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North American Prairie

J. E. Weaver
University of Nebraska

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TO MOST AMERICANS, the word "Prairie" suggests either a romantic element in pioneer fiction or a vast expanse of level land which must be crossed in going from one coast to another. But to the botanist, the American Prairie is a wonderfully complex society of living organisms.

This book tells the story of that society—the variety of its inhabitants; the constitution of its several communities; the internal struggles for domination of the society; and the battles of the Prairie as a whole against its two most vicious enemies, drought and overgrazing. Most striking, perhaps, is the story of that portion of Prairie which is seldom seen—the extensive and intricate "Prairie underground," with roots occasionally extending over 20 feet deep.

The information presented here is the product of long and painstaking scientific research; yet it is conveyed in terms that the general reader can understand, and it is made vivid by some 200 excellent illustrations. The expert on grasses will find here scientific data never before made available; the cattleman will acquire practical advice on how best to utilize the prairie grasses; and the layman will enjoy that rare experience of discovering a new world filled with life and struggle.

This is the first comprehensive book ever written about American Prairie. And it comes from the pen of the one man who, more than any other, is qualified by training and experience to write it—Dr. John E. Weaver. (*See back flap.*)

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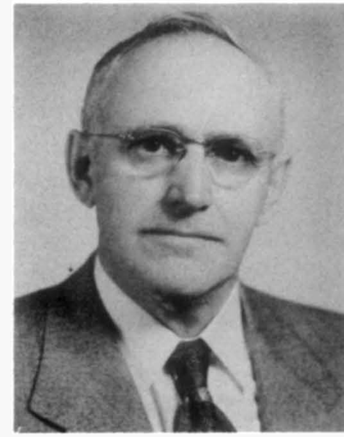

DR. JOHN E. WEAVER, professor emeritus at the University of Nebraska, is a man internationally known and respected for his work in the field of plant ecology. During the past 40 years he has authored or co-authored some 80 articles, 4 monographs, and 11 books. So valuable are his authoritative studies of root activities, drought, and the structure of grassland, that for 27 years he has been listed by *American Men of Science* as one of the nation's 100 outstanding botanists.

His professional experience includes 8 years as research associate for the Carnegie Institution of Washington, 10 years on the editorial board of the scientific journal *Ecology*, and 10 years on the National Research Council's committee on the ecology of grasslands of North America. He has been president of the Nebraska Academy of Sciences and the Ecological Society of America, and an honorary president of the 1950 International Botanical Congress.

Dr. Weaver has influenced the field of ecology not only through his own publications but also through his work as a teacher at Washington State College, the University of Minnesota, and (for 38 years) the University of Nebraska. Students from all over the United States and many foreign countries have come to Nebraska expressly to work under Dr. Weaver's tutelage. He has supervised about 40 doctoral dissertations, all of which have been published.

The present publication represents, indeed, the very peak of Dr. Weaver's achievement, for it distills the results of a lifetime's uninterrupted, laborious field research.

Dr. L. A. Stoddard, of Utah State Agricultural College, in reviewing an earlier work by Dr. Weaver, wrote:

There comes occasionally to every scientific field a man who is so enthusiastic, and so devoted to his work that it becomes his very life. To him nature seems to unfold her secrets in response to his devotion; his ability to understand and communicate with nature becomes an inspiration to students and fellow workers alike. Such a man is John Ernest Weaver in the field of American grassland ecology.

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NORTH AMERICAN PRAIRIE

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by J. E. Weaver
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To Martha Helen

Preface

PRAIRIE is composed of many different species of native American plants. It appears as an inextricable mass of endlessly variable vegetation. One glories in its beauty, its diversity, and the ever changing patterns of its floral arrangements. But he is awed by its immensity, its complexity, and the seeming impossibility of understanding and describing it. After certain principles and facts become clear, however, one comes not only to know and understand the grasslands but also to delight in them and to love them.

More than forty summers have now been spent by the author in a study of the annual renewal of growth, development, and fruition of North American grassland. This included the direction of numerous graduate students who became interested in some of the countless problems presented by vegetation. It has been my practice to write the story of the prairie and the studies made therein at the time the field work was under way. The intimate acquaintance one makes with plants by living with them month after month must be recorded completely and at once, lest it fade from memory with the passing of time. One cannot well describe a root system he excavated many years ago, any more than he can vividly relate the terrible life and death struggle of vegetation during severe drought, a long time after it has occurred. Moreover, the many observations, experiments, and findings made and recorded in the past must be correlated and judged in the light of other findings to the present day.

Early investigations have been recorded in scientific books and magazines, many of which are now out of print or difficult of access. It has long been the desire of the author to write a simple, coherent story of the prairie, scientifically accurate, but in nontechnical language for the general reader. It is the reader's right and heritage to share the wonders and the beauty of the living prairie landscape. A secondary purpose is the bringing together, so far as is possible, the findings of other workers—a record of accomplishment that is widely scattered through the literature. This could best be done by consulting and abstracting materials from various publications. Therefore permission was asked and promptly given by the Carnegie Institution of Washington, the Duke University Press, *Ecological Monographs, Ecology,* and several other botanical journals to re-use materials originally furnished by the author. Similarly, permission to re-use his numerous bulletins published by the University of Nebraska Conservation and Survey Division has been given. Such sources of materials are carefully cited in the text. Only by such cooperation has this book been made possible.

The writer has been fortunate in living in that portion of the prairie that has "resisted civilization" longest, and where numerous large typical areas of grassland have been accessible for study. The prairie has been thoroughly examined as to its way of life both above ground and deep into the soil, which it so efficiently protects. Extensive experiments have elucidated many problems. While teaching plant ecology and special courses on grasses and grasslands, the scope of the work has been broadened and deepened by the aid of a large number of advanced students who have sought graduate study in this field. It is now my final pleasure to bring together the findings of students everywhere and humbly tell the story of North American Prairie.

Both common and scientific 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, and common names are nearly all according to the second edition (1913) of Britton and Brown.

The author is indebted to Dr. Herbert Hanson and Dr. Raymond Darland for reading certain chapters and to Dr. I. M. Mueller for reading the entire manuscript.

NORTH AMERICAN PRAIRIE

CHAPTER 6.

ROOTS AND RHIZOMES OF GRASSES

CHAPTER 7.

ROOTS AND RHIZOMES OF FORBS

CHAPTER 8.

STABILITY, SEASONAL ASPECTS, AND OTHER STUDIES IN PRAIRIE

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NORTH AMERICAN PRAIRIE

CHAPTER 1

The Nature of Grassland and Grasses

When the white man came to North America a magnificent grassland occupied the central part of the continent. From Texas it extended Northward to Manitoba, where it gave way to Boreal Forest. From the forest margins of Indiana and Wisconsin it extended westward far into the Dakotas and half way across Kansas. This great area of waving grasses, bedecked with wonderful flowers, was designated by early settlers as Prairie. Beyond, an even more extensive but drier and sparser grassland stretched away to the Rocky Mountains. This was early designated as the Great Plains (Fig. 1).

The vast prairie is in summer a land of waving grasses. Except for its grandeur of expanse and the abundance of varicolored flowers, it appears almost monotonous in the general uniformity of its cover. The dominance of grasses, the paucity of shrubs, the absence of trees, except along rivers and streams, and a characteristic drought-enduring flora constitute its main features.

The prairie is a closed community. From a half-inch below the surface to a depth of 3 to 6 inches, the soil is occupied by roots and rhizomes, and less frequently by bulbs, corms, tubers, and their outgrowths. A dense network of roots extends several feet in depth. Everywhere the soil is so thoroughly threaded with plant parts as to form a dense sod. The mass of vegetation is limited by the available supply of water. Plants not native to prairie are kept out. Grasses constitute the bulk of the vegetation but forbs, scattered throughout, are an important part. Long life of the individual and much vegetative reproduction are characteristic of prairie. Many plants have a life span of 10 to 20 years and some may persist much longer. In winter the plants are alive only below ground. But renewal of growth is so rapid in spring that even where the former cover has been removed by mowing or burning, the foliage soon becomes so dense that light near the

FIG. 1. Examples of North American prairie. Portion of a several-hundred-acre prairie near Lincoln, Nebraska (upper); prairie stretching away to the horizon (center) in the Flint Hills near Manhattan, Kansas; and a close view of Iowa prairie northeast of Atlantic.

soil surface is often reduced to very low intensities. This occurs despite the fact that the prairie is typically a land of sunshine.

ORIGIN OF PRAIRIE

The origin of North American grassland dates back about 25 million years to Tertiary times. It resulted from the uplift of the Rocky Mountains and subsequent changes in climate, especially reduced precipitation. "As the mountains rose, they intercepted the moisture-laden winds from the Pacific Ocean. Water was precipitated chiefly on the west side of the mountains, and the winds which came over the mountains to the eastward were dry and produced comparatively little rainfall. There was developed on the eastern side of the mountains a region of low summer rainfall and still drier winters. In such a climate tree-growth was impossible and the forests gradually disappeared. They were replaced by a vegetation of herbaceous plants, chiefly grasses. This vegetation persists today on the great prairies and plains which occupy a triangular area in the center of the continent, with one side of the triangle along the Rocky Mountains from Texas to Saskatchewan and its base extending east to Indiana" (Gleason, 1952). Thus present day prairie is preglacial in origin and has descended from the climatic prairie of Tertiary times. It has undergone many vicissitudes during and following the glacial periods. But large portions of the southwest now occupied by prairie have never been glaciated. Gleason (1923) has given an extensive account of the vegetational history of the middle west from preglacial time to the period of settlement.

EXTENT AND UNIFORMITY

The prairie, now designated as True Prairie, originally occupied all the region lying east of the plains vegetation or Mixed Prairie and the western margin of the great Deciduous Forest. The westerly border of the forest from Minnesota to Texas was usually dominated by oaks but hickories also were more or less abundant. "True prairie extended from southern Manitoba diagonally through Minnesota to southwestern Wisconsin and included the northern two-thirds or more of Illinois and part of northwestern Indiana. It included northern and western Missouri and the eastern half of Oklahoma for the most part, passing into the coastal prairie in the region of the Red River" (Clements and Shelford, 1939). More recent, unpublished studies indicate that it extends southward about halfway across Texas (Allred and Mitchell, 1954). The topography which this grassland occupied was essentially a series of plains. Prairie covered level lands, knolls, steep bluffs, rolling to hilly land, valleys, and extensive alluvial flood plains.

In his studies of the prairies in Iowa, Shimek (1911) states: "No matter what may be the variation in the surface characteristics of the prairies there is comparative uniformity in the nature of their floral covering." The flora is the same though the vegetation may be thinner or thicker from moist borders of swamps, lakes and streams to the highest and driest ridges of loess. "Neither topography nor geological formation determined the character of the flora . . . the flora is practically the same . . . and this flora is the best ear-mark of the prairie."

The most significant test of the uniformity of prairie is afforded by the presence of certain dominant grasses throughout all or nearly all of the area. The writer has been deeply impressed by the general uniformity of the prairies he examined from Minnesota to Missouri and from Oklahoma and Kansas to the Dakotas. The general unity of true prairie is shown as strongly and even more visibly by the long-lived forbs as by the grasses. Many of these overtop and sometimes more or less obscure the grasses. About 225 species of grasses and forbs [1] of considerable importance were found in the Missouri Valley region (Weaver and Fitzpatrick, 1934). In a single square mile of prairie near Lincoln, Nebraska, 237 species of prairie plants occurred (Steiger, 1930). About 265 species made up the bulk of the prairie flora of Iowa (Shimek 1931).

Using as a standard the species lists in "The Prairie" monograph (Weaver and Fitzpatrick, 1934), Transeau (1935) found the proportion of species on the prairies of Ohio to be as follows:

Of the 11 major grasses	100%,
of the 22 minor lowland grasses	73%,
of the 67 lowland forbs	84%,
of the 25 minor upland grasses	58%,
of the 75 upland forbs	40%.

"As the upland prairies of the 'Monograph' contain many plains species it is not surprising that at the tip of the [Prairie] Peninsula the composi-

[1] Forbs are non-grasslike herbaceous plants.

tion of upland prairies differs floristically more widely than that of the lowlands." Moreover, the prairies of the Peninsula exhibited the same types or communities as those described in the prairie monograph. "The western element in Ohio [Prairie] consists of species which are characteristic of both wet or lowland prairies and the dry or upland prairies as defined by Weaver and Fitzpatrick (1934). However, many of the species which are in the lowland in the west are confined to dry prairie habitats in southern Ohio" (Thompson, 1939).

CLIMATE AND SOIL

Climate of True Prairie is less humid than that of forest but more humid than in Mixed Prairie. Along the southeastern boundary from Oklahoma to Illinois, mean annual precipitation is almost 40 inches. But northeastward along the boundary in northern Minnesota and Manitoba it decreases to about 23 inches. Rainfall along the western border in Oklahoma is approximately 30 inches, in Nebraska about 25, but it is only 20 inches in North Dakota.

Throughout the entire grassland the climate is more favorable to grasses than to trees or shrubs or, indeed, to any other type of vegetation. The prairie is characterized by a widely different climate than that of the plains grassland. Chief differences are the greater precipitation, deeper and more constantly moist soils, and a greatly decreased rate of evaporation. Precipitation varies from 23 inches in the west-central portion to 40 inches near the eastern forest border.

Transeau (1905, 1930, 1935) has studied the climate of eastern prairie and forest over a long period. He states that the annual and seasonal precipitation-evaporation ratios are undoubtedly lower in the Prairie Peninsula than in adjoining forest regions both north and south, as is also the midsummer relative humidity. Precipitation is notably irregular in its areal distribution on the Prairie Peninsula.

In his comprehensive study of the climate of the central North American grasslands, Borchert (1950) concludes: "The climatic region coincident with the prairies . . . is actually a broad boundary zone between steppe [Plains Grassland] and forest. In the climate of the prairie region forests have a better chance of survival than in the steppe. On the other hand, grass is better adapted to low winter rainfall, unreliable snow cover, and occasional severe summer drought of the region . . . . The prairie peninsula has had a climate more like that of the steppe than the eastern forests during most winters and the summers of major drought years. But during most summers its climate is more like that of the eastern forest."

There is much evidence that the prairie climate has been more hostile to trees than the climates of the surrounding forests. "For example, Transeau [1935] noted the death of thousands of oaks bordering the prairies in Illinois by the close of the 1913–1914 drought. Albertson and Weaver [1945] reported the widespread desiccation and death of forests and planted groves in the 1930's in eastern Nebraska. McComb and Loomis [1944] noted the death of, or severe damage to, hundreds of thousands of adapted trees on suitable or even protected sites . . . during the same period in Iowa. There was no such wholesale damage to woodlands outside the Grassland. During the dry years of the 1930's prairie grass associations moved into areas where trees perished" (Borchert, 1950).

Most of this grassland is on Prairie soil, but a rather large part in the Dakotas and Minnesota, and to a smaller extent southward, is on Chernozem soil. But here the layer of lime accumulation, normally with dry soil beneath, occurs at 3 to 6 feet in depth. Over 70 per cent of the precipitation occurs during the growing season in western prairie and is so well distributed (normally 3 to 4 inches each month of spring and summer) that the growth of the prairie plants is usually not limited by a deficient moisture supply. Both Prairie and Chernozem soils are of unusually good texture and structure. They are rich in humus and dark in color; in fact they offer nearly every feature generally considered favorable to plant production. The late summer and fall droughts, which occur frequently, are the natural result in part from the luxuriant growth and resulting expenditure of enormous amounts of water, and in part from the lack of rainfall. They are often responsible for wide-spread and destructive prairie fires. Within the prairie area is found the most valuable agricultural land. The grass crops—maize, wheat, oats, etc.—with their roots extending 4 to 7 feet into the earth and their bountiful yields, attest at once to the deep, moist, rich soil which was before them occupied by prairie grasses and forbs.

ECOLOGICAL GROUPINGS OF GRASSES

Aside from taxonomic classification, prairie grasses may be grouped, ecologically, according to their time of growth, habits of growth, height, drought resistance, relation to grazing, and dominance.

COOL-SEASON AND WARM-SEASON GRASSES

The prairie possesses grasses of various extraction. Species of northern origin are needlegrass (*Stipa spartea*), Junegrass (*Koeleria cristata*), Canada wild-rye (*Elymus canadensis*), and western wheatgrass (*Agropyron smithii*). Kentucky bluegrass (*Poa pratensis*) and penn sedge (*Carex pennsylvanica*) are other examples. They renew growth early in spring and

FIG. 2. (Above) Two cool-season grasses; needlegrass (*Stipa spartea*) (left), and western wheatgrass (*Agropyron smithii*). Both are about 2.5 feet tall and nearly ready to blossom. (Below) Little bluestem (*Andropogon scoparius*) (left), and big bluestem (*A. gerardi*). They are warm-season grasses. Photo at Lincoln, Nebraska, on May 18 of a normal spring.

make their maximum development from late March to early June (Fig. 2). Maturity is reached and seed produced in late spring or early summer. Then they become more or less semidormant during hot weather, but vegetative growth is usually resumed during the cool months of autumn and they remain green despite frosts. Thus, they greatly extend the length of seasonal activity and the period of green forage for grazing animals.

Grasses which have come from a warmer, southern climate are represented by little bluestem (*Andropogon scoparius*), big bluestem (*A. gerardi*), Indian grass (*Sorghastrum nutans*), prairie dropseed (*Sporobolus heterolepis*), and switchgrass (*Panicum virgatum*). They renew activity much later in spring but grow continuously until early fall and thus produce much foliage in midsummer. Flowering and seed production extends from midsummer until late autumn, depending upon the species. There is no late fall growth. Plants with these growth-habits are designated as warm-season grasses. Side-oats grama (*Bouteloua curtipendula*), blue grama (*B. gracilis*), and buffalo grass (*Buchloe dactyloides*) from the arid southwest are also warm-season grasses.

SOD-FORMING AND BUNCH-FORMING GRASSES

Some prairie grasses are sod-forming. They not only reproduce from seeds but also from underground stems or rhizomes. These extend horizontally a few inches to a few feet from the parent plant and produce new shoots from their tips or from the nodes of the stem. The result is a dense thicket of shoots such as one finds in a field of sloughgrass (*Spartina pectinata*), switchgrass, or western wheatgrass. Sod-forming grasses may rather rapidly and completely occupy the soil. This habit is also shown by buffalo grass, except that here the spreading results from horizontal stems or stolons above the soil. These may produce both roots and aerial shoots at the nodes as well as near the tip.

Many grasses form bunches by erect growth of all the shoots. They spread at the base by means of tillers so that several hundred stems may occur in a bunch. In prairie, little bluestem, Junegrass, and needlegrass are examples of bunch-formers.

Sometimes a single species may reveal both the sod-forming and bunch habit, depending upon conditions for growth; hence this grouping indicates only the general or usual habit. Big bluestem, for example, normally forms a sod, but it occurs as isolated bunches on dry slopes and also in wet, poorly aerated soil. Conversely, side-oats grama is usually considered as a bunch grass, but in shallow rocky soil it may produce rhizomes several inches long.

The ability of grasses to adjust themselves to the environment by various degrees of tillering and by rhizome and stolon production accounts in a large measure for their successful occupation of more of the land surface (about 38 per cent of the United States) than is occupied by any other life form. The growth form of grasses has also contributed greatly to their success. Although the linear and more or less erect leaves receive less light than if they were broad or spreading, yet grouped in mass and crowded together, the plant as a whole receives the greatest possible illumination. In midsummer a single acre of prairie may present 5 to 10 acres of leaf surface.

HEIGHT CLASSES

Prairie grasses may be classified into three groups according to the height they attain. This apparently simple classification is very helpful and fundamentally sound as an ecological principle, since it is an expression of the relation of vegetation to the water supply. Big bluestem, switch-

FIG. 3. Tall, mid, and short grasses: Big bluestem (left), needlegrass 4 feet high (center), Scribner's panic grass (*Panicum scribnerianum*) (above, at right), and blue grama (*Bouteloua gracilis*). The short grasses are 8 and 16 inches tall, respectively.

grass, and sloughgrass are examples of tall grasses. Any grass that normally attains a height of 5 to 8 feet or more belongs in this group (Fig. 3). These grasses were by far the most abundant in Illinois and other eastern prairies with relatively high rainfall. They also occupy moist lowlands and deep ravines throughout the prairie.

Where the climate is drier or where rainfall is not supplemented by runoff water, grasses of a medium height (2 to 4 feet) prevail. Examples are little bluestem, needlegrass, and prairie dropseed. These are designated as mid grasses.

In very dry places, such as crests of hills, ridges, etc., especially in western prairie, there is much loss of water through runoff and blowing away of snow. Moreover, the vegetation is subjected to great water loss resulting from exposure to high winds. Here one may find examples of a third height-class—short grasses. They are usually only 0.5 to 1.5 feet tall. Such short grasses as blue grama, hairy grama (*Bouteloua hirsuta*), and buffalo grass are not infrequent in true prairie, but they constitute relic areas of little extent, except where favored by overgrazing of other grasses.

Not only do the terms tall grass, mid grass, and short grass indicate an important characteristic of the species, but also the presence in abundance of any one of these in undisturbed grassland indicates much about the water relations of the habitat. Great Plains vegetation, for example, consists not of tall grasses but of mixed mid and short grasses or mostly of short grasses in the drier parts. The even more arid grassland of the southwest (Desert Grassland) is characterized by short grasses. But in true prairie the hilltops and slopes of hills are regularly covered with mid grasses; tall grasses usually populate only the more moist lower slopes and lowlands.

DROUGHT-RESISTANT GRASSES

Grasses may also be classified on the basis of their drought resistance. Species of great drought resistance, such as side-oats grama, blue grama, and buffalo grass, or those adapted to evade drought, such as western wheatgrass, usually occur in most of the prairie only in small amounts (Fig. 4). They are normally unable to endure the competition of taller prairie species. Consequently they do not normally compose one per cent of the plant cover. But these species are the reserves adapted to a drier climate. They spread widely when less drought-resistant, mesic grasses

FIG. 4. Side-oats grama (*Bouteloua curtipendula*) (upper left), and western wheatgrass (*Agropyron smithii*) (right). (Below) Basal portions of big bluestem and clipped bunches of needlegrass.

are fewer and less aggressive. They increase rapidly and occupy large areas when great drought occurs and most vegetation is swept away.

RELATION TO GRAZING

Grasses and forbs, as will be shown, may also be classified on the basis of their relation to grazing. Some, such as big bluestem and most legumes, are preferred and selected by livestock and consequently early disappear. Others, such as certain goldenrods and asters, are scarcely eaten by livestock. They remain in a pasture for a long time.

A mixture of many grasses denotes great potentialities of the vegetation as regards adaptation to seasons of growth, to wetter and drier sites, and to periods of moist years or to phases of drought. Grasses are admirably suited to withstand conditions of excessive moisture, great drought, grazing, and fire. Through thousands of years species best adapted to prairie conditions have been sorted out and now compose the present grass flora.

DOMINANT SPECIES

Certain species of prairie grasses are so vigorous and abundant that their influence upon the habitat and effect upon other species determine to a large degree the conditions under which all of the remaining species associated with them must develop. Such a species is called a dominant. The struggle for control or dominance between the two most important prairie grasses furnishes a fine example of adjustment to environment. The sturdy big bluestem with it great stature, long growing season, and ability to endure shading, occupies the well drained, alluvial soils and often the moist lower slopes almost to the exclusion of the smaller species, little bluestem. But this mid grass, although only half as tall, is a keen competitor in its way. It possesses a finer and apparently a more efficient root system and, having a smaller transpiring surface than big bluestem, it holds the drier upland and meets its competitor on equal terms on midslopes or even on the lower slopes of dry hillsides. Thus, the dominants not only reflect the impress of climate but also respond strongly to the environment of the particular habitat.

A dominant or controlling species in prairie has many or all of the following characteristics: great abundance, large size (height and volume) compared with the other components of the community, and a long life span, which permits permanency of occupation. It is vigorous and hence a good competitor, since it is best adapted to the particular soil conditions and climate. It also has a wide distribution.

In prairie, the grasses are the regional dominants, although forbs may dominate locally where they are densely grouped. The number of such dominant grasses is small. The types or communities of prairie are determined by their presence, singly or in two's or three's. These dominants are so controlling that one could write a fairly good story about the prairie if he understood only the significance of these. They are only about 10 in number. The number of important forbs is considerably higher. It is not the purpose of the author to list all the species that occur in prairie, which may be found in the taxonomic manuals, but to acquaint the reader with the most important ones.

IDENTIFICATION OF SPECIES

It is fortunate that one can learn to distinguish grasses, one from the other, by vegetative characters alone at any period in their development. For example, needlegrass is a bunch grass of small to medium size with long, gradually tapering leaves which are corrugated on the upper surface but smooth and shining green beneath. The attenuated leaf-ends are nearly always dead, and a conspicuous membranous growth, the ligule, occurs at the base of the blade where it joins the leaf sheath. Sloughgrass has saw-tooth margins on its very long, coarse, shining leaves. Side-oats grama possesses hairs with swollen bases on the margins of the leaves, especially near the base, and some plants retain the zigzag-topped flower stalks for a long time. The dried, dead, basal leaves are not brown or gray but bleached to almost white. Thus, each species has its own particular characteristics well known, of necessity, to the student of prairie and of pastures originating from prairie. They permit him to identify the species during the entire growing season or even in winter. The distinguishing characteristics of different forbs, before the flowers have appeared or after they have fallen, are even more marked than those of grasses.

STUDY OF WESTERN PRAIRIE

The prairie has not been studied uniformly throughout. In fact the eastern portion was almost destroyed before it was investigated by botanists. The part that has received continuous ecological study over a period of nearly 40 years includes the prairie in the western third of Iowa and eastern Nebraska, Missouri and Kansas as far south as the Kansas River, and also the southern part of South Dakota and Minnesota. The study of a single area of grassland, no matter how complete, gives only a fragmentary picture of the whole. As one travels from one portion of a region to

FIG. 5. Upland prairie at Corning, Iowa, (above) showing an abundance of widely scattered forbs. Mowed prairie near Lincoln, Nebraska, showing the old-fashioned method of mowing and raking hay. Photo June 25, 1920.

another, the vegetation varies because of differences in topographic and edaphic factors as well as from gradual climatic change.

During six growing seasons (1928–33) almost 200 separate prairie areas were investigated. Of these, 135 were selected in the six states as typically representative. Some were a square mile or a half square mile in area, many were 80 to 160 acres, but a few were only 30 to 40 acres in extent. They occurred on all types of topography from steep glaciated or loess hills and almost level upland, to broad areas of first and second bottom lands along the rivers. Although often separated by miles from another prairie and surrounded by cultivated fields and pastures, the native vegetation remained completely intact. Each prairie was regarded as a sample plot of the former magnificent prairie which 60 to 90 years earlier seemed to continue indefinitely. Prairie in this study included the territory from the borders of marshes, lakes, and ponds to the highest and driest hills.

