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NATIVE GRASSLAND OF SOUTHWESTERN IOWA

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INTRODUCTION

Studies of the prairie by the writer and Fitzpatrick during 1922-33 were both extensive and intensive. They were extensive in that they included an area of 60,000 sq. mi. in western Iowa, eastern Nebraska and portions of the four adjoining states. They were intensive in that a record of the kinds and distribution of grasses, the abundance and relative importance of forbs, and other pertinent data were ascertained and recorded separately for each of 135 selected areas. Since most of these prairies were examined two or more times each growing season, and many repeatedly during a five-year period, a clear, concise description of each was secured. In this study it soon became clear that the vegetation receiving an annual rainfall of 30-32 in. was better developed in many ways than that in the drier areas westward and northward with 25-29 in. mean annual precipitation. Some of these differences were pointed out by Weaver and Fitzpatrick (1932, 1934) but the prairie was considered in its entirety and space did not permit descriptions of individual prairies.

Further studies of the prairie as affected by the great drought of the 1930's (Weaver and Albertson 1936, 1944) and the history of their degeneration under grazing (Weaver and Hansen 1941) emphasized the importance of the isohyet of 32 in. as marking the place of beginning of rapid change from the mesic prairies of southwestern Iowa to the more xeric ones northward and westward.

During the first quarter of the present century

prairie hay for horses was still in considerable demand. But this was rapidly decreased with the general use of the automobile and especially the farm tractor. Not only did the need for hay decrease, but also the prairie was readily broken by use of plow and tractor. Moreover, the farmer could now easily cultivate his expanding fields of maize. Several fine remaining Iowa prairies some of 80 or more acres were broken during our earlier study and many others since that time. Indeed, it seems that all will vanish (Hayden 1946). Therefore it was decided to write the description of a typical tract of well-watered Iowa prairie that was visited many times during and since 1929.

Names of grasses are according to Hitchcock and Chase (1950) revised *Manual of the Grasses of the United States*. Other scientific names follow Gleason's (1952) *New Britton and Brown Illustrated Flora*.

AREA OF STUDY

The prairie covered a large hill half a mile in length along its level top, and the long slopes to the south, east, north and west. It also included several smaller hills with slopes extending in various directions. The large hill extended about 100 ft. above the adjacent valley but the smaller ones only 10-50 ft. The area presented some level upland, rounded hilltops, gentle to steep upper slopes and more gradual lower ones. Ravines extended downward between the hills to a limited amount of level lowland, where, in some places, small portions of wet meadows occurred. Broad

washes sometimes occupied the heads of ravines which united to form larger ones in the valleys, but no ditches had been formed. Thus, this 200-acre area was typical of the rolling to hilly topography of southwestern Iowa and the wide extent of grassland which formerly carpeted this portion of the state.

Unfortunately a single prairie of such large proportions no longer existed in the area in 1929. Hence, to a 100-acre tract at Guthrie Center there have been added prairies from Anita, Corning, and Creston to compose the prairie described. The composite description of the grasses, forbs, conditions for growth, etc. is a combined record from each of the several stations and is thus entirely typical of these mesic prairies. Exact locations of each prairie need not be given since the natural grassland cover has been greatly modified or destroyed since this study was made. The general area is 45 mi. west to 65 mi. southwest of Des Moines (Figs. 1 and 2).



FIG. 1. Prairie on north hillside near Anita, Iowa, June 22, 1938.

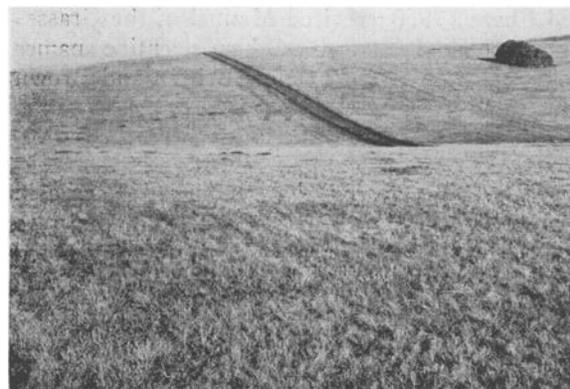


FIG. 2. Prairie in winter near Guthrie Center, Iowa.

CLIMATE AND SOILS

The prairie is located at about 94.5° W longitude and 41.5° N latitude. The climate is char-

acterized by moderately long, cold winters and a growing season of about 155 days (late April to early October) without killing frost. Average day summer temperatures are normally 75°-85°F., those of the night are about 10° less. But the maximum daily temperature may reach 100° or even 110°. The prairie soil freezes rather regularly in winter to a depth of 0.5-2 ft. The prairie is typically a land of sunshine, with about 60% in spring and 70% or more in summer. But under the cover of grass, light is frequently reduced to 20-30% of full sunlight at 12 in. above the soil and 2-7% near the soil surface. About 77% of the precipitation (31-32 in. mean annual) occurs during the growing season and 63% at night when evaporation is relatively low.

These studies were in the Shelby-Sharpsburg-Winterset Soil Association Area of southwestern Iowa. It is a loess-mantled drift plain cut by stream valleys. The crest of the ridges are 10-120 ft. above the bottoms of nearby valleys. These crests, where narrow, are round and have gentle slopes. Where the ridges are broad, they are also flat. These ridge crests are loess mantled. The adjacent steeper slopes to the bottom are usually glacial till with no loess mantle.

Shelby and Sharpsburg are the Brunizem (formerly called prairie) soils series which formed on the gently sloping to hilly uplands. They both have a dark-brown or very dark-brown A₁ or surface horizon, which is high in organic matter and contains numerous grass roots. The color becomes lighter with depth and the roots fewer. Shelby soils are on the steeper slopes, and they formed from glacial till. The Sharpsburg soils are on the gentle to rolling slopes, and they formed from loess. The Winterset soils are Humic-Gley and occupy the flat ridge divides. They have a darker and thicker A₁ horizon than the Shelby and Sharpsburg soils. The Winterset soils formed under tall and mid grasses in the loess that mantles the ridges.

All of these soils are medium to moderately fine textured, ranging from silt to clay loam. When covered with a good grass vegetation, they absorb water readily, and they have a good water-holding capacity (Simonson, Riecken and Smith 1952).

These soils offer approximately every feature favorable to plant growth. The precipitation is moderately low and the soil solution is relatively concentrated. They have abundant pore space and are nearly always well aerated to great depths. They are only slightly acid, and rich in organic matter and mineral nutrients. The natural vegeta-

tion as a product of soil and climate is the most vivid indicator of this excellent environment.

The year 1939 was the last and worst year of the drought. But during the entire growing season soil moisture depleted by the vegetation was restored more or less regularly and completely; at no time did plant growth appear to be retarded. Sampling at three stations throughout spring and summer revealed that water to a depth of 6 ft. was always available for growth, although in moderate amounts—2-5%, but usually 5-10%. This resulted not only from the amount of precipitation but also from its entrance into these silt to clay loam soils which were constantly maintained in a water-receptive condition by the continuous cover of grass. Unlike most prairies westward, this one had not been affected as regards change of structure or composition of vegetation by the great drought of 1934 or subsequently (Weaver and Albertson 1940).

TYPES OF GRASSLAND

Named after the most abundant and controlling species, this was bluestem prairie. The lower slopes and level land were clothed with a dense sod of big bluestem (*Andropogon gerardi*). On wetter land it became mixed with switchgrass (*Panicum virgatum*), which in sloughs was replaced by prairie cordgrass (*Spartina pectinata*). Hilltops and upper and mid slopes were dominated by little bluestem (*Andropogon scoparius*). It cannot compete very successfully with the taller big bluestem in well moistened soil where big bluestem produces dense shade. Hence, little bluestem is usually scarce or absent on lower slopes which receive considerable runoff and, possibly, seepage water.

On south and southwest slopes the transition from big to little bluestem usually occurs about one-third of the way up the slope, but on north and east slopes, which are less exposed to drying, this type often extends halfway up the hillside. Big bluestem extends farther up the hills along ravines, and on level hilltops it usually composes 10% and in some places nearly 50% of the vegetation. In fact, small amounts were found nearly throughout the little bluestem type. These two grasses alone composed fully 80% of the prairie cover.

COMPOSITION OF VEGETATION

In studying the composition of the vegetation, large numbers of sq in quadrats were examined. They revealed the distribution of the two bluestems as one proceeded up the hillsides. Representative examples are shown in Table I.

TABLE I. Percentage distribution of little bluestem (L) and big bluestem (B) as shown by 30 quadrats in various sites.

Species	Level base		Lower slope		Midslope		Upper slope		Level hilltop	
					South Slope					
L.....	0	0	0	2	57	61	84	66	76	59
B.....	94	93	95	87	33	31	9	17	22	32
					West Slope					
L.....	0	0	1	5	42	44	70	66	68	75
B.....	97	95	80	83	35	40	23	20	15	22
					North Slope					
L.....	0	0	3	0	50	35	65	62	64	46
B.....	92	98	90	94	44	55	25	27	25	39

The percentages are not based upon foliage cover (the area occupied by the spreading tops of the plants in the several layers of vegetation above the soil surface). This varies with the progress of the season and from dry to wet years. In July and later it was usually 85-100%. The basal or ground cover is the actual area occupied by the stems, mats, or tufts of plants about an in. above the soil surface. It is fairly stable and varies but little from month to month or year to year. The part of the total basal cover (considered as unity) composed by each species is that shown in Table I. The remaining basal cover was that of other vegetation.

