	15	0
Bouteloua curtipendula	..	2	1	66	84
Bouteloua gracilis	3	2	3	20	21
Bromus tectorum	..	4	2	10	21
Buchloe dactyloides	4	3	4	2	0
Carex	4	3	3	57	39
Festuca octoflora	3	1	1	71	93
Koeleria cristata	2	4	4	42	9
Poa pratensis	3	3	3	25	12
Sporobolus asper	5	4	3	19	3
NON-GRASSES					
Amorpha canescens	2	3	3	44	45
Aster multiflorus	1	1	2	64	60
Callirrhoe alceoides	1	5	4	0	3
Erigeron ramosus	1	3	3	33	30
Hedeoma hispida	4	4	2	40	69
Lepidium virginicum	..	5	2	18	39
Plantago purshii	4	4	2	31	66
Rosa arkansana	4	4	4	13	18

the influence of late summer rains, caused the two sides of the prairie to differ so distinctly in appearance that a sharp line of demarkation was visible between them one year later, that is July, 1936 (Fig. 18). On the east side

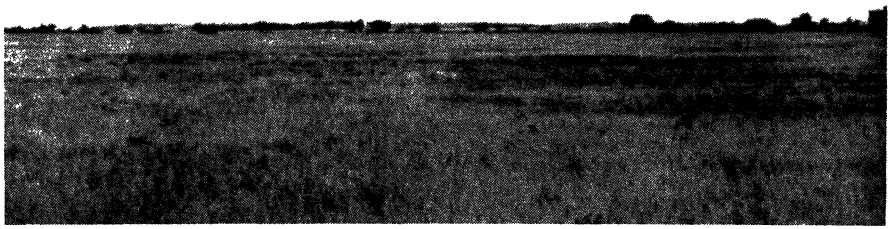

FIG. 18. Carleton prairie, July, 1936. The central line of demarkation resulted from difference in dates of mowing the previous year.

of this line *Sporobolus asper, Bouteloua gracilis, B. curtipendula, Andropogon furcatus,* and Amorpha had flowered after mowing. Species on that side seemed also to have gained in vigor for *Andropogon furcatus, Amorpha,* and *Bouteloua curtipendula* were denser, greener, and taller than just over the line marking the different dates of mowing. On the west side *Bromus tectorum, Festuca octoflora,* and *Agropyron smithii* were better developed.

Permanent plots were established on 14 carefully selected areas and found to contain 49 species. They were widely spaced and included all the important grasses. The prairie was not mowed in 1936. Wheat grass had

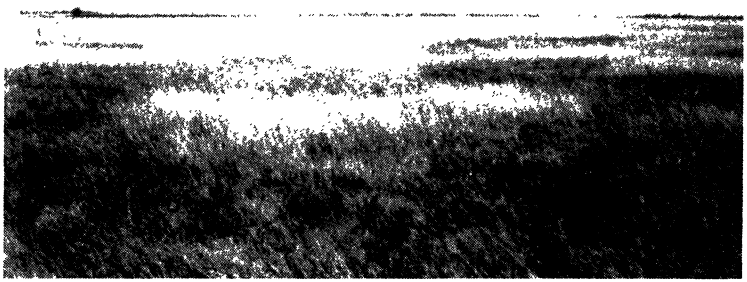

FIG. 19. Tension lines at Carleton, August, 1937. Big bluestem (dark) held its ground against the newly established wheat grass (white) in favored areas.

extended its territory considerably in 1937, side-oats grama was more abundant, and all native grasses appeared in better condition than in 1936. In many local, well-defined areas big bluestem still held complete dominance, having repelled the invading wheat grass and most of the annual grasses so conspicuous over the prairie (Fig. 19). The line caused by the difference in mowing dates was obliterated by the tall wheat grass. A summary of the data on the 20 principal species in the quadrats is presented in Table 15.

TABLE 15. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, TOTAL NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937, AT CARLETON, NEBRASKA

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
GRASSES						
Agropyron smithii	1,775	2,705	+ 52.4	14	0	0
Andropogon furcatus	925	645	— 30.3	12	0	0
Andropogon scoparius	1,134	172	— 84.8	8	1	1
Bouteloua curtipendula	1,244	1,322	+ 6.3	12	1	2
Bouteloua gracilis	779	405	— 48.0	9	1	4
Bromus tectorum	40	242	+505.0	8	3	1
Buchloe dactyloides	25.42*	2.79*	— 88.9	6	2	1
Carex	657	409	— 37.7	10	0	1
Festuca octoflora	(485)†	(830)†	+ 71.1	14	2	0
Koeleria cristata	434	29	— 93.3	10	0	5
Poa pratensis	384	708**	+ 84.4	11	0	3
Sporobolus asper	243	236	— 2.9	6	1	0
Stipa spartea	70	51	— 27.1	2	1	0
NON-GRASSES						
Amorpha canescens	52	31	— 40.4	7	0	0
Androsace occidentalis	41	405	+887.8	11	2	0
Aster multiflorus	879	392	— 55.4	10	1	2
Erigeron ramosus	75	110**	+ 46.7	9	6	0
Hedeoma hispida	104	697	+570.1	13	4	0
Lepidium virginicum	8	213	+2,562.5	13	9	0
Plantago purshii	42	367	+773.8	12	2	0

†Number of square decimeter units in which species occurred.
*Estimated cover in percent.
**Seedlings.

The deep-rooted Amorpha, occurring in 7 plots, suffered a loss of 40 percent. However, in the plots on the western side of the prairie the loss was 58 percent as compared with none on the eastern side which was mowed earlier. Aster was another deep-rooted species which decreased considerably. This is in accord with the long-known fact that because of the dryness of the subsoil below the claypan, alfalfa cannot survive drought on Crete silt loam. The loss for Aster was 68 percent on the west and 52 on the east side of the prairie. Other forbs with deep roots sustained smaller losses or none. Among the perennial grasses, buffalo grass, little bluestem, and June grass decreased by about 90 percent. Blue grama, big blustem, needle grass, and the sedges suffered smaller losses. Wheat grass made a large gain, side-oats grama a much smaller one. The large increase of bluegrass

was largely due to the appearance of a host of seedlings in one plot. Erigeron was present only as well developed seedlings, often 6 inches in height. Annual forbs as Androsace and Hedeoma and weeds such as Lepidium and downy brome gained more than 100 percent in these plots as well as becoming more widely distributed.

The percentage occurrence of the chief species in temporary random plots is given in Table 14 and may be considered as indicative of gain in territory occupied *(Festuca octoflora),* of no change in distribution *(Bouteloua gracilis),* or loss of territory *(Andropogon scoparius).*

A clearer conception of the trends of change in floristic composition may be obtained by an examination of Table 16. Annual grasses, present in all permanent plots, had 5 times as many stems in 1937 as in 1936, but perennial grasses were 43 percent fewer. Among the forbs the story is similar, again reflecting the presence of the claypan. . The short-lived, shallowly rooted weeds gained about 850 percent.

TABLE 16. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT CARLETON, NEBRASKA

	Number of species	Number of Stems		Percentage of change	Number of plots
		1936	1937		
Grasses	21	13,125	7,741	— 41.0	14
Annual	2	53	274	+416.9	8
	1	(519)*	(830)*	+ 59.9	14
Perennial	18	13,072	7,467	— 42.9	14
Forbs	22	1,445	2,364	+ 63.5	14
Annual	8	352	1,665	+373.0	14
	1	(34)*	(65)*	+ 91.2	2
Perennial	13	1,093	699	— 36.0	12
Ruderals	6	48	457	+852.1	13
Total	49	14,579	10,528	— 27.8	14

*Number of square decimeter units in which species occurred.

The average number of species of grasses per plot decreased from 9 to 8, annuals gaining and perennials losing approximately 20 percent. Perennial forbs lost about 7 percent but annuals and weedy species increased sufficiently to raise the average total number of species from 14 to 15.6.

In the total area of 10 square meters quadrated, 14 of the square decimeter units were bare in 1936 but only 3 in 1937. The most active invaders of these bare areas were, in order of diminishing importance, Agropyron, Festuca, *Bouteloua curtipendula,* Androsace, and Hedeoma.

The vegetation averaged two thirds taller in 1937 than its level of 6 inches in 1936. Annual grasses were 120 percent taller but annual forbs only one third higher.

Tests of the rate of infiltration of water into soils supporting 3 species of grass in pure stands showed that for the first 2 inches applied there was little

difference in time required (Fig. 20). The rate for blue grama and western wheat grass was almost the same until the addition of the third inch. In the cylinder having the slowest rate of absorption in wheat grass, only half of the third inch was absorbed after 14.3 hours and water had penetrated only 8.5 inches. In another cylinder, the upper inch of claypan was found to be wet after 14 hours of watering in the swale having only 8 inches of porous topsoil.

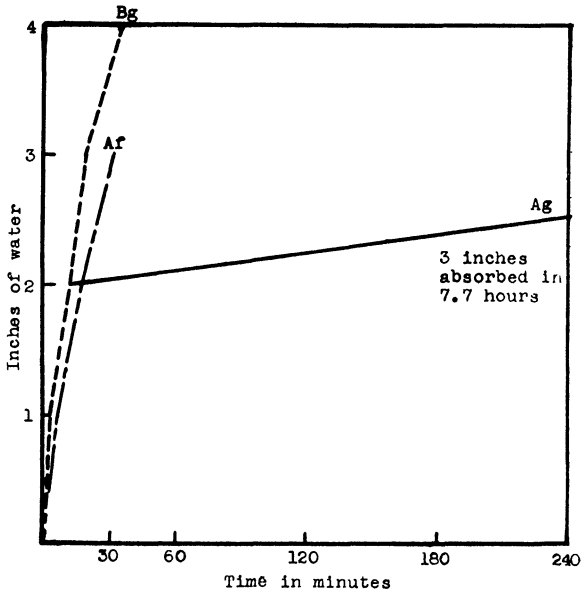

FIG. 20. Rate of infiltration of water into the soil in 3 types of vegetation at Carleton, Nebraska; blue grama (Bg), big bluestem (Af), and wheat grass (Ag).

A study of data given in Table 17 shows that in the wheat-grass swale the soil moisture was not depleted to such an extent as in well-drained soil occupied by big bluestem.