In using this plan one comes to know each sample intimately. All parts can be examined. The component communities are not too large to visualize from beginning to end. One can compare the differences in types in various areas and examine the transitions from one to the other. Then next month or next year he can return to reconsider his judgment in the light of other findings. This would have been the modern method— random sampling of prairie—even if the grasslands had been entirely intact. Studying the grassland as a continuous whole would have been almost overwhelming in such a complex entity as true prairie. Subsequent studies of many other prairies have shown that a sufficient number had been investigated to permit reliable conclusions as to the composition and structure of the vegetation. This study gives a general view of vegetation as a unit; it deals only with the more important facts, principles, and species.

Practically all of the prairies had been mowed annually, some for a period of 50 to 60 years. The removal of the plant cover by mowing after it has matured has no harmful effect upon the vegetation. Before the advent of settlers, prairie fires were common and enormous herds of antelope, bison and other grazing animals trampled the grass, at least locally. Thus this renovation of prairie was a natural occurrence. It has been shown that the accumulation of excessive debris modifies the composition of the vegetation. Even after mowing, the soil is protected from erosion by wind and water and sudden fluctuations of temperature. There remains a 2.5- to 3-inch stubble with dead basal leaves. Much fallen debris accumulates during "hay making," and nearly always there is some growth late in autumn.

METHODS OF STUDYING PRAIRIE

The methods of study were simple and direct. The survey was made with the assistance of Prof. T. J. Fitzpatrick and the aid of a graduate student. The first objective, upon entering a prairie, was to gain a preliminary knowledge of the types or communities of grassland it contained, their extent, and their relative importance. The various communities of grassland are delimited by the presence in abundance of a single dominant or two or three dominant grasses on somewhat equal terms. Even the farmer or grazier recognizes and understands what is meant by sloughgrass, switchgrass, needlegrass, or little bluestem prairie. Throughout the great expanse of prairie only six such major communities occur, three on upland and three on lowland.

Each prairie was traversed on foot until all parts of it were examined. The types of vegetation were studied in detail and the transitions from one community to another were carefully observed.

As one studies prairies, one after another and year after year over a wide area, he is impressed with the changes in grassland communities, as water content is affected by topography, which repeat themselves so vividly and faithfully. In fact he becomes able to visualize that the entire landscape is a great grassland, a picture mostly blotted out by man but one that can be reconstructed with such a high degree of clearness and certainty that it seems only yesterday that the grandeur of the prairie existed in its entirety.

The square-meter quadrat was uniformly employed in ascertaining basal area, foliage cover, and percentage composition of the vegetation. Basal area or ground cover may be defined as the area occupied by bunches, mats, or tufts or stems of plants near the soil surface. It is very difficult to clip off cover with mower or shears at the soil surface; even cattle cannot remove it so closely. Hence for convenience a height of about 1.5 to 2 inches is used in ascertaining basal area. Actually this is usually estimated, after experience, without removing the vegetation. Basal area is best estimated in small units of 1 to 5 square decimeters. It is always surprising to find that even dense grassland may have only a small basal area; perhaps only 15 per cent of the soil surface is actually occupied by plants (Fig. 4). Basal cover is very stable, since nearly all of prairie plants are perennial, and it usually varies but comparatively little from year to year.

Foliage cover is the area occupied by the spreading tops of the plants at the several heights that they may attain above the surface of the soil. It is very changeable, not only from dry to wet years or from hilltop to lower land, but also from time to time as the vegetation develops during the growing season. As one walks around a square meter of vegetation looking down upon it rather vertically, he may find that the soil is completely obscured by the grasses and forbs. Or perhaps 10 or 25 per cent of the soil area is revealed. In the first instance the foliage cover is 100 per cent, in the second 90 and 75 per cent, respectively.

The percentage abundance of the various grasses, sedges, and forbs—the percentage composition of the vegetation—was ascertained in more than 400 quadrats. The vegetation in any unit area is considered as 100 per cent. If a sample has five bunches of little bluestem and one clump of big bluestem as large as all of these, then the percentage composition is 50 per cent little bluestem and 50 per cent big bluestem. The size of a plant is determined solely by the soil surface it occupies—that is, the per cent of the total basal area of vegetation (100 per cent) which it composes.

The surveys to determine the composition of the cover and its structure (how the plants were grouped) were a fascinating study. Hundreds of yards in the many prairies were traversed on hands and knees, and in this way a very clear picture of the vegetation was obtained. This detailed study, with and without quadrats, revealed much concerning the habits and life histories of plants and interrelationships that might have been overlooked had only general observations been made. It resulted also in revealing the relatively unimportant species and the presence of inconspicuous ones. However, no species was recorded in the quadrats unless it composed at least 0.5 per cent of the cover. The amount of basal area occupied by forbs was not recorded for each species but for the group collectively. Usually it did not exceed 5 per cent. This character of a forb tells little about its ecology; hence forbs were grouped and studied separately from grasses (Fig. 5).

All forbs in each prairie were listed and their importance in grassland closely estimated. The criterion was the actual effect of the forb upon the cover of grasses, and the portion of the basal area and foliage cover that it occupied. Several important characteristics of each species were studied—abundance, size, duration, density of stands, basal and foliage cover. Examples follow: Lead plant which occurs throughout nearly all upland prairies is more abundant than the rose which, although growing in dense groups, is not so frequently encountered. Violets are often very abundant but they are so small that they are less important than a few of the large rosinweeds. Dogtooth violet endures only a few weeks above ground, and by midsummer the plants of many-flowered psoralea break off at the ground line and are blown away. But the button snakeroots are present in prairie through the growing season. Downy gentian usually occurs as isolated plants, but prairie cat's-foot is closely grouped in dense mats and, like the strawberry, spreads by stolons. Indian plantain may spread its large, broad, plantain-like leaves over a square foot or more, but the stem of the swamp milkweed may be no thicker than a pencil. Foliage cover is extremely variable. Some forbs by midsummer have their foliage spread quite above the grasses, as false indigo and water hemlock. Others are densely leafy from base to top, as false boneset and stiff goldenrod.

Some species of forbs possess all of these characters. For example the smooth goldenrod is an abundant perennial of large size. Stems occur abundantly in great clusters, the basal area is large, and the foliage is so dense that it almost excludes the grasses. Clearly this is a high-ranking forb. A few forbs possess almost none of these characters. Yellow flax is an annual with a single small stem and narrow leaves held far apart. Even when abundant, the plants are not closely spaced. Most forbs possess a few to several of the preceding characteristics. After long experience in prairie, one learns to evaluate all of these characteristics of a plant when its name is mentioned.

For each prairie studied, a complete list of the forbs was made. After careful observation each species was then placed into one of five groups, depending upon its importance. Those that occurred in great abundance and were of considerable importance throughout a prairie were designated by 1, as a society of the first class. Usually only 6 to 8 species in any prairie held such high rank, but sometimes 10 to 12 and rarely only 2 to 4. These were widely but not necessarily continuously distributed throughout the prairie. Other species which were of only slightly less importance were designated as 2, a society of the second class. Conversely, certain species were so rare that they were observed only once or a few times. These were placed in class 5. Others occurred in several places but not commonly. They formed only a small part of the plant cover because they were infrequent (class 4). Most of the forb population fell between the extremes of classes 1 and 2 on the one hand and 4 and 5 on the other. These were designated as belonging to class 3, one of intermediate importance. A classification of forbs was made separately for each prairie while it was being carefully studied. After familiarity with the species is attained it is thus possible to make this very useful classification which illustrates the relative importance of forbs. The constancy of a species, which is its more or less persistent occurrence in all of the plots (separate prairies), was thus ascertained. These estimates in 100 upland and 35 lowland prairies scattered widely throughout the 60,000 square-mile area, are believed to render averages that are more nearly correct than would be obtained from detailed counts in a few sample plots even if worked out in far greater detail.

The photographs which illustrate individual species and plant communities were made in every instance to show them as they occurred under undisturbed conditions. Almost constant air movement from gentle breeze to strong wind is characteristic of prairie, except in early morning. Because of bright sunshine and cloudless skies it is difficult to depict depth of detail in the vegetation. Only rarely are there times when diffuse light accompanies perfect calm. Many pictures in the field were taken with a curtained background. Numerous plants, with a block of moist soil in which they grew, were removed to the laboratory for proper conditions of lighting, etc., to portray the size, branching, flowering habit and detail of other characteristics.

The underground plant parts were also examined, a very laborious task. The methods employed will be described as well as the surprising results obtained.

Climax prairie is the outcome of thousands of years of sorting out of species and adaptations to the soil and climate. The vegetation represents not only an evaluation of the present environmental conditions but also those of the past. It is exceedingly complex and remarkably stable. Fully 95 per cent of the species are perennials, many with long life spans. Since the eastern part of the prairie was not studied until after it had been almost destroyed, the plan of the book is to acquaint the reader first with the western portion, scattered over six states in an area of 60,000 square miles. Here investigations have been conducted consistently throughout many years. They reveal the nature, development, continuity, and intimate structure of this grassland. They also furnish a background from which one may visualize the early descriptions of the white men who first viewed the prairie and compare the present results with earlier studies. They are a necessary background for an understanding of the deterioration and recovery of prairie during extended periods of drought, its damage due to fire, and the changes brought about by grazing.

CHAPTER 2

Grasses and Communities of Lowland

PRAIRIE of the wetter or more moist lowlands is dominated by grasses that are quite different from those typically forming upland communities. Five species, forming three plant communities, are chiefly concerned. These were the principal grasses and types of grasslands encountered by the explorers and early settlers on the plains of Illinois and along the river valleys westward and northwestward.

BIG BLUESTEM

Andropogon gerardi (*A. furcatus*) is one of the most widely spread and important dominants of the prairie (Fig. 6). Together with little bluestem of uplands it usually constitutes fully 75 per cent of the plant cover. Big bluestem was the most abundant species of the grasslands which occupied the broad valleys of the larger streams. It also grew thickly in tributary valleys and ravines and occurred on slopes and lower hillsides as well. Today the bluestems are the chief components of the great grassland areas (Flint Hills and Osage Hills) in Kansas and Oklahoma. They are also found far beyond the boundaries of true prairie.

Big bluestem is an erect perennial. It is a warm-season grass which begins growth in April.[1] Development of the shoot is rapid and the leaves are 8 to 16 inches high by the first of June. The abundant foliage reaches a height of 2 to 3 feet late in July or early in August. The leaves, which are often 16 to 24 inches long, spread gracefully so that the area of the top of a clump is usually 1.5 to 2 times that occupied by the base. The flower stalks begin to appear above the general level of the foliage early in July, but anthesis does not reach its maximum until mid-August or September. The height attained by the flower stalks and the number of finger-like

[1] Time of growth, flowering, etc., is given for the middle of the great north-south expanse of grassland. It is that of east-central Nebraska.

FIG. 6. Lowland prairie. (Upper left) Big bluestem 9 feet tall; (below) big bluestem mowed and piled in haycocks, showing the abundant yield. Relative height of sloughgrass (*Spartina pectinata*) in background and switchgrass (*Panicum virgatum*) in foreground on June 24.

racemes produced vary greatly with the season and factors affecting growth, especially the water supply. Flower stalks vary in height from 3 feet on moist slopes to 7 to 12 feet on rich bottom lands. The stems are often characterized by a purple or blue wax-like bloom. An abundant crop of seed is usually produced annually.

Seedlings develop rapidly when conditions are favorable to growth. Roots of mature plants are coarse, often 2 to 3 mm. in diameter, compared with those of most upland grasses. A great mass of roots are produced, however, and depths of 5 to 7 feet are usually attained. Tillering begins early and is pronounced. Tillers may begin to appear seven or eight weeks after germination and soon the seedling develops a small tuft or bunch. Rhizomes are also produced and the area occupied by both shoots and roots is thus greatly increased. The causes of dominance of big bluestem are found in its rapid growth, dense sod-forming habit, great stature, and tolerance of the plant and its seedlings to shade. Leaves of seedlings remain green and function under light intensities of only 5 to 10 per cent of full sunshine. The lower leaves of older plants also make food under light values of only 10 per cent, but at only about a third of the rate of fully lighted leaves. The individual stems in well established sod are usually spaced about half an inch apart. They are grouped into mats of sod with so much space intervening that the actual amount of soil occupied by them averages only about 13 per cent of the soil surface. Nevertheless the foliage is so dense and spreads so widely that the light is much reduced and invasion by other species is very difficult; it indeed forms a closed community.

Big bluestem is the best prairie grass for both pasture and hay. It is highly palatable and nutritious and very productive. Cattle show a greater preference for it than for any other grass. But unless it is grazed judiciously it will be replaced by inferior species. It also furnishes one of the chief constituents of prairie hay. It is highly valued as hay, but it should be cut in early bloom before the stems become too hard and fibrous for palatability. On lowlands, two cuttings are usually made each summer. The new growth rapidly develops and furnishes an abundant second crop. Yields of hay are not very different on comparable sites from Dakota to Oklahoma and are usually 1 to 2 tons per acre, but sometimes they may exceed 3 tons (Fig. 6).

INDIAN GRASS

Sorghastrum nutans is a tall, coarse grass with water requirement and habits of growth and flowering almost identical with those of big bluestem (Fig. 7). Both are warm-season grasses. Like big bluestem, Indian grass may form patches of sod or occur in bunches. It is readily distinguished from big bluestem by its slightly more erect habit of growth. The leaves

FIG. 7. Detail of Indian grass (*Sorghastrum nutans*) (left), switchgrass (center), and Canada or nodding wild-rye. Height is about 6 feet.

are usually broader and somewhat lighter green in color. The leaf blades spread at 45-degree angles from the stems and possess prominent ligules at their bases. The large yellowish-brown panicles, 4 to 12 inches long, are very different from the forked inflorescence of big bluestem. Indian grass, however, is much less abundant. It is of southern derivation and reaches its greatest abundance in the southern portion of the area. Here it may compose 90 per cent of the vegetation where almost pure stands occur in ravines, but the percentage is only 5 to 20 in most lowlands. The more usual percentages over the area as a whole are 1 to 5, and in many lowlands, especially northward, it is almost absent. Its occurrence in dense, big bluestem sod as isolated stems or very small clumps is usual and results from the fact that under severe competition it tillers, if at all, only poorly. Where portions of the big bluestem community are occasionally flooded or repeatedly burned, Indian grass greatly increases in abundance. The rather large seeds are usually viable and germinate readily unless buried more than half an inch deep. The vigorous seedlings endure a wider range of extremes as regards drought than most lowland species. This probably explains, in part, the habit of this grass of readily invading disturbed places throughout the prairie. Indian grass is excellent for grazing and for hay, ranking almost as high as big bluestem. If cut before the woody flower stalks develop, it is readily eaten by all kinds of stock.

KENTUCKY BLUEGRASS

Poa pratensis, contrary to common belief, is not indigenous to the United States. It was introduced from Europe with the coming of white settlers. It is a rather constant component of both lowland and upland prairie types. Several factors have contributed to the invasion of bluegrass along ravines and in lowlands and to its extension in smaller amounts to upland. Under natural conditions bluegrass can scarcely invade upland prairie and is kept out of lowlands where the tall grasses produce much debris and where shade is dense. Annual mowing or grazing usually removes this handicap. Where the stand of tall grasses on low ground is densest, bluegrass is often entirely absent. Even where this grass is well established, experiments show that it is shaded out in two or three years if the vegetation is left undisturbed. Prairie fires consume the debris but they also kill the bluegrass. In sections of the prairie where the old practice of annual burning is followed, bluesgrass occurs very sparingly or is absent.

The success of bluegrass in invading prairie is largely due to its early vigorous growth, since only a few prairie grasses are of the cool-season type. It is the first grass to renew growth in spring. Very early in May the flower stalks begin to appear and profuse blossoming occurs. Thus far it has received almost full light intensity. Not only has a crop of seed developed, but also much food has been made and stored in roots, rhizomes, and crowns in early spring. During the remainder of the summer it is less vigorous and, indeed, is usually semidormant during the hottest part of this season. After the September mowing it is revived by cooler weather and autumnal rains. It continues to grow well into winter. This smooth perennial, with long, flat leaf blades which fold during drought, is also the bluegrass of lawns. It is excellent for grazing, but yields are smaller than those of prairie grasses and it is far more sensitive to summer drought.

BIG BLUESTEM COMMUNITY

Among the several types or communities of prairie grass the two of greatest importance and widest extent are those dominated by big bluestem and little bluestem, respectively. The former is characteristic of level but well drained lowlands and lower slopes of hills; the latter is distributed over drier, upland soils. Sampson (1921) found that big bluestem (*Andropogon gerardi*) was the dominant of prairies that were too dry for sloughgrass over the whole state of Illinois, little bluestem being dominant only on the lighter types of well drained uplands. Somewhat similar conditions prevailed in true prairie of eastern Iowa and parts of Missouri and Minnesota (Vestal, 1914; Shimek, 1925). Westward, big bluestem is the most important dominant of grasslands which occupy the broad lowland valleys of Lake Winnipeg and the Red River of the Dakotas, the Missouri, the Platte and Arkansas, and other great drainages as well as the lowlands along their thousands of tributaries throughout the area of true prairie (Schaffner, 1926; Bruner, 1931). Wherever this type occurs it is nearly always dominated by a single species, big bluestem.

This type of grassland is best developed on lower moist slopes and well aerated lowlands and is practically in complete possession of them. Sometimes it occurs locally on well watered, nearly level upland. Contact of the big bluestem type on the xeric side is usually with little bluestem. In the western half of the true prairie, at least, it is overwhelmingly exceeded in extent by the little bluestem type; the two communities together, however, constituted fully 80 per cent of the grassland cover investigated. The big bluestem type of grassland is usually clearly defined.

COMPOSITION OF VEGETATION

Percentage composition of vegetation in the big bluestem type on low, level, second bottom prairie near Tarkio and Bigelow, Missouri, in 1930, was as follows, each column representing a square meter quadrat.[1]

Big bluestem	90	84	88	94	95	98	93	90
Indian grass	—	—	1	2	2	—	1	—
Bluegrass	1	1	2	—	1	1	2	—
Basal area	16	11	19	15	25	14	20	14

It may be noted that the three species composed 85 to 99 per cent of the vegetation. The remaining species will be considered later.

Sampling the well drained bottom lands along Salt Creek and the Platte River in eastern Nebraska gave very similar results, except that flooding in the area of the first three quadrats resulted in an abundance of Indian grass.

Big bluestem	65	67	33	95	86	95	87	79	66	78	92	82	84	80	90	86	95
Indian grass	30	25	54	2	—	—	—	—	—	—	—	—	—	—	—	—	—
Bluegrass	3	3	5	3	8	3	10	15	10	5	—	10	—	1	—	6	2
Basal area	12	9	3	10	11	12	8	—	—	—	—	—	—	—	—	—	—

Quadrats from west-central Iowa from hilltop to low level base or through the upland, little bluestem type into the lowland big bluestem type follow:

Species	Hilltop	Upper slope			Midslope		Lower slope		Level base
Little bluestem	70	70	56	44	44	40	—	—	—
Big bluestem	13	22	27	35	35	40	75	80	97
Bluegrass	7	3	10	10	10	5	5	15	1
Basal area	25	21	17	15	15	15	13	11	10

Here the gradual decrease of little bluestem and a corresponding increase in big bluestem is revealed as one proceeds down the long, west-facing slope. The findings also show that bluegrass occurs in the understory in both grassland types.

Numerous samples of the vegetation, each consisting of one square meter, were taken in the six states in the several grassland types. These were used to determine the average percentage composition of the vegetation. Their significance is greatly enhanced by the fact that the results

[1] Quadrats described here and in Chapter 4 and also table 1 (simplified) are from Weaver and Fitzpatrick, Ecological Monographs 4 (no. 2), 1934.

disclosed by their analysis were confirmed by literally hundreds of critical and detailed observations in 135 prairies in which these studies were made. About 12 species of grasses and the forbs composed approximately 99 per cent of the vegetation in each of these three major grassland types. For purposes of later comparison, these data are presented together in table 1.

An analysis of the quadrats in the big bluestem type revealed a number of important facts. Big bluestem constituted 78 per cent of the vegetation and was present in every sample. Its great abundance is shown by the fact that in a third of the quadrats it ranged between 80 and 89 per cent of the vegetation and in 22 per cent it constituted 90 per cent or more. It was less than 60 per cent in only 14 quadrats. Thus, it is truly the great dominant of lowlands.

Bluegrass was represented in all but 12 per cent of the samples and constituted 8.8 per cent of the basal area. But little bluestem constituted only 2 per cent of the basal cover and was found in only 19 per cent of the quadrats. It is not so tolerant of shade as is bluegrass. Indian grass, while occurring in 37 per cent of the quadrats, furnished only 1.9 per cent of the basal area. In only 6 samples did it constitute more than 10 per cent of the vegetation.

TABLE 1. Percentage composition of the vegetation and frequency of occurrence of each of twelve most important grasses in three communities of prairie.

Species	Big bluestem Type. 155 sq.m. % Comp.	% Freq.	Little bluestem Type. 180 sq.m. % Comp.	% Freq.	Needlegrass Type. 25 sq.m. % Comp.	% Freq.
Little bluestem	2.0	19	55.0	98	17.7	84
Big bluestem	78.0	100	24.8	99	17.5	96
Kentucky bluegrass	8.8	88	4.7	80	5.1	84
Needlegrass	1.9	31	2.5	40	51.2	100
Prairie dropseed	.1	1	2.7	20	1.4	12
Indian grass	1.9	37	1.8	51	.7	32
Side-oats grama	.1	7	.6	32	.9	32
Small panic grasses	.3	28	.4	36	.2	20
Junegrass	.1	10	.6	34	1.6	40
Nodding wild-rye	.1	12	.0	4	.2	16
Switchgrass	1.7	22	1.3	14	.1	8
Sloughgrass	.4	12	.0	0	.0	0
Forbs	3.6	74	4.1	90	2.4	72
Total	99.0		98.5		99.0	

The usual percentage where it was found was 1 to 3. Switchgrass, usually found in wetter soil, was distributed in about one-fifth of the unit areas. Its average basal area was less than 2 per cent.

Forbs were listed in three-fourths of the quadrats. They formed less than 5 per cent of the basal area in 58 per cent of those in which they occurred, and exceeded 10 per cent in only 10 per cent of the sample areas. Basal area alone does not give a fair estimate of their importance, however, and they will therefore be considered separately. The basal area of vegetation averaged 13.3 per cent. It was less than 8 per cent in only 11 samples and more than 20 per cent in only 3.

SLOUGHGRASS

Spartina pectinata, also called cordgrass and tall marshgrass, derives its generic name from a Greek word for cord, probably applied because of the toughness of the long coarse leaves (Fig. 8). It is found throughout

FIG. 8. Usual dense stands of sloughgrass (left) and switchgrass. The meter stick shows the height.

the grasslands of central North America occupying soil too wet and too poorly aerated for the development of big bluestem and switchgrass. Its demarcation of soils too wet, without drainage, for the growth of maize is clearly shown throughout the prairie. In countless areas the uplands and big bluestem lowlands have been broken, but the sloughgrass draws and flooded lands were left intact. They are too wet for cropping, at least in spring, but furnish hay, and the grass cover very successfully holds the soil against erosion. Many fields have become divided into several parts by deep ditches, impassable to farm machinery, where the prairie cordgrass was plowed under with the bluestems.

The seeds germinate readily in wet soil, and the seedlings develop so rapidly that the plants are a foot high in August and perhaps 2.5 feet tall at the end of the growing season. The plants ordinarily require two or more years' growth before flowering stalks are produced. By this time the foliage is 3 to 5 feet high and the photosynthetic surface very great. Because of its tall growth in dense pure stands, light values near the soil surface are only 1 to 3 per cent. Seedlings are not very tolerant of shade, and reproduction, except in bare areas, is undoubtedly almost entirely by rhizomes and tillers.

Beneath mature plants the surface 6 to 10 inches of soil is filled with a mat of coarse, thick, woody, much branched rhizomes. Because of its extensive rhizomes, this species always forms a dense sod. The roots are coarse and very long; they have been found to extend 8 to 11 feet deep.

Although this species renews activity rather late, often not until the second week in April, it grows more rapidly than any of the grasses of the prairie. By the first of June it is frequently in the fifth or sixth leaf stage and varies from 2 to over 3 feet in height. Where it shares marginal areas with switchgrass or big bluestem, it conspicuously overtops them (Fig. 6). The general height of the foilage at the end of the growing season ranges from 3 to 7 feet, depending upon the water supply. Flower stalks vary with soil moisture supply from 5 to 10 feet in height. Flowering begins about the second week in July, but the height of anthesis occurs approximately a month later and flowering may continue until frost. The large conspicuous panicles are 8 to 16 inches long and usually consist of 10 to 20 spikes.

Under the normally uniform cover of *Spartina* the shade is dense. Two or three of the basal leaves are generally dead by midsummer, leaving the stems bare to a height of 8 to 12 inches. Mature leaves are 15 to 18 mm.

wide and 2.5 to 5.5 feet in length. They are furnished with saw-tooth edges.

Sloughgrass furnishes moderately good hay if it is cut before the woody stems are much developed. The common practice is to mow the sloughs about three times each year. Since growth is quickly renewed and very rapid, heavy yields are thus obtained. Sloughgrass was widely used by pioneers for thatching roofs and covering haystacks and unroofed cribs of corn. Earlier, the Indians thatched their permanent lodges with sloughgrass before covering them with earth.

SLOUGHGRASS COMMUNITY

Spartina pectinata occurred over hundreds of square miles of first bottom lands along both the Mississippi and Missouri Rivers and their tributaries throughout the true prairie. It also grew in the edges of sluggish streams or ponds, but rarely in moist soils except in dry seasons or as relics in soils that had been drained. It represents the last stage in the succession from wet land or water to climax prairie. On its hydric side sloughgrass is bordered by various tall sedges, rushes, marsh grasses, and other hydrophytes forming wet-meadow vegetation. Toward the mesic side it usually gives way to a switchgrass—wild-rye community that is intermediate in its water relations. Sloughgrass is taller and coarser than most grasses of lowlands. It is dominant over great areas because of its height and the dense, pure stands resulting largely from propagation by rhizomes. Where best developed, the coarse, woody stems actually occupy only 1 to 3 per cent of the soil surface, since they are rather widely spaced. Nevertheless the shade produced is so dense—often 1 per cent or less of full sunshine—that where conditions for its growth are favorable other grasses are effectually excluded. In thinner stands, however, many tall, coarse forbs, some 9 or more feet in height, from both wetter and drier lowlands are found, as well as numerous smaller ones in the understory.