Actually the total basal cover is surprisingly low. As a result of several hundred determinations made during five years it was found to average only 13.3% of the total soil surface in the big bluestem type and 15.3% in that of little bluestem. In this prairie it was greater, 14.3 and 16.1, in the two types, respectively. This difference in amount of basal cover with little change in the kind of vegetation indicates here merely more favorable conditions for growth. Where the basal cover increases greatly it indicates change in the composition of the vegetation. In Iowa true prairie it is nearly always due to disturbance and increase in Kentucky bluegrass (*Poa pratensis*).

NATURE OF BLUESTEMS

The nature of these warm-season, perennial, dominant grasses should be clearly understood. Big bluestem is a tall, rather coarse grass, with a pronounced tillering habit. Its rapid development of rhizomes enables it to produce a characteristic sod, but in dry habitats it also occurs in bunches. Growth usually begins after mid-April and development of shoots in the perennial soil is rapid. Early in June there are usually 3-5 leaves with an average height of 10-16 in. Foliage usually reaches 18-34 in. in height on lowland and 12-18 in. on the hillsides late in July. By this time a few of the basal leaves in the deep shade

have died but the 4-8 green ones above spread gracefully outward and downward. The larger leaves are often 2 ft. in length and mostly 5-12 mm wide. Flower stalks may begin to appear in July but flowering reaches its maximum in August and September. On the best watered lowlands they sometimes attained a height of 8 ft., thus extending several ft. above the 36-40 in. general level of the foliage. Flower stalks may occur at the rate of 100 to 160 per sq m, but they are usually fewer and much shorter on dry hillsides.

Dominance of this grass results from its rapid development, early tillering and rhizome production, its dense sod-forming habit of growth, great stature, and the tolerance of seedlings to shade.

Little bluestem is smaller and finer than big bluestem. It forms dense, circular bunches of sod as a result of prolific tillering and the lack of well-defined rhizomes. Bunches vary in width from a few in. to 12 or more. The density of stems composing the bunch varies with the water supply and age of the grass. But the number of crowded stems, flattened at the base, may reach 150-300 in a bunch of medium size. The bunch habit is best developed on dry ridges. Ordinarily the plants form a much interrupted sod of mats and tufts so dense that other species cannot invade but must grow between the mats and closely aggregated small bunches.

Little bluestem is often of small stature on hill crests, taller on hillsides and tallest on lower slopes. Growth is rapid and by June 1 the foliage level may reach 8-12 in., but 16-24 in. by mid-summer. The leaves are usually 4-6 mm in width and 5-9 in. long, but some are 18 or more in. in length. Clusters of flower stalks extend upward in late summer and autumn 1.5-2 ft. in dry places but 3 or more ft. under a favorable water supply. They bear axillary racemes of clustered spikelets along much of the upper half of the flower stalk. Silky gray hairs are conspicuous in autumn.

Dominance of this grass is due in part to its vigorous seedlings that tiller both early and abundantly and create a compact, dense plant cover. A fine, extremely well branched root system threads the soil not only beneath the bunches or mats but also on all sides of them.

The struggle for dominance between the two bluestems furnishes a fine example of adjustment to environment. Big bluestem with its great stature and ability to endure shading occupies the well drained alluvial soils and moist lower slopes almost to the exclusion of little bluestem. But the latter, a mid grass of only half the size of its tall grass rival, is a strong competitor in its way. Endowed with a finer and apparently more ef-

ficient root system and having a much smaller transpiring surface, it holds the drier uplands and meets its antagonist on equal terms on most mid-slopes. The success of a plant adapted to a region depends upon its competitive ability. That of the bluestems is very great (Fig. 3).



FIG. 3. Detail of bluestem grasses (*Andropogons*) in mid-June.

Big bluestem is the more widely distributed over the prairie as a whole. It was found, at least in small amounts, almost everywhere, but little bluestem was often absent in the dense shade in the big bluestem type on lower, more moist soil (Fig. 4). This was well shown by Weaver and Fitzpatrick (1934) in the analysis of 155 quadrats in the big bluestem type in portions of six states. They considered the big bluestem type as occurring where the percentage of cover of this species exceeded that of little bluestem. Big bluestem constituted 78% of the vegetation and was present in every quadrat. Little bluestem composed 2% of the plant cover and was present in only 19% of the quadrats.

A comparison of the composition of upland prairie vegetation under a rainfall of 30-32 in. with that of drier areas (25-29 in.) was also made. This was based upon intensive field studies and 180 sq m quadrats. Average percentage of little bluestem in its type increased from 52 to 56 and that of big bluestem decreased from 29 to 23. This illustrates the delicate balance between the two species of bluestem and how the tall grass encroaches upon the territory of the mid grass where water content of soil becomes more abundant.

The foliage cover of little bluestem averaged 5-9 in. higher in the wetter area than in the drier one. That of big bluestem showed differences of 6-12 in. Moreover, bunches of little bluestem and other grasses were more completely filled with

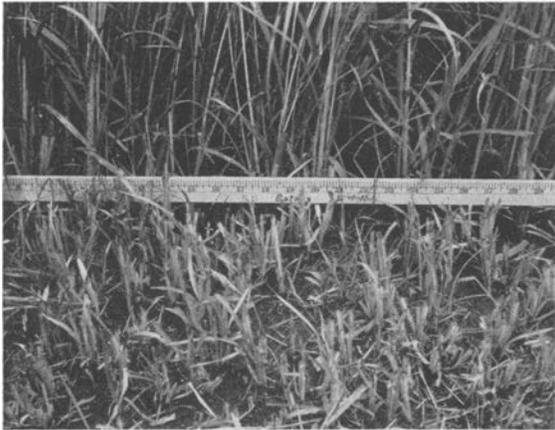


FIG. 4. Characteristic dense stand of big bluestem (*Andropogon gerardi*) in midsummer, with plants in foreground clipped to show basal cover.

stems in the area of higher rainfall. Flower stalks were larger and more abundant, and were produced even in dry years; yields of hay were also greater.

OTHER GRASSES

The little bluestem community is the only upland type (consociation) in this prairie. Here the sod is denser and the bunch habit less developed than in most prairies westward. The more xerophytic needlegrass (*Stipa spartea*) community and that of prairie dropseed (*Sporobolus heterolepis*) did not occur.

Needlegrass is a perennial, cool-season bunch grass. It usually forms relatively small, circular bunches 2-4 in. in width. It rarely exceeded 10% in abundance, and this amount was found only locally on the crest of a single ridge. Elsewhere it was usually absent or occurred only as scattered bunches intermixed with the bluestems. It renewed growth early, attained a height of 3-4 ft., blossomed and ripened its fruits, with long twisted awns, in June.

The warm-season, perennial prairie dropseed is distinctly a bunch former. It was more abundant than needlegrass. Bunches were mostly 4-8 in. in width but some attained large size, 10-18 in., by continued peripheral tillering over a long period of years. A height of 15-24 in. was attained by the long, attenuated leaves, and late in autumn the abundant flower stalks with broad spreading panicles were 2.5-3 ft. tall. It was of local occurrence on dry upper slopes in nearly pure patches or thickly intermixed with little bluestem. Isolated bunches were infrequent. In a few places this species intermixed with little bluestem on lower slopes as well. Here its percentage composition varied from 10-85%.

Side-oats grama (*Bouteloua curtipendula*), the tallest and least xeric of the gramas of true prairie, was found commonly only on the driest hills and slopes and was never abundant (Fig. 5).



FIG. 5. A large bunch of side-oats grama (*Bouteloua curtipendula*) ready to blossom.

Junegrass (*Koeleria cristata*) is a small, cool-season, bunch grass with foliage height of about 12-15 in. This was exceeded by the 25-in. flower stalks with their spike-like contracted panicles. It was scattered between the mats and bunches of little bluestem to the extent of 1-2% of the cover. Unlike most prairie grasses, it seems to depend more upon rapid reseeding than on a long life span to maintain its place in prairie.

Several low-growing perennial and interstitial panic grasses were found in small amounts. Chief of these were *Panicum scribnerianum*, *P. wilcoxianum*, and *P. praecocius*. Purple lovegrass (*Eragrostis spectabilis*) was not abundant. It is common in prairie westward and conspicuous in late summer for its reddish panicles which break off and are blown about by the wind. Prairie wedgegrass (*Sphenopholis obtusata*) and hairgrass (*Agrostis hiemalis*) were not at all abundant, and tall dropseed (*Sporobolus asper*) occurred only rarely and in disturbed places. Two sedges, *Carex festucea* and *Scleria triglomerata*, and

the slender rush (*Juncus tenuis*) were of infrequent occurrence.

