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## GRASSLAND PATTERNS IN 1940<sup>1</sup>

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Major changes in grassland have now been followed for a decade over a considerable portion of true prairie in Nebraska and Kansas. The replacement of portions of this association by mixed prairie has been described (Weaver, '43). This major change resulted from the enormous increase or invasion of western wheat grass (*Agropyron smithii*)<sup>2</sup> and the development of an understory of blue grama (*Bouteloua gracilis*) or buffalo grass (*Buchloe dactyloides*). But numerous areas of true prairie were only partially occupied by western wheat grass. Nearly all of the original cover of bluestems and associated species, however, was greatly opened if not completely destroyed by successive years of desiccation (1934 to 1940). Some degree of recovery was attained during the best years of the dry cycle and at the end of the drought several types or communities of vegetation formed a veritable mosaic in the prairie landscape. In this paper the vegetation of four representative prairies is described as it appeared at the end of the drought. This study, with the preceding one, gives an authentic record of conditions at the end of the period of great desiccation over the entire central portion of true prairie which has been so greatly damaged.

The communities of this prairie association and their composition and structure as they appeared just preceding the dry cycle have been described (Weaver and Fitzpatrick, '34). Root depth and

other characteristics of underground parts, which played such an important part in resisting drought, had been investigated even earlier (Weaver, '19, '20). The process of destruction itself as it occurred in 1934 has been described (Weaver, Stoddart, and Noll, '35), and the results of the drought in Iowa, Nebraska, and Kansas during the following year have been recorded (Weaver and Albertson, '36). In addition, the major changes in this grassland as a result of continued drought have been presented by Weaver and Albertson ('39 and '40). Contributions by Robertson ('39) and Weaver, Robertson, and Fowler ('40) added further information. Finally, a resurvey of grasses, forbs, and underground plant parts was made at the end of the great drought in 1940 (Weaver and Albertson, '43). In this last publication, however, the communities or types of vegetation, most of which were developed as such only at the end of the drought, were given but incidental attention. They now constitute the framework of the newly restored prairie wherever it occurs, and the course of their development, since the process has neared completion, is much more clearly perceived.

### BELLEVILLE PRAIRIE

Four miles east of Belleville, Kansas, there is a well-drained, north-sloping upland prairie. Originally it consisted of 30 acres but about half of it was set aside for pasture. The portion continuously studied consists of a 15-acre tract with long, east, west, and north slopes and a well-developed broad ravine along the entire north side. The soil is a pervious black loam derived from soft limestone parent material. It is a deep soil with good water-holding ca-

<sup>1</sup>Contribution from the Department of Botany University of Nebraska, No. 142. This study was made with the aid of a grant from the Penrose Fund of the American Philosophical Society.

<sup>2</sup>The nomenclature of grasses follows Hitchcock's Manual of the Grasses of the United States; that of other plants Britton and Brown's Illustrated Flora.

capacity and like the soil and subsoil at the other stations circumneutral in reaction.

It was first studied in 1931. The lowest part of the ravine bore a pure stand of slough grass (*Spartina pectinata*). About 5 acres supported an excellent stand of big bluestem (*Andropogon furcatus*) with a little Indian grass (*Sorghastrum nutans*), and with intermixed tall panic grass (*Panicum virgatum*) and nodding wild rye (*Elymus canadensis*) on the wetter margins. There was a good understory of Kentucky bluegrass (*Poa pratensis*). A small patch of western wheat grass occurred in one portion underlaid with a claypan. The higher land on all slopes was dominated by little bluestem (*Andropogon scoparius*) with about 15 per cent of June grass (*Koeleria cristata*) and a considerable amount of big bluestem. The steep portions of the hills showed locally almost pure alternates of buffalo grass and blue grama. About these, as well as throughout the bluestem sod, side-oats grama (*Bouteloua curtipendula*) was well distributed.

Drought began here in 1933 and was very severe in 1934. By 1935 the small wheat grass alterne had developed into a large one 2-3 rods wide and 10 rods long. Dust had covered most of the lowland 0.5-1 inch deep and nine-tenths of the bluestem area was occupied by a nearly pure stand of wheat grass. The slough grass area was much less extensive and had been replaced in part by tall panic grass and nodding wild rye. Some bluegrass still persisted. A dust cover of even an inch was very detrimental to the bluestem. Where dust, carried in from a field on the south, blew from the hillside and did not lodge on the steep bank, the uncovered area was still occupied by big bluestem. Otherwise these steep banks too were sodded over with wheat grass (fig. 1). Nearly all low-growing forbs were absent.