SWITCHGRASS

Panicum virgatum, a tall, coarse, sod-forming species, is an important dominant of low, moist land (Figs. 7, 8). It has migrated up ravines and draws and also occurs in disturbed areas on upland. It is perhaps the most mesic of prairie grasses, as is shown by its abundance in the drier portions of the sloughgrass community, where it occupies with nodding wild-rye and redtop (*Agrostis alba*) soils that are too poorly aerated for big bluestem.

Large seeds of this species are produced abundantly, but they do not germinate well until they have undergone a period of dormancy. Then, when planted, germination is prompt and seedlings develop rapidly both above and below ground. Like many other warm-season grasses of southern origin, switchgrass renews its growth late in April. Its height-growth for a time exceeds that of big bluestem and by early June the foliage is often 1.5 feet tall. Like big bluestem, the foliage reaches its maximum height by mid-July. A little later the panicles begin to unfold. These large, open, spreading panicles are 12 to 20 inches long and 16 to 20 inches wide. Flowering, which begins in July, reaches a maximum in August and continues until late autumn. Seeds are shed in winter or late fall. Mature plants attain a height of 4 to 7 feet. This tall grass is less tolerant of shade than big bluestem, nor does it tiller so readily or so abundantly. Owing to the scarcity of basal shoots and the wide spacing along the rhizomes of the unbranched stems, only 2 to 5 per cent of the soil surface is occupied. Hence, Kentucky bluegrass and shade-enduring sedges may occur as an understory. The roots are coarse and very deep.

Switchgrass is readily eaten by livestock as long as the stems remain green and are not much lignified. After this time the leaves and panicles, even of mature plants, are readily eaten. The grass makes excellent hay if it is harvested twice each summer. Yields are high.

NODDING OR CANADA WILD-RYE

Elymus canadensis is a tall, coarse grass of high water requirement (Fig. 7). Despite the fact that it is widely distributed, it is a dominant of much lower rank than any of the preceding. Reaching its best development on low land, it is also found on upland where increased water content of soil has resulted from local disturbances such as badger holes, gopher mounds, and other denuded places.

The relatively large seeds show a high rate of germination. Because of its northern derivation, seedlings of this cool-season plant do not ordinarily winter-kill. Mature plants renew growth two or three weeks earlier than big bluestem and other warm-season grasses. A foliage height of 2.5 to 3.5 feet is attained by the middle of June. Then the spikes begin to appear, since it flowers in midsummer. These, with the elongating stem, add another foot in height. The conspicuous spikes are usually 6 to 9 inches long and, if awns are included, often an inch in width. The rather woody, stout stems may occur in loose clumps. Often they are widely spaced, where the plants grow in an open sod. The broad green leaf blades, each with two auricles which clasp the stem, are only 8 to 15 inches long. As the seed ripens, the spikes bend over gracefully, which accounts for its common name, nodding wild-rye. Like practically all of the prairie grasses it furnishes good forage and hay. However, it should be harvested early. If left to mature, not only do the stems become lignified but the heads are often infested with ergot, which is harmful to livestock.

SWITCHGRASS–CANADA WILD-RYE COMMUNITY

This is a lowland community with water relations intermediate between sloughgrass and big bluestem. Originally hundreds of acres of bottom lands and other wet areas were clothed with dense stands of switchgrass more or less intermixed with Canada wild-rye. In the western prairies it was far less extensive than either of the preceding communities. However, broad areas were occupied by this community where the land sloped gradually, but where the changes in habitats were more abrupt the two preceding communities were usually separated by only a narrow belt of switchgrass and wild-rye or at least by one of these species. On both its wetter and less moist margins, extensive mixtures may occur.

Switchgrass is more abundant in the southeastern part of the western prairie, and wild-rye increases northward and westward. Characteristically, small areas of either or both species alternate with, or more or less intermix with, sloughgrass. In such places they may constitute 10 to 30 per cent or even more of the vegetation over many square miles of poorly drained bottom lands. In areas of wet soil this community may extend far up ravines and also occupy the broad sloping flats receiving water at the heads of ravines. The height of switchgrass often varies from 5 to 6 feet at the foot of the hill to only half this on the upland.

In mixture with switchgrass, nodding wild-rye seldom forms more than 1 to 5 per cent of the mixture but sometimes 10 to 15 per cent. But northward and westward it becomes more abundant, and on level land subject to overflow it may be the dominant grass over large tracts, where, when headed, it resembles thinly planted fields of barley. Basal shoots and leaves are few in midsummer, and only 5 to 8 per cent of the soil surface is occupied. Its early growth and excellent seeding habits compensate somewhat for its only moderately successful competition with other grasses of lowland.

In a low level area of grassland with a high water table and depressions here and there, vegetation may occur in patchwork fashion. But where the slope is gradually upward, the high degree of dominance of sloughgrass switchgrass, and big bluestem, respectively, clearly demarks the several communities. Where the slope gradient is steep they occur as narrow strip or belts often only a few feet wide. Each species seems best adapted to its own habitat. Sometimes sloughgrass follows far up a wet ravine where the change to well aerated moist soil is so abrupt that switchgrass and Canada wild-rye are not found or are represented only sparingly.

OTHER GRASSES OF LOWLANDS

About 20 other species of grasses are of considerable importance in lowlands. Many of these are found in or near areas of sloughgrass or in the more moist portions of the switchgrass and Canada wild-rye community. Some are also associated with big bluestem, especially in transitional areas.

Eastern gamagrass (*Tripsacum dactyloides*) is a tall, tufted perennial with very coarse, knotty, scaly rhizomes forming clumps 1 to 4 feet in diameter among other grasses or growing in continuous stands near lakes, swamps, and streams (Fig. 9). It is found mostly south of Nebraska in true prairie. The tall stems are 6 to 8 feet in height and have broad leaves much wider than those of most other prairie grasses. On springy hillsides it occurs as isolated bunches or small circular patches. Flowering begins late in June. This grass is not relished by livestock when other vegetation is plentiful, but if cut two or three times each growing season, the yield of hay is heavy.

Redtop (*Agrostis alba*) is an erect sod-forming grass 2 to 4 feet tall, often with a decumbent base, and vigorous rhizomes 2 to 6 inches long. It thrives in wet soil and also grows in depressions covered with water in spring and early summer. Thus, in nearly level bottom lands, islands of redtop often mark the depressions. The large, widely spreading panicles, 2 to 12 inches long and usually reddish in color, give this grass its common name. Blossoming occurs during midsummer.

Northern reedgrass (*Calamagrostis inexpansa*) and bluejoint (*C. canadensis*) are frequent in wet areas along the Missouri and Platte rivers and in other low or swampy grounds. They were not found in great abundance but were very important grasses in wet situations eastward and in Minnesota where the bluejoint often constitutes a distinct stage in succession between sloughgrass and switchgrass (Sampson, 1921).

Reed canary grass (*Phalaris arundinacea*) is a coarse perennial which, owing to rhizomes that spread widely, forms dense stands in wet places. The foliage reaches a height of 2.5 to 3.5 feet and the stems are 3.5 to 5 feet tall. The leaves are often nearly half an inch in width, and the inflorescence is a loose spike-like panicle.

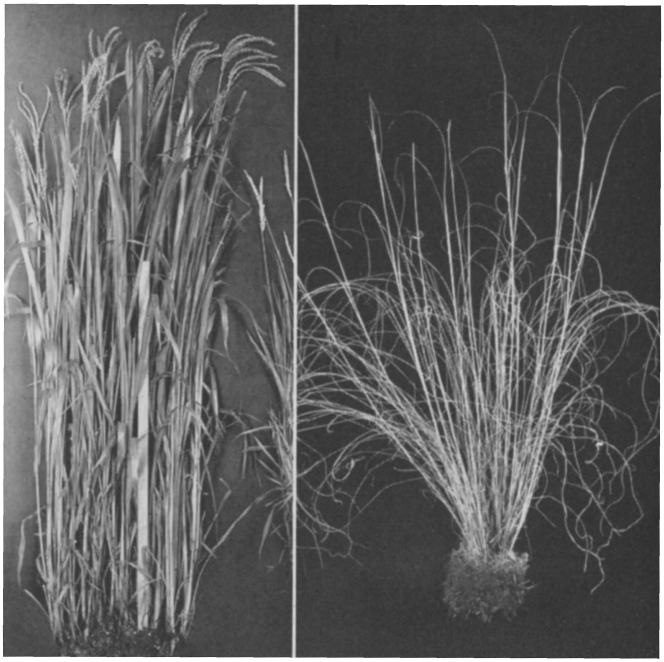

FIG. 9. A small clump of eastern gamagrass (*Tripsacum dactyloides*) (left) about 5.5 feet high. A mid grass, tall dropseed (*Sporobolus asper*), with leaves rolled as is often characteristic in late summer.

Saltgrass (*Distichlis stricta*) is infrequent except on the margins of saline areas. It nearly always grows in soil with a shallow water table. This perennial sod-former spreads widely by means of rhizomes. The foliage is only 6 to 10 inches high and is exceeded only a little by the flower stalks. It forms a dense sod when grazed and furnishes the best forage under close grazing. Western wheatgrass (*Agropyron smithii*), an upland grass to be described, populates small to extensive lowland areas often underlaid by a clay pan.

Other common grasses of lowland, varying from general distribution to local abundance, are Virginia wild-rye (*Elymus virginicus*), stout wood-reed (*Cinna arundinacea*), American sloughgrass (*Beckmannia syzigachne*), and fowl mannagrass (*Glyceria striata*). Rice cutgrass (*Leersia oryzoides*) and whitegrass (*L. virginica*), both with creeping rootstocks, are found in the wettest types of grassland. In comparison with the importance of the three great dominants, big bluestem, sloughgrass, and switchgrass, all of the preceding species are of minor significance.

Prairie is only partly composed of grasses. Forbs, as shown in the following chapter, also constitute a highly interesting and important part.

CHAPTER 3

Principal Forbs of Lowland

Forbs are always present and often abundant in prairie. They are an integral part of it. Often they are more conspicuous, although nearly always of less importance than the grasses. Some are rare; others occur only occasionally. All add tone to the landscape, and the beauty of the prairie is in a large part a result of their presence (Fig. 10). Nearly all of the legumes are valuable as forage, and they contribute considerable amounts to the total yield. The list of native forbs that are regularly eaten by livestock and hence decrease under close grazing is a long one; the list of those grazed but little or not at all and therefore increase in pastures is much shorter. Undoubtedly forbs provide valuable variety in the diet of livestock. In this extensive study on the composition of true prairie, approximately 150 species were found of sufficient abundance and of enough importance to warrant more or less individual study.

The following lists include the 58 most important species of forbs of lowland. They are arranged in order of decreasing importance, based upon the percentage of prairies in which they occurred in the two highest ranking groups, 1 and 2 (see page 20). Where numbers follow the name, the first number is the percentage of prairies in which the species occurred in the first, second, and third rank, and the second number in the fourth and fifth rank. The other numbers indicate similar rankings in upland prairies. Thus, stiff marsh bedstraw (*Galium tinctorium*) occurred in 70 and 4 per cent in the higher (1, 2, 3) and lower (4, 5) groups of lowland prairies, respectively. But on upland it was found in only 2 and 4 per cent of the prairies.

Materials for chapters 3 and 5 have been taken largely from "The Prairie," Ecological Monographs 4:111-292, 1934. The lists of forbs have been somewhat shortened and simplified, especially by the inclusion of common names. Descriptions of plants have been decreased in number and length, rearranged, and simplified. Somewhat more than half of the

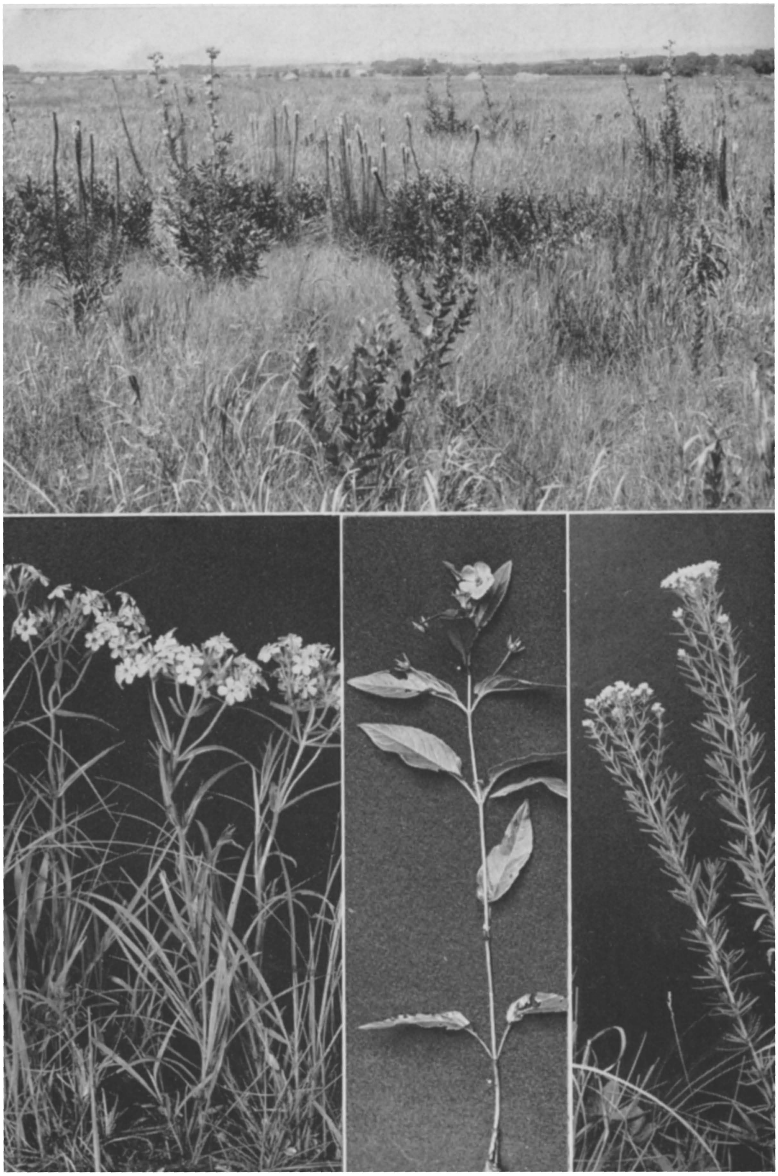

FIG. 10. View in August of low prairie in the Elkhorn Valley near Norfolk, Nebraska. Compassplant (*Silphium laciniatum*) and prairie button snakeroot (*Liatris pycnostachya*) are in bloom. (Below) Prairie phlox (*Phlox pilosa*), a single plant of fringed loosestrife (*Steironema ciliatum*), and mountain mint (*Pycnanthemum*).

photos have been re-used from "The Prairie" or from other papers by the writer published in Ecological Monographs.

TABLE 2. List and ranking of the 38 most important species of lowlands.

Galium tinctorium . . . . Stiff marsh bedstraw	70-4	2-4
Fragaria virginiana . . . Scarlet strawberry	52-20	27-18
Steironema ciliatum . . . Fringed loosestrife	74-26	1-3
Aster praealtus . . . . Willow aster	69-22	1-2
Anemone canadensis . . Canada anemone	50-13	4-2
Solidago altissima . . . . Tall goldenrod	72-14	9-18
Silphium laciniatum . . Compassplant	51-15	25-20
Phlox pilosa . . . . Prairie phlox	40-4	26-5
Silphium integrifolium. Entire-leaved rosin-weed	41-26	19-17
Helianthus grosseserratus Saw-tooth sunflower	54-28	4-11
Liatris pycnostachya . . . Prairie button snakeroot	40-16	15-12
Equistem laevigatum . . Scouring rush	46-17	22-15
Zizia aurea . . . . Golden meadow parsnip	35-14	6-10
Teucrium canadense . . American germander	52-31	0-7
Apocynum sibiricum . . Indian hemp	36-46	14-12
Viola papilionacea . . . . Meadow violet	31-29	3-8
Glycyrrhiza lepidota . . Licorice	43-14	3-12
Pycnanthemum virginianum and *P. flexuosum* . . . . . Mountain mint	18-2	2-4
Cicuta maculata . . . . . Water hemlock	30-32	0-0
Veronicastrum virginicum . . . . . . Culver's root	33-2	3-4
Asclepias verticillata . . Whorled milkweed	32-45	6-15
Asclepias sullivantii . . . Sullivant's milkweed	24-38	2-8
Equisetum arvense . . . . Scouring rush	16-16	4-4
Lythrum alatum . . . . . . Loosestrife	22-14	0-2
Erigeron annuus . . . . . Fleabane	18-10	5-4
Vernonia fasciculata . . Western ironweed	31-35	0-4
Helianthus tuberosus . . Jerusalem artichoke	19-18	0-4
Asclepias incarnata . . . Swamp milkweed	11-25	0-0
Hypoxis hirsuta . . . . . . Star grass	—	—
Heliopsis helianthoides. Oxeye	22-36	5-21
Thalictrum dasycarpum Tall meadow rue	13-31	1-4
Polygonum coccineum . Water smartweed	27-22	0-0
Rudbeckia hirta . . . . . . Black-eyed Susan	24-8	13-5
Ratibida pinnata . . . . . Coneflower	14-9	4-8
Senecio aureus . . . . Golden ragwort	11-5	2-3
Lycopus americanus . . . Water hoarhound	14-21	0-2
Silphium perfoliatum . . Cup plant	12-25	1-1
Vernonia baldwini . . . . Baldwin's ironweed	24-26	11-38

List of species of somewhat less importance in lowlands
(Read column on right following that on left)

Physalis heterophylla
Prairie ground cherry
Erigeron philadelphicus
Fleabane
Lobelia spicata
Pale spiked lobelia
Allium canadense
Wild onion
Helenium autumnale
False sunflower
Oxalis stricta
Yellow sheep sorrel
Rhus radicans
Poison ivy
Helianthus maximiliani
Maximilian's sunflower
Cirsium undulatum
Wavy-leaved thistle
Cacalia tuberosa
Indian plantain
Desmodium illinoense
Illinois tick trefoil
Antennaria plantaginifolia
Plantain-leaf everlasting
Physalis virginiana
Virginia ground cherry
Astragalus canadensis
Canadian milk vetch
Amphicarpa bracteata
Hog peanut
Gaura (all species)
Gaura
Oxalis violaceae
Purple sheep sorrel
Artemisia ludoviciana
Sage or mugwort
Lathyrus palustris
Marsh vetchling

Each of the 57 species in the preceding lists was far more abundant in lowlands where soil moisture was more plentiful than on uplands, but competition for light with the tall grasses was more severe. Although 10 other species were found in more than 10 per cent of lowland prairies, they are of far less importance than those that occurred regularly and abundantly.

STIFF MARSH BEDSTRAW

Galium tinctorium is a small perennial herb with 4-angled erect stems. The great importance of this species is shown by its occurrence as a society of the first class in over a third of the lowland prairies and of slightly lower rank in another third. The stems arise from the abundant, rather shallow underground parts. The plant is branched and leafy to near the base; the branches are mostly solitary and the leaves small, so that all are fairly well lighted even where, as usual, the plants are densely aggregated (Fig. 11). This bedstraw nearly always forms a dense understory in wet grasslands and sloughs. Growth begins early, and the plant grows nearly erect and to a height of 10 to 18 inches. The tiny, white, terminal flowers are present

FIG. 11. Canada anemone (*Anemone canadensis*) (above) forming a characteristic dense society; scarlet strawberry (*Fragaria virginiana*), and a few plants of stiff marsh bedstraw (*Galium tinctorium*).

from May until July, when they are usually replaced by the small, smooth, shining green fruits.

SCARLET STRAWBERRY

Fragaria virginiana is a widely distributed species, occurring throughout the region. In the more xeric western part it is found only in the lowlands and along ravines, but southeastward, with increasing rainfall, it is found on uplands as well. In many prairies it is rather uniformly distributed even over hilly land. It occurs in nearly half of the upland prairies but much more abundantly in about three-fourths of those on lowland (Fig. 11). The root system is less extensive and shallower than that of most prairie forbs. The strawberry is found not only as an understory where there is a dense stand of big bluestem but also occurs in wetter communities. Frequently the plants are densely aggregated. In early spring they are only an inch or two in height and the leaves are mostly spread near the soil surface. On uplands a height of 5 to 8 inches is usually attained, but the plant may extend upward 12 to 14 inches under the tall grasses. Propagation is mostly by long runners rather than by the short, thick, shallow rhizomes. The pretty white flowers are most abundant in mid May, and large clusters of the bright red, delicious fruits ripen during June.

FRINGED LOOSESTRIFE

Steironema ciliatum is the third most important forb of wet areas, where it forms extensive societies (Fig. 10). Its wide distribution is shown by its presence in every lowland prairie examined. In 20 per cent it ranked as a society of the first class, and it held second or third rank in about 55 per cent. This perennial herb renews growth early in spring, develops rapidly, and reaches a height varying from 1 to 3.5 feet. Because of underground stems, it grows in dense stands. The leaves are widely spaced on the unbranched stems, and the plant is very tolerant of shade. The pretty yellow flowers are held by the peduncles above the foliage. The plant remains green until frost.

WILLOW ASTER

Aster praealtus is a tall perennial that occurs rather abundantly on well watered lowlands or on the margins of ravines at the foot of slopes. It grows well also in wetter types of grassland, very frequently occurring with sloughgrass. Aster was found in all but 9 per cent of lowlands, usually ranking very high. Growth begins early and by May a height of 2.5 feet is attained. Mature plants range from 3.5 to 7 feet in height, depending upon the abundance of water and light. The bases of the woody stems defoliate. In September the much-branched tops are covered with a wealth of flowers.

CANADA ANEMONE

Anemone canadensis is a widely distributed, very conspicuous, and important forb of the more moist big bluestem prairies and wetter types of grasslands. Because of its propagation by rhizomes, it often forms dense, more or less circular patches a few to many feet in diameter. In less favorable sites it is often represented by scattered individuals. Plants range

FIG. 12. Tall goldenrod (*Solidago altissima*) standing far above the big bluestem; Culver's root (*Veronicastrum virginicum*) with leaves in whorls, and arrow-leaved aster (*Aster sagittifolius*).

from 8 to 18 inches in height. The large leaves are usually so thickly placed that they almost obscure the soil, and grasses are greatly suppressed. The white flowers, 1.2 to 2 inches in width, unfold during the latter half of May, and for several weeks areas of low prairie and broad flat swales in uplands are veritable flower gardens (Fig. 11).

TALL GOLDENROD

Solidago altissima is a common and conspicuous species of lowlands. It was found in all of them and as a society of the first or second class in nearly half. It is even more characteristic of the wetter types of grassland than of the big bluestem prairies. Until the plants reach a height of a foot or more, they have a definitely nodding top resulting from unequal lateral growth. Mature plants are 3 to 6 feet or more in height (Fig. 12). Growth is so rapid that at all times the plants stand well above the grasses. Where shade is dense the stems are defoliated by August to a height, often, of 2 feet. In ravines such dense stands may occur that only bluegrass can withstand the shade. In more moist prairies southeastward, this species occurs as an important forb of uplands and sometimes grows on hilltops. The large, golden flower clusters appear in late summer.

COMPASSPLANT

Three species of rosinweeds are found in the area (Fig. 13). The compassplant (*Silphium laciniatum*) is a very coarse, tall, yellow-flowered composite characteristic of low prairie and wet ravines in the north and west, but also occurs regularly on uplands, including hilltops, in the better watered areas south and east. Height varies from 3.5 to 10 feet and number of stems from 1 to 12 according to age and water supply. A single clump 6 to 9 inches in basal diameter may give rise to 100 or more coarse basal leaves which have a spread at or above the grass level of 3 to 5 feet. These leaves are often 20 inches long and 14 inches wide. A single clump may have a diameter of 2.5 to 5 feet, and in it and on its periphery the prairie grasses are shaded out. The vertical leaves, especially of younger plants, have the orientation of a compass, the sides receiving the morning and afternoon sun. From the involucres and upper parts of the stem much gummy material exudes and solidifies. The Indians and white settlers, especially the children, gathered it for chewing gum.

ENTIRE-LEAVED ROSINWEED

Silphium integrifolium is a tall, coarse perennial that often forms large clumps in low ground. It is found only sparingly in uplands, except in the prairies with the greatest rainfall, and is almost confined to ravines and lowlands in the western part of the area. The clumps consist of a few

FIG. 13. Three rosinweeds and two sunflowers. Cup plant (*Silphium perfoliatum*) (left) and, in sequence, entire-leaved rosinweed (*S. integrifolium*), young specimen of compassplant (*S. laciniatum*), and saw-tooth sunflower (*Helianthus grosseserratus*), with base of its stem at right. (Below) Jerusalem artichoke (*H. tuberosus*) with a quantity of the enlarged underground stems.

stems or there may be 15 to 25 or more. Since the very leafy plants are 2.5 to 5 feet tall, the effect of large clumps on the grasses is marked. This species, like the preceding, is one of the ten most important forbs of lowlands (Fig. 13).

CUP PLANT

Silphium perfoliatum is also a very large coarse herb. Its large opposite leaves are united at the base to form a cup which holds considerable amounts of water after a rain (Fig. 13). It usually reaches a height of 5 to over 8 feet, the several stems and coarse leaves occupying much space. It ranks fairly high as a lowland forb, but much less so than either of the two preceding.

SAW-TOOTH SUNFLOWER

Two species of sunflowers are common in the flora of lowlands. The saw-tooth sunflower (*Helianthus grosseserratus*) is a tall, coarse, single-stemmed composite. It is often abundant in ravines where it forms dense stands, and sometimes occurs, with reduced stature, on higher ground. Growth from the strong rhizomes and thick crown begins early in April and proceeds very rapidly, continuing until August when a height of 6 to 9 feet is attained. Where the sod is dense, stems are usually not closely spaced. A maximum showing of the large yellow flowers occurs in September (Fig. 13). This species was found in 82 per cent of the lowlands and was so abundant in 22 per cent as to form societies of the first class.

JERUSALEM ARTICHOKE

Helianthus tuberosus is characteristic of borderlands between prairie and woodland along ravines and streams. It thrives along draws or on lowland where the soil has been deposited by flooding. It is not so tall as the preceding species; its leaves are shaped much more like those of the cultivated sunflower (*H. annuus*); the heads are few and the ray flowers orange-yellow. The tubers are often of considerable size and abundance (Fig. 13). They were eaten by the Indians either raw, boiled, or roasted. It appears that they depended upon the natural supply and never cultivated the plant (Gilmore, 1919).