Kentucky bluegrass (*Poa pratensis*), although dominant in adjacent pastures, occurred from dry hilltop to sloughs, but only in amounts rarely exceeding 1-5%. Slight invasion of this European species had resulted from the annual mowing and removal of the forage. This permitted full light for growth of this cool-season, rhizomatous grass both in early spring and late autumn. A few other species are mentioned elsewhere.

The chief grass intermixed with big bluestem, but always in small amounts, was Indiangrass (*Sorghastrum nutans*). It is almost an ecological equivalent of big bluestem in time of renewing growth, height, flower-stalk production, and time of flowering and producing seed. It is readily distinguishable from big bluestem by its more erect habit of growth, its broader and less recurved leaves with prominent ligules, and its large, yellow-brown panicles. It occurred in dense big bluestem sod as isolated stems or small clumps. This probably resulted from the fact that it is slower than big bluestem under severe competition in producing tillers and rhizomes. Aside from a few patches in lowland and ravines where it composed 8-30% of the cover, it was found sparingly throughout the prairie as a whole.

Contacts of the big bluestem community were made with the switchgrass—Canada wild-rye (*Elymus canadensis*) type. This type occurred on soils where water content was intermediate in amount between big bluestem on the drier side and prairie cordgrass on the wetter one. Switchgrass is a coarse, rank, sod-forming species. From a height of 5 ft. at the bottom of ravines, it gradually decreases to about 3 ft. near the top, where it sometimes extends as bunches into drier land. In a few localities it intermixed with big bluestem in considerable amounts, otherwise it was nearly always of little importance. Canada wild-rye also spread, but not often abundantly, from lowland high up ravines. Elsewhere it occurred sparingly. A few other grasses including *Elymus virginicus* and *Muhlenbergia racemosa* were present. Since only fragments of the more mesic and hydric types of prairie were present, they will not be described (cf. Weaver and Fitzpatrick 1934, Weaver 1954).

The following grasses which occur, at least in small amounts, in more xeric true prairie westward and northwestward were not found. They are western wheatgrass (*Agropyron smithii*), red-three awn (*Aristida longiseta*), blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), buffalo

grass (*Buchloe dactyloides*), and plains muhly (*Muhlenbergia cuspidata*).

FORBS

Prairie forbs are very diverse in their nature and to understand their relationship to the grasses and to each other one must study them at different times during the year (Fig. 6). Many forbs of early spring always remain near the surface of the soil where they grow rapidly. Within a few weeks and before they are much shaded by the grasses they produce flowers and fruit. Thereafter they may wither and die, but usually they remain green in the subdued light of the understory for a long time. Dogtooth violet (*Erythronium albidum*), prairie violet (*Viola pedatifida*), and prairie cat's-foot (*Antennaria neglecta*) are examples.



FIG. 6. Prairie at Corning, Iowa, showing the large number of native forbs.

The hawkweed (*Hieracium longipilum*), Indian plantain (*Cacalia tuberosa*) and certain other forbs maintain their territory for a time in the form of compact rosettes but later carry the leaves upward on the elongating stems and thus beyond the dense shade of the grasses.

A different plan is pursued by flowering spurge (*Euphorbia corollata*), Sullivant's milkweed (*Asclepias sullivantii*), wild indigo (*Baptisia leucantha*) and other forbs. By producing an elongated stem, sometimes 8-10 in. in height, before unfolding leaves, they avoid for a time competition with the grasses for light. The lower leaves, if any, are scale-like. The widely spaced stems scarcely interfere with the grasses and the crowns are spread partly or entirely above them.

The most severe competitors are forbs with foliage that occupies much space from the soil surface to their leafy tops. They often extend to greater heights than the grasses; in addition, the tops of some spread far outward. Sometimes the grasses are completely routed. Examples are furnished by false boneset (*Kuhnia eupatorioides*),

various goldenrods (*Solidago*), and butterfly weed (*Asclepias tuberosa*). It is believed that the greater height of most species of lowland has probably resulted from a greater water supply and especially from the struggle for light.

The relative abundance and importance of each species of forb was studied and closely estimated. Its rank, whether high, intermediate or low, was ascertained only after examining the entire prairie. Size, abundance, duration, density of stand, and gregariousness were all considered. The general criterion for each species was the actual effect of the forb on the cover of grasses and the proportion of the basal and foliage cover that it composed. Such a grouping demands a rather detailed knowledge of the species, gained only after several years of field study.

Forbs that rated highest in all or nearly all of the preceding criteria were given first rank. In this prairie there were 8 such species in addition to 1 shrub and 1 half-shrub. On the other extreme, plants that were relatively few in numbers or of infrequent occurrence were assigned to a low rank. Most of the important forbs fell between these extremes. They did not qualify in enough of the criteria to rank high, but far exceeded in abundance, size, etc. those of low rank. This ranking of species into groups of relative importance is a process to which fixed measurements cannot be accurately applied but one which, as will be shown, gives a very useful classification.

Species forming societies of the first class

The prairie shoestring or lead plant (*Amorpha canescens*) is the most abundant and most important of all upland plants, except the grasses. It also grows on lower slopes and well drained lowlands in the big bluestem type. No other half-shrub or forb has so consistent a distribution. In mowed prairie the plants produce 2-5 or more stems from the crown. Plants frequently occur at the rate of 12 to more than 20 per sq m, but the number of stems may average 2 or 3 times as many. It furnishes very palatable forage in considerable quantity and may yield 150 lbs/A of air-dry hay. Stems develop rapidly from the stores of food in the root-crown and very deep, woody taproot. Nodules occur on the roots throughout their entire length which is often 16 ft. The plant attains a height of 1.5-3 ft. The stems instead of growing erect usually lean outward. In well developed societies the cover of grasses is always reduced, sometimes to two-thirds its normal stand.

Redroot (*Ceanothus ovatus*) is a xerophytic, leafy shrub that occurs only in well drained soil,

such as dry hillsides and ridges. Where abundant, it controls to a considerable degree the presence of other species. A single plant may consist of 50 or more stems that arise from an enlarged woody crown, spread widely, and despite annual mowing, reach heights of 1.5 to about 3 ft. A single plant affects the grass but slightly, but where many large plants grow thickly, 3-5 bushes per sq m, the shade is dense. By midsummer the fallen lower leaves cover the soil and an area of 4-6 sq ft beneath the plant is often devoid of vegetation. Redroot has a strong, deep, woody taproot, with widely spreading branches which compete vigorously with the grasses for water in the surface soil. Fortunately it propagates only by seed. Its large size and persistent occurrence as isolated plants and in patches, even if not continuous, materially reduce the yield of hay.

Stiff sunflower (*Helianthus laetiflorus*) is the most widely distributed and often the most abundant forb of upland prairie. It also occurs, but less frequently, in big bluestem territory. It is the most xeric of the numerous prairie sunflowers. Dense societies in which the grasses may be greatly thinned result from its rhizome habit of propagation. In early spring the leaves form rosettes on the soil but the new shoots elongate rapidly and the leaves are carried upward ahead of the grasses. In this prairie the plants reached heights of 2-3 ft, the leaves were large, and the flower heads were 3-6 or more in number. Westward the plants are smaller in every way and usually only 1-3 flower heads per plant occurred. Number of plants per sq m varied from 30-100 in societies of this sunflower. Blossoming began early in July but reached its maximum in August.

Prairie cat's-foot (*Antennaria neglecta*), one of the few mat-forming species, makes up in abundance and gregariousness for its small stature. It occurs, usually as societies, from moist lowland to dry hilltop but thrives in greater numbers in the drier sites where the grass is thinner. This stoloniferous plant has a conspicuous white-woolly appearance. Most of the small clumps or rosettes occur on or only a few inches above the soil in the interspaces between the tufts and bunches of sod. Almost leafless scapes, 2-5 in. long, are produced on warm slopes by the middle of April and perhaps 2 weeks later on northern exposures. Flowering precedes maximum vegetative activity. Some leaves remain green over winter and many new ones appear with the spreading of the stolons. Vegetative activity may continue all summer even in the weak light (1-5%) under the cover of bluestems (Fig. 7).

Coreopsis palmata, a stickseed, is a perennial



FIG. 7. Plants of spring and early summer. Prairie cat's-foot (*Antennaria neglecta*) (above) and spiderwort (*Tradescantia occidentalis*), the latter photographed by F. W. Albertson. Grasses have been removed.

composite that was found only on upland where it nearly always occurred densely aggregated into conspicuous societies. This resulted from its extensive propagation by rhizomes. The very leafy, rigid stems are 1-3 ft tall and simple or little branched. The deeply 3-7-lobed leaves are 2-3 in. long and so tolerant of shade that the stems become only slightly defoliated near the base. Under thickly grouped stems the stand of grass is greatly thinned. It almost disappears under dense societies, which may cover areas of 25 or more sq ft. The large yellow flowers appear in summer but persist for only a few weeks.