No moisture above the hygroscopic coefficient remained to a depth of 4 feet in the bluestem in August of both years. In the wheat grass it was exhausted in the upper 3 feet in 1936, but was present in small amounts at

TABLE 17. PERCENTAGE OF AVAILABLE SOIL MOISTURE IN TWO TYPES OF VEGETATION NEAR CARLETON, NEBRASKA

Depth in feet	Well-Drained Big Bluestem				Wheat-Grass Swale			
	Hygroscopic coefficient	1936	1937		Hygroscopic coefficient	1936	1937	
		Aug. 3	June 8	Aug. 11		Aug. 3	June 8	Aug. 11
0-.5	9.3	—3.3	20.0	—0.8	10.5	—3.7	12.0	1.8
.5-1	13.3	—1.6	7.3	—1.1	14.6	—0.3	—3.3	2.7
1-2	15.7	—0.9	8.0	—0.9	15.4	—0.3	3.9	1.6
2-3	12.9	0.0	2.7	—0.5	13.2	0.0	3.8	1.8
3-4	11.8	0.0	0.2	—0.3	11.6	0.7	2.2	2.8
4-5	12.0	0.9	...	0.3	11.9	1.2	...	3.8
5-6	12.4	1.0	...	0.4	12.2	2.6	...	4.2
6-7	12.0	2.0	...	1.0	12.2	2.9	...	7.6
7-8	11.6	4.0	...	1.9	11.4	5.7	...	7.4
8-9	11.0	4.3	...	...	11.9	5.8	...	...
9-10	11.2	4.7	...	...	11.6	6.4	...	...
10-11	10.9	5.8	...	...	10.9	8.3	...	...
11-12	9.9	6.6	...	...	8.3	7.9	...	...
12-13	9.5	6.4	...	...	10.3	6.2	...	...
13-14	9.7	5.3	...	...	13.2	6.4	...	...
14-15	10.7	5.3	...	...	14.0	5.9	...	...

most depths in 1937. Moisture content was less than the wilting coefficient of Briggs and Shantz (1912) to depths of 10 and 7 feet in big bluestem and in the wheat-grass swale, respectively, and at 10 to 15 feet the ratios were 1.02 to 1.1. Deep-rooted forbs were absent in the swale. At greater depths water was more plentiful during 1937 in the swale but less so in higher land. The higher hygroscopic coefficients at depths of 12 to 24 inches are correlated with the presence of the claypan, slow infiltration rate, rather dry subsoil, and high mortality among deep-rooted forbs.

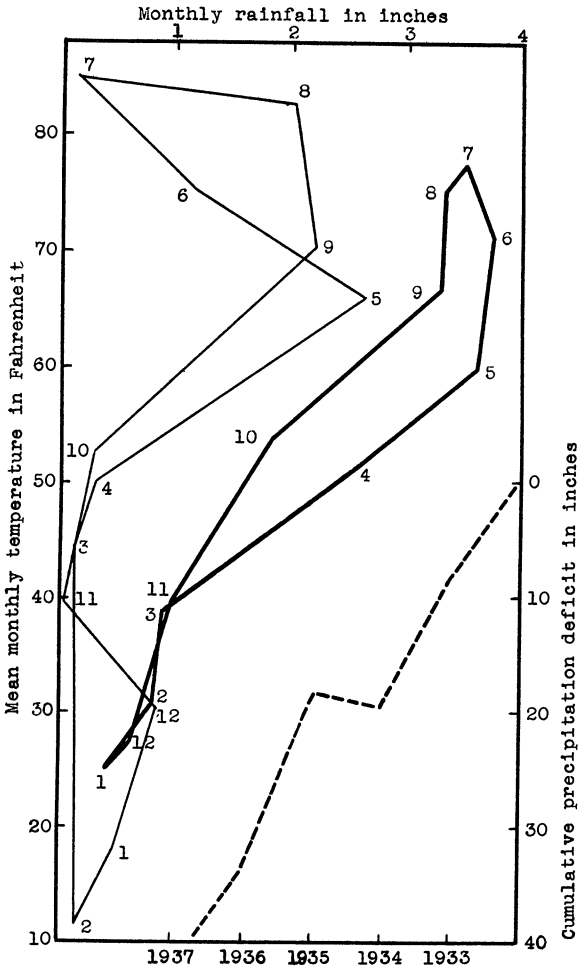

FIG. 21. Hythergraph of mean monthly temperature and rainfall for 1936 (light line) and for a 35-year period (heavy line) at Clay Center, Nebraska. The numbers 1 to 12 represent months. Broken line shows cumulative precipitation deficit from January, 1933, to August, 1937.

CLAY CENTER PRAIRIE

A well-drained, unbroken tract of about 10 acres lies 6 miles north of Clay Center, Nebraska. A shallow swale and an abandoned road cross it. As a rule the only disturbance has been annual mowing, but following the growing season of 1935 it was partially burned; in 1936 the vegetation was left intact. The soil is Hastings silt loam. It is readily penetrable by water and roots and has the lime layer at a depth of over 4 feet. This type of soil is considered excellent for corn and is almost entirely under cultivation in Clay County.

Prior to the drought, the dominant vegetation was a mixture of little bluestem of the bunch type and big bluestem. The former composed as much as 95 percent, and the latter frequently 20 percent of the vegetation. June grass, buffalo grass, and blue grama were fairly abundant while sand drop-

seed *(Sporobolus cryptandrus)*, six-weeks fescue, and wheat grass were present in small amounts. Lead plant was the most conspicuous forb.

The extent of drought injury to this prairie in 1934 and the damage by drought and dust in 1935 have been described by Weaver and Albertson (1936).

Clay Center received a total rainfall of 10.3 inches (40 percent of normal) in 1936. This was 3 inches less than in 1934, the driest previous year (Fig. 21). The mean summer temperature, which was 8.2° F. above normal in 1934, was 6.37° F. above the mean during 1936. The maximum temperature, 113° F., was the same each year. Two drought periods occurred in 1936. The first, of 24 days duration, began June 5 and was broken by a rain of 0.56 inch. It was immediately followed by a second of 37 days with only two measurable showers totaling 0.19 inch.

FIG. 22. Year-old bunches of *Bouteloua gracilis* attached by vertical rhizomes to the parent crowns which had been covered by 2 inches of dust in the early spring of 1935. Roots of the new crowns have been removed.

So weedy was this area in early July that only the presence of such deep-rooted forbs as Amorpha, Liatris, and Solidago proclaimed to the casual observer that it was unbroken prairie. Agropyron was the most abundant grass. It formed nearly pure stands on the higher ground where the dust deposited the previous year was 1 to 2 inches deep. The only other perennial grass to survive this burial was blue grama, which was able to develop rhizomes vertically and form new crowns on the surface (Fig. 22). Big bluestem was abundant but little bluestem and buffalo grass were scarce,

being outranked by June grass, side-oats grama, blue grama, Kentucky bluegrass, and sedges. The small panic grasses, especially *Panicum wilcoxianum,* were scattered everywhere. Many weedy types were scattered throughout. *Bromus tectorum* formed dense patches on lower ground, as did Plantago up the slope. Dense mats of seedlings of foxtail (*Setaria* spp.), red-root *(Amaranthus retroflexus),* and barnyard-grass *(Echinochloa crusgalli),* 2 to 3 inches tall and almost entirely dead, made up one third to one half of the cover. Abundance of other forbs was as follows in 1936 and 1937, respectively: Achillea, 5-0; Amorpha, 3-3; Aster, 1-3; Callirrhoe, 3-3; Hedeoma, 5-3; skeleton weed *(Lygodesmia juncea),* 3-4; *Meriolix serrulata,* 4-4; *Solidago glaberrima,* 1-3; and *S. mollis,* 3-3.

Eleven widely separated permanent meter quadrats were selected, one in each of several vegetation types. They included 51 of the 66 species observed here. A census was taken in the quadrats during the second week in July of each year. Table 18 shows that in these plots the perennial grasses reacted to the extreme conditions of 1936 and early 1937 in a strictly individual manner. The bouteloues, *Sporobolus asper,* and *Andropogon furcatus* held their own fairly well while the stems of *A. scoparius* were 65 percent fewer at the second counting. Losses of June grass, interstitial panic grasses, and Kentucky bluegrass were more than 80 percent, but this was partly offset

TABLE 18. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, TOTAL NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937, AT CLAY CENTER, NEBRASKA

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
GRASSES						
Agropyron smithii	1,448	1,663	+ 14.8	6	0	0
Andropogon furcatus	525	506	— 3.6	10	0	1
Andropogon scoparius	494	173	— 64.9	4	0	0
Bouteloua curtipendula	340	344	+ 1.2	10	0	0
Bouteloua gracilis	2.12*	2.11*	— 0.5	7	0	1
Carex	588	675	+ 14.8	9	0	2
Koeleria cristata	282	32	— 88.7	6	0	3
Panicum scribnerianum	226	44	— 80.5	5	0	2
Panicum wilcoxianum	514	37	— 92.8	8	0	3
Poa pratensis	498	95	— 80.9	9	0	5
Schedonnardus paniculatus	107	406	+279.4	2	0	1
Sporobolus asper	45	45	0	3	2	0
Sporobolus cryptandrus	113	142	+ 25.7	7	0	4
NON-GRASSES						
Amorpha canescens	26	14	— 46.1	5	0	1
Artemisia gnaphalodes	315	448	+ 42.2	8	0	2
Aster multiflorus	237	262	+ 10.5	5	1	0
Callirrhoe alceoides	52	74	+ 42.3	5	1	2
Lepidium virginicum	8	155	+1,837.5	10	8	0
Salsola pestifer	4	221	+5,425.0	11	8	0
Solidago glaberrima	434	307	— 29.3	7	0	1

*Estimated cover in percent.

by gains of Texas crabgrass *(Schedonnardus paniculatus),* sand dropseed, wheat grass and sedges.

Perennial grasses as a group decreased in density 15 percent while annual grasses increased 10 percent (Table 19).