PRAIRIE PHLOX

Phlox pilosa is a perennial occurring abundantly on lowlands (44 per cent) and uplands (30 per cent), even ranging over the hilltops in Iowa and Missouri. Westward it is nearly confined to low ground. The slender, erect, mature stems, 1 to 2.5 feet high, for a long time stand well above the grasses. The long narrow leaves are too few to produce much shade even where several stems occur in a single square foot (Fig. 10). But the large clusters of beautiful pink-purple or rose-red flowers are a conspicuous feature of the landscape during May and June.

PRAIRIE BUTTON SNAKEROOT

Liatris pycnostachya is characteristic of big bluestem areas and is rarely found in much drier or much wetter grassland types (Fig. 10). Except very locally, it is confined to the areas of higher precipitation southward and eastward. A height of 3 to 5 feet is attained by this species. The unbranched stems arise from a strong corm, 3 to 4 inches in diameter, and growth is rapid. The basal leaves, often 100 or more, while narrow, are very long. At first they are almost vertical, but later they spread widely. Flowering begins late in July and, since the inflorescence is 10 to over 12 inches long, for several weeks the landscape is ablaze with purple.

GOLDEN MEADOW PARSNIP

Zizia aurea was found in half of the low prairies and ranked as a society of the first class in 19 per cent. It is an erect, branched perennial that reaches a height of 1 to 3 feet. Although there are often only 1 to 8 stems per plant, the many basal and lower long-petioled leaves which are bi- or triternately compound give it a bushy appearance. During May and June, when blossoming occurs, the large yellow-flowered umbels are conspicuous.

AMERICAN GERMANDER

Teucrium canadense occurred in 83 per cent of lowlands but ranked first in only 14 per cent. This perennial, odorless mint springs from coarse, much-branched rhizomes well supplied with whorls of fibrous roots. The rigid, square stems, with their rather large leaves, reach a height of 1 to 3.5 feet, including the dense wand-like racemes which, when mature, are 6 to 12 inches long (Fig. 14). The abundant, small, light purple or pink flowers are conspicuous. Blossoming occurs throughout the summer.

CULVER'S ROOT

Veronicastrum virginicum rapidly develops its unbranched stems and all reach a height of 2 to 7 feet in late June or July. Frequently the clumps are 2 or more feet in diameter. It competes with the grasses for light at all levels; under dense clusters of plants the soil is almost bare. The fragrant, white flowers occur in spike-like racemes and are so numerous as to be very conspicuous (Fig. 12).

FIG. 14. Water hemlock (*Cicuta maculata*) with long-petioled basal leaves and carrot-like flowers, and rhizomes and erect stems of American germander (*Teucrium canadense*).

WATER HEMLOCK

Cicuta maculata is a stout, erect, much branched, perennial herb that is found only in moist or wet soil. The base of the great, hollow, glabrous stem is frequently an inch thick. The plant varies in height from 3 to 6 feet. The general height of the blades of the bi- or tripinnate, basal leaves usually varies between 16 and 32 inches. The petioles are mostly 1 to 2 feet long. The stems are leafy to the top; the leaves rapidly decrease in size with an increase in height of stem (Fig. 14). The plant is supplied with several fleshy roots, some of which may reach an inch in diameter. Both stems and roots possess a carrot-like odor. This plant is poisonous. It was found in about two-thirds of the low prairies, often in soil wetter than that occupied by big bluestem.

FIG. 15. Native blue flag (*Iris versicolor*), a denizen of wet lowland.

OTHER SPECIES

There are many wonderful plants in the lowland, and each has its own peculiar characteristics and special preferences and exerts its individual impress upon the grassland. Associated with water hemlock are several mints (*Mentha*), hedge nettle (*Stachys*), marsh marigold (*Caltha*), water hoarhound (*Lycopus*), and blue flag (*Iris*) (Fig. 15). The whorled milkweed (*Asclepias verticillata*), even when growing thickly, has only a minor effect upon the grass. Nor does the large, coarse, Sullivant's milkweed (*Asclepias sullivantii*), since the plants occur in very open stands.

In the sloughgrass, the five-foot swamp milkweed (*Asclepias incarnata*) retains its leaves only near the top of the stems, so dense is the shade. Yellow star grass (*Hypoxis hirsuta*) blossoms in spring and early summer not far above the soil. The yellow and the purple sheep sorrels (species of *Oxalis*) are also low-growing plants, blooming mostly in summer. A small, showy, herbaceous vine, purple vetch (*Vicia americana*), sometimes forms dense but limited societies in moist soil. Dense societies of the

FIG. 16. Wild bergamot (*Monarda fistulosa*), tall meadow rue (*Thalictrum dasycarpum*) about 7 feet tall (center), prairie coneflower (*Ratibida pinnata*), and Baldwin's ironweed (*Vernonia baldwini*) at extreme right.

purplish or blue-flowered spiderwort (*Tradescantia bracteata*) occur in almost pure stands; while here and there are found the mountain mints (*Pycnanthemum* spp.) (Fig. 10) and poison ivy (*Rhus radicans*). Other species common on lowlands are wild bergamot (*Monarda fistulosa*), tall meadow rue (*Thalictrum dasycarpum*), coneflower (*Ratibida pinnata*), and Baldwin's ironweed (*Vernonia baldwini*) (Fig. 16). The black centered, orange-yellow flowers of black-eyed Susan (*Rudbeckia hirta*) beautify the landscape. This is a brief glimpse into nature's wonderful flower garden—lowland prairie.

CHAPTER 4

Grasses and Communities of Upland

VEGETATION of upland prairie is quite different from that of lowland. The dominant grasses are nearly all of the mid-grass type. Five species, distributed in three plant communities, are chiefly concerned. Upland grasses cannot compete successfully with tall grasses on lowland because of the dense shade produced by them. Conversely, upland soils are usually not sufficiently moist to promote development of tall grasses, especially in competition with the more xeric mid grasses. Of course, there is much intermixing of species on lower slopes, and mid grasses are often scattered sparingly over low ground. Likewise big bluestem, mostly in the bunch form, occurs, sometimes abundantly, beyond its general area of dominance. The adopted Kentucky bluegrass is a small component of each of the six grassland communities.

LITTLE BLUESTEM

Andropogon scoparius is an erect, warm-season, perennial grass which puts forth new shoots usually about mid-April. The early and abundant tillering of the vigorous seedlings results in a very compact bunch or sodded area (Fig. 17). The slender leaves, often 8 to 14 inches long when mature, with prominent midveins, are partially folded. The foliage usually varies in height from 7 to 15 inches, depending upon soil fertility and especially available moisture. It may attain 20 inches in the warmer and more humid southern areas. The flower stalks, produced in late summer and autumn, range from 1 to 3.5 feet high (Fig. 18). Flowering begins usually in August and continues for several weeks. Flower stalks are thickly grouped, and seeds are produced in great abundance. Propagation is by seed, by tillers, and by very short, inconspicuous rhizomes.

An open sod is produced where moisture is sufficient, but bunches 6 to 8 inches or more in diameter are formed in drier sites. Several hundred

FIG. 17. Typical stand of little bluestem (*Andropogon scoparius*) in July. The bunches are about 18 inches tall. Prairie near Pierce, Nebraska, on September 15, after mowing and stacking the hay. The stubble and mulch give efficient protection to the soil.

closely aggregated shoots, which are flattened at the base, may occur in a single bunch. On lower land and in areas with abundant precipitation the whole sod may consist of closely crowded stems. These sod-mats are sometimes several square feet in area, but usually they are much smaller.

Often the sod consists of small tufts closely aggregated. The overlapping leaves furnish a foliage cover of 80 to 100 per cent, but the basal area is seldom greater than 20 per cent. The usual bunches of this grass have a spread of foliage often twice that of the base of the bunch. Deterioration of the bunches and mats nearly always occurs first in the older central part and proceeds toward the periphery, but they often have a long life span. The beautiful coloration of upland prairie in autumn and winter is largely due to the various shades of yellows, reds, and bronze presented by the drying of this grass.

Little bluestem is highly palatable throughout the true prairie, particularly during early stages of development; like big bluestem it furnishes a rather uniform amount of forage throughout the summer. Less foliage of this and many other grasses is produced farther northward where the growing season is short; in northern Texas some leaves remain green all winter. When properly managed, the best native pastures are dominated by bluestems, and if harvested early little bluestem also produces an abundant crop of hay of good quality (Fig. 17).

SIDE-OATS GRAMA

Bouteloua curtipendula is a warm-season, perennial mid grass with short scaly rhizomes. It forms small to large tufts or a very open sod (Fig. 18). It is drought-resisting, and when other grasses succumb to drought it may develop large bunches. In habit it approaches that of an interstitial species. On steep banks of ravines, on dry ridges, and in slightly disturbed places, it may form 10 to 60 per cent of the plant cover. It ranges widely, from the big bluestem community throughout all of those on uplands, but normally composes only 1 to 3 per cent of the vegetation. It rarely exceeds a few square yards in area in rather pure stands. Growth is renewed early in April, and a height of 3 to 3.5 feet is attained when the flowers are produced. Abundant tillers and new shoots from rhizomes produce much foliage. Flower stalks appear about the first week in July, and blooming continues into September. The inflorescence consists of 35 to 50 pendulous spikelets on a slender flower stalk. The zigzag appearance of the rachis is very characteristic, as are also the hairy margins of the leaf blades and the dry, curled, whitish basal leaves. The plant is tolerant to shade and has an excellent root system.

The nutritious forage furnished by this *Bouteloua* is readily eaten by livestock. This grass withstands well both grazing and drought and is a principal species in many pastures where it has largely replaced the bluestems.

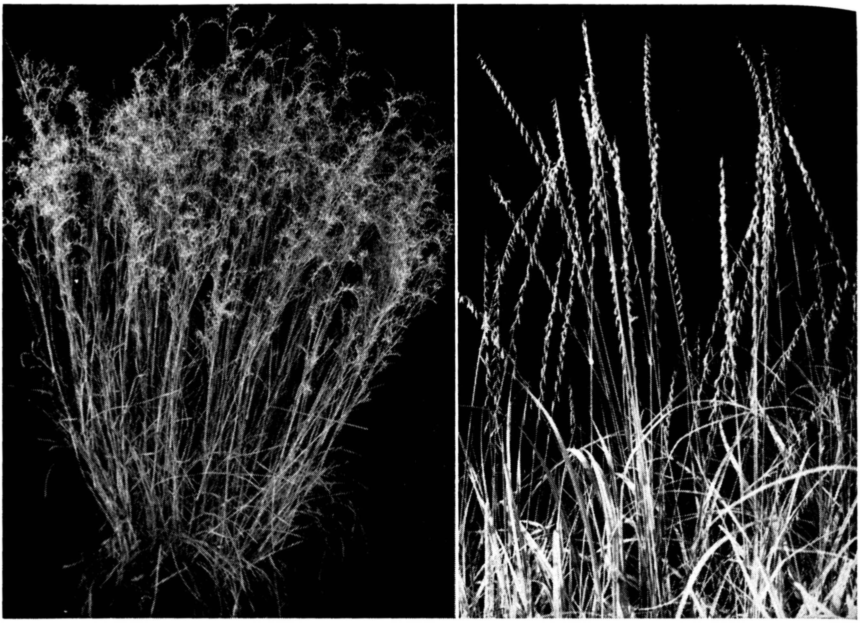

FIG. 18. Large bunch of little bluestem in seed in September, and (right) a sod of side-oats grama in seed in August.

JUNEGRASS

Koeleria cristata is a cool-season, perennial, bunch-forming grass of boreal origin (Fig. 19). It is most abundant in the northern and central prairie region, where it occurs in the needlegrass, the little bluestem, and the prairie dropseed communities. But not infrequently it is found on lower mid-slopes and well drained lowland. It usually composes 1 to 3 per cent of the prairie cover, but sometimes as much as 10 per cent. The bunches of this mid grass are mostly about 2 inches in diameter. The abundant flower stalks, with their densely flowered, contracted, spike-like panicles, 2 to 5 inches long, appear not unlike those of timothy. The rather dense foliage attains a height of only about 12 inches; flower stalks are 20 to 30 inches tall. The rather short leaves are soft, irregularly corrugated on the upper surface, and conspicuously dark green. Blossoming begins late in May, and the height of anthesis is attained by the middle of June. The roots are only about 1.5 to 2 feet deep. Following the fruiting season the plant experiences a period of summer dormancy, after which it makes considerable growth in autumn. It seems to depend more upon rapid reseeding than on a long life span to maintain its place in prairie. Junegrass is an excellent forage plant and is relished by all kinds of grazing animals.

Needlegrass and prairie dropseed also occur rather regularly as minor components of the little bluestem community. Since each grass also forms a distinct community of its own, they will be described where these communities are discussed.

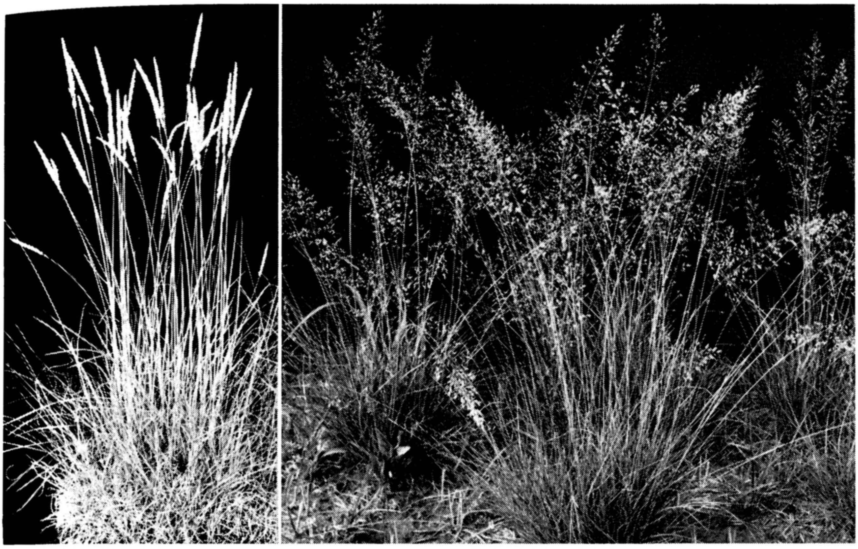

FIG. 19. A bunch of Junegrass (*Koeleria cristata*) near the time of blossoming, on June 15. (Right) Bunches of prairie dropseed (*Sporobolus heterolepis*) with other vegetation cleared away. The plants are in flower and fruit, Sept. 15.

LITTLE BLUESTEM COMMUNITY

Little bluestem is the most important dominant of this most extensive upland type. On an average it alone composes 55 per cent of the vegetation in the western prairie area, and it sometimes furnishes 90 per cent. Like big bluestem its dominance extends widely. Little bluestem ranges over the uplands eastward, but especially southward, while westward it extends far into mixed prairie. This species easily exceeds in importance all other upland grasses combined. It ordinarily forms an interrupted sod; the mats or tufts are very dense. Accompanying species grow between the mats. The roots form a continuous dense mass in the upper 2 to 3 feet of soil and many reach 4 to 5 feet in depth. A pronounced bunch habit occurs on steep slopes where much water may be lost by runoff. Here the large bunches are more widely separated. This community is less abundant in the northwestern part of true prairie where, on poor soils with much runoff, it either intermingles with needlegrass or is, in many places, almost replaced by it. In the richer, more moist soils of the Iowa-Missouri-Kansas area its chief competitor is big bluestem. This tall grass intermingles with it throughout, often in almost equal amounts in the Flint Hills of Kansas, and sometimes exceeds it in abundance even on midslopes. This type gives way to big bluestem slowly on gradual slopes but more abruptly on steeper ones.

COMPOSITION OF VEGETATION

A series of square meter quadrats from the top to the base of a long, rather gentle south slope near Topeka, Kansas, gave the following percentage composition in July, 1930. Each column represents a quadrat.

Species	Upper slope				Mid-slope		Lower slope		Level base	
Little bluestem	65	40	81	69	52	75	15	18	16	5
Big bluestem	10	9	10	8	30	20	63	60	80	89
Prairie dropseed	15	50	—	—	6	—	—	—	—	—
Switchgrass	—	—	2	8	10	4	—	5	2	—
Foliage cover %	50	50	50	60	75	80	90	100	100	100
Basal area %	14	10	13	15	12	18	13	13	15	13

Little bluestem was outranked by prairie dropseed in one place on the upper slope. Seepage on the mid slope permitted the growth of some switchgrass. Otherwise decrease of little bluestem and an increase in abundance of big bluestem from upper slope to level base is shown clearly. This was accompanied by a marked increase of foliage cover but with no change in basal area. Similar changes occurred in all of the six states where samples were taken. Those from a station in central Iowa have been shown on page 29.

Percentage distribution of little bluestem on ridges and steep upper slopes in relation to needlegrass is shown for three stations as follows:

Species	Northwestern Ia. (Cherokee)				Northeastern Neb. (Allen)				Southeastern Neb. (Neb. City)				
Little bluestem	61	44	30	15	—	5	—	69	25	13	29	21	4
Big bluestem	10	15	15	12	65	24	40	25	7	41	38	30	25
Needlegrass	15	30	48	45	20	45	50	—	50	36	26	38	56
Bluegrass	3	2	5	8	5	5	6	2	—	1	1	2	6

Needlegrass was an important constituent of the vegetation in twelve quadrats, chiefly to the detriment of little bluestem, and it was the chief dominant in 7 sample areas. The line of quadrats crossed the ridges and upper slopes at right angles; bluestems, and usually little bluestem, were the dominants both above and below the areas of needlegrass.

A total of 180 quadrats was made throughout the little bluestem type in the six states. The average basal area was 15.3 per cent. It was less than 10 per cent in only 17 samples and exceeded 20 per cent in only 20 units. Little bluestem composed 55 per cent of the vegetation and was present in all quadrats save three. In only 20 per cent of the quadrats did it constitute less than 40 per cent of the vegetation, and in 31 per cent of them it exceeded 70 per cent (Table 1).

The average percentage composition of the most abundant grasses in this type was little bluestem 55, big bluestem 24.8, bluegrass 4.7, needlegrass 2.5 and prairie dropseed 2.7. The per cent frequency of each species was, in the same order, 98, 99, 80, 40, and 20. The large amount of big bluestem was due in part to its considerable abundance on lower midslopes and on well watered, less rolling upland areas. Some of the quadrats, moreover, included transitional areas between the big and little bluestem types.

The two bluestems together constituted 80 per cent of the plant cover. The wide distribution and great abundance of bluegrass are of much importance (Table 1). It ranked as the third most abundant species.

Needlegrass and prairie dropseed each furnished about 2.5 per cent of the basal cover, but the dropseed had only half the frequency (20 per cent) of that of needlegrass. Table 1 shows that needlegrass occurred both more frequently and in greater amounts in this type than in that of big bluestem. Prairie dropseed was almost confined to uplands.

Indian grass played a very minor role here, as it did also on lowlands. Junegrass, side-oats grama and the two low-growing panic grasses each composed approximately 0.5 per cent of the cover. This percentage occurrence in about a third of the quadrats was the same. Very little nodding wild-rye occurred anywhere, but switchgrass constituted 30 to 62 per cent of the cover in several quadrats in the southern section of the area.

Forbs furnished only 4.1 per cent of the basal area notwithstanding their abundance and conspicuousness. They occurred in nine-tenths of the quadrats. Although the forbs may often seem far more important, and sometimes actually are so, yet as regards their part of the basal area the percentage rarely averaged much more than 5 to 12. It must also be kept clearly in mind that even the grasses, often with a foliage cover of 100 per cent, actually occupy on an average only about 15 per cent of the surface of the soil.

This, then, is the partial answer to the question, of what is true prairie composed? Quadrats were supplemented by extensive and thorough examinations of the plant cover over the entire prairie.

NEEDLEGRASS

Stipa spartea is typically an upland species, but it is also frequently more or less abundant on flat lands at the heads of draws, and on broad washes on lower slopes where heavy rains may cause some erosion and deposit of soil. It is a perennial, cool-season bunch grass of boreal origin. It renews growth with Canada wild-rye and Kentucky bluegrass very early in spring. The usually circular bunches are relatively small, ordinarily only 1.5 to 2.5 inches in diameter. But some, by extensive tillering, may finally exceed 4 inches in width. They are usually rather widely spaced in mature stands and intermixed more or less with other grasses. Height of foliage ranges from 15 to 36 inches, varying with the amount of available water and the degree of competition. Growth is so rapid that a height of 2 feet may be attained by the first of June. The leaves are smooth and shiny beneath, and corrugated and somewhat glaucous above. The attenuated ends of the long, slender leaves are mostly dead and dry even early in summer. In drought the leaves roll upward and inward. They may remain green or partly green all winter when covered with snow or when the weather is mild.

Flower stalks are well developed by the first of June (Fig. 20). They are from 2 to 4 feet tall and vary in number from 1 or 2 to about 18, depending somewhat on the size of the bunch. Flowering follows quickly, and by June 10 the twisting of the 4- to 6-inch awns indicates the ripening of the seed.

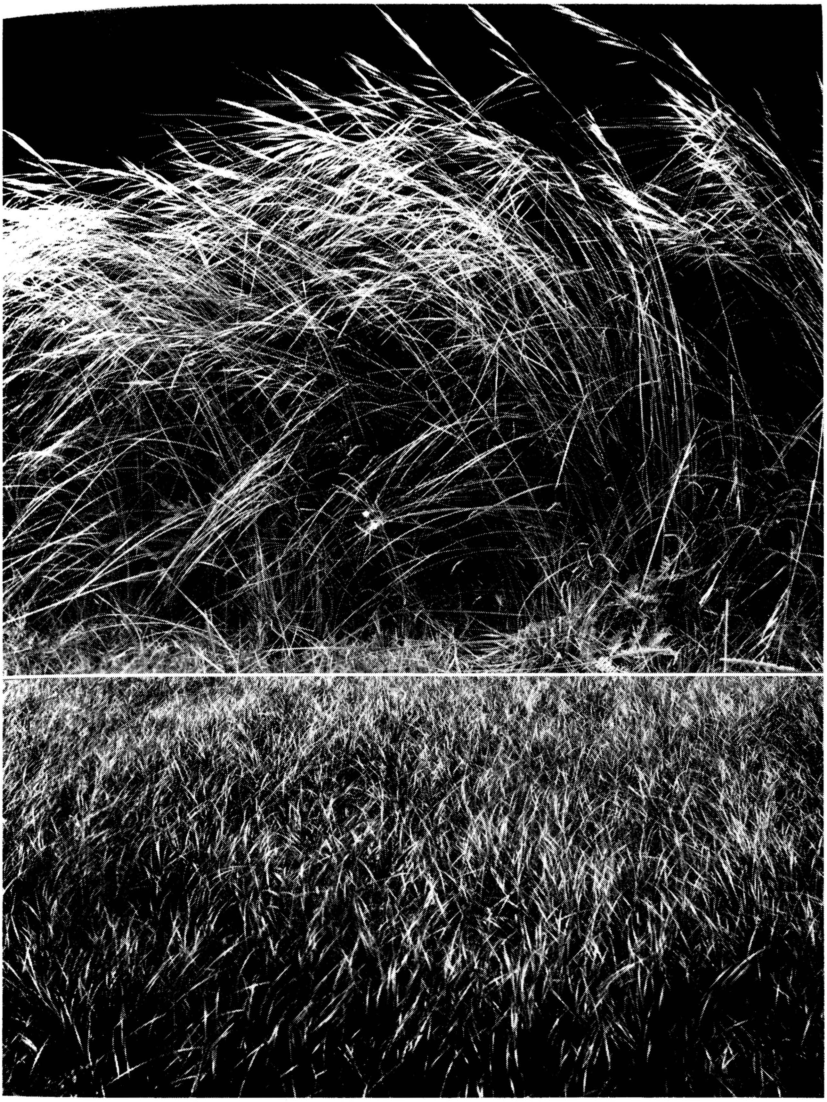

FIG. 20. Typical view of needlegrass on July 1. Bending is not due to the wind but to the crop of heavy seeds. (Below) A pure, thick stand of needlegrass before the production of flower stalks.

"A field of fruiting Stipa is a magnificent sight. The tall, wand-like stems are often so thick, as they bend gracefully under the weight of the seed, and the foliage cover so dense that the general appearance, until one separates the crowns, is that of a sod-former rather than a bunch grass. Actually the basal cover is very small, only about 11 per cent. . . . After the fall of the seed [usually by the first week of July] the four-foot stems, now bleached white, become erect. They and the broad shiny glumes remain for several weeks and clearly demark the boundaries of the needlegrass community" (Weaver and Albertson, 1944).

The seeds (which, as in all grasses are really fruits) may be blown a considerable distance by the wind, especially when the long awns twist together in clumps. Unlike most other grasses, the seed gives the best germination when planted deeply. The fruit is buried in the soil by the torsion of the bent and twisted awn, which is held from turning by the bases of stems near the soil surface. Seeds from a single stem are relatively few, perhaps only a dozen or two, but all are apt to be planted to the proper depth of about 2 inches and are thus insured better conditions for germination than on the soil surface. The root system is fine and very efficient.

Stipa in its early growth furnishes excellent forage, and, because of its development before most other prairie grasses, it is frequently exterminated by grazing animals. It should not be mowed for hay until the seeds have fallen.

NEEDLEGRASS COMMUNITY[1]

Needlegrass is the chief dominant of a very much smaller grassland type than that of little bluestem. This bunch grass is of little importance in northeast Kansas and Missouri and is found only occasionally from central Kansas southward. But it gradually increases northward, where the type becomes well developed. In Dakota, north of the area studied, needlegrasses (species of *Stipa*) are the chief dominants over vast areas. Steep, dry ridges and xeric slopes, especially where the soil is thin and perhaps sandy or gravelly, are frequently dominated by needlegrass. In hilly lands in the central and northern parts of the prairie, communities of needlegrass may cover from one-fifth to one-third or even more of extensive up-

[1] This and the following community description were adapted from "The Prairie" (Ecological Monographs, 4).

lands. Here it may comprise 50 to 80 per cent of the plant cover. Such areas alternate with the little bluestem pattern or with that of prairie dropseed. The chief associates of needlegrass are the bluestems, Junegrass, and side-oats grama, but it is found in various groupings. It also occurs with big bluestem on lowland but seldom extensively. An analysis of 25 quadrats is given in table 1.

Where needlegrass is fairly thick, the basal area is small; and the greater the apparent density of this species, the more the bare soil. This results from the smaller amount of little bluestem and other less conspicuous elements. Frequently the basal area is only 7 to 9 per cent, but it is usually about 11.