Flowering spurge (*Euphorbia corollata*) is a perennial species of wide distribution, especially in prairies with rather high precipitation. Here it occurred on upland, but in drier western grassland it is infrequent even on low ground. The plants consist mostly of single stems 3-5 ft high, but clusters of 2-3 and sometimes 25 occur. Leaves to a height of about 6 in. are scale-like; the remainder are small, narrow, and not wide-spreading. In midsummer the wand-like stems terminate in a whorl of branches which bear the very numerous, rather small, white flowers in widespread umbels.

Compassplant (*Silphium laciniatum*) is a characteristic low-prairie species in the northwestern prairie but in the more moist areas south and east it is common to abundant on upper slopes and hill-

tops as well. Height varied greatly, increasing from 4-5 ft to 10 ft in more favorable habitats. Number of stems increased from 1-3 on young plants and to 10 or more on long established ones. The coarse lacinate leaves, nearly 2 ft long and more than a ft in width, are mostly clustered at the base of the clump. Those of young plants, especially, have the orientation of the compass; thus the sides receive the morning and afternoon sun. The upper third of the stem bears an abundance of flower heads of very large size. This forb ranks high more because of its size and destructive effect on the grasses than because of great abundance.

Downy phlox (*Phlox pilosa*) is a perennial of early growth which reaches its mature height of nearly 3 ft early in May or in June. Then its cymes of bright pink-purple or rose-red fragrant blossoms, with an occasional white flowered individual, are very conspicuous in the landscape. Even where it is abundant, because of its long narrow grass-like leaves, it seems to disappear with the close of the period of flowering in June. But the dried flower parts are not shed for some time and the foliage remains green until fall. Plants occurred in great abundance, singly or in clumps.

Liatris pycnostachya is the largest, most mesic and most abundant of a group of 3 blazing stars found in this prairie. Tall gayfeather varies in height from 3 to about 5 ft; a third of its stature is attained by the first of June. Hence it is well fitted to grow in areas of big bluestem and it is rarely found in much wetter or much drier grassland types. But under a rainfall of 30 or more in. it spreads throughout the little bluestem type as well. The basal leaves are long, narrow, and very abundant. At first they are nearly vertical but later spread widely and thus occupy a considerable area from which the grass is excluded. The several unbranched stems are densely clothed with short grass-like leaves but only to two-thirds of their height. The stems terminate in showy spikes 10-15 in. long. Flowering begins in late July. Where 3-15 stems occur per sq m, the prairie for several weeks is ablaze with purple.

In a few well-watered prairies, including this one, the sky-blue (*Aster azureus*) and arrow-leaved aster (*Aster sagittifolius*) ranked in the first class. Both are perennial from strong rhizomes, from which an abundance of fibrous roots have their origin. The stems of the first species, often 4-10 in number, are more or less grouped and reach heights of 1-4 ft. The large, abundant, broad leaves cast considerable shade, to which the plant is very tolerant. The stems, branching

above, give rise in late summer and autumn to a wealth of bright flower heads, about an in. wide, on the ends of long peduncles. The arrow-leaved aster, with its large, mostly sagittate basal leaves, is somewhat taller, 2-5 ft. The great racemes of light-blue or purplish flowers are thus held well above the grasses. The flower heads are only half as large but more abundant than those of sky-blue aster.

DISCUSSION

The 10 species of highest rank that formed the most abundant societies in this prairie included only 5 of the 15 species ranking highest in 100 upland prairies studied by Weaver and Fitzpatrick. Seven others from their group were present but they were only of intermediate rank. They were many-flowered aster (*Aster ericoides*), daisy fleabane (*Erigeron strigosus*), prairie clovers (*Petalostemum*), pale purple coneflower (*Echinacea pallida*), prairie rose (*Rosa suffulta*), Missouri goldenrod (*Solidago missouriensis*), and stiff goldenrod (*Solidago rigida*). Two others, silver-leaf psoralea (*Psoralea argophylla*) and ground plum (*Asragalus crassicaarpus*) occurred here only infrequently and a third, blazing star (*Liatris punctata*), was not found. These 10 species are all xeric forbs that extend far westward into mixed prairie. Moreover, 3 mesic species that ranked high in this prairie were also of highest rank in many lowland prairies over the general area. They were *Phlox pilosa*, *Silphium laciniatum* and *Liatris pycnostachya*.

A number of high ranking species, typically of lowlands, are of interest here. Stiff marsh bedstraw (*Galium tinctorium*) and fringed loosestrife (*Steironema ciliatum*), denizens of very wet places occupied by switchgrass and big bluestem, where they form dense societies, are rarely found elsewhere in western prairies. But here they flourished far up the ravines. Golden meadow parsnip (*Zizia aurea*), Canada anemone (*Anemone canadensis*), and willow aster (*Aster praealtus*) of similar habitat preferences, not only migrated far up the ravines but also often spread outward onto uplands. Golden ragwort (*Senecio aureus*) and Sullivant's milkweed (*Asclepias sullivantii*) likewise greatly extended their upward range.

Species of Intermediate Rank

The following is a list of species of intermediate rank, most of which formed societies, but some were merely scattered throughout.

<i>Antennaria plantaginifolia</i>	<i>Aster ericoides</i>
Plantainleaf pussytoes	Many-flowered aster

<i>Chamaecrista fasciculata</i>	<i>Pycnanthemum virginianum</i>
Showy partridge pea	<i>P. flexuosum</i>
<i>Comandra umbellata</i>	Mountain mint
Common comandra	<i>Ratibida pinnata</i>
<i>Coreopsis tinctoria</i>	Coneflower
Plains coreopsis	<i>Rosa suffulta</i>
<i>Desmodium canadense</i>	Prairie rose
<i>D. illinoense</i>	<i>Silphium integrifolium</i>
Showy and Illinois tick trefoil	Entire-leaved rosinweed
<i>Echinacea pallida</i>	<i>Silphium perfoliatum</i>
Pale purple coneflower	Cup plant
<i>Equisetum laevigatum</i>	<i>Sisyrinchium campestre</i>
Smooth horsetail	and <i>S. angustifolium</i>
<i>Erigeron strigosus</i>	Blue-eyed grass
Fleabane	<i>Solidago altissima</i>
<i>Eryngium yuccifolium</i>	Tall goldenrod
Rattlesnake master	<i>Solidago graminifolia</i>
<i>Fragaria virginiana</i>	Bushy, fragrant goldenrod
Scarlet strawberry	<i>Solidago missouriensis</i>
<i>Hieracium longipilum</i>	Missouri goldenrod
Hawkweed	<i>Solidago rigida</i>
<i>Liatris scariosa</i>	Stiff goldenrod
Blazing star	<i>Solidago speciosa</i>
<i>Liatris squarrosa</i>	Showy goldenrod
Scaly blazing star	<i>Tradescantia bracteata</i>
<i>Pedicularis lanceolata</i>	Bracted spiderwort
<i>P. canadensis</i>	<i>Vernonia baldwini</i>
Swamp and early lousewort	Ironweed
<i>Petalostemum candidum</i>	<i>Veronicastrum virginicum</i>
White prairie clover	Culver's root
<i>Petalostemum purpureum</i>	
Purple prairie clover	

Aster ericoides formed societies of the highest rank in about 44% of the upland and 25% of the lowland prairies. The lesser abundance of this xeric species here is of considerable significance. *Fragaria virginiana* is a widely distributed species, occurring from areas of prairie cordgrass through big bluestem to hilltops clothed with little bluestem, as it did in this prairie. But in the more xeric western ones it is confined to lowlands and moist ravines. *Leptandra virginica*, *Pycnanthemum flexuosum* and *P. virginianum*, and *Solidago altissima* are species that are almost confined to lowland westward, but here as in other well-watered prairies they spread far upland along ravines and sometimes even into drier soil.

Petalostemum candidum and *P. purpureum* are widely distributed in true prairie. They ranked third among the most important legumes and were exceeded only by lead plant and silver-leaf psoralea. Renewal of their growth in spring began with that of the bluestems. It proceeded rapidly and the plants attained heights of 2-2.5 ft when blossoming began about the first week in July. The compound leaves are composed of 3-9 rather small leaflets. The stems were defoliated to a height

of 5-8 in. by midsummer and the remaining foliage was not dense. Usually only 1 or a few stems were produced from the crown of the taproot but long-established plants had 15 or more. In open stands only 5-10 plants occurred per sq m, but in dense societies more than 50. Only when the plants were large and crowded did they produce much shade. Although the two species formed mixed groupings, in this prairie and others northward the white-flowered plants were far more abundant. Both species were most abundant on uplands.

Silphium integrifolium is confined to ravines and lowlands in prairies with low rainfall but here it also occurred on upland. The plant grows rapidly in spring, constantly overtopping the grasses. Isolated, small, open clumps had little effect upon the grasses, but when several large groups, each with 12-20 very leafy stems, aggregated nearly all other vegetation was excluded. Yield of hay was correspondingly reduced. In many big bluestem prairies of Iowa this species was among the high-ranking forbs (Fig. 8).