TABLE 19. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT CLAY CENTER, NEBRASKA

	Number of species	Number of Stems		Percentage of change	Number of plots
		1936	1937		
Grasses	21	7,200	6,220	—13.6	11
Annual	7	443	487	+ 9.9	7
Perennial	14	6,757	5,733	—15.2	11
Forbs	20	1,196	1,178	— 1.5	11
Annual	5	13	17	+30.8	8
Perennial	15	1,183	1,161	— 1.9	11
Ruderals	15	561	937	+67.0	11
Total	54	8,518	7,852	— 7.8	11

It may be seen in Table 18 that five of the species which dropped out of a greater number of plots than they invaded were species that made definite gains in abundance. The data show that there was a strong tendency among these species for larger plants and denser stands to increase while small plants and sparse stands died. That the development of above-ground parts of a species is proportional to that of roots is well known, and considerable data indicate that deep roots and drought resistance are closely related in prairie plants.

Perennial forbs were also inconsistent, Artemisia gaining 42 percent and Missouri goldenrod losing 29 percent. For the group, gains nearly made up the losses. Annual forbs increased one third and weeds two thirds with percentage increases of Salsola and Lepidium in the thousands. In several plots in 1936, the hundreds of dry weed seedlings less than 3 inches tall were not counted but their percentage cover merely noted. In 1937 these areas were bare but overshadowed by fewer, larger plants of Salsola and other weeds (Fig. 23).

The unusually large number of species per quadrat (14.4) in 1936 was only one less the following year. Annual and perennial grasses and perennial forbs decreased while weeds and annual forbs increased in number of species per plot.

Of the 1,100 square decimeter units in the quadrats, 59 were bare in 1936 and 136 in 1937. However, only 16 were bare both years. The large scale depopulation accompanied the disappearance of 26 species from the unit areas. Chief among these were the weeds, red-root, stink-grass *(Eragrostis major),* and foxtail, the grasses, Poa, *Panicum wilcoxianum,* and Koeleria, and the

forb, *Solidago glaberrima.* Salsola, *Bromus tectorum,* Artemisia, Lepidium, and Agropyron were the foremost of the 19 species of invaders.

Certain changes, though not shown by the plots, were obvious. The lush vegetation of June, having used the surface moisture, was very dry on July 10 (Table 20). The early annual weeds, unusually large because of reduced competition, were no longer making demands on the habitat, but were breaking the force of the hot winds and casting slight shade over the withering grasses. Wheat grass had spread over most of the area, and the large, well-developed bunches of the grama grasses were quite conspicuous. Downy brome appeared to dominate the lower side of the prairie.

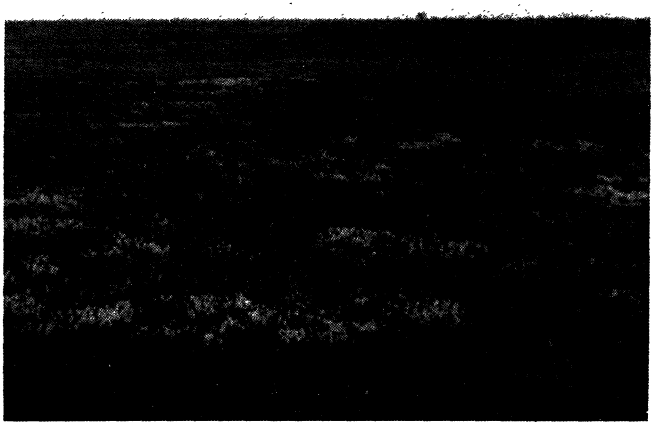

FIG. 23. Clay Center prairie in July, 1937. *Artemisia gnaphalodes* (white) with a height of 14 inches was overtopped only by wheat grass. It was the most conspicuous plant on the prairie.

Rates of infiltration in 4 types of vegetation were compared on August 17. Soil moisture had been slightly replenished since July 10 by eight showers totaling 3.8 inches (Table 20).

TABLE 20. PERCENTAGE OF AVAILABLE SOIL MOISTURE DURING THE SUMMER OF 1937 AT CLAY CENTER, NEBRASKA

Depth in feet	Hygroscopic coefficient	June 7	July 10	August 17
0-1	8.4	18.1	-0.9	2.5
1-2	9.5	5.4	0.0	1.2
2-3	10.5	1.7	0.9	1.2

In the lead plant, side-oats grama, and blue grama types, the 4 inches of water penetrated very rapidly and with no marked difference in rate according to type. Neither was there any relation between the number of stems

enclosed by a cylinder and the rate of infiltration. Among the three types, the greatest variation between the fastest and slowest rate per cylinder was from 10 to 24.5 minutes, the average time being 14.7. The four cylinders, pressed into the ground through two inches of dust, which had not been disturbed since its deposition in March, 1935, required an average time of 28 minutes for 4 inches of water to penetrate, and ranged from 21 to 35 minutes (Fig. 24). Thus, soil bearing either grasses or forbs absorbed twice as rapidly as bare, consolidated dust.

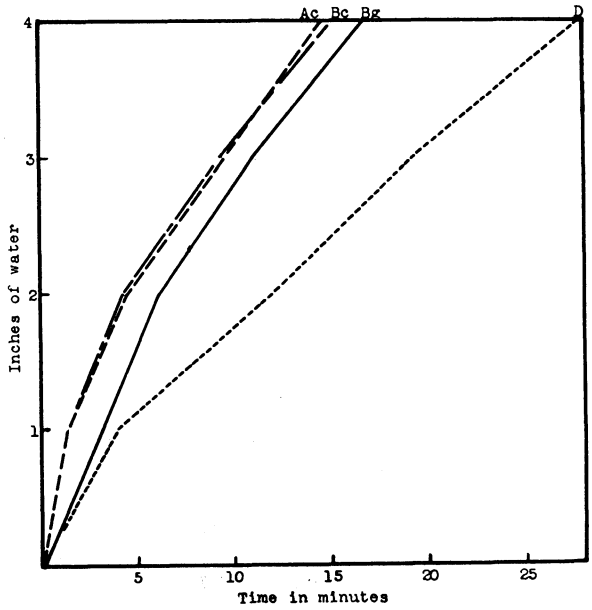

FIG. 24. Rate of infiltration of water into the soil in 4 types of vegetation at Clay Center, Nebraska; lead plant (Ac), side-oats grama (Bc), blue grama (Bg), and a deposit of dust 2 inches deep (D).

The composite of random soil samples taken to a depth of 2 inches and kept watered in the greenhouse for 5 months yielded more than 300 plants of 21 species. Perennials constituted 29 percent of the species but only 3 percent of the seedlings. Six-weeks fescue was the most abundant species, with downy brome next in rank.

NELSON PRAIRIE

This is an upland prairie of 20 acres 5.5 miles northeast of Nelson, Nebraska. It slopes gently eastward to drop abruptly near its edge into ravines which together include not more than one tenth of the area.

The soil of the upland is Crete silt loam, as at Carleton.

In 1931, the dominant vegetation was *Andropogon scoparius* with a good mixture of *A. furcatus*. Alternes of *Bouteloua gracilis* occurred and in them there was an abundance of Plantago, Hedeoma, and Festuca. *Bromus tectorum* was an invader. Although the prairie was very grassy, both grasses and forbs were of small stature and the latter were less abundant than farther eastward.

In 1935 only remnants of little bluestem were found, and big bluestem was greatly depleted by drought and wind-deposited soil. Side-oats grama and blue grama also were injured, while wheat grass had invaded. Festuca

occurred in as many as 212 bunches per square meter on the upper, dust-covered half of the slope where it was codominant with downy brome. Where this deposit approached an inch in depth, small, thriving alternes of wheat grass were present. The usual interstitial plants were rare and more than two thirds of the ground was bare.

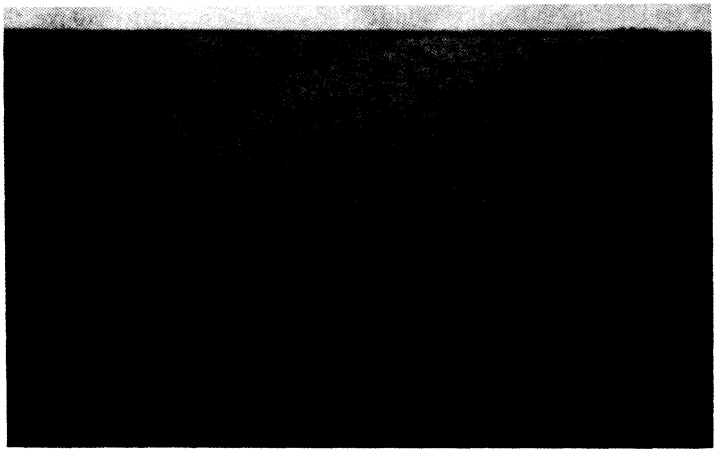

FIG. 25. Big bluestem buried by silt in 1936 at the Nelson prairie.

The vegetation of this prairie, when examined on July 4, 1936, appeared to be in a critical condition. Two days previously a local cloudburst accompanied by much hail and violent wind had laid the already dwarfed vegetation still lower and covered much of the grass with eroded topsoil and debris. The absence of leaves on all but the protected south sides of plants, and the bruised stems of such forbs as Liatris, Kuhnia, and Amorpha bore witness of the direction and severity of the storm. Such mature and brittle plants as Festuca and Erigeron were pelted into the ground, which was packed very hard, or washed down the slope to lodge in small dams against living clumps or stems. Numerous, widely branching cracks were everywhere on the upland, where they must have received considerable runoff from intervening areas as well as from the field above the prairie. In a swale at the north end, some of the best big bluestem on the prairie was buried under 4 to 6 inches of alluvium (Figs. 25 and 26).

In early August the vegetation was drought stricken. The cumulative rainfall deficiency had nearly doubled since 1934. The average mean temperature for the 3 summer months was 6.7° F. above normal, 2.2 degrees less than for 1934 (Fig. 27).

Nevertheless, an impressive change of aspect had been wrought in the vegetation since July 4. Viewed from the sky the prairie would have appeared as a network of green spread over a gray-brown field. The soil cracks had

not closed but presented a border of 8 to 12 inches on each side consisting of a lush growth of big and little bluestems and side-oats grama. Leaves and racemes of the last were 8 and 20 inches tall, respectively. Away from the cracks, much big bluestem had made no growth during July while the rest had grown slightly at the base. Little bluestem, however, had put out many new stems and was much more conspicuous than a month earlier. No efficient rain had fallen since the cloudburst, and no moisture above the hygroscopic coefficient was present, except near the cracks, at least to a depth of 3 feet (Table 22).