PRAIRIE DROPSEED

Sporobolus heterolepis is a warm-season perennial which is distinctly a bunch-forming grass (Fig. 19). The mostly circular bunches are usually 4 to 8 inches in width, but widely spaced ones may attain a diameter of 12 to more than 18 inches. Growth of the narrow, yellow-green leaves begins early in spring. Ordinarily the shoots are closely aggregated within the bunch, sometimes as many as 100 to 200 occurring in a single bunch of medium size. During drier years the number is much reduced. The leaves, which are 18 to 40 inches long and are attenuated and dry at the tips, curve gracefully outward and downward in summer. In winter, still attached to the stems, they lodge thickly in such a manner as to provide a mulch to a distance of 10 to 14 inches around the base of the plant. Old bunches deteriorate as a result of the death of the central part and often break up into several tufts. The enlarged rounded bases of the stems beneath the debris collected in the bunches, the 4 or 5 leaf blades originating at about the same height, and the very fine veining of the leaves, are all characteristic of this species. The abundant fibrous roots reach a depth of 4 to 5 feet.

The foliage height on uplands is about 8 to 18 inches, but on low ground it may reach 24 inches or more. Although flower stalks begin to appear in July, anthesis reaches its height late in August and September. The broad, spreading panicles are held 2.5 to 3 feet above the soil surface. Each spikelet bears a single large seed which readily falls upon reaching maturity, hence the name dropseed. This grass is palatable to all kinds of stock and furnishes considerable forage when it is not allowed to mature.

PRAIRIE DROPSEED COMMUNITY

A very minor but distinct upland community is dominated by the bunches of prairie dropseed. Despite the wide distribution of this species, it was not found in many of the prairies in this survey. It is always most abundant on the driest uplands, where it often dominates local patches, forming 80 per cent or more of the cover. The areas over which it holds control are much less extensive than are those of the needlegrass type. They vary from a few square rods to a few acres in extent, and all degrees of intermingling with the needlegrass type and with the little bluestem community occur. Prairie dropseed more often occurs as scattered bunches with little bluestem or needlegrass, where it constitutes 1 to 20 per cent of the vegetation. Sometimes isolated clumps occur in big bluestem prairie. Following the drought of 1934–40 this community increased very greatly in area and importance.

The bunches are so widely spaced that the basal area is usually only 8 to 15 per cent, but the widely spreading foliage obscures the unoccupied soil between the bunches and the sod-like, smaller tufts. The foliage cover is often 80 to 90 per cent in good stands. Usually only the more xeric upland forbs occur in this community, since the entire soil is thoroughly threaded by the roots of this xerophytic grass.

About the same species of upland grasses that occur with needlegrass were found here. In 10 representative quadrats little and big bluestem each composed about 11 per cent of the vegetation and bluegrass about 4 per cent. Needlegrass, Junegrass, and Indian grass were each represented by about 1 per cent, but they occurred in 30 to 50 per cent of the quadrats.

OTHER UPLAND GRASSES

About 25 minor species of grasses and sedges occur more or less regularly on uplands. Only a few of these are of considerable ecological importance and will be briefly described. Others will be mentioned elsewhere. Scribner's panic grass (*Panicum scribnerianum*) is a low-growing perennial that occurs throughout the prairie on both moist and dry soil (Fig. 3). It is a species of the understory, growing between the bunches and tufts of other grasses. In winter, the broad, smooth leaves form a rosette-like cluster near the soil, but the erect stems in summer ordinarily reach heights of 12 to 15 inches, except in shade on lowland where they may be

18 or more inches high. The bunches or tufts are small (1 to 5 inches wide) but the tops spread widely. This grass develops best where the vegetation is not dense. Flowering often begins early in June. The panicles, with their large spikelets, are conspicuous. Because of its wide distribution and rather common occurrence, it is one of the most important secondary species.

A considerable number of other panic grasses of small stature occur. Among these Wilcox' panic grass (*P. wilcoxianum*) is most frequent and of greatest abundance. It is of smaller stature than Scribner's panic grass; leaves, panicles and fruits are distinctly smaller than those described, and in addition leaves and stems are very hairy. Both this and the preceding have good forage value.

Tall dropseed (*Sporobolus asper*) is a perennial bunch grass which is very drought resistant and takes on great importance during drought cycles (Fig. 9). It normally forms only a small part of the vegetation. The plant is 1.5 to 4 feet tall. Stems are mostly unbranched, and the compacted panicle, which is enclosed in the upper leaf sheath, varies from about 3 to 10 inches in length. Flowering occurs in autumn. The long, very fibrous leaves bleach white, as do the stems in winter. They are frayed by the wind but may remain in place a second summer. Tall dropseed also occurs in low prairie, especially where there is a clay pan or slight disturbance. It is common in native pastures, but is of low forage value.

Penn sedge (*Carex pennsylvanica*) is an understory species which attains a height of 5 to 9 inches, but the flower stalks are a little taller. Excellent rhizomes enable it to form tufts, singly or in small groups between the dominant grasses. Growth is renewed early in spring, and blossoming occurs during April or early May. Where best developed, as on dry ridges and upper slopes, it may form at least 10 per cent of the vegetation. It is a species of wide distribution. Certain other sedges are more or less common in prairie, especially *Carex meadii, C. festucacea,* and *C. scoparia.*

Western wheatgrass (*Agropyron smithii*) was found only sparingly in the west-central area of true prairie before the great drought, although it was plentiful northward and in the mixed prairie westward (Fig. 4). Immediately after the beginning of drought it became increasingly abundant in true prairie, where it spread over all types of terrain until in many places it became the most important grass west of the Missouri River. In addition to being a good seed-former, large areas where other species were practically absent indicated its excellent method of migration by underground stems. It will be discussed in the chapters on drought.

Purple lovegrass (*Eragrostis spectabilis*) is sparingly distributed throughout the prairie. It is a perennial of a somewhat weedy nature. It grows in low tufts but becomes very conspicuous when the large, widely spreading, purplish panicles appear. These separate from the plant and are scattered widely by the wind.

Blue grama (*Bouteloua gracilis*) is a short grass of great importance in mixed prairie (Fig. 3). In true prairie it occurs sparingly and usually only in the driest situations, where mid grasses grow poorly and shade is not dense. This very palatable, drought-resistant grass forms a continuous sod, by the close spacing of the bunches, or a sod interrupted by other grasses, depending upon available soil moisture. The numerous leaves, which vary in length from 1 to 4 inches, are mostly basal and grow so thickly that the sod is almost continuous. Flower stalks are 8 to 12 inches high and have 2 or 3 spikes about an inch long. Flowering may occur at any time during summer when soil moisture is available. Forage matures well on the ground, and this species, unlike most prairie grasses, furnishes excellent feed both summer and winter.

Hairy grama (*B. hirsuta*) is similar in stature and general appearance to blue grama, except that the leaves are very hairy and that it grows in small bunches. Very little occurs in the region under present consideration but it is abundant on thin droughty soils and rocky hilltops in the extensive grasslands known as the Bluestem Hills in Kansas and the Osage Hills in Oklahoma.

Buffalo grass (*Buchloe dactyloides*), like the preceding short grasses, cannot endure the shading of taller competitors and is of little importance in true prairie (Fig. 21). It spreads rapidly by stolons which root readily when they come in contact with moist soil. It is usually associated with blue grama on the thinner soils of upland in the western edge of prairie but is also found in draws or on clay pan lowlands where it sometimes forms pure, dense mats of limited extent. The plants are seldom more than 4 to 5 inches tall and the leaves grow so near the soil that much of the green tissue remains even when closely grazed. Staminate spikes occur in groups of 2 or 3 on slender erect culms usually only 4 to 6 inches high. The pistillate spikes or heads, which produce the seeds, are hidden within the foliage.

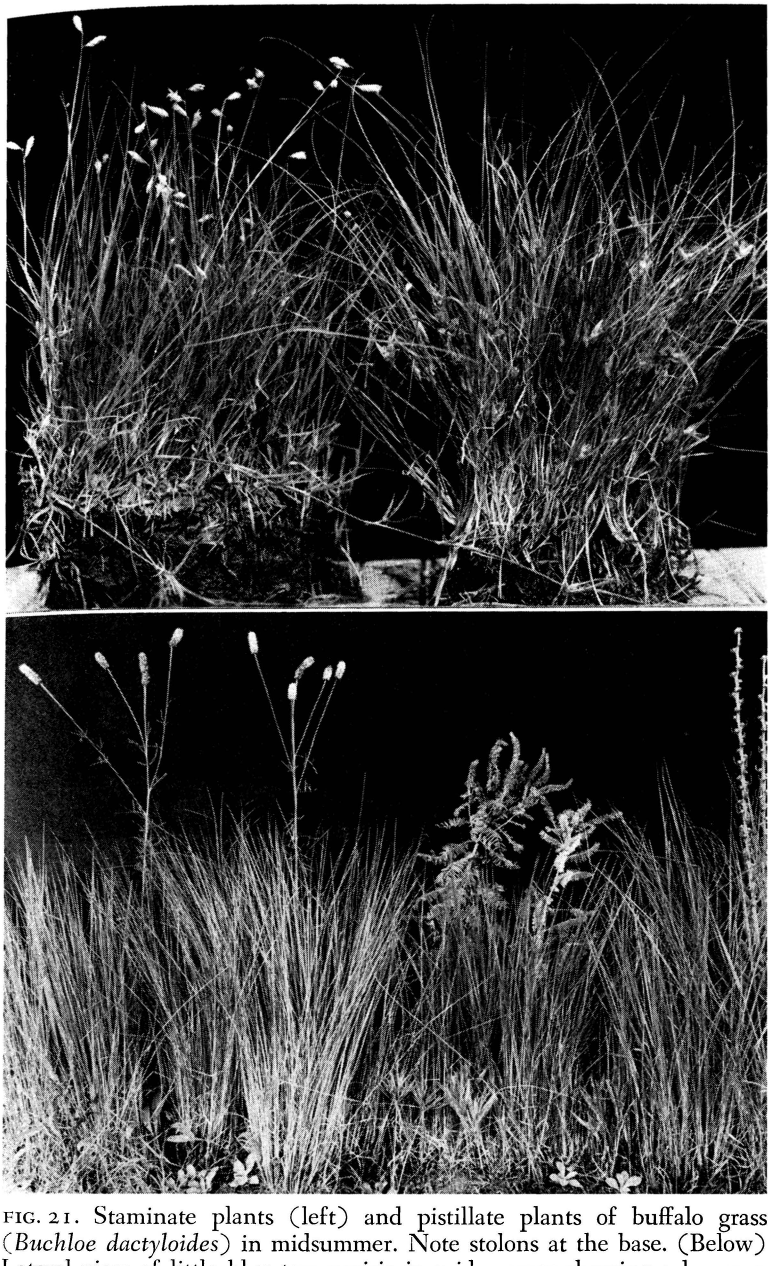

FIG. 21. Staminate plants (left) and pistillate plants of buffalo grass (*Buchloe dactyloides*) in midsummer. Note stolons at the base. (Below) Lateral view of little bluestem prairie in midsummer showing a lower, a middle, and an upper layer of vegetation. The forbs are white prairie clover (*Petalostemum candidum*) (left), lead plant (*Amorpha canescens*), large button snakeroot (*Liatris scariosa*) (right), and prairie cat's-foot (*Antennaria neglecta*) on the soil. (From Ecological Monographs)

CHAPTER 5

Principal Forbs of Upland

Forbs of upland were studied and listed in the same manner as those on more moist soil. A group of 75 species that were most abundant and important on uplands occurred in at least 10 per cent of the 100 prairies examined.

Table 3. List and ranking of the 35 most important forbs (and a few shrubs) of uplands.

Amorpha canescens Lead plant	87-6	18-34
Helianthus laetiflorus Stiff sunflower	80-7	38-11
Aster ericoides Many-flowered aster	80-5	50-25
Antennaria neglecta Prairie cat's-foot	72-6	25-19
Erigeron strigosus Daisy fleabane	76-9	40-32
Solidago missouriensis Smooth or Missouri goldenrod	64-12	24-20
Psoralea argophylla Silver-leaf psoralea	56-18	19-24
Petalostemum candidum and *P. purpureum* White and purple prairie clover	52-22	10-24
Echinacea pallida Pale purple coneflower	40-26	6-18
Euphorbia corollata Flowering spurge	33-7	11-24
Solidago rigida Stiff goldenrod	48-26	26-31
Astragalus crassicarpus Ground plum	36-21	0-9
Liatris scariosa Large button snakeroot	39-23	6-10
Rosa suffulta Prairie rose	48-26	41-24
Coreopsis palmata Tickseed	34-3	0-0
Kuhnia eupatorioides False boneset	37-41	14-16
Psoralea tenuiflora Psoralea	22-16	3-3
Sisyrinchium campestre Blue-eyed grass	40-11	15-7
Ceanothus ovatus Redroot	24-16	0-0
Liatris punctata Dotted button snakeroot	23-25	0-2
Desmodium canadense and *D. illinoense* Tick trefoil	29-29	41-16
Aster laevis Smooth aster	17-7	3-6
Artemisia ludoviciana Sage or mugwort	36-34	28-28
Lespedeza capitata Bush clover	28-27	26-28
Schrankia nuttallii Sensitive briar	10-5	3-0
Solidago speciosa Showy goldenrod	20-28	6-6

Aster azureus .... Sky-blue aster	7-6	0-6	*Baptisia leucantha* .... Large white wild indigo	12-22	6-17
Linum sulcatum ..... Yellow flax	29-25	8-8	*Baptisia leucophaea* ... Large-bracted wild indigo	19-27	0-20
Achillea millefolium .. Milfoil or yarrow	16-35	13-27	*Salvia pitcheri* .... Pitcher's sage	9-16	0-14
Senecio plattensis ..... Prairie ragwort	15-11	12-3			

List of species of somewhat less importance in uplands
(Read column on right following that on left.)

Ratibida columnifera
Prairie coneflower
Pedicularis canadensis
Lousewort
Salix humilis
Upland willow
Anemone cylindrica
Long-fruited anemone
Comandra richardsiana
Bastard toadflax
Liatris squarrosa
Scaly blazing star
Ruellia humilis
Hairy ruellia
Viola pedatifida
Prairie violet
Solidago graminifolia
Fragrant goldenrod
Plantago purshii
Pursh's plantain
Lygodesmia juncea
Rush-like lygodesmia
Solidago mollis
Velvety goldenrod
Oxytropis lambertii
Locoweed
Eryngium yuccifolium
Rattlesnake master
Polygala alba
White milkwort
Polygala sanguinea
Field milkwort
Pedicularis lanceolata
Lousewort
Callirhoe alcaeoides
Poppy mallow
Potentilla arguta
Cinquefoil
Physalis lanceolata
Prairie ground cherry
Lithospermum incisum
Narrow-leaved puccoon
Onosmodium occidentale
Western false gromwell
Psoralea esculenta
Prairie turnip

Each species in the preceding lists was far more abundant in uplands than in lowlands. There were 15 other less important species that were found in more than 10 per cent of the 100 upland prairies.

LEAD PLANT

Amorpha canescens is perhaps the most conspicuous and characteristic shrub of uplands. The prairie flora includes a few half-shrubs and shrubs in addition to *Amorpha. Rosa suffulta, Ceanothus ovatus,* and *Salix* *humilis* are common examples. In unmowed prairie, as in the Flint Hills of Kansas or along roadsides, *Amorpha* may develop into bushes 2.5 to 4 feet tall and the stems are sometimes 0.5 inch in diameter. This is several times the width of annual stems, which, however, become quite woody by midsummer. Under annual mowing the plant produces 2 to 5 or more basal stems. Frequently 12 to 20 plants occur per square meter. On lighter, poorer types of soil a maximum of 50 to 60 plants have been found. In limited areas they even exceed the grasses in importance (Fig. 22).

Growth begins about May 1, and by early in June the plants, where they are at all abundant, give the landscape a leaden-colored tone. Late in June when the foliage is about 1 to 2 feet tall, flowering begins; then the height may reach 3 feet or more. The tiny dark violet-purple flowers, despite the fact that they contain but a single petal, are so abundant that the clustered spike-like racemes are very conspicuous. Seedlings, which are often abundant, are very tolerant of shade.

During late summer drought the stems may become partly defoliated. This also occurs in deep shade of lowlands. But the remainder of the leaves remain green until frost. This plant produces much shade. It is important throughout the season, but because of its deep root system its competition with the grasses for water and nutrients is greatly reduced. Lead plant ranked as one of the leading societies of upland in 74 per cent of the prairies. It occurred in about half of the lowland prairies but in greatly reduced numbers.

SILVER-LEAF PSORALEA

Psoralea argophylla is a high-ranking legume that forms extensive societies, especially on lower hillsides and steep slopes along ravines. It is also usually distributed over well drained, moist, level lands. It occurs mostly where the little bluestem type intermingles with considerable big bluestem (Fig. 22).

The naked shoots appear early in April and the leaves unfold several inches above the soil. Blossoming begins in June, but the plants are conspicuous because of the silvery foliage rather than the small blue flowers. Mature plants are 12 to 28 inches high. The usually single stem has practically no leaves on the lower 6 to 12 inches. The branched open crown is 5 to 10 inches wide. Although 30 to 60 individuals may occur in a single square meter, they seem to be only slightly detrimental to the grasses, which appear normal in density when this legume is removed. Late in summer an abscission layer causes the stem to break near the soil surface and the tops tumble over the grasses before the wind.

In 74 per cent of upland prairies silvery psoralea was present, and it

FIG. 22. Little bluestem prairie with fine societies of lead plant (upper) and silver-leaf psoralea (*Psoralea argophylla*). Guthrie Center, Iowa, June 5.

formed societies of first rank in 37 per cent. Although occurring in 43 per cent of lowlands, here it was far less abundant.

MANY-FLOWERED PSORALEA

Psoralea tenuiflora (*P. floribunda*) is a legume of wide but irregular distribution in upland prairies. It seldom occurs in lowlands. The thick stems, sometimes 1 but often 4 to 15, are bare and unbranched to a height of 4 to 6 inches when young and to 8 to 10 when fully grown. Mature plants are often 2 feet tall and have much branched, spreading tops, 18 to 24 inches or more wide. The small blue flowers appear early in June. A single large plant may produce nearly 20,000 individual blossoms. Late in summer an abscission layer near the soil weakens the stem. It is broken by the wind and the plant then becomes a tumbleweed.

PRAIRIE TURNIP

Psoralea esculenta ranked sixtieth in importance on upland prairie and seldom occurred on lowland. Although the mature plant may attain 20 inches in height, neither it nor its rather few small blue flowers are conspicuous. It is of special interest because of the swollen portion of its taproot, a few inches below the surface of the soil, which in mature plants is often almost spherical in shape and 2 inches in diameter (Fig. 23). This is said to have been one of the food plants of greatest importance obtained from the prairie by the Indians. "After the roots were peeled they were eaten either raw or after cooking. Large quantities were dug in June or early July to peel and dry for the winter food supply. The peeled roots were braided in long strips by the tapering ends, as strings of garlic are braided by the tops" (Gilmore, 1919).

PRAIRIE CLOVERS

Petalostemum candidum and *P. purpureum* are widely distributed species which ranked third among the most important legumes. Numbers vary from 5 or 10 plants per square meter in open stands to 50 or 60 where they are frequent, but in well developed societies the number is even larger. A single taproot gives rise to 1 to 3 stems, but sometimes there are 10 to 12. Occasionally bunches 7 inches in basal diameter with 60 stalks may occur. Prairie clovers begin growth with the grasses but soon outstrip them in height. When blossoming begins, about the first

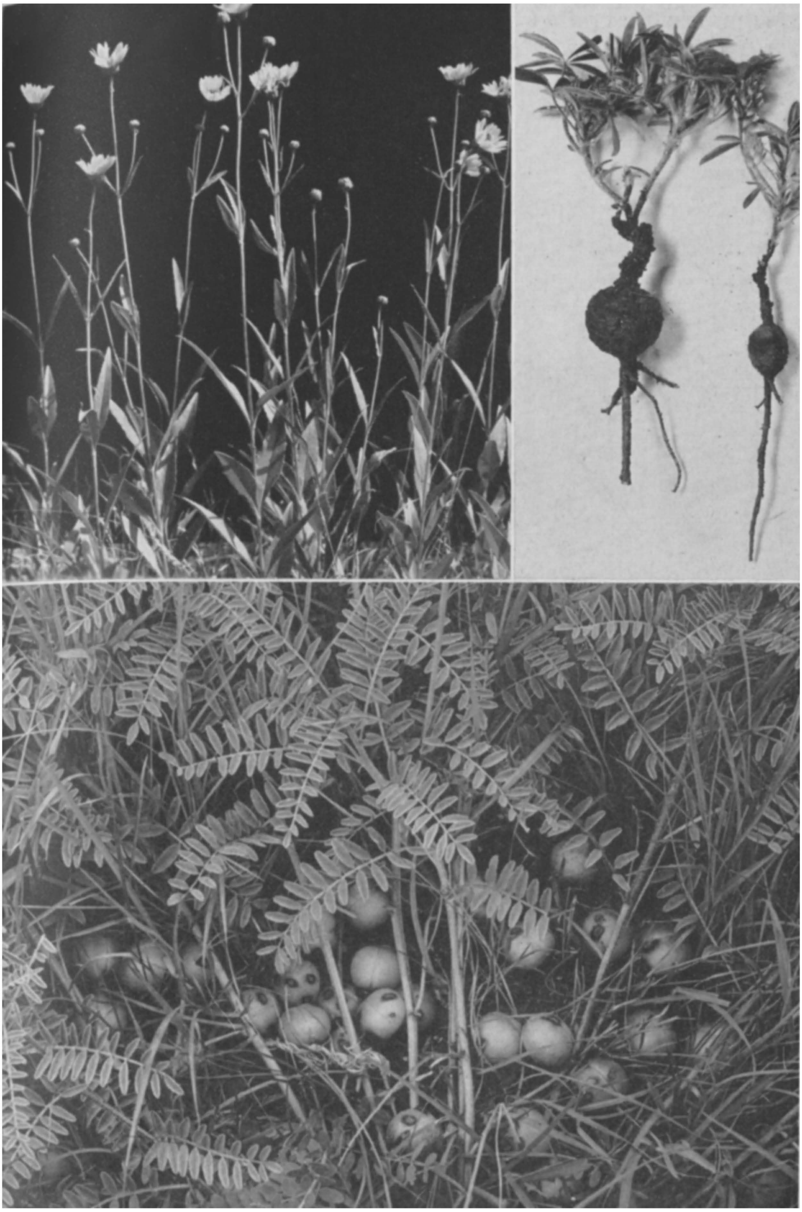

FIG. 23. Flourishing plants of stiff sunflower (*Helianthus laetiflorus*) (left), and tops and enlarged roots of prairie turnip (*Psoralea esculenta*). (Below) Ground plum (*Astragalus crassicarpus*) in fruit.

week in July, the plants are 2 to 2.5 feet tall (Fig. 24). The leaves of the purple prairie clover are smaller than those of the white-flowered species but they clothe the stems more thickly. The conspicuous heads, 0.5 to 2.5 inches long, are terminal on the branched tops and are held far above the general level of the grasses. Only in dense stands do the plants cast much shade. Although they grow in mixed societies, yet the purple clover prefers higher ground. Northward the white-flowered species was far more abundant. On uplands these legumes were present in three-fourths of the prairies, where they attained first rank in 22 per cent. On lowlands they were far less abundant.

FIG. 24. Flowering spurge (*Euphorbia corollata*), Indian plantain (*Cacalia tuberosa*), white prairie clover (*Petalostemum candidum*), and (in foreground) a stem of Illinois tick trefoil (*Desmodium illinoense*).

GROUND PLUM

Astragalus crassicarpus is a conspicuous legume of spring and early summer well known by the early settlers. It is a typical plant of the upland,

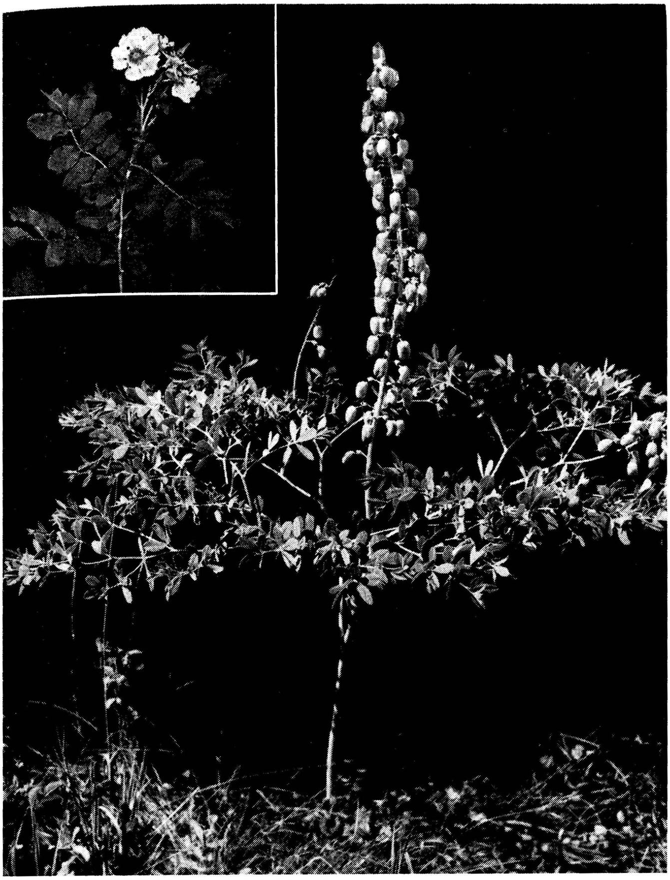

FIG. 25. Large white wild indigo (*Baptisia leucantha*) with foliage spreading 3 feet above the soil surface. Height of flower stalk is nearly 6 feet. (Upper left) Prairie rose (*Rosa suffulta*).

where it occurred in 57 per cent of the prairies. It is a large, coarse, decumbent legume, rarely exceeding 8 inches in height. The numerous stems spread widely in a somewhat radial manner, covering a circular area 2 to 3 feet in diameter. Its abundant, large, violet-purple flowers are attractive, as are also the plum-sized fruits (Fig. 23). When mature the abundant fruits are nearly an inch in diameter, somewhat longer than wide, and beautifully colored with a blotch of red on the upper side away from the soil.

FIG. 26. Pale purple coneflower (*Echinacea pallida*) (upper left), and prairie with patches of daisy fleabane (*Erigeron strigosus*). Below is a portion of large-bracted wild indigo (*Baptisia leucophaea*) in blossom, and a top view of rosettes of prairie cat's-foot (*Antennaria neglecta*).

Large white wild indigo (*Baptisia leucantha*) is a unique legume. The fully grown plant, with single stem and widely branched crown, resembles a miniature tree standing 2 to 4 feet above the general level of the grasses

FIG. 27. Smooth or Missouri goldenrod (*Solidago missouriensis*) (left), rattlesnake master (*Eryngium yuccifolium*) and large button snakeroot (*Liatris scariosa*).