FIG. 8. Nature's garden on lower slope at Anita, July 16, 1940. Prominent forbs are pale purple coneflower (*Echinacea pallida*) and rosinweed (*Silphium integrifolium*).

Vernonia baldwini is a plant of peculiar interest. Widely distributed on lowland and in ravines of drier prairies, it occurs here on the hilltops as well. Although possessed of strong, thick rhizomes, it rarely produces more than 1-3 tall, leafy stems. But when the competing grasses are weakened by grazing or other disturbance, it rapidly increases its area and develops bushlike clumps covering several sq ft.

Among the 4 species of *Liatris* of common occurrence in true prairie, *L. punctata* is the most xeric. It extends quite across the mixed prairie as well, but was not found in this mesic Iowa prairie. *L. squarrosa*, also a xerophyte occurred

most abundantly on dry ridges and hillsides. It was only 6-24 in. high but the plants were often abundant locally. The very leafy stems grew in clumps of 10-30 and there were often 3-5 clumps per sq m. Beneath them the soil was bare except for a small amount of bluegrass. The much taller *L. scariosa* has fewer stems, usually only 2-3 per plant, but it was more widely distributed. Less xeric than the preceding, it occurred on hillsides as well as on lowlands. Fifty to 100 or more flower heads per stem were held aloft above the grasses even on hilltops. The wealth of rose-purple flowers and the colored tips of the large bracts form, in autumn, a pleasing and impressive sight. Most of the other forbs of common occurrence will be mentioned later.

Several species of very high rank elsewhere do not occur in either of the preceding groups. Scruppea (*Psoralea floribunda*) was not found and false boneset (*Kuhnia eupatorioides*) and ground plum (*Astragalus crassicaarpus*) were infrequent. The greatly increased size of *Kuhnia* is remarkable. In dry grassland the bush-like top is usually only 2 ft tall and 1-1.5 ft in width. But here bushes, perhaps 20 yrs old, had a basal diameter of 6-8 in. where 100 or more stems arose from the crown of the very deep, thick taproot. Heights of 3-3.5 ft were attained and the tops spread over an area 2-3 ft in width. The native prairie grasses were shaded out; only a little bluegrass remained.

Species of low rank

A considerable number of species of low rank will be mentioned in the discussion of seasonal aspects. To complete the record for those who may be especially interested, the following list of forbs is presented. It does not include species of wet land unoccupied by big bluestem.

<i>Acerates angustifolia</i>	<i>Lithospermum incisum</i>
<i>Acerates hirtella</i>	<i>Lobelia inflata</i>
<i>Acerates viridiflora</i>	<i>Lobelia spicata</i>
<i>Achillea millefolium</i>	<i>Lygodesmia juncea</i>
<i>Allium canadense</i>	<i>Lythrum alatum</i>
<i>Anemone cylindrica</i>	<i>Oxybaphus linearis</i>
<i>Apocynum cannabinum</i>	<i>Oxybaphus nyctagineus</i>
<i>Artemisia ludoviciana</i>	<i>Monarda fistulosa</i>
<i>Asclepias verticillata</i>	<i>Oenothera biennis</i>
<i>Aster laevis</i>	<i>Onosmodium occidentale</i>
<i>Aster oblongifolius</i>	<i>Physalis heterophylla</i>
<i>Aster patens</i>	<i>Physalis virginiana</i>
<i>Aster sericeus</i>	<i>Polygala verticillata</i>
<i>Astragalus canadensis</i>	<i>Potentilla arguta</i>
<i>Cypripedium candidum</i>	<i>Prenanthes aspera</i>
<i>Delphinium virescens</i>	<i>Ratibida columnifera</i>
<i>Equisetum arvense</i>	<i>Ratibida pinnata</i>
<i>Eupatorium perfoliatum</i>	<i>Rhus radicans</i>
<i>Gaura biennis</i>	<i>Rudbeckia hirta</i>
<i>Gaura parviflora</i>	<i>Rudbeckia triloba</i>

<i>Gentiana andrewsii</i>	<i>Salix humulis</i>
<i>Glycyrrhiza lepidota</i>	<i>Scutellaria parvula</i>
<i>Habenaria leucophaea</i>	<i>Solidago gigantea</i>
<i>Helenium autumnale</i>	<i>Solidago nemoralis</i>
<i>Heuchera richardsonii</i>	<i>Specularia perfoliata</i>
<i>Hieracium scabrum</i>	<i>Strophostyles helvola</i>
<i>Houstonia nigricans</i>	<i>Tradescantia virginiana</i>
<i>Lactuca biennis</i>	<i>Verbena hastata</i>
<i>Linum sulcatum</i>	<i>Vernonia fasciculata</i>
<i>Lithospermum carolinense</i>	

In addition, a shrub (*Corylus americana*), which is an occasional invader of prairie in Iowa, occurred in one small area of big bluestem. Hazel has thick woody rhizomes and very deep roots. It persisted despite annual mowing and produced much shade. A small amount of *Symphoricarpos orbiculatus* was also found.

FURTHER CONSIDERATION OF PRAIRIE

The prairies are not of recent origin. Their beginnings date back about 25 million years to Tertiary times and resulted from the uplift of the Rocky Mountains and subsequent changes in climate, especially reduced precipitation (Clements 1936, Gleason 1952). Present day prairie is preglacial in origin and has descended from the climatic prairie of the Tertiary period (Gleason 1923). Seeds of about 30 species of prairie grass have been found as fossils in Miocene and Pliocene deposits (Elias 1942). Borchert (1950) has shown that the grasslands have a climatic distinctiveness as compared with surrounding regions. The evidence from deeply buried soil profiles (fossil soils) gives strong support to the view that grasslands existed during interglacial periods (Thorp, Johnson & Reed 1951, Fry and Leonard 1952, Simonson 1954). A recent discussion on central North American grasslands has been written by Wedel (1957).

Climax prairie is extremely resistant to invasion. Large tracts are uninvaded by weeds except to the extent that trails or roads have been made through them or soil has been washed into the ravines from adjacent fields. Local invasions of short duration may also occur where the grasses have been destroyed by stacks of hay or burrowing by gophers, badgers or other animals. It is indeed impressive to find isolated prairies entirely uninvaded, although surrounded by cultivated crops with their accompanying annual weeds or by pastures with their usually longer-lived weedy flora. There is lack of invasion despite the fact that the number of invaders is quite as large as the number of prairie species and their methods of competition diverse. According to Cratty (1929) the immigrant flora of Iowa consisted of 263 species. In the present paper approximately 165

prairie species are listed (Fig. 9). Shimek (1931) states that 265 species make up the bulk of the prairie flora of Iowa. Such stability denotes a high degree of equilibrium between the native vegetation and its environment under the control of a grassland climate. The slight but rather general invasion of bluegrass has resulted from the disturbance produced by annual mowing and removal of the forage.



FIG. 9. Societies of blazing star (*Liatris scariosa*) and black-eyed Susan (*Rudbeckia hirta*) in Iowa prairie.

We may well consider now why the numerous species of grasses and forbs are able to grow with great rapidity. All except a relatively few species are perennial. No time is lost each spring in germination and establishment. The plants are already wonderfully well established. Only those who have studied the prairie underground can fully appreciate its amount and extent in the soil. Here occur the stem bases, rhizomes, tubers, corms and bulbs. They are mostly within a few in. of the soil surface, a great potential food resource for the new crop of prairie plants. They, with food stored in roots, make possible rapid growth in early spring and summer.

The network of fine, wonderfully branched roots of the grasses in the little bluestem community are about twice as deep (4-5.5 ft) as the plants are tall. In the big bluestem community grass roots, although coarser, are even deeper. Those of big bluestem extend downward commonly 6-7 ft, which is also often the height of the grass. The

number of grass roots both on upland and on lower ground averages about 650 per sq ft. In early spring roots may absorb more vigorously in the warmer soil at 5 or more ft in depth than in the recently thawed upper soil. The wave of summer heat traveled downward slowly and reached these depths in late winter. By weight there is more material in the surface 4 in. of soil alone (3-4.5 T/A) than in the entire crop of vegetation above ground, which in this prairie was usually 1.5-2 T/A. The total oven-dry root-weight varied from 4.6-6.4 T/A; like the yield of tops it was greater in the big bluestem type. These amounts are also 20-28% greater than those found in similar prairies of eastern Nebraska.

The dark humified organic matter alone ranged from 30-40 T/A in the top 6 in. of soil (Thorp 1948). "It acts as a home and as food for the microscopic plants and animals that prepare the soil for the use of higher plants, and as a water reservoir to supply plants with needed moisture and to cushion them against drought. Much of the all-essential nitrogen is stored in the organic material waiting to be made available by micro-organisms for the use of higher plants" (Thorp 1948).

Penetrating throughout the masses of fibrous roots of grasses are the underground parts of forbs. Their root habits follow closely three general patterns. Many have strong taproots, $\frac{1}{4}$ to more than 1 in. in diameter. These produce several large branches, in the first 3 ft of soil, that spread outward and downward. Like the main roots they may branch repeatedly and penetrate as deep and often much deeper than roots of grasses. Numerous legumes belong to this group. Many produce root tubercles throughout their entire depth.