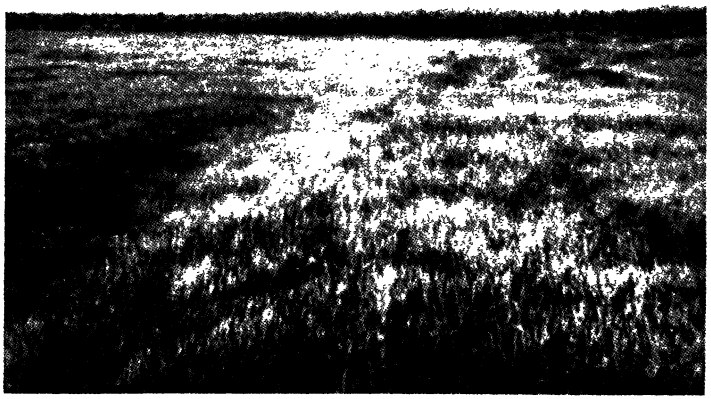

FIG. 26. The same area dominated by downy brome in 1937.

Big bluestem and six-weeks fescue were the most abundant grasses, with little bluestem and side-oats grama next in rank. Wheat grass was common, but only one percent had spikes. Only one clump of hairy grama *(Bouteloua hirsuta)* was found. Sand dropseed was more abundant on a ridge in the center of the prairie than elsewhere. Here it was mixed with wheat grass, plantain, peppergrass, and blue grama, the total basal cover scarcely exceed-

TABLE 21. RELATIVE IMPORTANCE OF THE CHIEF FORBS AT NELSON, NEBRASKA, EXPRESSED IN ABUNDANCE CLASSES. CLASS VALUES AS IN TABLE 7

Species	1931	1936	1937
Amorpha canescens	3	3	3
Antennaria campestris	1	0	0
Aster multiflorus	1	3	4
Erigeron ramosus	3	3	4
Hedeoma hispida	3	4	3
Kuhnia glutinosa	3	4	4
Lepachys columnaris	2	4	0
Lepidium virginicum	0	3	2
Liatris punctata	1	3	4
Plantago purshii	3	2	3
Solidago glaberrima	3	5	0

ing one percent. During the first night on the prairie .5 inch of rain fell slowly and by morning near the cracks the inflorescences of big bluestem, which were not visible in the evening, had unfolded at a height of 28 inches.

Relative abundance of the important forbs is shown in Table 21. It was obvious that deep-rooted perennials had not been able to maintain their former density after the drought of 1936.

FIG. 27. Cumulative precipitation deficit from January 1, 1933 to August 31, 1937 (line) and average mean monthly departure above normal temperature for June, July, and August (bars) at Nelson, Nebraska. Temperature data are based on records from three nearest Weather Bureau stations.

Selection of 8 permanent plots with a total area of 16 square meters was made in 6 different types of vegetation on the upland, and a census was taken during the second week of August each year.

In early June, 1937, the higher one fourth of the prairie was found to be buried under eroded topsoil from the field above to a depth of 2 inches. Only the stiffer forbs, wheat grass and a scattering of big bluestem were able to emerge through this deposit. It was largely populated by the annual foxtail, pigweeds, Russian thistle, and downy brome. The cracks, though still open, seemed to be of small benefit to the vegetation, as it was equally dwarfed everywhere. The cracks evidently permitted rapid evaporation as well as rapid entry of water. The topsoil was moist but the second foot was extremely dry (Table 22).

Precipitation for all but three months since the previous visit had been below normal and the winter had been especially dry and cold. The approximately normal precipitation of 6.3 inches during June and July, however, was sufficient to increase soil moisture slightly below the first foot, and to improve the condition of the vegetation somewhat. By the middle of August the grasses along the cracks were again flourishing although dwarfed elsewhere. This formed a pattern visible a quarter of a mile away (Fig. 28).

TABLE 22. PERCENTAGE OF AVAILABLE SOIL MOISTURE ON THE UPLAND AT NELSON, NEBRASKA

Depth in feet	Hygroscopic coefficient	August 6 1936	June 7 1937	August 16 1937
0-1	9.8	-1.7	5.3	1.3
1-2	12.4	-0.6	0.6	2.8
2-3	12.1	-0.7	0.7	2.0

Side-oats grama and sand dropseed were abundant and conspicuous among the generally distributed but dead Festuca, Bromus, and Plantago. Wheat grass was not fruiting. Indeed its presence was revealed only by careful search. Many of its stiff, dry spears 4 to 5 inches tall were dead and decayed at the soil surface. Several new clumps of hairy grama were found and the one old clump previously noticed had 42 percent more stems. The character of the cover on the lower half of the prairie is well represented in Figure 29. The plot census data confirmed, in the main, the general observations (Table 23).

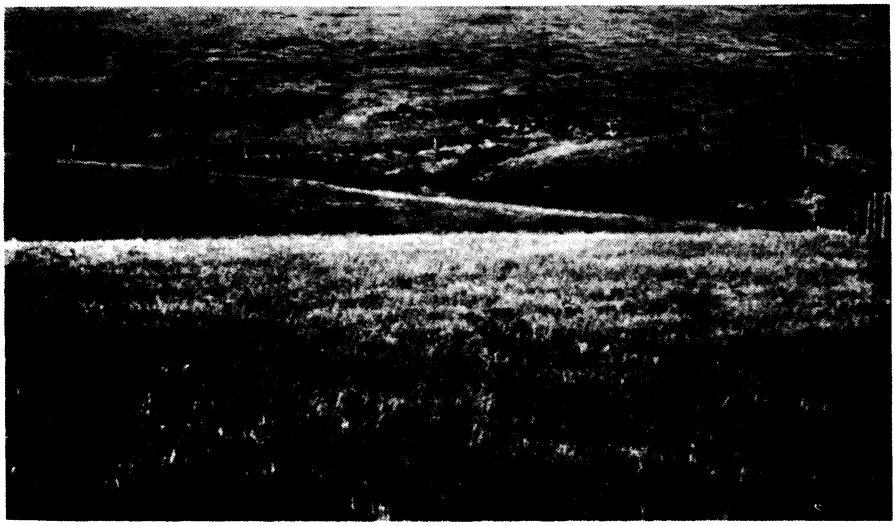

FIG. 28. Lush growth of grass along cracks at Nelson, Nebraska, August, 1937.

Although already decimated by the drought of 1934, big and little bluestems, in 6 and 4 plots, respectively, were again reduced. The same was true of June grass, bluegrass, and the small panic grasses, but the losses were still greater. Wheat grass, usually on the increase, had all but disappeared while the three grama grasses showed gains ranging from 26 to 87 percent. Sand dropseed was 3 times as abundant. Among the deep-rooted perennials only Amorpha held its own while Kuhnia and Liatris were much less numerous in the permanent plots in 1937. Artemisia and Aster had disappeared.

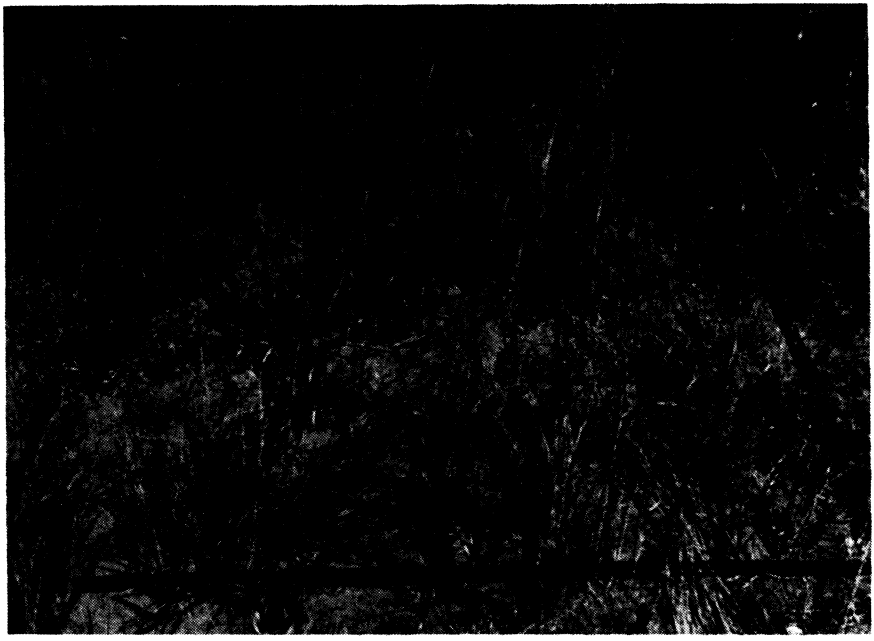

FIG. 29. Open cover typical of the lower half of the Nelson prairie in 1937.

Of the five groups compared in Table 24, four lost and one (annual grasses) made only a slight gain. The loss of perennial grasses, although smaller in percentage than that of forbs, signifies a much greater lowering of the total density.

Annuals of all kinds appeared to be as generally distributed in 1937 as in the preceding year. The number of species of weeds per plot was larger the second year, but perennial forbs lost nearly one and perennial grasses more than two species per plot. The average total number of species per plot, however, remained nearly constant (Table 24).

The number of bare square decimeter units had increased 56 percent.

TABLE 23. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, TOTAL NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937, AT NELSON, NEBRASKA

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
GRASSES						
Agropyron smithii	550	108	— 80.4	3	0	0
Andropogon furcatus	700	409	— 41.6	6	0	1
Andropogon scoparius	568	147	— 74.1	4	0	1
Bouteloua curtipendula	1,133	2,123	+ 87.4	6	0	0
Bouteloua gracilis	459	579	+ 26.1	2	0	0
Bromus tectorum	116	47	— 59.5	3	0	1
Carex	195	187	— 4.1	6	0	2
Festuca octoflora	(309)*	(410)*	+ 32.7	6	0	0
Koeleria cristata	227	13	— 94.3	5	1	3
Panicum scribnerianum and *P. wilcoxianum*	24	3	— 87.5	3	0	2
Poa pratensis	136	0	—100.0	5	0	5
Schedonnardus paniculatus	128	65	— 49.2	2	0	1
Sporobolus cryptandrus	25	83	+232.0	4	1	0
NON-GRASSES						
Amorpha canescens	187	184	— 1.6	2	0	0
Aster multiflorus	36	0	—100.0	2	0	2
Erigeron ramosus	106	1	— 99.1	3	0	2
Plantago purshii	(133)*	(113)*	— 15.0	4	0	0
Salsola pestifer	0	23	+	3	3	0

*Number of square decimeter units in which species occurred.