(Fig. 25). Its large, cream-colored flowers occur in very large racemes, and the inflated, small seeded pods are outstanding features of the lower slopes where the plant is mostly found. Large-bracted wild indigo (*B. leucophaea*) is a coarse, widely spreading perennial that occurs in about half of the upland prairies, often on lower slopes. It has 2 to 12 thick stems which branch and spread widely so that the tops of the plants are 2 to 3 feet in maximum width. When blossoming begins in May, the large racemes of cream-colored flowers extend conspicuously beyond the foliage (Fig. 26). When a part of the plant is crushed, the sap, upon exposure to the air, becomes dark purple in color, hence the name "false indigo."

BUTTON SNAKEROOTS

Several species of button snakeroots and blazing stars occupy a prominent place in the vegetation of prairie and add grace and beauty to the autumnal aspect. *Liatris punctata* is a coarse, perennial composite well adapted by its long life, extensive root system, and harsh narrow leaves to grow in dry soil. This dotted button snakeroot was found in 58 per cent of upland prairies, where it ranked first in 10 per cent. Large button snakeroot (*Liatris scariosa*) was found in nearly two-thirds of the uplands and in 16 per cent of lowlands. It ranges in height from 1 to 5.5 feet. The linear leaves, especially the basal ones, are 7 to 12 inches long and fairly broad, although they are reduced to mere bracts near the inflorescence (Fig. 27). The wealth of rose-purple flowers as well as the colored tips of the large bracts form a pleasing and impressive sight.

PRAIRIE MUGWORT

Prairie mugwort (*Artemisia ludoviciana*) is a conspicuous plant in prairie both because of its social habit of rhizome propagation and its whitish appearance against the background of green. The latter is due to a dense coat of hairs, which can be removed by rubbing, thus exposing the green leaves (Fig. 28). Mature plants are often 2.5 feet tall and very leafy with their tops much branched. This sage is rather local in its occurrence, but where it is found the plants are often aggregated. It occurred in 70 per cent of upland prairies and in more than half of the lowlands. Where sage grows thickly, the undercover of grasses is considerably thinned.

STIFF SUNFLOWER

Helianthus laetiflorus ranks next to lead plant as the most characteristic, widely distributed, and abundant species of upland forb (Fig. 23). Typically its home is on the uplands, where it may grow in very poor, dry soil. It begins growth in early spring, especially from abundant rhizomes, forming rather dense groups of stems where the sod is open. New shoots develop rapidly. In early spring the leaves form a rosette on the soil, but soon the stem elongates and exceeds little bluestem in height. Mature plants in dry

FIG. 28. Western red lily (*Lilium philadelphicum*) (upper left), and a detailed view of lead plant. Below is the sage or mugwort (*Artemisia ludoviciana*) with big bluestem, and (right) many-flowered psoralea (*Psoralea tenuiflora*) showing the naked stems holding the young foliage. May 15.

soil may attain a height of only 12 to 18 inches, but if water is more plentiful they extend upward in excess of 3 feet. The size of the leaves may more than double, and the size of the flower head as well. Indeed, 3 or 4 flowers may develop, in contrast to the single one of drier soil. Stiff sunflower usually begins to bloom in the first week of July, reaches a maximum in August, and continues well into September.

The plants ordinarily shade the grass but moderately, since the lower leaves often assume a semivertical position, and usually dry and shrivel after midsummer. Then the 4 or 5 pairs of upper leaves constitute the entire scanty foliage. Over extensive areas 40 to 50 plants may occur per square meter, but sometimes as many as 100. This sunflower was found in 87 per cent of upland prairies, with first rank in 66 per cent. It was found in about half of the lowlands, where it ranked in first class in 19 per cent. Its distribution is often rather uniform over large areas.

MANY-FLOWERED ASTER

Aster ericoides (*A. multiflorus*) is a species of wide distribution both in dry and moist soil. This perennial makes a vigorous new growth by mid-April; the stems stand well above the level of the grasses early in May, and attain a height of 12 to 18 inches in June. Sometimes the largest bush-like clumps are 12 to 18 inches or more in diameter and 2 feet tall (Fig. 29). More usually it occurs as isolated individual stems 12 to 20 inches tall, or in groups of only a few stems. Plants are often connected by tough, woody rhizomes, some of which are more than 8 inches long. Many-flowered aster is especially conspicuous from the time its abundant white or purplish flowers begin to appear in late August or early September until the seed is ripe in late autumn. Often the flowers are so densely clustered that they almost obscure the rest of the plant.

This plant occurred in 85 per cent of upland prairies and held first or second rank in 59 per cent of them. It also was found in 75 per cent of the lowlands and held first rank in 25 per cent. Although this aster usually overtopped the grasses, yet because of its scattered growth and the small expanse of the leaves, the shading effect was not pronounced.

PRAIRIE CAT'S-FOOT

Antennaria neglecta, one of the most abundant prairie forbs, is a mat former. Beginning growth by the middle of March, it avoids for a time

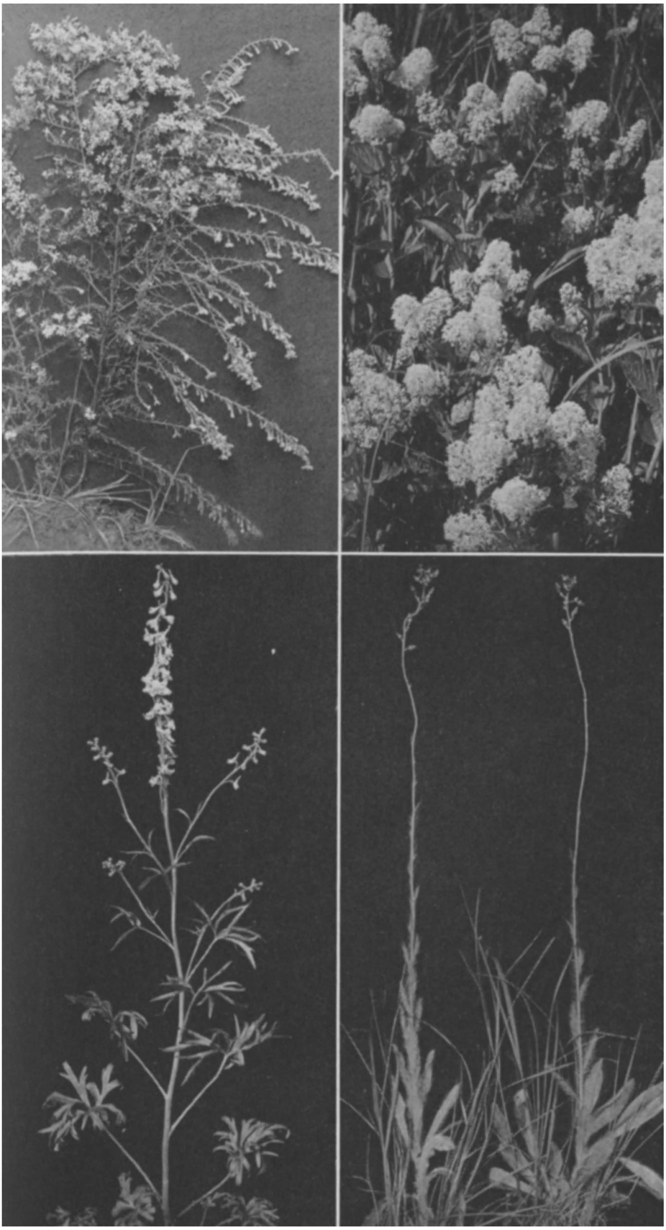

FIG. 29. Many-flowered aster (*Aster ericoides*) (upper left), and portion of a bush of redroot (*Ceanothus ovatus*). (Below) Prairie larkspur (*Delphinium virescens*), and hawkweed (*Hieracium longipilum*).

excessive competition with the grasses. Some of the leaves remain alive all winter, and soon new ones appear (Fig. 26). Early activities are directed toward production of flower stalks. Although some new leaves and stolons are produced, yet vegetative activity reaches its maximum after the period of flowering. The species is dioecious; usually the mats or small dense patches are composed of either staminate or pistillate plants. Blossoming begins about mid-April and continues for 3 to 4 weeks. The heads are born on erect, almost leafless scapes usually 2 to 5 inches high. Sometimes 50 to 75 flower stalks occur in a single square foot. After fertilization, the pistillate scapes elongate to approximately twice their former length, thus placing the bristly fruits in a favorable position for wind distribution.

Prairie cat's-foot occurs almost exclusively in the bare places between the bunches and tufts of sod. Leaves of the small clumps or rosettes do not all lie flat on the ground, but they seldom rise more than 3 inches above it (Fig. 26). The plant is so tolerant of shade that it may continue vegetative activities throughout the summer even in areas of big bluestem sod. It is shallowly rooted and rather readily affected by drought. This species was found in 78 per cent of upland prairies, ranking first in 39 per cent and second in 20 per cent. It occurred in 44 per cent of the lowlands, where it was usually much less abundant.

DAISY FLEABANE

Erigeron strigosus differs from nearly all the other leading forbs in its short life span. It is an annual or short-lived biennial, the rosettes of the first summer producing flower stalks the following growing season. Growth is resumed early in spring and blooming begins near the end of May, when the plants usually range from 8 to 24 inches in height. The number of flower heads varies from 15 to over 100 on the branched top of a single plant (Fig. 26). The number of plants varies from 25 to 50 per square meter, but where thickest from 100 to 125. The plants are mostly single stemmed but some have 2 to 5 stalks. They are only moderately well clothed with narrow leaves, and branching occurs well above the level of the grasses. Hence even in thick stands they have little effect in shading the grasses. Daisy fleabane ranked in the first class in 47 per cent of upland prairies and was represented in 85 per cent of them. It was also present in 72 per cent of low prairies, ranking high in 30 per cent. Its abundance varied greatly from year to year.

SMOOTH GOLDENROD

Solidago missouriensis is the most widely distributed and most important of the numerous goldenrods of the prairie. It occurred in three-fourths of the upland prairies and held a high rank in more than half of them. But in big bluestem prairies it was both less widely distributed and less abundant. It is a coarse perennial that spreads widely by means of stout rhizomes, mature plants reaching a height of 1 to 3 feet (Fig. 27). The stems ordinarily are not densely clustered but form an open growth. By the first week in May the rosette-like clusters of leaves, common in mowed prairie, stand out conspicuously above the grass level. Where plants are abundant, the vigor and density of the grasses are considerably reduced, since 50 to more than 75 stems may occur in a single square meter. The stems of large plants are quite woody. Plants may be leafy to the base or, because of drought or deep shade, defoliated to a height of 6 to 20 inches. Blossoming begins late in July and helps to usher in the autumnal aspect. Then the prairies are aglow with the yellows of various goldenrods, sunflowers, and, a little later, the purple of blazing stars and button snakeroot.

STIFF GOLDENROD

Solidago rigida is a perennial of wide distribution on both upland prairies (74 per cent) and lowlands (57 per cent). Growth is renewed in early spring. Soon the stiff, unbranched stems become prominent. Usually they are in groups of 2 to 8. Because of the large, broad leaves even a small clump of the stems, which are 1.5 to 3.5 feet high, casts considerable shade. When the plants are at all closely spaced the immediate area is usually free of grass.

FLOWERING SPURGE

Euphorbia corollata is a species of much prominence and wide distribution in the southeastern half of the area. This tall perennial occurs mostly as single stems, 3 to 5 feet high, but it is often grouped in clusters of 2 or 3 and sometimes as many as 30 (Fig. 24). It has long, stout rootstocks. The leaves in the grass, some of which are scale-like, fall from the base of the stem, and those remaining above are small and not widely spreading. By the middle of July many of the wand-like stems terminate in a whorl of branches, bearing the numerous, rather small, white flowers.

PALE PURPLE CONEFLOWER

A very conspicuous composite when in bloom, is the pale purple coneflower (*Echinacea pallida*). The plant usually consists of 2 to 5 mostly simple stems, each with a single terminal flower head. These are born well above the grasses when blossoming occurs in early summer. The large purple flower heads are often 3 inches wide but in rich, well watered soil much larger. The ray flowers last about a month, but the black central cones are conspicuous until late autumn (Fig. 26).

PRAIRIE ROSE

Rosa suffulta is a half-shrub which was found in three-fourths of the prairies but in only 65 per cent of those on lowlands. In drier prairies westward, it is more or less confined to low ground, but with increasing rainfall it is scattered over the hills as well. When unmowed, this rose becomes a shrub 2 to 3 feet high, but it rarely attains a height greater than 20 inches where mowed annually; consequently on uplands the leaves partly overtop the grasses. The stems occur singly or in groups of 3 to 5. They are very leafy, and where abundant, they shade the grasses to a considerable degree (Fig. 25). This plant has an abundance of rhizomes. Early in June the large pink buds unfold into the wonderful, white and pink-tinted blossoms. The beautiful, reddish, shining fruits appear abundantly late in July and are very conspicuous in autumn.

FALSE BONESET

Each species of forb differs in appearance, habit of growth, size, and abundance from the others. False boneset (*Kuhnia eupatorioides*) (*K. glutinosa*) develops a strong, thick, taproot 15 to 17 feet deep and does not grow well in poorly drained soil. Above ground it develops a bush-like top, often with a basal diameter of 6 to 8 inches but a spread of the scores of stems of 2 to 3 feet. Length of life is perhaps 25 to 30 years.

WHITE LARKSPUR

Delphinium virescens has a stout stem which arises from a thick, woody root (Fig. 29). The usually isolated or widely spaced plants are conspicuous largely because they stand so prominently, usually 1 to 2 feet, above the general level of the grasses. The large, white flowers, sometimes tinged with bluish spots, appear mostly in May and June and readily attract attention.

PRAIRIE VIOLET

Viola pedatifida arises early in spring from a short vertical rootstock. These small plants rarely exceed 2 to 7 inches in height. The violet flowers of this modest little plant appear late in April but are most abundant in May. This understory species is soon obscured by the overtopping grasses.

TICK TREFOIL

Desmodium illinoense grows so slowly that it is only 6 to 8 inches tall early in June. But the leafy stalks develop rapidly thereafter, and the long, terminal racemes that appear about July 1 ultimately reach a height of 5 to 6.5 feet (Fig. 24). The small purple or purplish flowers of this legume are succeeded by the jointed loments. Soon they begin to stick to ones clothing, and later they are a veritable pest where the plants are at all abundant.

OTHER SPECIES

The abundant white flowers of the shrubby redroot (*Ceanothus ovatus*) adorn the hillsides, especially during May and June (Fig. 29). The great, bushy butterfly weed (*Asclepias tuberosa*) furnishes an abundance of brick-red bouquets where it occurs on lower slopes. Sky-blue asters grow in rich soil. Other species commonly found on uplands are hawkweed (*Hieracium longipilum*), rattlesnake master (*Eryngium yuccifolium*), Indian plantain (*Cacalia tuberosa*), tick trefoil (*Desmodium illinoense*), and western red lily (*Lilium philadelphicum*). These may be seen in figures 29, 27, 24 and 28, respectively.

The beauty of the prairies is so impressive, as one wave of blossoming plants is followed by another from early spring to late autumn, that the seasonal aspects have been described separately in Chapter 8.

CHAPTER 6

Roots and Rhizomes of Grasses

THAT half of the plant and often much more is hidden from view, is particularly true of prairie vegetation. Rhizomes, bulbs, corms, and other plant parts for food accumulation are buried in the earth, and roots of both grasses and forbs extend far into the soil. Indeed, in winter prairie retreats underground. Prairie climate is one with only moderate rainfall, but the aerial environment is such as to promote high water loss by transpiration and by evaporation from the soil surface. Prairie soils are deep, mostly well aerated, rich, and moist. While a few species have roots which are sparse and relatively superficial, most prairie plants develop underground parts that equal or greatly exceed the extent of tops.

METHODS OF STUDY

Two methods have been used in studying the root systems of prairie plants. The first has been designated as the trench or direct method; a more recent one is the monolith method. Each gives certain values and together they enable one to gain an excellent understanding concerning the depth, spread, quantity, and interrelations of various root systems.

The first method was fully described (Weaver, 1926) after it had been used by the writer and his co-workers in excavating hundreds of root systems during a period of 12 years. First the plants to be examined are selected and a trench is excavated 8 to 12 inches from them. One 6 to 12 feet long, 3 feet wide, and 5 to 7 feet deep is most convenient. Next is the task of excavating and describing the root system. There is no easy method of uncovering the roots, and it can be done successfully only at the expense of considerable time and energy and by exercising a great deal of patience. But once started, the work is not only interesting but even fascinating. A small hand pick with cutting edge, an ice pick, a tape measure and a meter stick, pencil, note book, and drawing paper are the only equipment needed. The object is to remove the soil about the roots. With careful, painstaking study, especially after considerable experience has been obtained by practice, what at first appeared as a tangled root mass begins to unfold into a more or less definite pattern—that of the particular species of the plant concerned. The general characters of the root system of a species are often as marked and distinctive as those of the plant parts above ground. Although it may be profoundly modified when subjected to different environmental conditions, it still maintains the characteristic impress of that species in its usual habitat.

When the root description was completed it was tried on other plants of the same species, as yet undisturbed in the trench walls, and any marked variations were noted. Such a method is a great aid to exact observation and promotes a high degree of accuracy. The most satisfactory method is to draw the roots on a large scale in the field, building up the drawing as the number and length of roots, branching habit, and number of branches are ascertained. The drawing is then inked, the size being greatly reduced when the engraving for publication is made.[1]

The monolith method is used in securing a representative sample of an entire root system (Weaver and Darland, 1949a). This is done by mark ing out the size of a wooden frame on the vertical wall of the trench. The frame is usually one foot wide and of sufficient length (3 to 5 or more feet) to encase even the deepest roots of many prairie grasses. The trench wall on both sides of the marked area, as well as below it, is cut away in such a manner that the monolith protrudes from the wall at least 3 inches. The frame, which is really a box 12 inches wide and 3 inches deep inside and with the upper end removed, is fitted tightly over the monolith. While it is held in place, the monolith is then cut from the trench wall in such a manner that a block of soil exactly 3 inches thick but 3 to 5 feet long is obtained. A temporary top is placed over the box and the monolith is transported without cracking or breaking to the laboratory.

After many hours of soaking in water, the box containing the monolith is placed horizontally or tilted at any desired angle on a low table for washing. A "flaring rose" nozzle attached to a garden hose is employed in spreading the water uniformly over the sample. The amount of water

[1] Root descriptions, much abbreviated, and drawings are from the writer's "Ecological Relations of Roots," and "Root Development in the Grassland Formation," Carnegie Institution of Washington publications 286 and 292.

used and the pressure with which it is applied vary with the soil type and the soil horizons in the sample. Often it is necessary to wash the soil away under water, and even then the more delicate roots must be protected by the hand. Efficiency and success in the operation are gained only by experience. But one feels well repaid for the time spent when after 3 to 5 hours the complete root system alone is left in almost perfect condition in the bottom of the box.

The roots are prepared for photographing and quantitative study by transferring them to an appropriate background covered with black felt. Much detail is lost, of course, by photographing a five-foot root system on a 5 by 7 film.[2] But this difficulty may be overcome in part by photographing representative areas life size.

ROOTS OF LOWLAND GRASSES

Five to 12 root systems of each species of grass were excavated and examined, often in several different types of soil. The descriptions are those of the root habits of the plants in their normal prairie habitat. Those of grasses most abundant on moist soil of lowlands will be described first.

Sloughgrass or Prairie Cordgrass

Spartina pectinata, like various other species which thrive in low wet soil and furnish an abundant yield of forage, has very coarse, rather poorly branched but very deep roots (Fig. 30). These thick roots, often 3 to 5 mm. in diameter, originate from the base of the clumps in groups of 2 to 5 or more. They also arise, usually singly, at distant intervals along the rhizomes. They spread very little but penetrate almost vertically downward to depths of 8 to 13 feet, frequently extending into waterlogged soil. They taper so gradually that at a depth of 7 to 8 feet they are still 1 to 1.5 mm. thick. The lateral branches are thread-like and very abundant but only about 1 to 3 inches long and poorly rebranched. But in very wet soil or when growing in shallow water, many fine and much branched but more shallow roots also occur. Like the roots of cattails and many other plants of swamps and marshes, these have large air-conducting spaces in the cortex. This grass has the coarsest roots of any examined; coarse, deep roots are common to several of the species with dense foliage which thrive best

[2] Photographs of roots from monoliths are mostly from Weaver and Darland, Ecological Monographs 19, 1949.

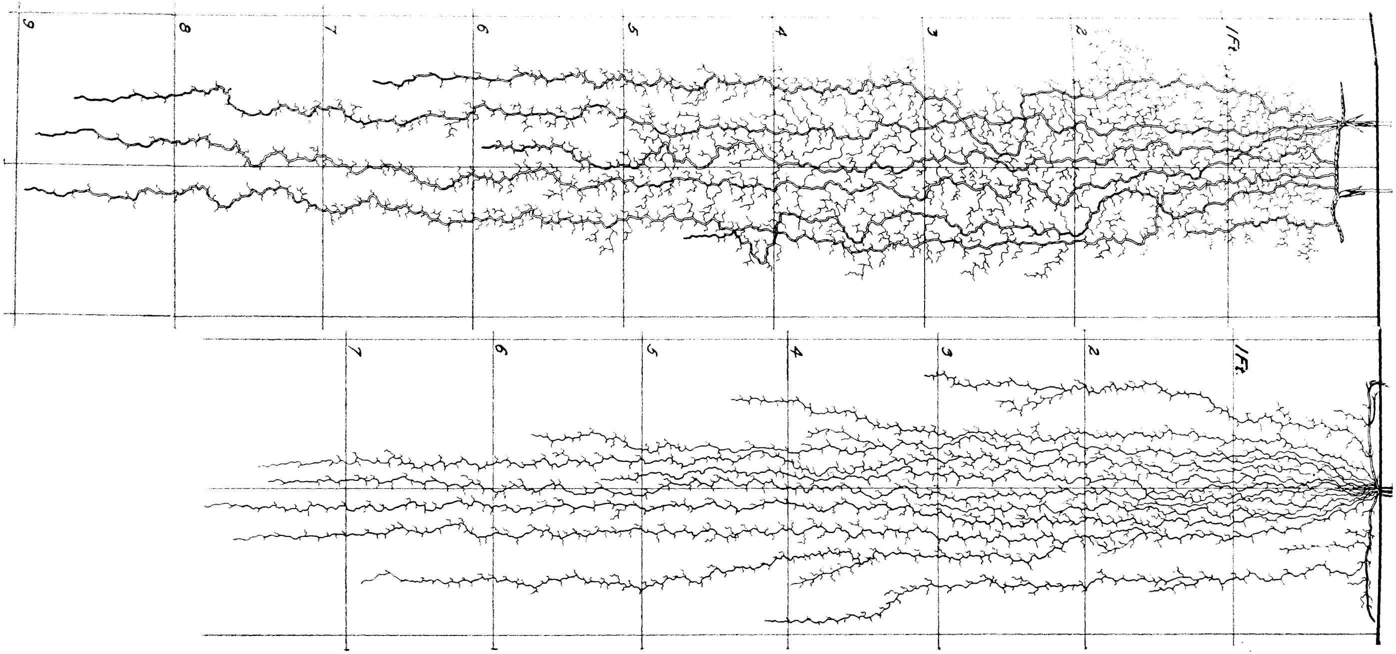

FIG. 30. Roots and rhizomes of prairie cordgrass (*Spartina pectinata*) (left), and western wheatgrass (right).

in situations wet in spring but often dry to a depth of several feet late in summer.

The rapidity of development of the roots of native grasses is exceeded only by those of cultivated crops. Growth is slower under the exceedingly keen competition for light, water, and nutrients in undisturbed grassland, but in disturbed areas where the sod formed by roots and rhizomes has been broken, development is very rapid. Under these conditions seedlings of sloughgrass and switchgrass may reach depths of 4 feet at the age of 3 months, a growth rate of half an inch per day. This rate is not uncommon among prairie grasses. Moreover, tillering begins early. When the plants are only 4 to 5 weeks old, tillers begin to appear and, simultaneously with these, a sufficient number of adventitious roots to supply these new shoots with water and nutrients. Once fully grown, the roots remain functional for many years.

Switchgrass

The roots of *Panicum virgatum* are also very coarse, often 3 to 4 mm. in diameter (Fig. 31). They penetrate nearly vertically downward to a depth of 8 to 11 feet, spreading but little in the surface soil. In comparison with most grasses the branching in moist soil is very poor. But, as with nearly all species of grasses, the branching habit is greatly modified by variations in soil conditions. On plants excavated from dry soil, branches were exceedingly numerous and, with the great depth of penetration, enabled the plant to occupy many cubic feet of soil.

Big Bluestem

At least 25 plants of *Andropogon gerardi* have been excavated and studied. The very abundant roots grow both vertically and obliquely downward, a few almost horizontally, and at once thoroughly occupy the soil and form a dense sod (Fig. 32). The roots may extend more than a foot obliquely away from the place of their origin before turning downward. The larger roots vary from 0.5 to 3 mm. in diameter and may reach a depth of 5 to 7 feet or more. All of the roots branch profusely; the main laterals are 2 to 6 inches long. The amount of branching and the length of laterals vary with soil structure; they are less in compacted soils. The main roots taper so gradually that at 4 feet they are nearly as large as at the surface. They thoroughly occupy the surface few feet of soil, and the ends of the roots are extremely well branched to the very tip. Their color is reddish-brown and quite unlike the white or tan-colored roots of switchgrass and sloughgrass. Life-size roots of big bluestem and switchgrass are shown in figure 33.

Indian Grass

The root system of *Sorghastrum nutans* is not quite so coarse as that of big bluestem, and usually it does not reach a depth greater than 5 to 5.5 feet. The roots, like those of big bluestem, spread laterally but little in the dense sod. Roots are abundant and branch profusely to the second and third order.

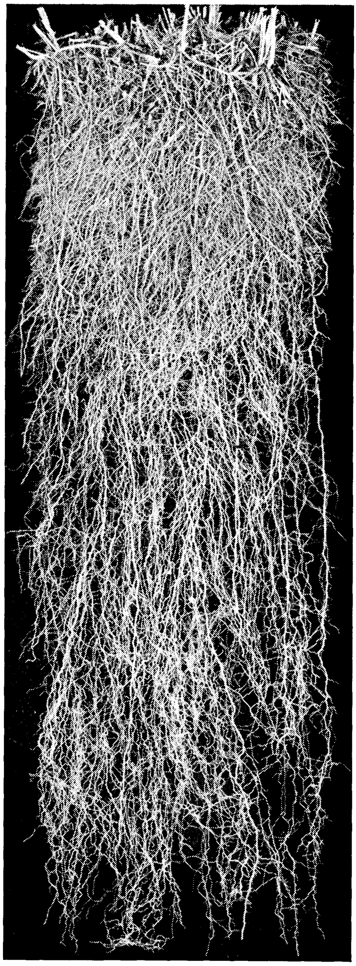

FIG. 31. Detail of roots of switchgrass from a monolith 12 inches wide and 3 feet deep.