Where much dust was deposited on the uplands, an open stand of wheat grass

prevailed with only relicts of former grasses. Here the basal cover usually did not exceed 2 per cent. Little bluestem was all dead on the west-facing slope, and only traces remained on the east one. Big bluestem was represented by mere relicts. In fact, fully 95 per cent of the original tall grass had died; where most sheltered, scarcely 25 per cent remained. There was no Indian grass, only a little side-oats grama, and small amounts of June grass. Many plants of cactus (*Opuntia humifusa*) had died and decayed.

Although both blue grama and buffalo grass had suffered considerable losses, as shown by marked thinning of the stand, they were rapidly recovering. They still held their former areas and buffalo grass especially was spreading rapidly. New centers were being established over the slopes. *Aster multiflorus*, only 8 to 12 inches tall, formed great patches and was rapidly repopulating the bared soil.

Great bare areas were everywhere and erosion by wind and water was imminent. Plants of the understory had disappeared. Weeds populated the soil thinly in places, elsewhere they grew thickly. The chief invaders were *Bromus secalinus*, *B. tectorum*, and *Festuca octoflora*. Other weeds of much importance were *Silene antirrhina*, *Lepidium densiflorum*, *Hordeum pusillum*, *Plantago purshii*, and *Chenopodium album*.

Although 1936 was a very dry year, the deficiency below normal rainfall at this station was only about half that of 1934. Vegetation on low ground grew well until late in June, but that on upland was dwarfed and the cover was very open. Blue grama and buffalo grass thrived, however, and formed nearly pure communities on exposed slopes.

In 1937 the growing season was one of low rainfall. All but the most xeric grasses were again reduced in abundance, although the drought-evading wheat grass thrived. Vegetation was much



FIG. 1. (Upper) lower steep portion of the north-facing hill at Belleville, Kansas, showing the relict big bluestem (*Andropogon furcatus*) on the slope with western wheat grass (*Agropyron smithii*) above and below. Photo July 15, 1938.

FIG. 2. (Lower) characteristic sharp boundary line which occurred between different types of vegetation late in the drought cycle. By 1942, when this picture was taken, both the blue grama-buffalo grass community in the foreground and the big bluestem type in the background had greatly increased in density, but the boundary line established during drought was still maintained.

dwarfed. There was a great decrease in the weedy *Aster multiflorus* and most other forbs. Annual grasses and ruderals were abundant in spring. There was much further reduction in the density of little bluestem and such a marked increase in western wheat grass that the dominance of the widely spreading big bluestem was challenged. Many more

or less clearly defined types of vegetation were becoming established.

In 1938 there was considerable thickening of the vegetation under a greatly increased water content of soil. On low ground, big bluestem had formed numerous dense bunches in 1936. The following year the interspaces were occupied in part by bluegrass, nodding wild rye,

tall panic grass, and other species. Big bluestem, during this growing season, changed rapidly to a sod former, and occupied much territory even on high ground (fig. 2). In places on lowland it had been heavily invaded by wheat grass and formed either the big bluestem-wheat grass type or was second in rank to wheat grass. During this excellent year for growth, this prairie, which had suffered so long from repeated desiccation, showed very definite types of vegetation. Hence, the entire area was mapped during the summer of 1938 by means of a plane table and alidade with the assistance of Dr. J. H. Robertson and Dr. R. L. Fowler. To secure greater accuracy, the smaller communities were first mapped on a large scale and then reduced to the smaller one shown in figure 3. It may be noted in the legend of figure 3 that there were only five types which were almost pure. Each of the other five were clearly dominated by two species. In some areas dominated by *Agropyron smithii* and *Bouteloua gracilis*, the wheat grass was more abundant. This is indicated by the symbol for wheat grass standing out more clearly than that of blue grama. Conversely, where blue grama was more abundant its symbol is darker than that of wheat grass. The same scheme was used for mixed *Andropogon* and *Bouteloua*, and *Andropogon* and *Agropyron*. Thus, so greatly had drought disturbed the cover that there were 8 mixed types. The mapping was done accurately to within 3 feet of the actual community boundaries which were very distinct in nearly every instance (figs. 4 and 5).

Upon entering the prairie from the north, one faced the steep north slope of the hill which was about 25 feet above the valley. Several ravines had been eroded into this slope, but their rounded bottoms were sodded as was also that of the main drainage way along the entire north side, which began on the north-east side (note contour lines on map).

Any runoff water from the steep north-east-facing slope in the southwest portion of the prairie and the east-facing one on the west side entered another ravine, also completely vegetated. This ravine extends to the northwest corner. The southwest and west slopes beyond the ravine are only moderately steep. The hilltop is broad and slopes gently both west and east. It extends northward from the southeast side, where it is highest, and ends in the steep bank along the northern border. The east slope is gentle and in the south part of the prairie extends to the eastern border.