TABLE 24. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT NELSON, NEBRASKA

	Number of species	Number of Stems		Percentage of change	Number of plots	Species Per Plot	
		1936	1937			Average 1936	Percentage of change 1937
Grasses	18	4,233	3,793	—10.4	7	9.2	— 25.4
Annual	4	(427)*	(457)*	+ 7.0	6	1.5	+ 10.7
Perennial	14	4,233	3,793	— 10.4	7	7.7	— 32.6
Forbs	11	388	244	—37.1	7	2.8	—23.3
Annual	3	133	59	—55.6	6		
	1	(133)*	(113)*	—15.0	4	1.7	+ 9.6
Perennial	7	255	185	—27.5	5	1.2	—71.8
Ruderals	5	(118)*	(47)*	—60.2	6	.67	+173.1
Total	33	4,622	4,061	—12.1	8	10.5	— 1.9

*Number of square decimeter units in which species occurred.

This depletion in cover was caused largely by the death of Festuca, Erigeron, *Bouteloua curtipendula,* and *Andropogon furcatus.* Festuca, *B. curtipendula,* and Hedeoma were the chief invaders of the units bare in 1936.

The infiltration rate of water into soil bearing three types of vegetation was measured (Fig. 30). The cylinders were placed so as to enclose bunches

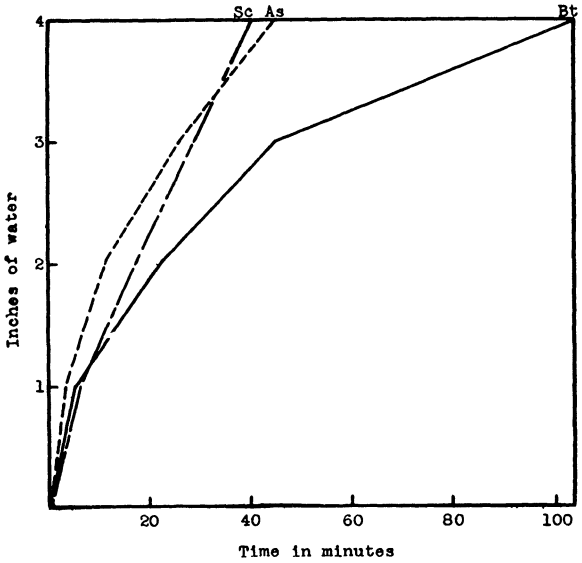

FIG. 30. Rate of infiltration of water into the soil in 3 types of vegetation at Nelson, Nebraska; sand dropseed (Sc), little bluestem (As), and downy brome (Bt) on an alluvial deposit one year old.

of sand dropseed and of little bluestem a few feet distant; also in the alluvium covered by downy brome which is shown in Figure 29. Soil in the little bluestem type absorbed the first 2 inches more rapidly and the last 2 more slowly than did the sand dropseed type. It required 44 minutes as compared with 40 minutes in the latter for the absorption of 4 inches of water. In the alluvium average time for 4 inches was 104 minutes. The first inch of water disappeared in 5.7 minutes but the rate gradually lessened, the fourth inch requiring 59 minutes. In no instance was there any correlation between the amount of visible vegetation enclosed by the cylinders and the rate of infiltration.

MONTROSE PRAIRIE

Four miles southeast of Montrose, Kansas, there is a rectangular upland prairie of about 20 acres undisturbed except by frequent burning. On the east it is bordered by a newly-fenced 30-acre pasture which in 1931 was part of this ungrazed prairie. Other contacts are with cultivated fields. The relatively level north end is separated from the long, north-sloping southern part by a shallow ravine which drains across it eastward from the plowed field. The soil in the ravine is Lincoln silt loam, colluvial phase; that of the slopes is Colby silty clay loam, which comprises 95 percent of the prairie. The 6-inch layer of eroded topsoil is a dark, pervious mantle of silt loam underlain by a subsoil consisting of about 20 inches of grayish to light brown, slightly compacted silty clay loam above unweathered loess. Bennett (1935) reports that on this soil type little bluestem and grama grass were over 3,000 times as effective as clean cultivated Kafir corn in preventing erosion, and 400 times in preventing runoff.

In 1931 most of the area was dominated by a mixture of *Andropogon furcatus* and *A. scoparius,* the former (mixed with *Sorghastrum nutans*) having full possession of protected slopes and ravine bottom while the latter

increased to 80 percent of the mixture on much of the higher ground. *A. scoparius* was present in both the sod and bunch types. *Bouteloua curtipendula* and Koeleria were common, especially on dry slopes. A few spears of Agropyron, as well as tufts of Buchloe and *Bouteloua gracilis,* were present but nowhere abundant. *Sporobolus cryptandrus* and *S. asper* were uncommon.

Study of the area in July, 1936, revealed a vegetation characterized by a singular uniformity in height and composition. Alternes were relatively few, being restricted to 2 or 3 of Agropyron and *Andropogon furcatus,* unless several patches of *Bouteloua gracilis* and *B. curtipendula* only 1 to 5 square feet in area are included. Big bluestem was in unusually good condition immediately surrounding numerous small piles of hay—old haycocks and accidental leavings. It was still abundant over the prairie as a whole but was at least equaled in abundance by Agropyron. *Bouteloua curtipendula* and *B. gracilis* were almost as important as *Andropogon furcatus. A. scoparius,* Buchloe, Poa, Elymus, and *Panicum virgatum* were not common; *P. scribnerianum,* Sorghastrum and Schedonnardus were rare; but *Sporobolus cryptandrus* and *S. heterolepis* were not seen.

Artemisia, Allionia, Kuhnia, Rosa, Linum, Sideranthus, Vernonia, Aceroates, and Lepachys appeared to be as abundant as described by Weaver before the drought. Amorpha (the only conspicuous forb), Aster, Solidago, Psoralea, and Antennaria, though still present, had decreased in abundance while Astragalus, Silene, Physalis, Salvia, and Liatris could no longer be found. On the other hand, Hedeoma had increased so that much of the ground fairly bristled with it. Androsace, Chenopodium, Ambrosia, Tithymalus, Lepidium, Salsola, and *Eragrostis major* were present although not recorded here before the drought. Where possible, members of the above groups are listed in order of decreasing abundance in 1936. The increase in ruderals, although primarily due to drought disturbance, was greatly abetted by the presence of numerous weedy stack sites and by the extreme weediness of adjacent fields.

One of the chief ecological features of this prairie was an area near the top of the hill at the south end which, in the spring of 1935, had been buried under a deposit of wind-blown gray dust ranging in depth from one foot near the fence to one-fourth inch six rods down the slope. The dust came from the adjacent field and had been deposited in this short distance after entering the prairie. A rather pure stand of wheat grass with a scattering of big bluestem and weeds formed a very open cover, considerable areas being nearly bare and quite unprotected from sheet erosion except by the interlacing rhizomes of Agropyron in the surface soil. At the shallower edge of the deposit, many dead crowns and rhizomes of little bluestem, side-oats

grama, and big bluestem lay exposed on the surface and to 1.5 inches above it, suggesting that, after covering them, the dust plus some of the original topsoil had been eroded away by water in the absence of any living protective cover. Dust deeper than 0.5 inch appeared to have destroyed most of the big bluestem, and that deeper than 1 inch, all of it. Wheat grass was fruiting here and in a few other scattered spots.

About midway down the long north slope, a belt of fine big bluestem 1 to 2 rods wide extended across the prairie from the east as if acting as a barrier to the invading horde of Agropyron descending the slope. Below it, Agropyron occurred in only a few scattered patches and in the ravine bottom. In this alterne of big bluestem, smooth sumac *(Rhus glabra)*, a shrub common to forest-prairie ecotones, was present in considerable numbers in spite of annual mowing.

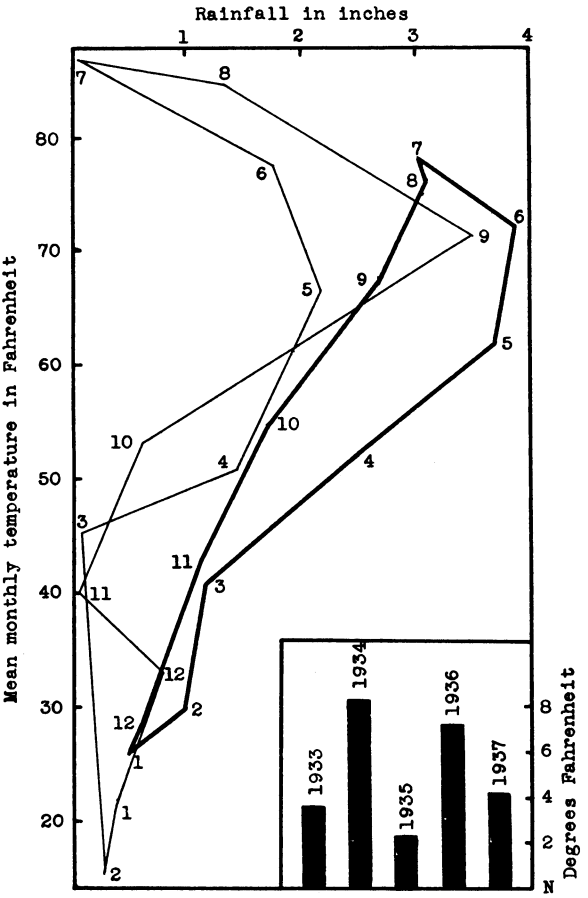

FIG. 31. Hythergraph of mean monthly temperature and rainfall for 1936 (light line) and for a 36-year period (heavy line) at the Montrose prairie. The numbers 1 to 12 represent months. Inset: Departure above the normal mean temperature for 3 summer months.