Canada Wild-Rye

Elymus canadensis has a shallower but more widely spreading root system than any of the preceding grasses of lowland. The obliquely running roots reach distances of nearly 2 feet on all sides of the base of the plant, but root depth on any plant examined did not exceed 2 feet. The tough, wiry roots branch to the third and fourth order.

ROOTS OF UPLAND GRASSES

The roots of upland grasses are not so coarse as those of lowland, and they usually do not reach such great depths. But they are nearly always much better branched, and finer rootlets are much more thoroughly distributed throughout the soil.

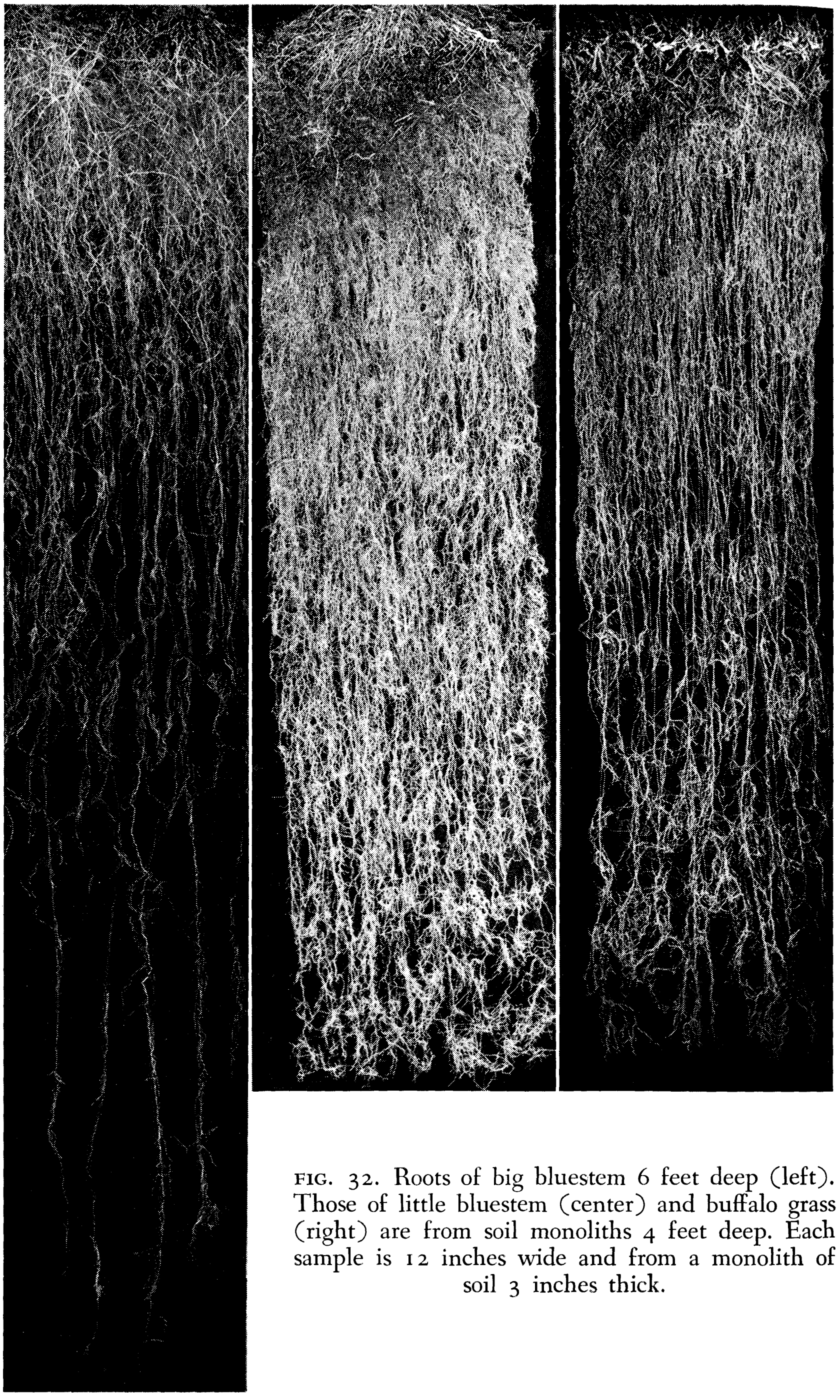

FIG. 32. Roots of big bluestem 6 feet deep (left). Those of little bluestem (center) and buffalo grass (right) are from soil monoliths 4 feet deep. Each sample is 12 inches wide and from a monolith of soil 3 inches thick.

Little Bluestem

The roots of *Andropogon scoparius* are much finer than those of big bluestem, being only 0.1 to 1 mm. in diameter. The lateral spread is similar to that of big bluestem but more pronounced. Some roots extend laterally near the surface soil; many run outward and downward 12 to 18 inches or more from the base of the crown. But the great bulk of the roots run nearly vertically downward to depths of 4.5 to about 5.5 feet. Roots are so abundant as to form a dense sod, almost completely occupying good soil at least to 2.5 feet in depth. The surface is especially well occupied by dense masses of finely branched rootlets. All of the roots branch profusely to the third and fourth order; many of the branches are over 30 inches long. Even the deeper soil is fairly well occupied (Figs. 32, 33).

Whether or not a root of one species is a foot or two longer or shorter than that of its competing neighbor may seem of little consequence. But sometimes, as during the great drought of 1934–1940, it has been of tremendous importance. Where little bluestem was intermixed with a smaller amount of big bluestem on the upland, the available water initially became exhausted in the first and second foot of soil. But by midsummer repeated sampling showed that no water was available to a depth of 4 to 4.5 feet. Nearly all of the little bluestem died, but much of the big bluestem was able to absorb enough water below 4.5 feet to maintain life until rains finally came.

Needlegrass

The bunches of *Stipa spartea* are regularly smaller than those of little bluestem and the root system is usually shallower and proportionately smaller. Strong fibrous roots from 1 to 1.5 mm. in diameter descend rather vertically into the soil, often to a maximum depth of only 2 to 3 feet but sometimes, where the soil is mellow and deep, to 4 or 5 feet. Others spread rather horizontally but mostly in a diagonally downward direction to a distance of 10 to 18 inches. Numerous smaller roots fill the surface soil, while the larger roots produce many laterals to a depth of 1.5 to 2 feet. At greater depths the main roots often divide into many fine branches.

Prairie Dropseed and Side-oats Grama

The root habit of *Sporobolus heterolepis* is very similar to that of little

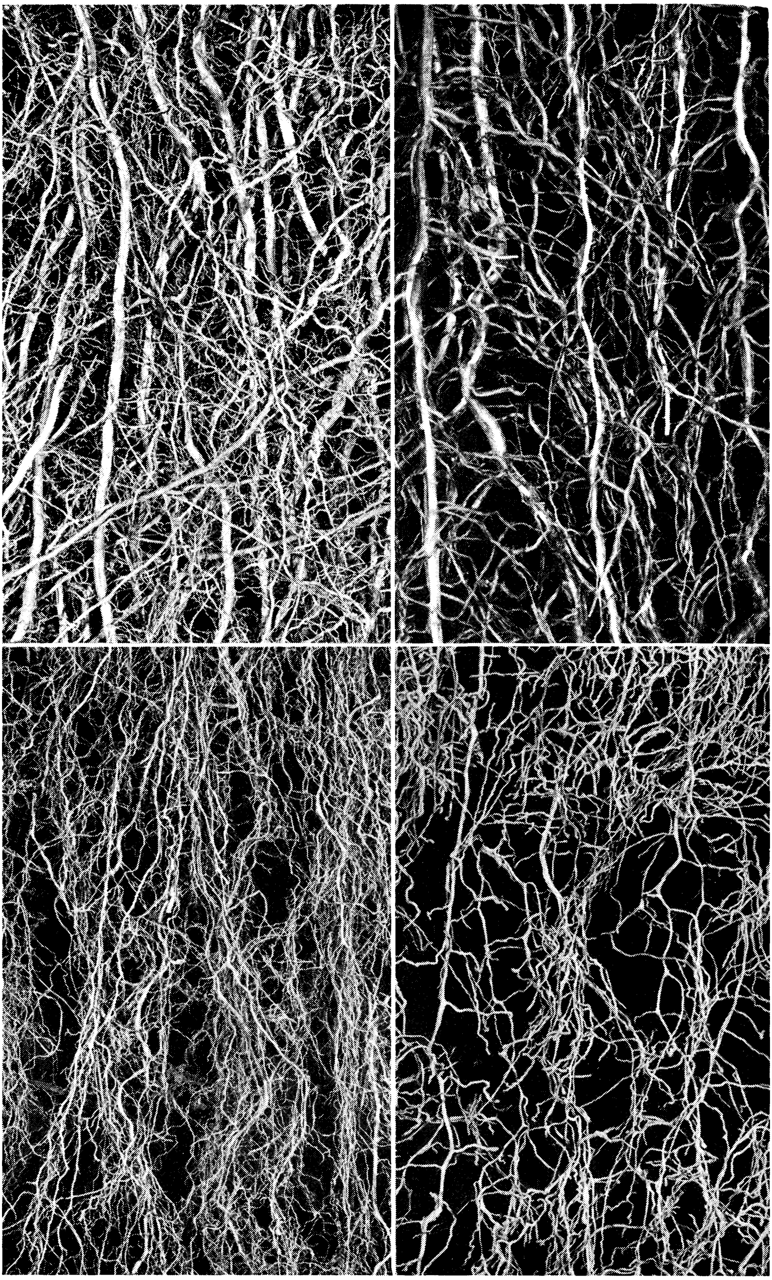

FIG. 33. View of roots, natural size, in 3-inch slabs of soil. Plants and approximate depths of roots are switchgrass, 3 in. (upper left); big bluestem, 27 in. (upper right); little bluestem, 30 in. (lower left); and western wheatgrass, 36 in. (lower right).

bluestem, although its roots may spread even more widely between the large bunches. Depth of penetration varies, but it is usually 4 feet or more. *Bouteloua curtipendula* has great mats of rather fine roots beneath a sod of this species. They are especially dense and well branched in the surface 12 to 18 inches, but many extend into the fourth foot of soil.

JUNEGRASS

Several species of grasses abundant in upland prairie are characterized by rooting habits considerably different from those described. *Koeleria*

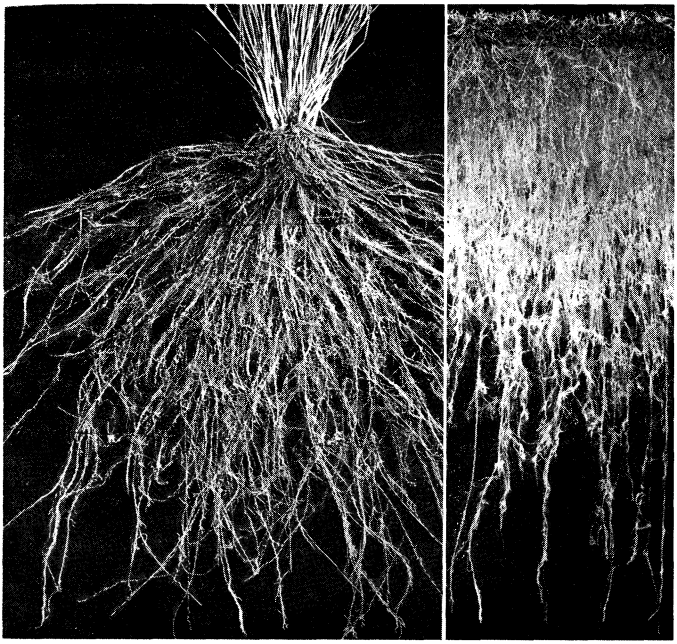

FIG. 34. Root system of Junegrass with depth and spread of about 20 inches, and roots of Kentucky bluegrass (*Poa pratensis*) from a 3-foot monolith.

cristata is a small but common bunch grass. Its early growth in spring, blossoming in June, and summer dormancy may be correlated with its shallow root-habit which seems to be hereditarily fixed. The general shape and extent are shown in figure 34. Average root depth is about 18 inches, although a few roots in mellow loess soils have been found to extend somewhat deeper. A great abundance of fine rootlets spread outward from the base of the plants, some in the surface inch of soil, and occupy the soil to

8 or 10 inches on all sides of the base. The roots are less than 0.2 mm. in diameter.

Scribner's Panic Grass and Penn Sedge

Panicum scribnerianum, which occurs in the understory between the bunches of dominant grasses, has roots that spread laterally 8 to 10 inches before turning downward and others that grow obliquely or directly downward. They reach depths of only 2.5 to 3.5 feet. *Carex pennsylvanica,* common on uplands, has more widely spreading roots, but they are scarcely so deep as the preceding.

Kentucky Bluegrass

Poa pratensis, which now occurs almost everywhere in true prairie, has a very fine, thickly branched root system. But only the surface 1.5 to 2 feet of soil is usually well occupied by roots, although the longest ones may reach a depth of about 3 feet (Fig. 34).

Western Wheatgrass

Another grass which grows on level lowland, in ravines, or on top of the driest hills—any place where it can enter a bared place in prairie—must be considered. This is western wheatgrass (*Agropyron smithii*), a species that spread everywhere during the great drought and one against which the other plants had to compete in reclaiming their former home.

The individual stems, usually several hundred per square yard, are connected by tough, frequently branched rhizomes which extend widely in the surface 3 to 4 inches of soil. From these and from the base of the stems arise the tough, white or light-colored roots. They are only 0.5 to 1.5 mm. in diameter, and do not extend much laterally from their place of origin. In general they penetrate almost vertically downward, branching profusely and somewhat regularly, many to a depth of 6 feet and some a foot or two deeper. The main roots and their usually short branches rather completely occupy the soil (Fig. 30).

Blue Grama and Buffalo Grass

These grasses occur somewhat regularly, even if sparsely, in the western portion of true prairie. Both are important dominants in mixed prairie westward. They have replaced the bluestems over large areas which have been heavily grazed. *Bouteloua gracilis,* especially, became abundant during the years of great drought. Despite the low stature of these short grasses, which are usually 4 to 10 inches tall, the root system is extremely well developed. The roots are very fine. The coarsest in either species do not exceed 0.5 mm. in diameter, but they have great tensile strength. In true prairie they spread much less laterally than in the drier soil westward, where many threadlike roots extend outward near the soil surface 8 to 10 inches from the place of their origin. The dense mat of roots that penetrate vertically downward may reach 1.5 to 3 feet, depending upon the type of soil. The laterals are usually not more than 0.5 to 1 inch in length. But often the mat of roots is quite thick even beyond the 3-foot depth, and some of the longest roots are found in the fifth and even the sixth foot of soil. The root habits of these two short grasses, which have been examined in many places, are so similar that both may be fairly well comprehended by the examination of one (Fig. 32).

RHIZOMES OF GRASSES

Many prairie grasses and sedges possess, in addition to extensive root systems, underground stems or rhizomes. These not only propagate the plant but they are also a storehouse for food. Rhizomes may readily be distinguished from roots by the presence of nodes to which scale-leaves are attached. These show little superficial resemblance to aerial leaves. The end or apex of a rhizome is a terminal bud. This and other buds on the rhizome may either produce aerial shoots or develop new rhizomes. Those of certain grasses form a dense network in the surface soil. Rhizomes of the same species of plant always occur at approximately the same depth under similar conditions for growth. If the depth of soil above the rhizome is changed either by erosion or deposit, it may descend or ascend accordingly and again produce rhizomes and new shoots at the former level. The rhizomes of most prairie plants are relatively shallow and are confined to the upper 4 or 5 inches of soil.

One can not study the roots of plants without also becoming familiar with rhizomes from which, in many plants, great numbers of roots develop. But special experimental studies have greatly increased our knowledge of the behavior of these underground stems (Mueller, 1941). Experimental results and many other data to be presented are from this source.

Sloughgrass and Switchgrass

Rhizomes of sloughgrass occupy the upper 6 to 10 inches of soil, forming a network of coarse, woody, very much branched stems (Fig. 35). These vary in diameter from 5 to 10 mm. They are all sheathed when young with hard-pointed scales which are sometimes longer than the internodes. Terminal buds are rigid and sharp-pointed. New rhizomes begin to form early in summer, and by autumn they may attain a length of 12 inches or more. Where erosion has occurred they may be shallow, but even after more than six inches of soil has been deposited upon them they may grow upward and produce shoots above the new soil level.

The network of rhizomes of switchgrass is also shown in figure 35. These stems vary in diameter from 3 to 7 mm., and new rhizomes develop in early summer.

Big Bluestem

When a sod of big bluestem is washed free from soil, a close network of gnarled rhizomes is revealed (Fig. 35). New rhizomes often extend outward early in spring. During summer, great food reserves are concentrated in them. The numerous large buds that develop remain dormant until the following spring. Then some grow immediately into shoots while others produce horizontal rhizomes 1 to 3 inches long before the terminal bud turns upward and develops an aerial shoot. New leafy shoots continue to appear throughout the summer. This species shows limited ability to grow up through soil when the deposit exceeds 2 to 3 inches in depth. Although the rhizomes are relatively short, they are closely matted in the sod. During two years a total length of 319 feet of rhizomes was produced in a single square meter of bare soil (Mueller, 1941).

Indian Grass and Canada Wild-Rye

Rhizomes of *Sorghastrum nutans* are not greatly unlike those of big bluestem, but their development is somewhat delayed compared with those of big bluestem, both in seedlings and mature plants (Fig. 35). Consequently, big bluestem has a great advantage in rapidly spreading into bared places. Rhizomes of *Elymus canadensis* tend to be inclined or somewhat vertical rather than horizontal. They are only an inch or two in length and are produced almost entirely in the surface two inches of soil.

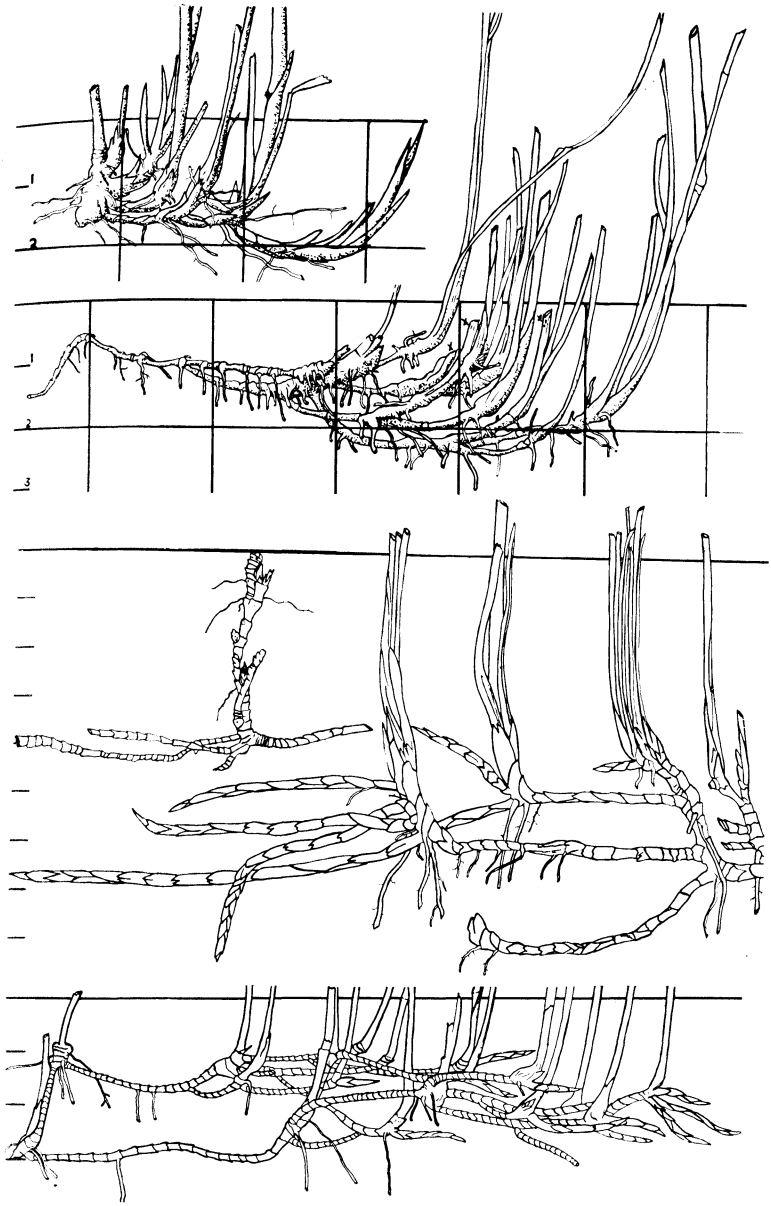

FIG. 35. Rhizomes of various grasses. In order, from top downward, they are: Indian grass, big bluestem, sloughgrass, and switchgrass. Scale is in inches. (After Mueller, Ecological Monographs: 11)

Side-oats Grama

Bouteloua curtipendula has short rhizomes which are usually confined to the surface two inches of soil. Ordinarily they are only 2 to 3 inches long, but lengths of 5 or more inches have been recorded. New rhizomes, 2 to 3 mm. in diameter, usually develop early in summer, and new roots extend outward and downward from the nodes.

Western Wheatgrass

During the years of great drought when the prairie populations began to shift rapidly, it became increasingly necessary for one to acquire detailed information concerning vegetative propagation of the various species. Otherwise the rapid, wide-spreading of *Agropyron smithii* and certain other grasses and forbs could never have been clearly understood. Rhizomes of wheatgrass were from 6 inches to more than 3 feet in length and grew very rapidly. The result was an enormous increase in territory. Moreover the vitality of the rhizomes and their resistance to drought were very great. During years unfavorable for growth they gave rise to few aerial stems, which grew poorly and failed to produce flowers. But once liberated by drought from competing species, a thousand stems per square yard often occurred. They reached a height of 2.5 to 3.5 feet and flowered so abundantly that the whole appearance of the prairie was changed.

Growth periods of rhizomes correlated with the growth of tops; new rhizomes began to develop early in spring. If overtaken by drought the food reserve was concentrated just back of the terminal bud; the remainder of the rhizome appeared wilted. But it became active again with returning available soil moisture (Mueller, 1941).

Wheatgrass was an early invader, frequently the first into soils that had drifted over the vegetation, causing its death (Fig. 36). Sometimes this was due to the rhizomes growing vertically upward through 10 to 12 inches of compacted soil, a phenomenon which has been shown experimentally by covering the sod with soil of variable depths. Many plants grew through 6 inches of soil and some produced seed. A few penetrated through a foot of soil and produced a normal amount of foliage. During an experiment extending over two years, 600 feet of rhizomes were produced in one square meter. Some rhizomes elongated 7 feet in a single growing season (Mueller, 1941).

UNIFORMITY OF ROOT DISTRIBUTION IN PRAIRIE

Examination of the roots from a single soil monolith 12 inches wide presents accurate information on the appearance of the roots throughout the general area under sod-forming grasses. Thus, under a sod of big bluestem, western wheatgrass, or switchgrass there is a nearly uniform pattern of vertically descending roots. They are nearly the same throughout in size, in depth, and in spacing. To the pocket gopher or other burrowing

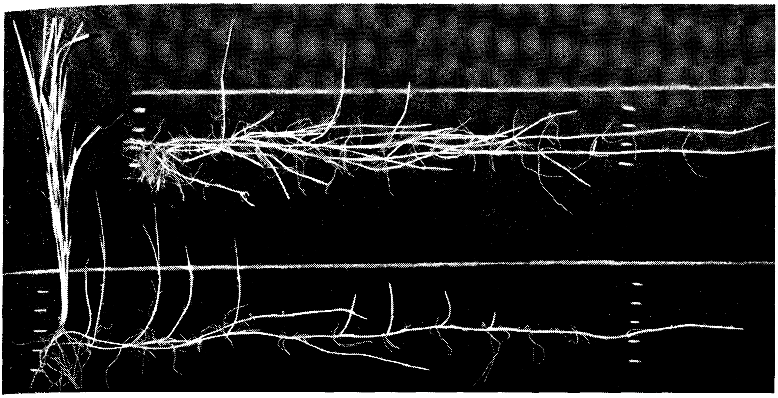

FIG. 36. Rhizomes of western wheatgrass; white lines indicate soil surface, and depth is shown in inches.

animal moving horizontally within the zone of root depth, they present a continuous network uniformly threading the soil. But with monoliths that are taken directly beneath a bunch-forming grass there is still some doubt in regard to the amount of root material between the bunches.

Studies by Weaver and Voigt (1950), using soil monoliths 3 feet wide, have shown that below the 3-inch depth, root distribution under and between bunches of little bluestem and prairie dropseed is not unlike that of sod-forming grasses. In upland prairie then, a chief obstruction to the forward progress of a burrowing animal through the network of grass roots would be the presence of large taproots or branch roots of forbs. Since they are sometimes 1 to 3 inches in diameter and very woody, the animal might do well to by-pass them.

ROOT DEPTH AND WATER ABSORPTION

Efficiency of absorption of roots at different depths has been shown experimentally by Nedrow (1937). During the great drought of 1934, many species of upland prairie were wilted and dried due to the exhaustion of available water to a depth of 4 feet. A narrow trench 4 feet long was dug on a hillside to a depth of 32 inches. Water was poured into the trench and maintained at a depth of 6 inches during a period of 7 days. Both little bluestem and Indian grass had renewed growth for a distance of two feet down the slope. But bluegrass, prairie cat's-foot, and Scribner's panic grass, all species of lesser root extent, made no recovery. It was ascertained that water was available only at depths of 2.5 to 4 feet.

Representative sods of thoroughly wilted and dried little bluestem and Kentucky bluegrass were selected with special reference to uniformity of stand. Trenches were dug about them in such a manner that columns of soil 10 inches in diameter and 30 inches deep were closely encased in galvanized iron cylinders. Three columns for each species were secured. They were cut off even with the base of the cylinders and removed to a greenhouse where a bottom was sealed over the lower end of each cylinder. By means of a soil tube, cores of soil an inch in diameter were obtained from the middle of the columns to depths of 4, 15, and 24 inches, respectively. Then glass tubes three-fourths inch in diameter were inserted to each of these depths, and the space between the soil and tubes completely filled with packed soil. The tubes permitted watering at the several depths. Three liters of water were added to each core, and losses of water by transpiration were periodically determined by weighing, and then replaced.