*Panicum virgatum*, growing in a nearly pure stand, occupied the lowest portion of the north ravine including territory where a good growth of *Spartina pectinata* occurred before the drought. *Elymus canadensis* occurred as a belt a few feet wide in the lower portion of the southwest ravine.

Even casual observation of the map shows that big bluestem either in pure or mixed stands occupied the largest part of the prairie. In pure stands on low ground it had suffered least from desiccation and formed a dense cover, often with considerable amounts of *Sorghastrum nutans*. As in the preceding lowland types, there was a fairly good undergrowth of bluegrass, and a slight intermixture of other tall grasses. Forbs were scarce. Big bluestem had occupied some of the area which before the drought had been inhabited by wild rye or tall panic grass. On the lower slope a thick stand occurred, since this was originally big bluestem vegetation. But higher up the slopes and especially in the large area on the hilltop the stand was thinner. For here, as in smaller relict patches of this type, little bluestem had died several years earlier and big bluestem had made only intermittent progress in spreading its rhizomes into the spaces thus bared. In fact, the stand of big bluestem on upland was originally only 10 to 20 per cent. It had increased greatly; in some places there was a dense

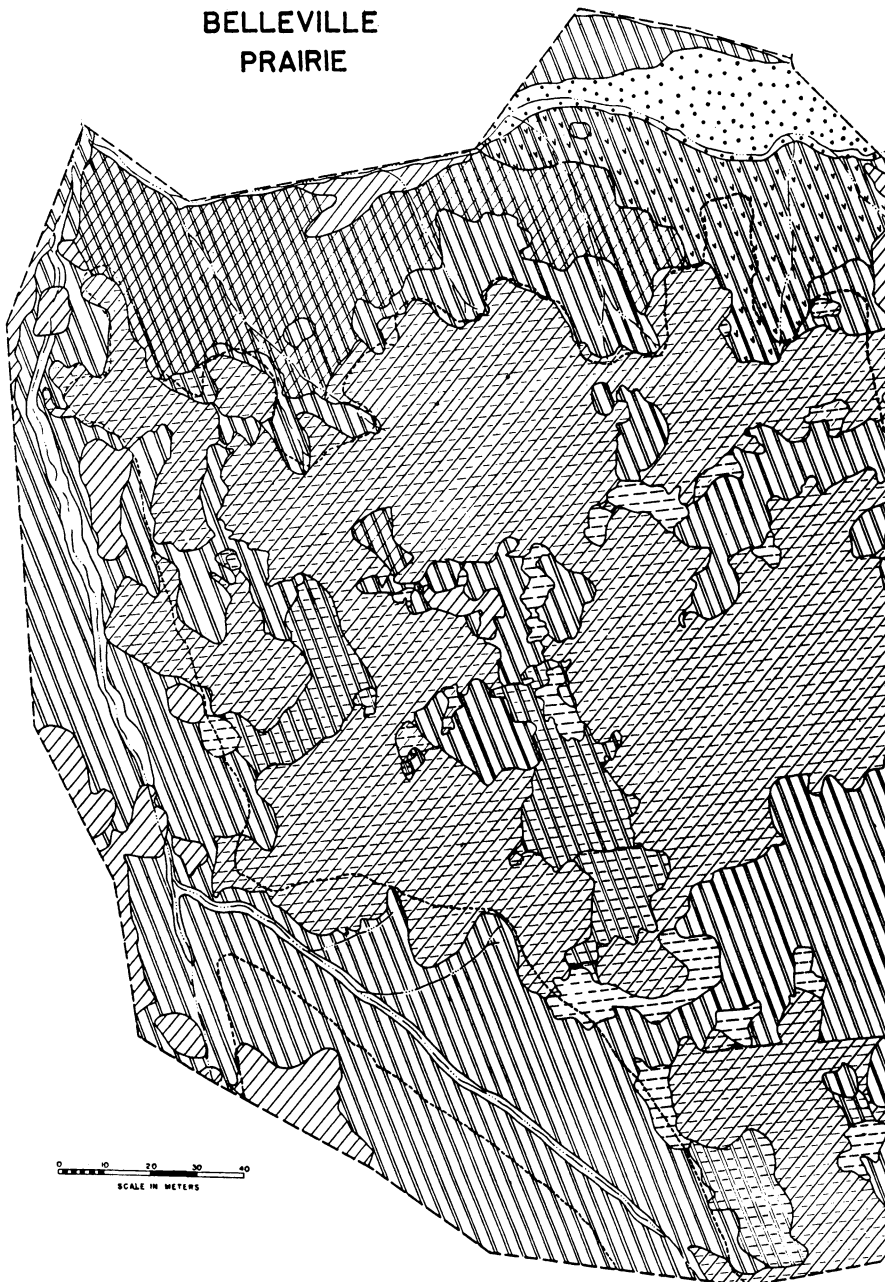
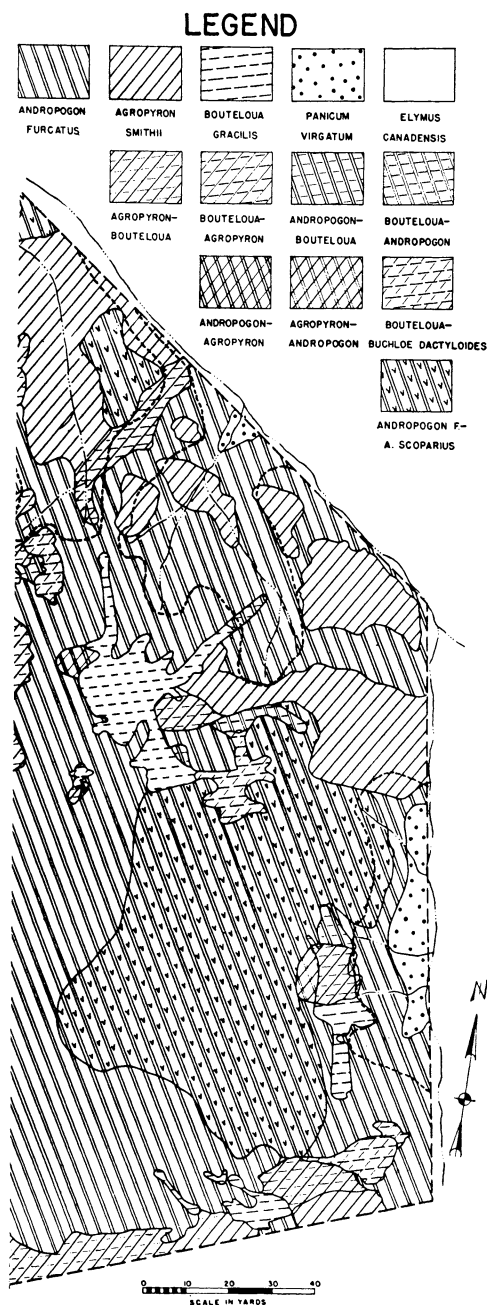