A different pattern, common among many species, consists of a strong taproot or several main roots that produce relatively few or no branches but penetrate deeply, often to 8-10 ft. When branches occur they are usually from the deeper part of the root system. Purple coneflower (*Echinacea pallida*) has this root pattern. A third root type is exhibited by the large group of forbs with rhizomes, root offshoots or corms with numerous main roots of about equal size. They likewise penetrate deeply, usually deeper than the grasses. All absorb vigorously in the surface soil and are strong competitors of the grasses. Several asters and goldenrods illustrate this type.

Roots of forbs may add another 0.5-0.75 T/A (a very low estimate) to the total root weight. Thus, upon reflection one may understand that the bulk of the prairie is below and not above the

surface of the soil. "It was not by chance that grasslands of the Mississippi and Missouri valleys became the scene of the greatest corn and wheat production in the world. There were many reasons for this, but the most significant were depth of soil, abundance of available humus and minerals, presence of lime, readiness of nitrification, and number and abundance of nitrogen-fixing plants. Virtually the only limiting factor was water, whose amount was restricted by rainfall which decreased progressively to the westward and by recurrent periods of drought" (Clements 1938).

PRAIRIE IN EARLY SPRING

Prairie is a very complex community. To some it appears as an inextricable mass of vegetation, varying endlessly. In one's early study it seems somewhat elusive, not easy to visualize and difficult to describe. This vagueness of understanding can be overcome, once the species are known, by visiting the prairie several times during the growing season, examining it closely, often on hands and knees, and always with a very definite purpose in mind.

The prairie maintained its appearance in winter until the last of April, at least at a little distance. The soil was completely obscured by the 2.5-3 in. of grass stubble with its dead basal leaves and the fallen debris from "hay making" in addition to the dried forage from late fall growth. A continuous layer of mulch a few mm thick covered the ground. Lichens and mosses sometimes occurred on the damp, spongy soil between the tufts and mats of sod.

The earliest plants in blossom appeared on ridges and upper south-facing slopes about the second week in April. On north exposures they were often 7-10 days later. Sometimes growth in spring was delayed by a late heavy snow. Bluestem grasses renewed growth after mid-April. But the drab colors of winter were not entirely replaced by the green of new vegetation on lowlands and north exposures until early in May. Then the numerous yellow and purple spikes of *Carex pennsylvanica* outlined the patches of this small sedge. *C. meadii* with bluish-green leaves and large, yellow staminate spikes was less abundant.

Patches of *Antennaria neglecta* occurred scattered throughout. Sometimes there were 50 or more of the 4-6 in. flower stalks per sq ft. Blossoming began about the middle of April and the fluffy fruits were first scattered by the wind early in May. A few plants of *Anemone caroliniana* bloomed on sunny slopes, but the far more conspicuous pasque flower (*Anemone patens*) was

found farther northward (Hayden 1943). Dog-tooth violet (*Erythronium albidum*) occurred on the lowland. The prairie violet (*Viola pedatifida*) appeared late in April but became more plentiful in May. The new green of scattered plants of bluegrass, Junegrass, needlegrass and Canada wild-rye was sparse. The chill of spring was still in the air and soil; the prairie was slowly recovering from a long period of dormancy. This was only the beginning of a wonderful period of development. Each week from April to October witnessed a new crop of fruits and seeds of various prairie plants.

VERNAL ASPECT IN MAY

A survey of the prairie during the first week in May revealed that the new growth of the bluestems obscured the drab vegetation of late winter. Prairie dropseed added verdure to the landscape as did also the rapidly developing cool-season Junegrass, needlegrass, and Canada wild-rye. Kentucky bluegrass was beginning to produce flower stalks. From the last week in April until late in May, many plants came into bloom. The crests of the prairie ridges were white with the innumerable, panicked flowers of redroot, which continued blossoming during the first weeks of June. The conspicuous, pretty white flowers of strawberry, often in dense clusters, began to appear when the leaves were only half grown, and the bright red fruits ripened during June. The white or purplish tinged flowers of blue-eyed grass (*Sisyrinchium*) and the golden-yellow ones of star grass (*Hypoxis hirsuta*) occurred in patches, sometimes thickly, from lowland to hilltop.

Dense societies of golden ragwort (*Scnecio aureus*) and scattered plants as well were plentiful in May; the hoary heads of fruits were held high above the grasses and scattered by the wind during June. *Viola papilionacea* rapidly developed both foliage and flowers before the light was too greatly obscured by the grasses. Clusters of purplish flowers occurred in the patches of vetch (*Vicia americana*), mostly associated with big bluestem. The yellow flowers of *Oxalis stricta* and the larger rose-purple ones of *O. violacea* were found, usually in patches, among the grasses during both May and June.

The abundant white flowers of *Anemone canadensis*, 1.5-2 in. wide, were held by long peduncles well above the mass of leaves, which was sometimes so dense as to almost obscure the grass. Blossoming began in mid-May, and continued for several weeks. The erect spikes of the yellow or reddish flowers of the louseworts (*Pedicularis*) were not uncommon. Spiderworts (*Tradescantia*

bractcata and *T. occidentalis*) presented an abundance of purple flowers where they occurred in numbers. Flowering of false indigo (*Baptisia leucophaea*) began only after the thick, naked shoot had rapidly grown upward 5-9 in. and the leaves unfolded. Then the great racemes of large cream-colored flowers extended conspicuously beyond the foliage. The scattered plants usually occurred singly.

Golden meadow parsnip (*Zizia aurea*) is a large, somewhat bush-like plant about 2.5 ft high. The wide, yellow-flowered umbels were conspicuous in May and June. A single plant was noticeable at a distance and they were sometimes densely grouped in the territory of big bluestem. Downy phlox, scattered thinly to thickly through the grass, was perhaps the most impressive species of springtime. Its abundant bouquets of pink and purple flowers were held high above the grasses, even in June when big bluestem was 2 ft tall.

May also initiated rapid vegetative growth of plants which blossomed in summer and autumn. Tall-growing forbs such as sunflowers, rosinweeds and goldenrods and many other late bloomers far outstripped even the tall grasses in rate of growth. Many were a ft high on May 1 and 2.5 ft tall by June 15. The new shoots of blazing stars, asters, prairie clovers and lead plant again decorated the landscape. Now the long period of dormancy had ended; spring was really here and one could almost feel that the prairies pulsed with life.

To one who views the annual renewal of growth in prairie in spring and observes the brown landscape become carpeted with green, it is always impressive. To students from tropical countries who witness the greening and blossoming of the prairie for the first time, it seems almost a miracle. Although beautiful, quiet and inspiring, the prairie landscape is also a field of battle. The struggle for mere existence, for light, water and nutrients, has been going on for centuries and is renewed each spring. The prairie is enormously overcrowded for the best development of the individuals even in its present condition of dynamic stabilization.

PRAIRIE IN SUMMER

A visit to the prairie in summer showed at once that many changes had occurred. These began during the last week in May. Many plants of spring had then ceased to bloom and their fruits were now to be seen. Several others such as phlox, redroot, golden meadow parsnip and Canada anemone continue to blossom, but they too were soon to wane. Their prominence in the landscape was being replaced by that of a host of

estival bloomers. With an increase in temperature and length of day, there was a distinct transition from spring to summer.

In early June the uplands were covered with foot-high foliage of little bluestem. In valleys, ravines and lower slopes big blue-stem exceeded this height by 4-6 in. The scattered plants of bluegrass had blossomed and the extended purplish stigmas of low-growing panic grasses were exposed to the wind. The timothy-like spikes of Junegrass were beginning to expand, and scattered plants of needlegrass were often in full bloom. But prairie dropseed and the bluestems did not produce flower stalks for several weeks. Unlike the preceding they are warm-season species. The fact that they continued vegetative growth until late July and only then began to blossom and ripen seed, a process which continues until late fall, indicates the usual continuous supply of soil moisture at all times during the growing season.

Branched tops of prairie clovers, now about 20 in. high, stood above the level of the grasses. The terminal heads of white or purple flowers varied from 0.5-3 in. in length. They were both abundant and conspicuous. The prairie rose (*Rosa suffulta*) began to unfold its large, pink buds into the beautiful white and pink-tinted blossoms early in June. Flowers continued to appear until well into July, and the reddish fruits were decorative until the prairie was mowed in autumn.

Rosettes of the winter annual, *Erigeron strigosus*, were of common occurrence in spring. By the end of May the erect stems were taller than the grasses. Ten to 20 plants sometimes occurred in a single sq m and each branched top produced 25 or more white flower heads. The dark violet-purple or indigo flowers of *Amorpha canescens*, each with a single petal but numerous stamens, were conspicuous for several weeks on this widely distributed and abundant plant. *Echinacea pallida* also blossomed in June. The flower heads were 3-4 in. in diameter. They terminated stalks somewhat taller than the bluestems. The black central cones were conspicuous for many weeks after the purple or rose-colored ray flowers were gone.