The condition of the vegetation was again noted a month later. During the interim 0.04 inch of rain had fallen and the mean temperature had been nearly 9° F. above normal (Fig. 31). On the upper slope wheat grass had produced heads on about one fourth of the plants and most of the leaf bases were green. Big bluestem was brittle to within an inch of the ground, having made no additional growth. The leaves of blue grama were dry 3 inches from the tip, but side-oats grama was still green though not in flower. Artemisia was drying up without flowering; Kuhnia was three-fourths defoliated and

half the leaves of *Solidago mollis* were dead, but *Allionia linearis* was flowering. Only the older plants of buffalo grass had any green leaves.

Twelve permanent plots with a total area of 10.5 square meters were located in eight different types of vegetation widely distributed over the area. These were quadrated about July 1 during both years. The most readily observed change was that produced by the great extension of wheat grass. It had migrated down the slope and across the ravine from its previous position on the dust deposit, which was now cemented so firmly that a steel quadrat pin could be forced into it only with difficulty. All grasses were in a condition of reduced activity and cracks in the soil were beginning to open. *Andropogon scoparius* and Poa appeared to have been reduced, but Buchloe seemed more abundant. A part of the data for 20 chief species included in the permanent plots is given in Table 25.

TABLE 25. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, TOTAL NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937, AT MONTROSE, KANSAS

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
GRASSES						
Agropyron smithii	1,588	2,688	+ 69.3	11	0	0
Andropogon furcatus	1,714	869	— 49.3	12	0	1
Andropogon scoparius	211	42	— 80.1	3	1	0
Bouteloua curtipendula	4,935	4,513	— 8.6	10	0	0
Bouteloua gracilis	0.96*	1.61*	+ 67.7	6	0	1
Buchloe dactyloides	47.57*	59.75*	+ 25.6	3	1	0
Carex	301	240	— 20.3	10	0	1
Festuca octoflora	28	1,446	+5,064.3	11	8	0
Koeleria cristata	65	34	— 47.7	2	0	1
Panicum scribnerianum	197	7	— 96.4	5	0	2
Panicum virgatum	30	0	—100.0	2	0	2
Poa pratensis	140	207	+ 47.8	1	0	0
NON-GRASSES						
Allionia nyctaginia	15	14	— 6.7	3	1	1
Amorpha canescens	70	43	— 38.6	6	0	1
Androsace occidentalis	21	345	+1,542.9	7	3	0
Aster multiflorus	133	68	— 48.9	8	0	1
Erigeron ramosus	36	58	+ 61.1	4	1	0
Hedeoma hispida	39	491	+1,159.0	10	4	0
Lepidium virginicum	4	122	+2,950.0	7	4	0

*Estimated cover in percent.

The native mid and tall grasses all appeared to have suffered losses ranging from 100 percent among the panic grasses to 9 percent for *Bouteloua curtipendula*. Increase in abundance was shown by wheat grass, blue grama, and buffalo grass, all species characteristic of mixed prairie. Little bluestem was an exception as it had only 20 percent as many stems in 1937 as in 1936. Festuca, an annual grass, Lepidium, an annual weed, and Hedeoma, an annual forb, all increased enormously while Aster and Amorpha, deep-rooted perennial forbs, suffered marked losses.

The 12 plots were found to contain 56 of the 72 species listed. The trends of change in floristic composition are summarized in Table 26.

Although the grasses originally producing the best hay decreased, perennial grasses as a group remained constant. Because of the larger number of annuals, forbs as a class increased although the number of perennials was greatly reduced.

TABLE 26. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT MONTROSE, KANSAS

	Number of species	Number of Stems		Percentage of change	Number of plots
		1936	1937		
Grasses	18	22,074	22,093	+ 0.1	12
Annual	3	(49)*	(254)*	+418.4	10
Perennial	15	22,074	22,093	+ 0.1	12
Forbs	24	377	1,068	+183.3	12
Annual	6	91	905	+894.5	11
Perennial	18	286	163	— 43.0	12
Ruderals	14	105	168	+ 60.0	10
Total	56	22,556	23,329	+ 3.3	12

*Number of square decimeter units in which species occurred.

At the second quadrating, the average number of species per plot had increased only 1.8 percent but changes shown by the different ecological groups were more marked. Gains ranged from 232 percent and 100 percent for species of annual grasses and forbs, respectively, to 25 percent for weeds. Perennial grasses had 18 percent and perennial forbs 37 percent fewer species per plot. In 1936 the numbers of species per plot were: total, 11; annual grasses, .25; perennial grasses, 6.3; annual forbs, 1.25; perennial forbs, 2.5; and weeds, 1.0. Certain annual grasses are weeds.

The vegetation was about 7 percent taller than the 1936 average of 11 inches. Grasses and forbs showed approximately the same increase in height.

Fifty of the 1,050 square decimeter units in the plots were without vegetation in 1936, and the following year 43 were bare, although only 11 were bare both years, *i.e.* 39 were invaded and 32 depopulated between studies. Agropyron was the chief invader (27 squares) followed by Festuca, Hedeoma, and *Bouteloua curtipendula*. A few bunches of the last exhibited a diseased condition characterized by dwarfing, chlorosis, and excessive proliferation. Agropyron, *Bouteloua curtipendula, Amaranthus* spp., and *Andropogon furcatus* were most important of those creating bare areas by their death.

Soil samples taken at 6 different places were found to be very uniform as to structure, color, compaction, and moisture content at corresponding depths, regardless of vegetation type. For example, samples taken at a depth of 12 to 24 inches on the upper slope in the big bluestem alterne, in wheat grass seven yards distant, and in Kentucky bluegrass near the bottom and at

the upper north side of the ravine contained 16.1, 16.3, 16.1 and 16.0 percents of water, respectively. To a depth of 4 feet on the upper slope and to three feet near the ravine, there was no soil moisture above the hygroscopic coefficient on August 5, 1936. This is understandable in the light of temperature and precipitation data shown in Figure 31. Every month of 1936, up to and including August, was drier than normal while the mean temperatures of the three summer months averaged 7.6° F. above normal. The 20.65 inches of moisture received during the next 11 months was 1.2 inches below normal and effected an increase in moisture content of only the upper 4 feet of soil, but this was largely exhausted in the second to fourth feet during the next six weeks. The available moisture in the surface foot was provided by a 0.6-inch rain 6 days before the samples were taken (Table 27).

TABLE 27. PERCENTAGE OF AVAILABLE SOIL MOISTURE AT CORRESPONDING PERIODS IN 1936 AND 1937 AT MONTROSE, KANSAS

Depth in feet	Upper Slope				Lower Slope			
	Hygroscopic coefficient	Aug. 5 1936	June 30 1937	Aug. 13 1937	Hygroscopic coefficient	Aug. 5 1936	June 30 1937	Aug. 13 1937
0-.5	9.2	—1.6	1.2	3.3	....	...	...	...
.5-1	12.3	—1.0	2.1	0.4	10.4	—1.7	—0.6	1.5
1-2	15.5	—0.6	4.0	—0.9	14.4	—1.1	2.3	—1.2
2-3	13.3	—0.6	2.8	—1.2	12.0	—0.3	3.5	1.0
3-4	13.0	—1.5	0.0	—0.5	11.5	1.0	1.0	1.4
4-5	12.0	0.2	...	1.0	10.4	3.0	...	4.2
5-6	11.1	1.6	...	2.8	11.9	5.5	...	3.3
6-7	10.8	2.6	...	...	12.1	3.5	...	...
7-8	12.3	2.8	...	...	12.4	5.8	...	...
8-9	13.3	3.5	...	...	13.0	6.2	...	...
9-10	14.3	4.9	...	...	14.0	6.8	...	...
10-11	14.6	6.2	...	...	13.9	7.9	...	...
11-12	14.9	6.1	...	...	14.6	7.0	...	...

Rates of infiltration of water into the soil in four types of vegetation were somewhat different. The first inch required periods ranging from 3.5 minutes in Amorpha to 9.5 minutes in Agropyron on the dust deposit 250 yards distant. The 4 cylinders were placed around 2, 3, 5, and 7 stems of Amorpha, a shrubby species having a long taproot. Time required for the 4 inches to enter the ground ranged from 28 minutes where 3 stems were enclosed to 68 minutes where 2 stems were present, and averaged 53 minutes for the replication of four. In Buchloe, five rods distant on the same level, the rate for each inch was approximately the same as for Amorpha, and the range among cylinders was 29 to 72 minutes (Fig. 32). Except for the first inch, the rate in the alterne of *Andropogon furcatus* previously described was considerably the highest of 4 types. The average time for 4 inches was 34.2 minutes, the range being from 20 to 52 minutes. Again no correlation could be shown to exist between the number of shoots included within the cylinder and the infiltration rate. In the wheat grass growing on a dust deposit, the

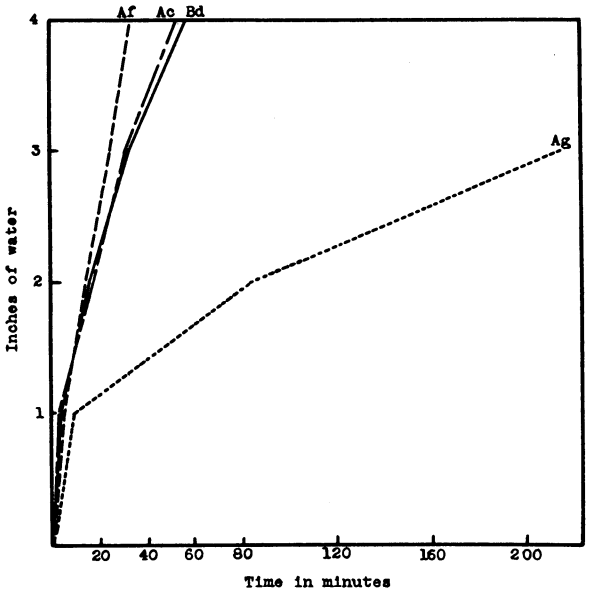

FIG. 32. Rate of infiltration of water into the soil in 4 types of vegetation at Montrose, Kansas; big bluestem (Af), lead plant (Ac), buffalo grass (Bd), and wheat grass (Ag).

average rates were 9.5, 75, and 132 minutes for inches 1 to 3, respectively. The range was from 39 to 474 minutes for three inches and in this instance the larger the number of plants per cylinder, the more rapidly the water was absorbed.