FIG. 3. Map of Belleville prairie made in the summer of 1938. The central area is a nearly flat hilltop, highest in the southeast and sloping gently northwestward but also to the east and southwest. The long broken lines alternating with dots indicate ravines. The short broken lines follow the brows of hills.

*(Part of Fig. 3 on opposite page.)*



stand and in nearly all a good cover of debris.

The original upland prairie cover of mixed little and big bluestem remained in two areas of considerable size. It is designated as the *Andropogon furcatus*-A.

*scoparius* type, since in most of it big bluestem was the more abundant near the end of the drought. In fact, little bluestem had made only slight recovery. The north area was nearly all on the north-facing slope, the larger south one on the middle and lower east slope (fig. 3). Both occurred where drought was least severe. Only in a few places did little bluestem compose 50 per cent of the cover; in these locations it had been as much as 80 per cent. Here the bunch type prevailed, but the sod-mat type was found where a large percentage of big bluestem occurred. Side-oats grama and June grass were other common mid grasses, and tufts of blue grama and buffalo grass were found. This type had maintained more forbs than any other but even here they did not exceed 20 perennial species. Nowhere was the cover dense; the understory had been all but destroyed by drought.

A large area of mixed *Andropogon furcatus*-*Agropyron smithii* occurred on the nearly level land near the north ravine. High south winds had carried in dust from the adjacent field. Some was deposited on the hilltop and a portion was blown over the steep north slope and deposited at the base of the hill. Dust deposit, however, was only supplementary to drought in causing the opening of the original prairie cover. Wheat grass soon became abundant in the semi-bared soil and large amounts of side-oats grama also thrived and waned on alternating years, depending upon amount and distribution of precipitation. It was the third most important grass in this type and sometimes occurred in small, almost pure patches. A single area of *Agropyron*-*Andropogon* mixture occurred near the southeast corner.

*Agropyron smithii* occurred in many small pure stands, mostly on peripheral parts of the prairie. On the south and west its dominance had resulted from dust covering the original vegetation. The sparseness or complete absence of other species, including forbs, in this



FIG. 4. (Upper) community of *Agropyron-Bouteloua* in the foreground and *Andropogon furcatus* in the background. This view on the gentle north slope was photographed August 11, 1939.