The yellow flowers of *Coreopsis palmata* appeared in the summer aspect. Societies of this composite make a pleasing display. *C. tinctoria*, although less abundant, is similar in the production of large orange-yellow flowers. After mid-July the abundant white flowers in the umbels on the wand-like stems of *Euphorbia corollata* brightened the landscape. The tiny but densely grouped white flowers of *Pycnanthemum flexuosum* made the societies of this forb very conspicuous wherever

they occurred. Blossoms were abundant in July and later summer (Fig. 10).

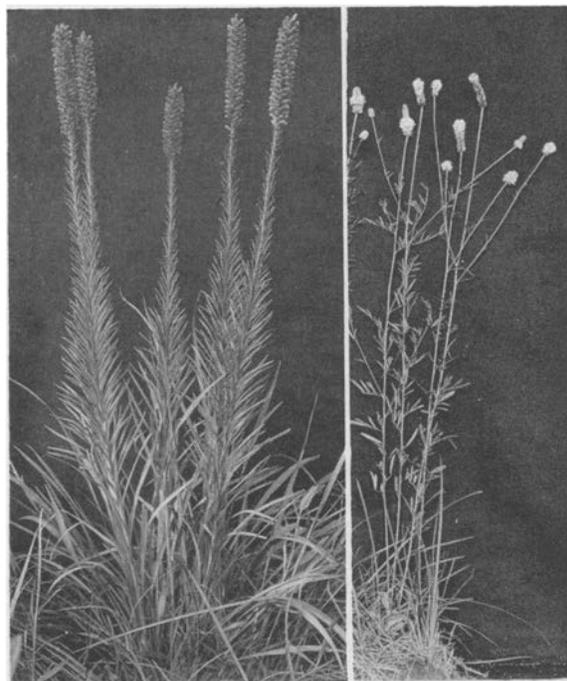


FIG. 10. Blazing star (*Liatris pycnostachya*) in fruit and white prairie clover (*Petalostemum candidum*) in blossom.

A few of the taller species of summer were *Hieracium longipilum*, two species of *Desmodium*, and *Baptisia leucantha*. The first, the hawkweed, occurred as individual plants, standing 3.5 ft high in July. The small yellow flowers of this slender, woolly plant were less showy than the hoary pappus of the ripe achenes. Flowers and fruits were present all summer. The tick-trefoils had a foliage height of only 2-3 ft until the very long terminal racemes of bluish or purplish flowers appeared early in July and reached a height of 5-7 ft. Both flowers and fruits were conspicuous; the plants often grew in large clumps. Plants of false indigo were nearly always few and widely scattered. The single stem was without leaves or branches to a height of about 3 ft where it spread its branches horizontally and widely above the grasses. The central stem of this legume usually terminates in a long, upright raceme of cream-colored flowers, thus increasing the height to about 5 ft. Other racemes are produced on lateral branches. The plants have no harmful shading effect upon the grasses beneath them.

Western red lily, although infrequent, was very noticeable because of its height and very large attractive flowers. The large, coarse plants of Sullivant's milkweed, found mostly scattered in

big bluestem, had an abundant display of flowers with delicate shades of pink and rose and, later, large erect pods. Butterfly weed (*Asclepias tuberosa*) grew singly, often forming bush-like clumps. It was very attractive because of the profuse production of brick-red flowers and the varicolored butterflies which usually hovered about them.

Several species of legumes, abundant to common westward, were almost absent. One was the large, coarse, decumbent, ground plum (*Astragalus crassicaepus*) which has abundant violet-purple flowers and very conspicuous plum-sized, fleshy fruits. Prairie turnip (*Psoralea esculenta*) was rare and silver-leaf psoralea (*P. argophylla*) far from abundant. Scurfpea (*P. tenuiflora*) is a tall plant with bushy top well above the grasses. The color of the very abundant, small, blue flowers mingled with the light gray of the leaves give a distinctive tone to many western prairies. Here it was absent.

During June and July many flowers adorned the prairie. The patterns formed by the groups or societies of various individual or intermingled species were extremely variable but all were beautiful. Each week new flowers appeared as others declined with the advance of the season. While the total number of forbs blooming in spring was about 35, those of summer were more abundant, approximately 60.

Height of forbs at the different seasons is of interest and importance. All of the prevernal plants were of low stature and carried on their life processes near the surface of the soil. None ever attain the midsummer level of the grasses, but most persisted in the understory throughout the remainder of the year. Of the numerous species that blossomed during May, about $\frac{3}{4}$ were of low stature. Only a few were conspicuous after midsummer at or above the level of the grasses. Forbs blooming in summer were of greater height than those of spring. Only a few were hidden in the grass. Conversely, about half extended well above the grasses into full sunlight. The remainder, about 40%, were nearly the same height as the grasses and, consequently, fairly well lighted. Autumnal-flowering forbs, next to be considered, were all tall.

AUTUMNAL ASPECT

The autumnal aspect began late in July. The grasses had reached their maximum foliage development. Little bluestem averaged 18-20 in. tall on uplands but a few in. taller on lower slopes. Big bluestem and Indian grass were 30-36 in. high in the wetter soil. They were passing from a stage

of active development to one of flower-stalk production, fruition, and maturity. Most of the forbs, so prominent in summer, had either finished blooming or would soon do so; flowers of others were being replaced by fruits; only a few continued blooming for a time. But it was clear that over the prairie the scenes were again being shifted, this time from those of summer to autumn. The coming of fall was clearly portended by the yellowing of the inflorescences of goldenrods and the blossoming of sunflowers, rosinweeds, and various blazing stars.

Nearly 40 species, mostly composites, bloomed during August and September. Forbs of the autumnal aspect, with rare exceptions, were coarse and of large size. They averaged much taller than those of summer, although some did not appear to do so, because their lower parts, often considerably defoliated, were hidden by the grasses. Week by week during spring and summer the struggle for light had become increasingly more severe. But the autumnal forbs had continued their rapid growth to sufficient height usually to extend quite beyond the level of the grasses. Some were 6-9 ft tall.

Helianthus grosseserratus is a tall, coarse, single-stemmed sunflower with large toothed leaves. Growing from strong rhizomes and thick crowns, the plants attained heights of 10-25 in. early in May and 6-9 ft in late summer. With *H. maximiliani*, a plant of similar stature, it had migrated from ravines and occurred as somewhat dwarfed individuals in drier sites. Oxeye (*Heliopsis helianthoides*), a plant 3-5 ft tall that superficially resembles a sunflower, occurred sparingly on lowland. All of the preceding had large yellow or orange flower heads. They developed very rapidly, overtopped the grasses, and blossomed profusely in late summer and autumn. None was abundant. Rosinweeds (*Silphium integrifolium* and *S. perfoliatum*), also tall coarse plants with large yellow flower heads, were scattered about in moist areas.

Aster azureus and *A. sagittifolius*, both of great abundance, displayed their wealth of bright blue or purplish flowers at heights of 2.5-4.5 ft and thus well above the grasses. Less abundant were plants of *A. ericoides* with white to purplish blossoms, and the blue and violet flowered *A. laevis*.

While no goldenrod attained first rank in this prairie, 4 species were of common occurrence. *Solidago missouriensis* was the first to bloom. Its panicles of tiny golden flowers were held aloft just above the sea of green. A single bushy plant produced great masses of flowers, and plants were

well scattered throughout (Fig. 11). *S. rigida* produced flat-topped inflorescences of similar beauty and equally conspicuous. A little later *S. altissima*, much taller and somewhat more mesic than the preceding species, also presented a wealth of golden blossoms. *S. speciosa* was among the last to bloom. This plant grows as single stems or several grouped in clumps 2-3.5 ft tall. Height of blossoming was attained in September. The beautiful golden flowers often covered the upper third of the plant.

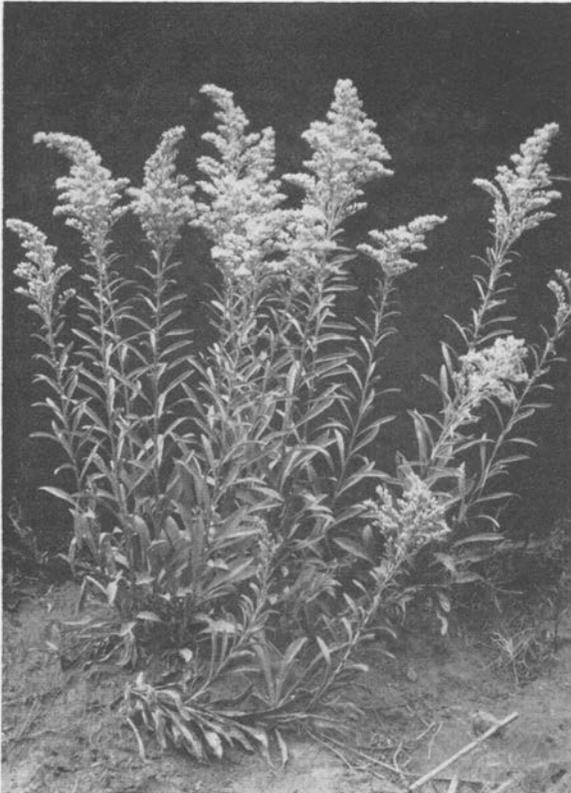


FIG. 11. Typical plant of Missouri goldenrod (*Solidago missouriensis*) in full bloom late in July; grasses have been removed.