Seeds of 18 species were present in the composite of 20 random shallow soil samples taken from this prairie in August, 1937. Of the seedlings appearing during 5 months in the greenhouse, one seventh of the plants and one sixth of the species were perennials. Nearly half of the seedlings were ruderals, but the most abundant species was an annual grass, *Festuca octoflora.*

DISCUSSION

A study of the data from the 9 prairies reveals that native perennial grasses and forbs suffered a further reduction in density following the drought of 1936 (Table 28). At some time during each summer soil moisture was non-available to a depth of 4 feet. On the upland, less than 2 percent was available to 8 feet. The zone in which the activity of roots has but slight effect upon soil moisture content thus appears to lie below 8 feet in upland prairies of this region. Weaver (1920) used the bisect method on upland prarie to ascertain that few grasses penetrate deeper than 5 feet, and few forbs deeper than 8 feet. During the drought of 1934, Nedrow (1937) showed that Antennaria, *Poa pratensis* and *Panicum scribnerianum* did not recover from wilting when watered at a depth of 32 inches, while *Andropogon scoparius* failed to respond when watered at 42 inches. The last lost 75 percent of its stand in 1936. This was accompanied by smaller but severe losses of Koeleria, *Sporobolus heterolepis, Carex* spp., *Andropogon furcatus,* and Stipa. However, where rainfall was above normal in 1935 and normal up to the time of quadrating (the Hebron prairie) in 1937, *Andropogon scoparius* increased its density by 15 percent. Thus, it is apparent that the fate of this species was controlled by soil moisture at the

TABLE 28. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES IN PERMANENT PLOTS ON ALL PRAIRIES, NUMBER OF PLOTS IN WHICH SPECIES OCCURRED (A), NUMBER OF PRAIRIES ON WHICH SPECIES OCCURRED (B), AND NUMBER OF PRAIRIES ON WHICH SPECIES SUFFERED LOSSES (C)

Species	Number of Stems		Percentage of change	A	B	C
	1936	1937				
GRASSES						
Agropyron smithii	9,187	11,985	+ 30.5	63	9	1
Andropogon furcatus	10,031	7,198	— 28.2	87	9	9
Andropogon scoparius	5,450	1,355	— 75.2	49	9	8
Bouteloua curtipendula	10,140	11,014	+ 8.6	71	9	4
Bouteloua gracilis	20.3*	19.0*	— 6.4	40	8	4
Bromus tectorum	768	3,413	+344.4	32	9	1
Buchloe dactyloides	81.6*	69.4*	— 14.9	14	5	2
Carex	3,625	2,522	— 30.4	74	9	5
Festuca octoflora	(1,248)†	(2,829)†	+126.7	56	8	0
Koeleria cristata	4,902	1,509	— 69.2	57	9	9
Panicum scribnerianum	628	407	— 35.2	46	9	6
Panicum wilcoxianum	737	56	— 92.4	31	9	8
Poa pratensis	10,410	5,448	— 47.7	57	9	7
Sporobolus asper	723	1,045	+ 44.5	25	8	3
Sporobolus cryptandrus	163	283	+ 73.6	16	5	1
Sporobolus heterolepis	1,368	510	— 62.7	16	5	5
Stipa spartea	886	648	— 26.9	18	5	3
NON-GRASSES						
Achillea occidentalis	77	12	— 84.4	9	6	5
Amorpha canescens	517	466	— 9.9	42	9	7
Antennaria campestris	35	23	— 34.3	7	2	2
Artemisia gnaphalodes	1,119	1,045	— 6.6	25	6	5
Aster multiflorus	2,906	2,612	— 10.1	64	9	6
Callirrhoe alceoides	58	87	+ 50.0	12	4	1
Erigeron ramosus	1,031	2,392	+132.0	61	9	2
Hedeoma hispida	290	4,126	+1,322.8	63	8	0
Helianthus rigidus	76	46	— 39.5	13	6	3
Lepidium virginicum	231	3,651	+1,480.5	70	9	0
Liatris punctata	61	28	— 54.1	5	4	3
Linum sulcatum	11	356	+3,136.4	23	6	0
Lithospermum linearifolium	31	43	+ 38.7	17	8	2
Plantago purshii	442	5,635	+1,174.9	29	5	1
Psoralea floribunda	19	30	+ 57.9	11	3	1
Rosa arkansana	40	40	0	9	4	2
Solidago glaberrima	614	538	— 12.4	39	9	5

*Estimated cover in percent.
†Number of square decimeter units in which species occurred.

working depth of its roots, rather than by temperature or humidity. All interstitial grasses sustained general losses. *Panicum wilcoxianum* was nearly wiped out, and *Poa pratensis* was reduced one half, while *Panicum scribnerianum* and *Eragrostis spectabilis* were less affected. Part of the injury to Poa in 1937 was due to the close grazing of grasshoppers. The moisture deficit was so great on the eastern prairies that even the short grasses were unable to hold gains made in 1935 and early in 1936. *Buchloe dactyloides* and *Bouteloua gracilis* were reduced 15 and 6 percent, respectively. Savage and Jacobson (1935) observed that these grasses were considerably injured by drought in 1934, even when aided by artificial watering.

These general losses were partly offset by gains by *Schedonnardus paniculatus* and *Sporobolus cryptandrus* on the western prairies and by general increases of 45 and 30 percent by *S. asper* and *Agropyron smithii*. The latter had spread widely from dense stands on hard, low ground and dust deposits, while *Sporobolus asper* was able to fruit in the absence of the customary late mowing. On the Nelson prairie, where stems of wheat grass were moldy or decayed below ground, an 80 percent loss was recorded. Change in *Bouteloua curtipendula* ranged from a 65 percent loss at Jamaica to a gain of 87 percent at Nelson. The result was a small net increase. The invasion of bared uplands by *Elymus canadensis* from ravines is understandable in the light of its high rate of germination and rapid root penetration (Blake 1935). Stipa was most abundant eastward and absent south and west of Carleton, while *Sporobolus heterolepis* was present only on the 3 prairies nearest Lincoln.

Festuca octoflora was the most abundant and rapidly increasing native annual grass. Its occupancy of square decimeter units rose from 1,200 to 2,800 and the increase in abundance was over 600 percent in plots where stems were counted. It was absent on only one prairie.

Perennial forbs as a group lost 10 percent although small gains were recorded for a few species, for example *Callirrhoe alceoides, Lithospermum linearifolium,* and *Meriolix serrulata* (Table 29).

TABLE 29. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS ON ALL PRAIRIES, NUMBER OF PLOTS IN WHICH SPECIES OCCURRED (A), NUMBER OF PRAIRIES ON WHICH SPECIES OCCURRED (B), AND NUMBER OF PRAIRIES ON WHICH SPECIES SUFFERED LOSSES (C)

	Number	Number of Stems		Percentage of change	A	B	C
		1936	1937				
GRASSES							
Annual	8	1,254 (1,521)*	4,612 (2,423)*	+267.8 + 59.3	67	9	0
Perennial	29	90,088	69,920	— 22.4	98	9	8
FORBS							
Annual	13	1,965	14,544	+640.2	84	9	1
Perennial	42	6,376	5,745	— 9.9	90	0	6
Ruderals	24	1,812	7,913	+336.7	86	9	1
Total	109	100,486	99,500	— 1.0	100	9	5
Bare sq. dm. units	...	(378)*	(402)*	+ 6.3	..	9	..

*Square decimeter units.

By far the most abundant perennial forb, *Aster multiflorus* occurred in 64 of the 100 plots and decreased 10 percent in spite of gains ranging from 1 to 105 percent on the three eastermost prairies. Both Aster and Agropyron are able to take possession of adjacent bare areas very quickly by production of numerous, vigorous, interlacing rhizomes. This habit, together with dissemination of seeds of Agropyron from occasional original areas,

gave this species dominance over considerable territory. Their gains in 1937, however, were limited to areas where over-abundance had not been reached the previous year, and, in general, losses were recorded where they were most abundant in 1936. Thus, it appears that even species favored by drought are subject to control during such periods by the same factors which limit activities of the true dominants.

Although Amorpha gained on two prairies, its general abundance was slightly reduced. The roots of this species penetrate deeply into the subsoil where the moisture-supplying power was low during the summer of 1936, as was shown by the daily folding of the leaves. Under such conditions, photosynthesis is retarded or stopped. That the time of grazing or mowing, as well as their frequency and closeness, influences mortality through its effect on food reserves is well known. Mortality of Amorpha with respect to dates of mowing (as at Carleton) suggests that ability to enter the winter with adequate reserves was the direct contributing factor in survival of this species during drought. Other species showing losses of about 10 percent were *Lygodesmia juncea* and *Solidago glaberrima,* while *Helianthus rigidus, Liatris punctata, Kuhnia glutinosa,* and *Achillea occidentalis* lost 40 to 84 percent. Solidago was severely defoliated by grasshoppers both years. The small, interstitial forb, *Antennaria campestris,* formerly so common, decreased one third on the two prairies where it occurred in plots.

Unlike the perennials, annual forbs and ruderals were sparse in 1936 but formed a dense growth under the favorable conditions of topsoil moisture in the spring of 1937. Hedeoma and Plantago were about ten times more abundant, the former usually interstitial in Agropyron, while Plantago often appeared to take temporary dominance on dry slopes depleted of *Andropogon scoparius* and *Bouteloua gracilis.* In 1935, both seedlings and mature plants of Erigeron were present. In 1936, it was represented mostly by mature plants but in 1937 by seedlings. These, however, made the species 130 percent more abundant than the previous year. Silene was absent in 1936 but abundant on eastern prairies the following year, and seedlings of *Solidago glaberrima* were also common the second year. The clearest annuation was shown by *Linum sulcatum,* which was common in 1935, rare in 1936, and common to abundant in 1937.

Although the prairies were invaded by many ruderals such as species of Amaranthus, Cirsium, Chenopodium, Setaria, and Eragrostis, only two achieved importance. These were Lepidium, which became more abundant on all prairies with increases of 5- to 90-fold, and *Bromus tectorum,* which was present on all prairies and made a 3-fold gain. Tragopogon and Lactuca were important eastward and Salsola westward. Steiger (1930) found that only 4 percent of prairie species were annuals. In 1937, annuals had increased to 19 percent.