FIG. 5. (Lower) view showing the usual sharp boundary between the *Agropyron smithii* type (foreground) and relict *Andropogon furcatus-A. scoparius* type in the background. Photo June 15, 1938.



type was a striking phenomenon. Transition to the adjacent big bluestem or other types was always abrupt, the ecotone rarely being more than three feet wide. In old stands, the stems were very numerous but between them the black soil showed plainly since there was little debris. Bluegrass was never found under wheat grass although it occurred regularly under bluestem and other more mesic grasses. Often the heavy growth of wheat grass on lowland lodged and formed a complete foliage cover. This springy mat, about 1 to 2 inches thick, was held 5–8 inches above the soil.

Numerous, irregularly shaped areas of *Bouteloua gracilis* occurred on the uplands. These were both much larger and more widely distributed than before the drought. Where the soil was partly or entirely bared seedlings of this species grew even during certain dry years, while established relict bunches released from competition developed into large mats. Thus, old areas were enlarged and many new ones established. Frequently the islands of this xerophyte were in direct contact with big bluestem (fig. 2). The blue grama stand varied from a rather dense one with open spaces only between the pieces of sod to others where individual bunches were fairly well aggregated. While pure stands of *Buchloe dactyloides* did not occur, mixtures of these short grasses were not uncommon. The mixed sod was denser than where blue grama grew alone. These low-growing grasses had thick mats of dead leaves in 1939, which with older debris covered much of the soil with a carpet 3–4 inches deep. When a few weeks of good weather prevailed, the hillside was covered with dense foliage 8–12 inches high even in years of severe midsummer drought. Interspaces in the mats, even if small, were filled with annuals, especially *Festuca octoflora*, *Hordeum pusillum*, *Bromus tectorum*, or *B. commutatus*. In fact, the short grass communities could be distinguished at

some distance from adjacent types by the light color of these dried annuals.

As early as 1935–36 western wheat grass occurred in many places on the drought-swept and partly dust-covered hilltop. It usually extended just beyond the brow of the north-facing slope but stopped abruptly in contact with the relict big bluestem (fig. 1). From these centers it spread rapidly and widely often forming pure stands. Synchronously with the spreading of wheat grass, the short grasses migrated by seed and stolons and established new holdings. Mutual invasions by mid grass and short grasses had resulted by 1938 in a very large area of mixed grasses—the Agropyron-Bouteloua type (fig. 3). Buchloe was much less widely distributed than Bouteloua.

Wheat grass is the only species that regularly invaded short grasses, although side-oats grama was found, even abundantly, in the openings between the sod-mats before wheat grass invaded. The establishment of the understory of short grasses was not complete over the entire area but continued its spread in 1939. The soil was fairly well covered with debris in the mixed prairie type.

The spring and early summer of 1939 were moist but midsummer drought was severe. The bluestems wilted, wheat grass dried, and even half of the foliage of the short grasses lost its green color. In early summer blue grama thickened its stand under the wheat grass and here also buffalo grass extended its stolons widely. The stands of both short grasses also became denser in their own types or mixtures. Wheat grass more completely invaded short grass areas. This grass was always taller on its invading periphery than in soil where it had already greatly depleted the water content. The normal 8-inch foliage height in June in well established stands increased to 18 inches in the open territory newly occupied. Growth was more rapid here too. In addition to the leaves being a third to a half wider, they were also

more numerous on the more rapidly growing culms. The interspaces between mats of blue grama were threaded with branched rootstocks 3 feet long but at first with only 10–12 widely spaced vigorous stems. In older stands, stems often occurred at the rate of 12–24 per square decimeter. Wheat grass was the only species which spread, even if thinly, throughout well-established sod of short grasses. Seedlings and mature plants of side-oats grama, however, were often found in the larger interspaces which were otherwise unoccupied, at least above ground. Wheat grass also thickened its stand where it occurred in mixture with big bluestem.

The mosaic of grassland types stood out clearly everywhere in 1940 as it did in 1938. Short-grass types adjacent to the flourishing bluestems appeared as depressions in the landscape. The seven-year drought had finally terminated.

Detailed examinations of the upland soil to a depth of four feet in the margins of adjacent communities revealed no differences. This was not surprising, since most of the soil was formerly occupied by bluestems. The various grassland patterns had resulted from a bared or nearly bared soil being repopulated by different groups of species. The present mosaic cover is certainly not the climax. It is only a very definite stage in progress towards stability.