The blazing stars with their purple and rose-purple flowers added much color to the prairie in late summer and autumn. Great clusters of small purple flowers also appeared after midsummer at the top of the long, stiff stems of ironweed (*Vernonia baldwini*). They were conspicuous during fall. The grayish-white flowers and fruits of false bonaset (*Kuhnia eupatorioides*) added pleasing variety to the wealth of autumnal colors. There were many others. Among the last of late fall bloomers was the blue gentian (*Gentiana puberula*). It would scarcely be noticed in the understory except for its large blue flowers.

In September the abundant flower stalks of little bluestem stood thickly 2.5-3 ft high. The panicles

of Indian grass and the forked inflorescences of big bluestem were on flower stalks 6-8 ft tall. The description of prairie in autumn by Weaver and Fitzpatrick (1934) may well be repeated here. "About the first week in September, or earlier if the season is dry, *Andropogon*, *Panicum*, and *Sorghastrum* begin to lose their green color and slowly take on the red and bronze and golden tints of autumn. With the progress of the season, these gradually deepen until the landscape presents a color scheme rivaled in beauty and delicacy of painting only by the autumnal coloration of the great deciduous forest. . . .

"During September and later fall, the great fields of fruiting grasses are beautiful to behold. On low ground scores of the forked inflorescences of big bluestem may occur on each square meter. The golden panicles of Indian grass glisten in the sun. The spikes of *Spartina* offer a pleasing pattern of a different variety and vie in splendor with the broad, delicate panicles of *Panicum virgatum*. The dried heads of nodding wild-rye stand thickly in ravines while on the uplands the abundant flower stalks and whitish fruits of little bluestem add pleasing variety. Here also the open panicles of *Sporobolus heterolepis* are held aloft above the level of the foliage."

PRAIRIE IN WINTER

The few cool-season grasses, such as needlegrass and Kentucky bluegrass, showed some renewed growth even after the September mowing. If the fall was late, the bluestems also produced some new foliage. The rosettes of certain species of aster, goldenrod, strawberry and prairie cat's-foot were still green during freezing weather, and when protected by an early snow they sometimes remained green all winter. But except for fruits and seeds, the living prairie population, in a dormant state, was found almost entirely within the protecting soil and scarcely at all above it.

In unmowed prairie in winter the dry leaves of numerous forbs still remained as withered things clinging to the bare stems; others had fallen in scattered patches on the soil. Most of the inflorescences had also fallen to earth, others remained as dried remnants of summer bouquets. The leaves of the bluestems, as those of other grasses, had dried in place on the erect stems. By late November their shades of reds and bronze had been replaced by tints of somber reddish brown or gray. Winter winds had swept away the numerous spikelets of little bluestem. The finger-like racemes of big bluestem for a long time adorned the winter landscape, especially on lower ground. Indian grass here and there re-

tained a few of its fruits on its dried panicles. A few spikes of Canada wild-rye were seen in the ravines, and in wetter places the tall erect stems of prairie cordgrass still maintained their spikes, though dry and bleached in the winter's cold.

Where the cover of vegetation is not removed for a period of years by mowing, fire, or grazing and trampling, changes in its composition are marked. In one upland prairie, the 15-yr-old natural mulch was 4.5-8 in. deep, and 6-9 T/A in amount. A nearly pure stand of big bluestem covered 80% of the area, but somewhat less thickly than normal. The usual midgrasses were few or none. Only a few of the taller forbs remained and the understory species had all but disappeared. Where large bunches of prairie dropseed prevailed the deeply mulched soil was free of other vegetation (Weaver & Rowland 1952) (Fig. 12).

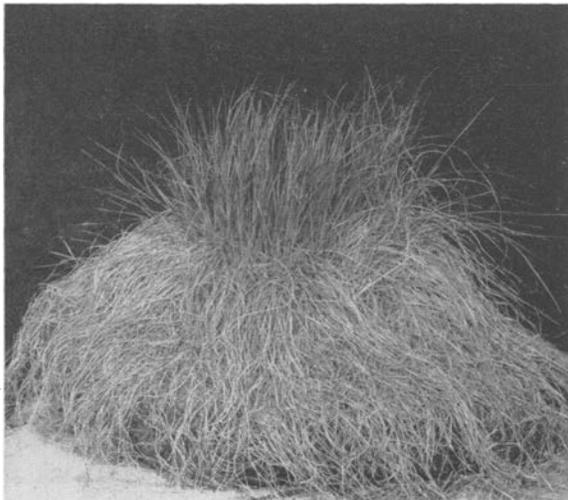


FIG. 12. Large bunch of prairie dropseed (*Sporobolus heterolepis*) in unmowed prairie, showing a great accumulation of dead leaves.

SUMMARY

The vegetation on a 200-acre tract of native grassland in southwestern Iowa and the environment in which it grew have been described. The study began in 1928, continued throughout the great drought of 1933-40, and intermittently since that time. It describes typical, annually mowed prairie under a precipitation in excess of 30 in. on the border line between the more mesic prairies eastward and southward and the more xeric ones westward. This grassland was scarcely affected by the drought. It was the last large area of natural vegetation found in southwestern Iowa, and has now been plowed or pastured.

Topography is rolling to hilly. Climate is one of cold winters with frozen soil and a warm to hot growing season from late April to early October,

with predominately sunny weather. Soils of the Brunizem series were formed from loess on the flat ridges and on gentle to rolling slopes, and from glacial till on the steeper slopes. They are of medium texture, absorb water readily, and retain it well. They formed under a cover of grass and are well aerated, high in organic matter and mineral nutrients.

The prairie is of ancient origin, extremely resistant to invasion, and very complex in composition. Most of the species are long-lived perennials. The very abundant grass roots on upland usually penetrate 4-5.5 ft deep and those on lowland 6-7 ft. The total oven-dry weight of roots varies from 4.6-6.4 T/A. The dark humified organic matter in the top 6 in. of soil ranged from 30 to 40 tons per acre.

Only one type or consociation prevailed on the upland; this was little bluestem (*Andropogon scoparius*). Needlegrass (*Stipa spartea*) and prairie dropseed (*Sporobolus heterolepis*) occurred but not abundantly. The big bluestem (*Andropogon gerardi*) consociation prevailed on lower slopes and on lowland. The two bluestems alone composed 80% of the vegetation. Their nature and causes of dominance are described.

Compared with similar prairies in eastern Nebraska, little bluestem in its community decreased nearly 5% and big bluestem increased 6% in amount. Foliage of these grasses averaged 5-8 in. and 6-12 in. higher, respectively; the bunches and sod were better filled with stems, and flower stalks were more abundant, taller, and produced even in dry years. Total yield was $\frac{1}{4}$ - $\frac{1}{2}$ T/A greater. Root weight was about 25% greater.

Forbs were classified according to their size, abundance, density and effect upon the grasses. All but about 25 of the 142 species that the writer and Fitzpatrick found to occur in 10% of the 135 prairie areas they examined were also found here. A total of about 165 species were found. Compositae furnished about $\frac{1}{3}$ of the forbs and Papilionaceae about $\frac{1}{8}$. Eight forbs, a half-shrub and a shrub formed societies of the first class. Each is briefly described.

Several forbs of high rank westward were of low rank here; others were infrequent or absent. Thirty-five species were of intermediate rank. They mostly formed societies but some were scattered throughout. Forbs were more abundant and much better developed than similar species westward. Several species found only in wet lowlands westward here flourished far up the ravines and many others also extended their range upward. Species of lower rank are either listed or mentioned in the text.

The prairie was studied throughout the growing season to ascertain the beginning and rate of growth, adjustments to light, duration of foliage and defoliation in dense shade, flowering and fruiting. Species of the vernal, estival and autumnal aspects all renewed growth at about the same time, and development was continuous until midsummer. The vernal species forged ahead in development of the ever increasing wave of estival and autumnal bloomers. Week by week the struggle for light became more severe. Species of early spring were low-growing, and about $\frac{3}{4}$ of those of the vernal aspect were also of low stature. In midsummer estival species attained a moderate height, about half of them were taller than the grasses; those of autumn continue growth until they overtopped the grasses, but their leaves to a height of 1-2 ft died. Only a few species blossomed until late in April, about 35 in May, and a larger number, perhaps 60, in summer. In the autumnal aspect, beginning late in July nearly 40 species bloomed; approximately 85 were tall, coarse composites.

The ancient origin, complex composition, and resistance of this grassland to invasion have been discussed. The interrelations of grasses and forbs, their role in the formation and maintenance of a rich, deep, productive soil have been emphasized.

Prairie vegetation and prairie soils are closely related, intimately mixed, and highly interdependent upon each other and upon the climate. But the once "magnificent, endless prairie" is now near extinction.

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