That topography has certain strong influences upon plant habitat is well known. It affects temperature, moisture and even soil structure by its influence upon erosion, runoff, infiltration of water, drifting dust and snow, and upon degree and direction of exposure to the wind and sun. As a rule, slopes lose more runoff water than level areas, but the latter are often less pervious owing to the presence of claypan near the surface. North and east slopes may be expected to have lower evaporation rates in summer because of lower insolation and better protection from hot southwest winds. Conditions of drought thus appear most severe on southwest and least on northeast slopes.

Table 30 permits a comparison of three classes of permanent plots, namely, 20 plots on xeric south, southwest, and west slopes, 36 on less xeric north, northeast, and east slopes, and 27 on level ground. The density (number of stems per square meter) of perennial grasses on mesic slopes was higher in 1936 and the loss in 1937 was less than elsewhere. Both lowest density and greatest injury to perennial grasses occurred on level ground, with only slightly less injury on xeric slopes. The scarcity of annual grasses on dry slopes in 1936 and their great increase are correlated with the differences in early season growing conditions. The density of annual forbs was progressively higher from moister to drier slopes in 1936, but the following year they were most abundant on north to east slopes and least on the level. Perennial forbs, which draw chiefly on subsoil moisture, showed both highest density and greatest losses on level ground, while on xeric slopes they made a gain of 10 percent. The weedy *Aster multiflorus* was largely responsible for the gain. Here, too, ruderals were least dense in 1936 and made their largest gains. Total densities on mesic slopes were but little higher than on more xeric ones, while plots on level land contained an intermediate number (1,130) of rooted shoots of all species per square meter. The variation in behavior of a species toward drought on different slopes may depend largely upon the stage of its development and upon its physiological condition, *i.e.* its metabolic preparedness when drought strikes. This, in turn, is determined by the suddenness of the inception of drought and the excellence of prior conditions for growth. A plant which, by virtue of its "favored" position on a north slope, is able to produce a vigorous shoot with minimum development of root hairs and root branches may be unable to adjust itself quickly enough to sudden onset of drought.

Owing to the presence of more available moisture in 1937, the vegetation of all prairies was much taller than the preceding year. The total density of the cover was reduced on the eastern and western prairies but increased on the ones in the southern and central parts of the area where there was more precipitation. An increase in number of bare units per plot was generally accompanied by a decrease in number of species and in total density. The principal invaders of bare areas, in order of decreasing importance, were

TABLE 30. NUMBER OF STEMS PER SQUARE METER AND CHANGES IN FLORISTIC COMPOSITION WITH RESPECT TO TOPOGRAPHY

	MESIC SLOPES				LEVEL GROUND				XERIC SLOPES			
	Average density 1936	NUMBER OF STEMS		Percentage of change	Average density 1936	NUMBER OF STEMS		Percentage of change	Average density 1936	NUMBER OF STEMS		Percentage of change
		1936	1937			1936	1937			1936	1937	
Grasses												
Annual	19.0	565	2,096	+270.0	36.2	800	1,900	+137.5	0.6	10	149	+1,390.0
	*(24.8)	*(737)	*(1,125)	+ 52.6	*(19.3)	*(426)	*(680)	+ 59.6	*(15.0)	*(247)	*(391)	+ 58.3
Perennial	1,112.6	33,045	28,096	— 15.0	960.2	21,220	16,341	— 23.0	1,055.7	17,420	13,512	— 22.4
Forbs												
Annual	20.9	622	8,758	+1,308.0	23.4	518	1,473	+ 184.3	31.1	514	2,260	+339.5
Perennial	57.5	1,718	1,495	— 13.0	93.7	2,072	1,561	— 24.6	75.9	1,253	1,375	+ 9.7
Ruderals	14.3	426	2,450	+475.1	51.2	1,139	3,131	+174.0	8.4	138	973	+605.1
Total	1,181.1	35,079	42,049	+ 19.9	1,130.3	24,979	23,391	— 6.4	1,170.8	19,318	18,343	— 5.0
Bare sq. dm. units	*(5.9)	*(176)	*(120)	— 31.5	(3.2)	*(71)	*(139)	+ 95.8	*(6.1)	*(101)	*(103)	+ 2.0

*Square decimeter units.

Festuca, Hedeoma, Lepidium, *Bouteloua curtipendula,* and Agropyron. Similarly, the species whose death caused bare areas were Poa, *Andropogon furcatus,* Erigeron, *Bouteloua curtipendula,* and *Andropogon scoparius. Bouteloua curtipendula* thus appears to have been the most unstable of the perennial grasses.

Investigations of soil reaction, chloride and moisture contents did not disclose the reasons for the sharp and prevalent alternation shown by perennial grasses. It must be kept in mind, however, that the supply of available soil moisture was abnormally low during this study. That such a study would throw light on the question of the causes of alternation if carried out at weekly intervals during a normal period is not unlikely. Cain (1931) found that contiguous forest communities could not be separated on the basis of reaction alone. Emmett and Ashby (1934) applied statistical methods to show that for Pteridium and Vaccinium there is no optimum pH within their pH range. This may well be true also for prairie grasses.

The range in soil moisture content at a depth of 2 feet was greater, that is higher and lower, under *Andropogon furcatus* than under any other type, while near roots of *Bouteloua gracilis* less moisture with a narrower range was the rule. Soils of unlike structure and permeability were found to differ markedly as to their vegetative cover.

Wheat grass was commonly the dominant on deeper deposits of dust and on shallow soils underlain by claypan. Particles of drifted soil sometimes become very firmly cemented into a brick-like layer. This is probably due to the presence of an excess of colloidal material. Fly (1935) reports that both dust and drifted soil had a higher percentage of total colloids than was present in normal surface soil. For this reason, the rate of infiltration of water into the soil in wheat-grass alternes was measured in hours rather than in minutes as in other types of vegetation. No marked difference in rate of penetration by water was found between undisturbed bare soil and vegetated soil close at hand. Soil ramified by fine, fibrous root systems was neither more nor less pervious than that penetrated by large, deep taproots such as those of *Liatris punctata, Amorpha canescens,* and *Rosa arkansana.* These results are not in agreement with those of Pearse and Woolley (1936), who used different equipment and a procedure which involved the flowing of a thin sheet of water over sloping ground and brought into play the damming action of the vegetation. However, Musgrave and Free (1936), who used the cylinders, found that neither alfalfa nor bluegrass increased infiltration enough to account for their effectiveness in reducing runoff. Infiltration into the loose, granular soil characteristically occupied by the sod form of big bluestem was consistently more rapid than into soil of the 11 other types tested. Dead crowns failed to absorb even the first two inches as quickly as big bluestem. Whether grasses, such as big bluestem and wheat grass, have the ability to change the structure of the soil or whether they

merely are better adapted to loose and hard soils, respectively, remains to be shown.

Although the sod-forming grasses have been badly depleted by drought, little erosion by water is likely to occur on prairie slopes. That the soil is unusually high in decaying plant material was indicated by the abundance of certain saprophytic fungi, notably *Simblum sphaerocephalum*. In addition, numerous rapidly growing annuals quickly clothe areas bared by death of perennials. Composite shallow soil samples taken at random from each of 5 prairies yielded seedlings of 42 species during 5 months of care in the greenhouse. Annuals constituted 34 of the species and 92 percent of the seedlings, most of which appeared the first month. Six-weeks fescue was by far the most abundant species.

SUMMARY

The drought of 1936 continued the destruction which in 1934 so greatly changed the composition of native vegetation of the true prairie. The summer of 1936 was the hottest and driest ever recorded in eastern Nebraska.

Studies were made of 100 permanent list plots, together with estimates of abundance of all species occurring in randomly selected temporary plots on nine annually mowed, but ungrazed, prairies in 1936 and 1937.

Perennial grasses were reduced in abundance 22 percent, perennial forbs 10 percent. Annual forbs, ruderals, and grasses were 3 to 6 times more abundant in 1937 than in the preceding year. Big bluestem was reduced 28 percent in abundance and 20 in percentage occurrence. Similarly, little bluestem lost 75 and 68 percent; blue grama, 6 and 9 percent; June grass, 69 and 43 percent; and Kentucky bluegrass, 48 and 57 percent. Western wheat grass increased 30 percent in abundance and side-oats grama over 8 percent. The corresponding increases in percentage occurrence were 36 and 100 percent. The total density of the vegetation remained nearly constant in the permanent plots, since annuals replaced the perennials.

The increase of 6 percent in number of bare square decimeter units of observation in permanent plots was due largely to disappearance of *Poa pratensis, Bouteloua curtipendula, Andropogon furcatus,* and *Erigeron ramosus.* Among the invaders of bared units, Festuca, Hedeoma, *Bouteloua curtipendula,* and Agropyron ranked foremost.

Greenhouse care of composite random samples of bare surface soil secured in August, 1937, showed that seeds of 8 perennial and 34 annual species were present. Annual plants constituted 92 percent of the population.

There was an increase of 5 percent in the number of species per plot (13.1) in spite of consistent losses of perennial grass species. Perennial forbs were inconsistent but annual grasses, annual forbs, and ruderals, almost without exception, made gains.

The general height of the vegetation was greater in 1937 in response to a supply of moisture which was more nearly normal than in 1936. No dwarfing occurred which could be attributed to drought injury received the preceding year.

Slope exposure had a marked influence on behavior toward drought. Perennial grasses were more dense and suffered a lower loss on mesic slopes than on xeric slopes or on level ground. Long-lived forbs were most dense and most injured on the level but they gained 10 percent on xeric slopes. Other factors than slope exposure which modified the effects of drought were deposition of drifting soil and alluvium, burning, hail, grasshoppers, variation in previous dates of mowing, and variation in permeability of the soil to water.

The widest range in soil moisture content was found in big bluestem, while soil occupied by blue grama had a lower average content and a narrower range. No consistent relationship could be found between any kind of alterne and the chloride content, carbonate content, or pH of the soil underlying it. However, the rate of infiltration of water into the soil in certain types of vegetation was characteristic. Steel cylinders 4 inches in diameter were pressed into the soil to a depth of 14 inches and 4 inches of water were added, one at a time, to the inch of cylinder remaining above the surface of the soil. Big bluestem soil absorbed most readily and the soil occupied by wheat grass least rapidly of the twelve types measured. Large taproots did not differ from fine, fibrous ones in their influence on the rate of infiltration when the damming action of the vegetation was barred.

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