#### HEBRON PRAIRIE

This prairie is a rolling upland tract of about 30 acres. It lies two miles south of Hebron, Nebraska. The soil is a silt loam into which water infiltrates readily and one of good water-holding capacity. It is a deep chernozem soil, the carbonate layer occurring at about 48–55 inches. Before the drought, the prairie was dominated by *Andropogon scoparius* of the xeric bunch grass type intermingled with 5 to 20 per cent of *A. furcatus* on the upland generally but on dry slopes with a high percentage of

*Bouteloua curtipendula* and *B. gracilis*. *Buchloe dactyloides* was rare but *Koeleria cristata* and many species of forbs were abundant. *Poa pratensis* occurred more or less throughout the understory.

Losses of vegetation by drought in 1934 varied from 95 per cent on upper and middle slopes of south-facing hills to 10 per cent near their bases. With a few exceptions, they were only slightly less on north hillsides. The native perennial grasses were completely killed over many square rods and relict patches remained only in ravines and other favored places.

An excess of 10.5 inches above the normal rainfall fell in 1935. This permitted drought survivors to develop, and made a survey of actual losses more certain. The most conspicuous feature was the dead bunches of little bluestem, since that species had been most abundant. Shoots had appeared, however, around the periphery of many clumps. The dead crowns of big bluestem were also everywhere. All species of grasses had suffered severe losses, but blue grama was injured the least. Surveys showed that 90 per cent of the basal cover was dead in the driest places on the slopes. This decreased to 20 or even 10 per cent at their bases. Over the prairie as a whole, 60 per cent of the former vegetation had succumbed. Even the best remaining cover was very open.

Two large areas of western wheat grass had become established in places covered 0.25 inch to more than 1 inch deep with dust. Later, several smaller ones appeared and all remained intact until the end of the dry cycle, although much modified by an understory of blue grama or, less frequently, buffalo grass.

Whole hillsides were covered with *Festuca octoflora* which the wind had sown thickly in most places but left others bare. By midsummer this annual had dried and given the landscape a brownish tinge. Elsewhere, *Hordeum pusillum* and *Bromus tectorum* were common. But they also soon matured

and the dried cover was relieved only by the green leaves of the widely spaced, surviving bluestems and other perennial grasses. An abundant crop of *Koeleria cristata*, 6 inches high by midsummer, had developed from an ample supply of seed. Survivors of *Bouteloua gracilis* were common; even small amounts of *Poa pratensis* were found in the most protected places.

Several forbs, relieved from competition of the perennial grasses, increased enormously. *Aster multiflorus* was abundant nearly everywhere. Rosettes of *Erigeron ramosus* formed almost a continuous understory over wide areas while matured plants with dried stems 2 feet tall occurred nearly throughout, sometimes in hundreds per square meter. Large plants of *Silene antirrhina* were common, and *Leptilon canadense* thrived as if growing in a field. *Ionoxalis violacea* occurred in such dense stands that its foliage almost concealed the soil. Propagules of all species found much open soil for invasion, since the perennial grasses had been so greatly thinned. Such gains as the grasses made toward recovery in 1935, however, were more than offset by further losses during the extremely dry year which followed.

In 1936 two long periods occurred without rain, one of 39 days duration from mid-June until late July and another of 20 days in August. Precipitation for the entire year was slightly less than 13 inches. Maximum temperatures reached 108°, 111°, and 109° F. in June, July, and August, respectively. Moreover, burning the prairie had been used as a method of weed control. Vegetation already weakened by previous adverse conditions was further depleted, since the year was about as dry as 1934. *Koeleria*, which had seeded widely the preceding year, was usually abundant over most of the prairie both as seedlings and more mature plants. It was most conspicuous along the cracks in the soil on poorly covered ridges.

Environment in 1937 was somewhat

less severe. Vegetation grew vigorously but weedy grasses and forbs still largely prevailed. Downy brome grass (*Bromus tectorum*) was distributed thinly over the whole prairie. Little barley (*Hordeum pusillum*) and six-weeks fescue (*Festuca octoflora*) were more abundant than in the preceding year, despite a general increase in the density of the perennial vegetation. Bluegrass had become rare but June grass was especially abundant.

There was marked improvement in 1938. The weedy stages of the subsere had nearly disappeared. Even downy brome grass was much less abundant. Big bluestem had taken over the ravines and lower slopes and it grew to a remarkable size even on the uplands. Here it spread rapidly into soil formerly occupied by little bluestem; in fact, it promptly reclaimed most of this space. Little bluestem, now reduced to only 5 or 10 per cent of its predrought stand, was recovering and spreading slowly in the most mesic sites. Side-oats grama had spread very widely and filled in many interspaces between other grasses. Large patches of blue grama, though still very open, were becoming denser as an abundance of tillers and seedlings developed. June grass, partly as a result of fire, was extremely abundant and reclothed much bare soil. As many as 30 bunches were found commonly in a single square meter and the very numerous spikes per bunch produced an enormous seed crop. Forbs, with few exceptions, had been greatly reduced. *Ionoxalis violacea*, however, was still extremely abundant and widely distributed. Aster, although still abundant, was usually suppressed. There was much less total bare ground since the interspaces between perennials were smaller, but six-weeks fescue remained an interstitial of great importance. Over the prairie as a whole, aside from western wheat grass, the order of abundance of grasses and sedges was big bluestem, side-oats grama, blue grama, six-weeks fescue, little barley, brome-

grass, Pennsylvania sedge, little bluestem, buffalo grass, and bluegrass.

A summary of the outstanding conditions in 1938 was as follows: A fairly complete occupation of the soil by grasses (although some were weedy annuals) and a correspondingly great reduction in bare ground. Suppression to pre-drought normal of nearly all forbs that had greatly increased, and the nearly complete absence of weeds. A remarkable spread of big bluestem, side-oats grama, blue grama, and the beginnings of recovery of little bluestem. Lastly, there were numerous narrow ecotones between wheat grass and big bluestem where competition was especially severe.

In 1939 moist soil prevailed in spring and early summer but there was a severe midsummer drought. As a result of the excellent early growth vegetation became thicker and a mosaic of alternates or types became clearly evident. They were even more sharply defined in 1940.

The most extensive type was *Andropogon furcatus*. Where the bluestem prairie was partially covered with dust on its southern (upper) slope, little bluestem succumbed but much of the big bluestem survived. It had since thickened its stand until it was 80 to 95 per cent; there were only a few other grasses, including some relict little bluestem. For a long time big bluestem resisted drought in the bunch habit; only in 1938 did it become a sod former. Other extensive alternates of this species occurred in ravines and on lower slopes. Over part of its area there was an intermixture of side-oats grama, blue grama, or recovering little bluestem. In very local areas side-oats grama composed as much as 30 per cent of the cover. But usually both the main areas and widely scattered fragments of this type were overwhelmingly big bluestem. Nowhere was it intermixed with western wheat grass (fig. 6).

A second type was relict big bluestem and little bluestem. Little bluestem

showed a good recovery in 1939 and on certain north-facing slopes a rather open mixture of these two species occurred. The patches covered only a few square rods but were clearly demarked notwithstanding the presence of much of the rapidly seeding but poorly competing June grass. As in the big bluestem type, there was a fairly good cover of debris, but here the understory of various low-growing species was beginning to return.

A third type was *Bouteloua gracilis*. The largest area occurred just below the belt of big bluestem near the hilltop. It was about 100 yards long and half this distance in greatest width. In addition, long arms of short grass extended far down the hill and on ridges clear through the big bluestem belt on the lower slope to the ravine. In most places it was composed of very large predrought bunches spaced 5-10 inches or more apart. This year the prairie was remarkably free from weeds, and irregular patches of the black soil 5-12 square feet in extent could sometimes be seen. But usually abundant smaller bunches partly filled the spaces and portended a dense future cover. In this type neither wheat grass nor buffalo grass occurred. In the mixed short-grass type where buffalo grass was present, it was beginning to fill in the spaces with its dense mats of stolons. In addition to several extensive large areas of the blue grama type, many smaller but very distinct ones occurred (fig. 6).

Western wheat grass was found only rarely in dense pure stands. Almost everywhere an understory of short grasses had developed. In fact, blue grama had replaced it over parts of its former territory (Weaver, '43). Some formerly pure but open stands of blue grama had likewise been invaded by wheat grass. The result of these mutual invasions was the *Agropyron-Bouteloua* type. Frequently blue grama was the leading dominant and wheat grass was represented by only a few stems per



FIG. 6. (Upper) alternates of prairie types at Hebron, Nebraska, during the July drought of 1940. Light foreground is blue grama and dark vegetation is dried big bluestem. The light type beyond is western wheat grass which recurs again beyond a second alternate of (dark) big bluestem.

FIG. 7. (Lower) portion of a rolling prairie near Lincoln, Nebraska, invaded by western wheat grass in seven distinct places during the great drought. These are the dark patches of vegetation, except the long one in the ravine (foreground) which is Kentucky bluegrass, an invader on soil washed in from an adjacent field. In this fall-mown prairie the wheat grass is 5 inches tall; the bluestems have not yet renewed growth. Photo May 2, 1940.

square meter. This represented either an early invasion of wheat grass or its later suppression. Both conditions had given rise to the *Bouteloua-Agropyron* type.

Intermixtures of many species with little expression of dominance occurred rarely and only on the steepest and driest ridges where the original cover had been almost entirely destroyed. Even traces of the weedy seral stages remained here. Interstitial species of grasses and those which usually occur in disturbed places in prairie were intermixed here in equal amounts with the regular type dominants. These included side-oats grama, June grass, hairy grama (*Bouteloua hirsuta*), tall dropseed (*Sporobolus asper*), Scribner's panic grass (*Panicum scribnerianum*), purple lovegrass (*Eragrostis spectabilis*), and others.

Over this former bluestem prairie as a whole, there was now a population which was estimated, after long and careful study, as containing the following percentages of grasses: big bluestem 40, blue grama 25, side-oats grama 16 (but never occurring as a type), wheat grass 8, little bluestem 8, and other species 3 per cent. These grasses composed the several well defined types with such sharp boundaries that they might have been mapped along their narrow ecotones. This was the condition in 1940 when good rains came.

#### OTHER PRAIRIES

A prairie near Lincoln, reserved for experimental work, was early invaded by western wheat grass. In 1940 it was in control of numerous widely separated patches, mostly a few square rods in extent (fig. 7). The most extensive type was needle grass (*Stipa spartea*). This species had spread widely from its original small holdings and formed several distinct communities some of which covered several acres. The prairie dropseed (*Sporobolus heterolepis*) type was also well represented in several smaller but distinct units. The

relict bluestem type was found only on lower slopes. A few ravines and one well-protected east slope maintained excellent representation of the degenerate type dominated by nearly pure stands of Kentucky bluegrass. A somewhat equal mixture of several grasses still covered about one-third of the prairie, and one bared hilltop was dominated locally by sand dropseed (*Sporobolus cryptandrus*). Thus, this 20-acre prairie also presented a patchwork of types, usually with rather sharp boundaries. The basal cover, however, was considerably less than that which was present before the great drought.

Near Crete, Nebraska, a 120-acre prairie had developed a very extensive community of nearly pure needle grass on a long south slope and ridge, and smaller ones elsewhere. Western wheat grass had completely occupied even a larger territory in great alternates and numerous, smaller, isolated patches. Big bluestem, the almost sole occupant of extensive areas, since scarcely any little bluestem survived, had thickened its stand during 1935 and 1938 and presented a distinct type. Certain areas were claimed by prairie dropseed as the dominant. Even bluegrass which remained in a large ravine had spread over flat land at its head and in clothing the nearly bared soil formed another grassland type. But in 1940 much territory was occupied by a considerable mixture of many species on more or less equal terms. They added a sixth pattern to the greatly diversified prairie landscape.

#### DISCUSSION

Conditions presented at Belleville, Hebron, Lincoln, and Crete have been found regularly in nearly all true prairie that was not completely overwhelmed by western wheat grass.

It is of great interest that such changes and adjustments as have occurred under the stress of this great drought are among the species of prairie alone.

Ruderals have been only transient, and the xeric species which rose to dominance had previously been normal components of true prairie even if minor ones.

The mosaic of grassland patterns at the end of the dry cycle represents merely a phase in recovery of the vegetation. Only the period of occupation of all of the territory has neared completion. Many years with approximately normal precipitation will probably be required for the less xeric grasses to suppress the more xeric ones and to regain their great abundance and wide distribution characteristic of these dominants under the usual climatic control. Much time will also be required for this grassland to develop its numerous societies of forbs, to restore its layered structure, and to regain its usual high degree of stability (Weaver and Flory, '34). The beginnings of these changes have already been observed within the three-year period (1940-43) of postdrought.

#### SUMMARY

The numerous communities or types in true prairie at the end of the dry cycle (1934-40) were so fragmented but possessed such definite boundaries that they appeared as a mosaic of various grassland patterns.

In true prairies not entirely overwhelmed by western wheat grass, characteristic types in 1940 were big bluestem, needle grass, western wheat grass, blue grama, and prairie dropseed. Other common communities were relict big bluestem-little bluestem, mixtures of several species without expression of dominance, and co-dominance of big bluestem and wheat grass, wheat grass and blue grama, and blue grama and buffalo grass.

One 15-acre prairie with 5 pure and 8 mixed types was mapped, so clearly were the boundaries between communities defined.

A brief statement of the original composition of the vegetation and its degree

of destruction is given for prairies at Belleville, Kansas, and Hebron, Nebraska. The temporary possession of the bared soil by a weedy flora among the terribly decimated prairie grasses, and its loss with the recovery of the grasses is described. The origin of each community and its development into the late-drought patterns are briefly discussed.

Prairie types at Lincoln and Crete, Nebraska, are pointed out to illustrate their wide variety and general distribution in a prairie cover which represents only a stage in the restoration of climax true prairie.

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