Growth began earliest and number and dry weight of shoots were greatest in those cores where water was applied nearest the soil surface. Little bluestem produced 124, 57, and 16 shoots with average heights of 8, 5, and 3 inches and dry weights of 7.0, 1.8, and 0.4 grams, respectively. Dry weights of new tops of bluegrass were 5.8, 4.3 and 0.4 grams, respectively. There was a direct relation between the amount of dry weight of tops produced and the amount of water absorbed.

The ability of many species of native and cultivated plants to absorb both water and nutrients from great depths has been demonstrated (Crist and Weaver, 1924; Hunter and Kelley, 1946).

CHAPTER 7

Roots and Rhizomes of Forbs

EXTENSIVE surveys have shown that among the most abundant prairie forbs the compositae alone furnish one-third of the species. Of the ten most important forbs of upland, three are legumes and six are composites. The underground parts of sunflower, goldenrods, asters, button snake-roots, and other compositae of prairie have been examined and will be briefly described.[1]

STIFF SUNFLOWER

Helianthus laetiflorus is the most widely distributed and abundant forb of upland prairies. Like many other prairie forbs, it propagates by means of rhizomes (Fig. 37). A number of these, with diameters of 2 to 4 mm., arise from the base of the plant and extend outward usually at a depth not greater than 6 to 8 inches and often in the surface 3 to 4 inches of soil. They vary in length from only a few inches to about 1.5 feet. Ordinarily they have few or no roots. They are often enlarged throughout the six inches nearest the tip. Roots vary from those that are fibrous, herbaceous, and only 0.5 mm. thick to those that are tough, woody, and 6 to 7 mm. in diameter. The form and depth of the root system are shown in figure 37. The finer, shorter roots as well as the more numerous branches from the larger ones provide for ample absorption in the surface soil. Thus, the roots are not only deep, but this species is also fairly well adapted to absorb efficiently in the surface foot of soil, especially below a depth of 4 inches. The spreading of a society of this sunflower was repeatedly observed. It advanced by rhizomes along a common front about 21 feet during 9 years.

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[1] Drawings and root descriptions are from Carnegie Institution of Washington publications 286 (1919) and 292 (1920).

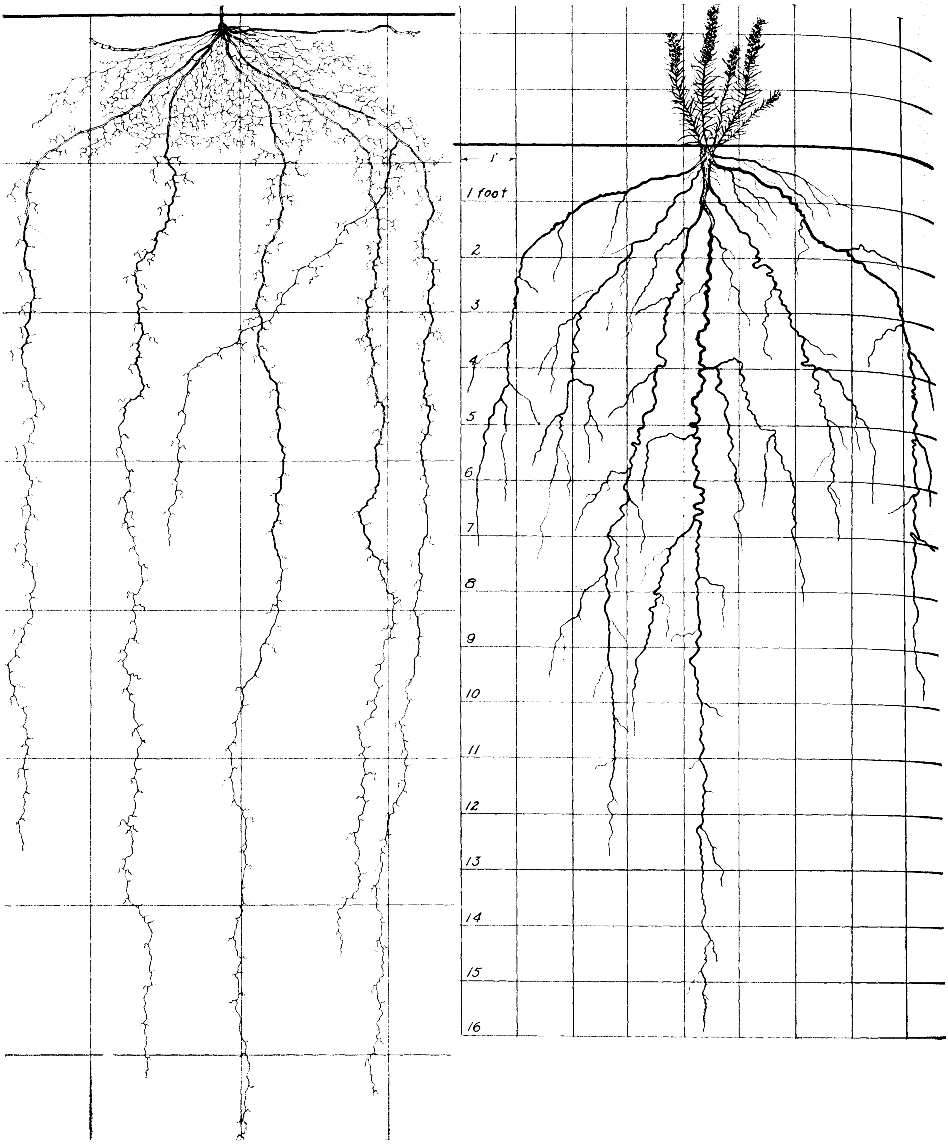

FIG. 37. Roots and rhizomes of stiff sunflower (*Helianthus laetiflorus*) (left), and dotted button snakeroot (*Liatris punctata*). Scale in both drawings is in feet.

MANY-FLOWERED ASTER

Aster ericoides is found regularly and abundantly especially in upland prairies. Clumps of this rather bushy plant are connected by tough, woody rhizomes 4 to 5 mm. in diameter, and from 1 to over 8 inches in length. Frequently they are short and then the plants are densely matted together. The plant is supplied with numerous fibrous roots usually 2 mm. or less in diameter. Their depth and distribution are similar to that of the sunflower, but the main roots are often about twice as numerous. Branch roots are sometimes 10 or more inches in length, but more frequently 0.5 to 3 inches. The root system is deep-seated, and very little provision is made for absorption in the surface 6 inches of soil (Fig. 38).

STIFF GOLDENROD

Solidago rigida is a very widely distributed prairie species and often becomes a weed when prairie is grazed. The fibrous roots spread widely immediately below the soil surface. Many of the numerous small roots pursue an oblique direction and spread from 12 to 18 inches from the base of the plant before turning downward. Most of the roots are only about 1 mm. in diameter and poorly branched. They are very abundant in the first 2 feet of soil, and maximum depths of over 5 feet are attained. Roots are yellowish-brown and have a smooth cortex, except the deeper ones which are silvery white.

SMOOTH GOLDENROD

Solidago missouriensis is a very important component of prairie vegetation. It propagates by woody rhizomes 3 to 8 mm. in diameter and from 2 to more than 12 inches in length. Adventitious buds producing slender rhizomes frequently arise from roots (Mueller, 1941). At the base of the clump and along the rhizomes, clusters of roots are produced which are from 0.5 to 3 mm. in diameter. Many of these are relatively short, repeatedly branched, and end in the first foot or two of soil. The larger, white, cord-like roots descend laxly and obliquely. The root system is spread 12 to 20 inches from the base of the plant. Branches are rather few and short, but the main roots nearly all reached a depth of 5.5 feet, and some extended well into the seventh foot. A maximum depth of 8.2 feet was attained. This goldenrod is similar to many-flowered aster in

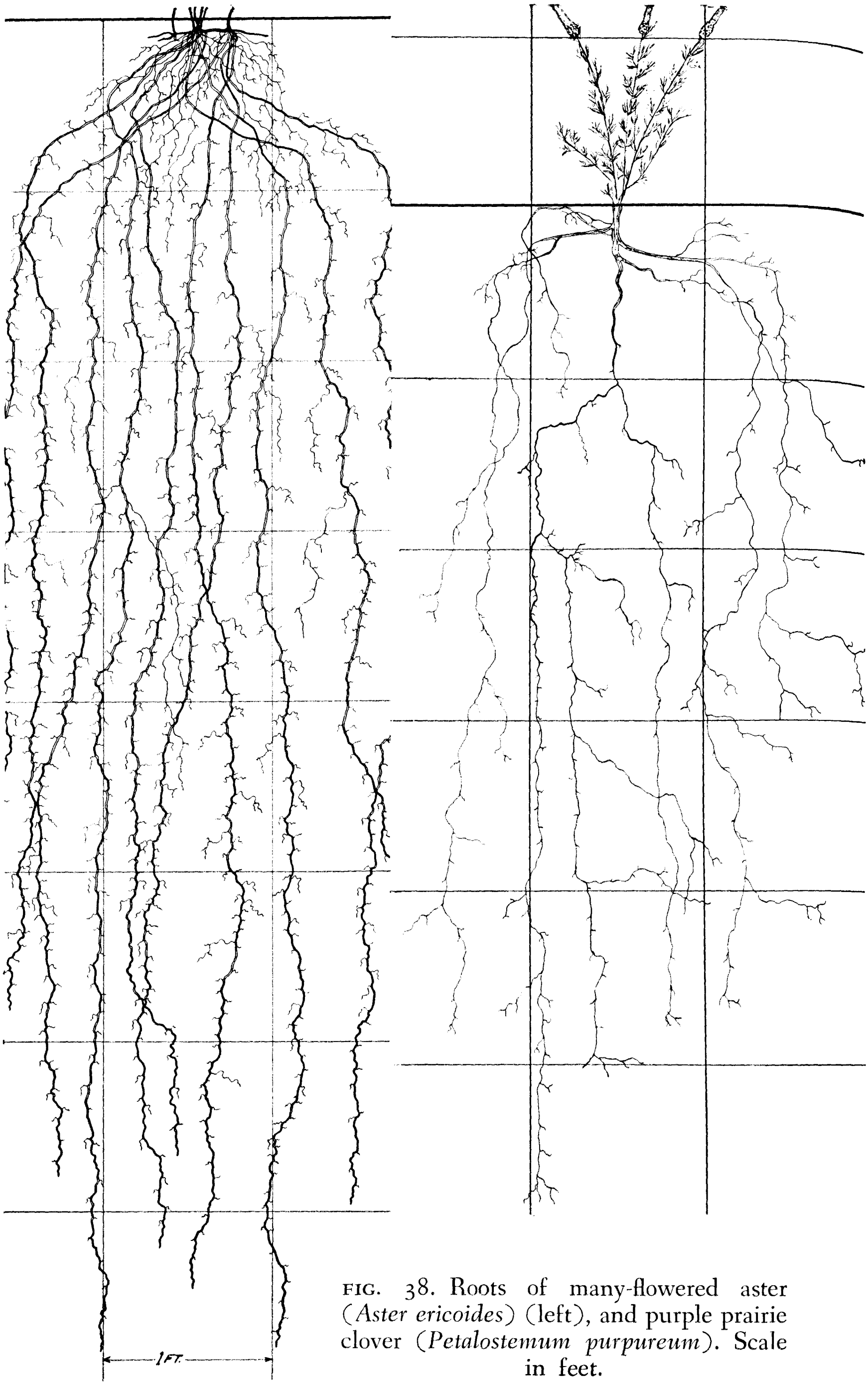

FIG. 38. Roots of many-flowered aster (*Aster ericoides*) (left), and purple prairie clover (*Petalostemum purpureum*). Scale in feet.

penetrating deeply and relying but little upon the surface soil layers for water and solutes.

CANADA GOLDENROD

Solidago canadensis propagates by means of strong woody rhizomes, 10 mm. or less in diameter, which run horizontally about 2 inches below the soil surface. The fibrous roots are about 1 to 2 mm. in diameter. They descend rather vertically into the soil. From these abundant roots, numerous laterals arise, beginning just below the surface and continuing to a depth of 9 to 11 feet. However, the main roots maintain their identity throughout their course and are very poorly branched throughout the last foot. The soil was well occupied by the roots of this species, and few other roots were found in its area.

BUTTON SNAKEROOTS AND BLAZING STAR

Unlike the preceding forbs which possess many roots of almost equal size and depth, numerous other species develop a prominent taproot. Each of many individuals of dotted button snakeroot (*Liatris punctata*) had a strong taproot. These penetrated to a depth of 7 feet in a heavy clay soil but in lighter soil they attained depths of 11.5 to 16 feet. In figure 37, as is usual, all of the root system is included; the roots are pictured as occurring in one plane. On some plants small laterals were scarce to a depth of 9 feet, while at 12 feet the soil was filled with small, silvery white, sparsely branched rootlets. This better branching, sometimes at 9 feet in depth, was observed on several plants. This forb apparently does not compete greatly with the much more shallowly rooted grasses of uplands where it often occurs abundantly. The older roots are woody and chocolate brown in color.

Large button snakeroot (*Liatris scariosa*) is characterized by a woody corm 3 to 4 inches in diameter, from which arise very numerous fibrous roots. These are only 1 to 2 mm. in diameter, and about 2 to 4 feet in length, but they are finely branched. During the great drought (1934–40) this rather shallowly rooted species almost disappeared from the western true prairie, but the deep taproot maintained the preceding species throughout the drought. The scaly blazing star (*Liatris squarrosa*) has very similar underground parts. The abundant fibrous roots spread 1.5 to 2 feet from all sides of the corm, and many reach a depth of 2.5 feet.

COMPASSPLANT

The deep taproot of *Silphium laciniatum* varies from 1 to more than 2 inches in diameter just below the crown. It descends vertically and tapers so rapidly that at 3 feet in depth it may be only a half-inch in diameter. Roots pursue this general vertical direction to depths of 9 to nearly 14 feet. The entire root is reddish-brown, and the cortex of the first 18 inches is very much ridged and wrinkled. There are relatively few large branch roots, although a few small and mostly short branches do occur. The large branches frequently run off horizontally for a distance of 3 to 4 feet before turning downward. When removed from the soil, the roots shrink to about half their former thickness (Fig. 39).

FALSE BONESET

Kuhnia eupatorioides (*K. glutinosa*) is another prairie forb with a very extensive root system. Depths of 16 to 17 feet were found on four different plants. Near the soil surface, the taproot is often more than an inch in diameter, and it seems probable, because of its bark-like covering, that little absorption occurs in the upper two feet of soil. But the deeper portions of these roots are glistening white and well branched and absorb water and nutrients far below the part of the soil that is filled with the roots of grasses (Fig. 40).

PRAIRIE ROSE

Rosa suffulta is shown with the preceding species in figure 40 only for convenience. It is not a forb but one of the few half-shrubs that are found in the grassland. It is widely distributed throughout the prairies, especially on uplands. The rose possesses strong, thick, woody rhizomes. By this means a single individual may give rise to many other plants, often from rhizomes placed 12 to 18 inches deep. These spread in all directions to distances of 5 or more feet. This largely accounts for the societies of this rose in prairie. In figure 40 the main root from the second plant (left) reached a depth of 15 feet; the root of the older plant pursued a nearly vertically downward course to a depth of 21 feet.

The upper 3 to 5 feet of the deep taproots of several species of prairie plants were separated from the soil by Nedrow (1937) without injury to them and encased in galvanized-iron cylinders 5 inches in diameter. The

FIG. 39. (Left) Rush-like lygodesmia (*Lygodesmia juncea*) with a taproot, in two sections, more than 21 feet long. (Right) Pale purple coneflower (*Echinacea pallida*) with a deep, somewhat fleshy root. In both figures the scale on left is in feet. (Center) Upper 5 feet of the thick, fleshy root of compass-plant (*Silphium laciniatum*); total depth was nearly 14 feet.

cylinders were 3, 4, and 5 feet long. This was done in late fall of the great drought, 1934, the plants being left intact in the field. The cylinders were tightly sealed about the roots at the bottom, filled with dry sand, and then sealed at the soil surface. Eleven plants of the following species were used: *Kuhnia eupatorioides* (*K. glutinosa*), *Liatris punctata, Silphium laciniatum, Amorpha canescens,* and *Rosa pratincola* (*R. suffulta*). These deeply rooted plants had been able to produce their normal growth during a season of drought (1934) when no available moisture occurred in the first four feet of soil. After the roots were encased so as to prevent absorption to depths of 3 to 5 feet, the plants continued to develop normally during a second summer, absorbing only in the deeper soil.

PALE PURPLE CONEFLOWER

Echinacea pallida is one of the ten most abundant forbs of upland prairie. It differs from most plants by having a thick, deep, fleshy, and almost unbranched taproot (Fig. 39). These are woody and chocolate-brown to nearly black in color. The roots ranged from 0.5 to over 1 inch in diameter. They tapered very slowly to the end at 6 to 8 feet in depth. If laterals occurred, they were short and sparse.

BALDWIN'S IRONWEED

The tall, dark-red, composite of lowlands and ravines (*Vernonia baldwini*) is better known as a weed in old pastures where bluegrass has replaced the prairie grasses. It propagates by strong rhizomes a quarter-inch or more in diameter, which occur usually 3 to 4 inches below the soil surface (Fig. 41). Roots are abundant, 20 to 30 arising from a single plant, and very different from any other roots examined. They are tough, smooth, yellowish-white, and unbranched throughout the first few feet of their course. The cortex is fleshy, and the diameter of the roots is 3 to 9 mm. Some extend vertically downward but many spread about 20 inches from the base of the plant before turning downward. At about 3 feet in depth they begin to branch and branches become more numerous in the deeper soil. Most of the finer branches and terminal rootlets, however, occur at 9 to 10 feet. On seven plants examined, all penetrated to a depth of about 11 feet. Thus, although able to compete but little with the grasses in the upper soil levels, this species can absorb at greater depths than most grass roots occur.

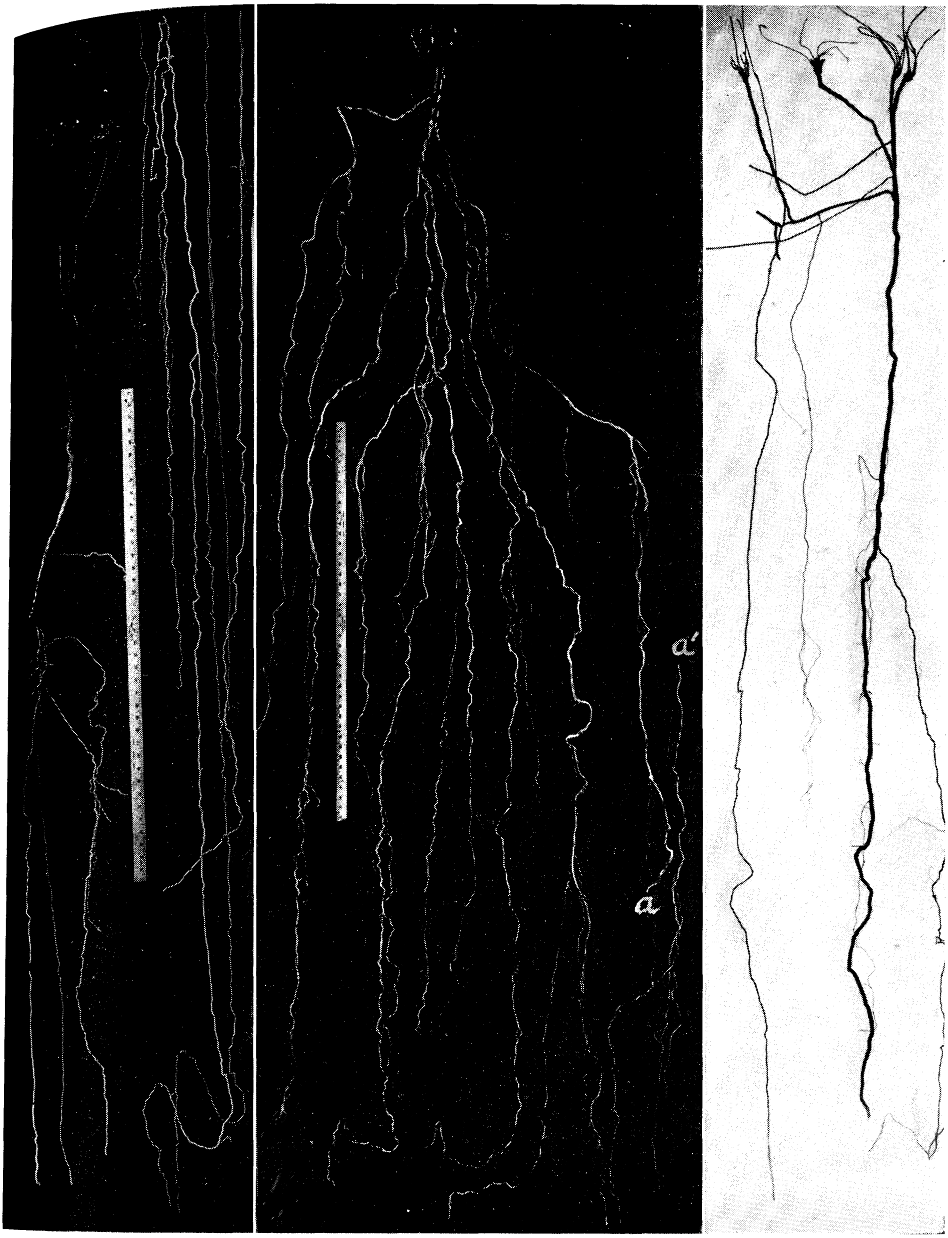

FIG. 40. Roots of false boneset (*Kuhnia eupatorioides*) 17 feet deep (left), and licorice (*Glycyrrhiza lepidota*) about 12 feet deep (center). The measuring stick is a meter long. Part of the roots of both plants are in two sections. (Right) Upper 9 feet of the rootsystem of prairie rose (*Rosa suffulta*). A depth of 21 feet was reached by the large taproot.

PRAIRIE CLOVERS

The purple and white prairie clovers (*Petalostemum purpureum* and *P. candidum*) are very important prairie legumes. Legumes, aside from grasses, rank next in abundance to composites in true prairie. They are especially important because of their ability to increase the nitrogen supply by means of bacteria in their tubercules. A great variety of legumes have been examined. Prairie clovers rank among the ten most abundant species of forbs. Figure 38 shows the characteristic features of a typical root of the purple-flowered species. Three to 7 large laterals usually arise in the sur-

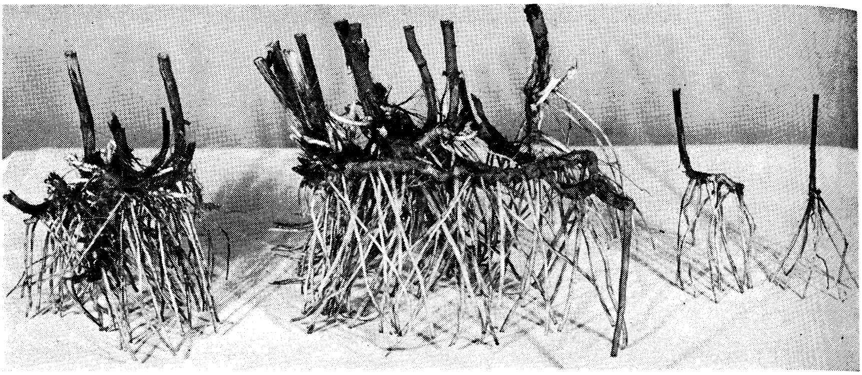

FIG. 41. Coarse roots and rhizomes of Baldwin's ironweed (*Vernonia baldwini*) showing several stages in their development.

face 1 to 4 inches of soil. They spread laterally 8 to 18 inches before turning abruptly downward. They are often minutely branched and compete with the grasses for water. Taproots 6 to 10 mm. in diameter penetrated to depths of 5.5 to 6.5 feet, respectively. The roots occurred quite abundantly at 5 to 6 feet in depth, through a soil mass 3 to 4 feet square under the plant. Even the finest roots could be distinguished from their competitors by their orange-brown color.

On one plant of white prairie clover a group of more than 8 stems arose from a woody taproot 17 mm. in diameter. The main root divided into three major parts. These extended downward and gave off but few branches. Further studies showed that the white prairie clover is poorly supplied with absorbing roots in the surface 18 inches of soil. The main branches are few and run downward with little spreading. Below the second foot, branches arose frequently. They were very long but not much rebranched. In the third to the fifth foot of soil, laterals were fine but very numerous to the root ends at 5.5 feet. Sometimes roots extended somewhat deeper.

PSORALEAS

Many flowered psoralea, (*Psoralea tenuiflora*) (*P. floribunda*) is frequently so abundant that for a time it overtops and obscures the grasses. The strong taproot is sometimes an inch or more in diameter. It gives off many large, widely spreading branches, especially in the first and second foot of soil, many of which extend to depths of 5 to 7 feet. The main root seldom branches finely in the surface foot and absorbs but little in the surface two feet of soil. But it penetrates rather vertically downward to distances of 8 to 9 feet or more.

Silver leaf psoralea (*P. argophylla*) also has a taproot which is a half-inch or less in diameter and tapers very rapidly with depth. It reaches about the same depth as the preceding species but is very poorly branched.

GROUND PLUM

Astragalus crassicarpus has a large taproot with many strong, widely spreading branches, most of which arise in the surface foot of soil and often in the surface 3 to 4 inches. They may spread outward 10 to 12 inches before turning downward and penetrating many feet into the soil. Root depths of 6 to 8 feet are not unusual. As in many native legumes, nodules occur at all depths, even near the root tips.

LARGE-BRACTED WILD INDIGO

Like the preceding legume, *Baptisia leucophaea* has little provision for absorption in the surface foot or two of soil. Its many rather woody main roots extend widely from the base of the plant and, although never branching profusely, absorb water and nutrients at great depths, even to 7 or 8 feet.

LEAD PLANT

Amorpha canescens is a half-shrub, but under annual mowing the top, like that of forbs, is renewed each spring. It is the most abundant and one of the most widely distributed species in prairie. Many of the tough, woody roots spread more or less parallel to the surface at a depth of only a few inches. When the prairie is plowed these break with a characteristic snap, thus giving rise to the colloquial name of prairie shoestring.

This long-lived legume has a very extensive, woody root system which grows far into the earth. Very little absorption occurs in the surface 2 to 4 feet of soil. Thus, grasses frequently grow vigorously between the spreading roots where they doubtless suffer little competition. A seven-year-old plant gave off from the knotty crown, 11 woody roots 8 to 14 mm. in diameter. They ran off at various angles, from almost parallel with the hillside soil surface to vertically downward, where the roots were somewhat grouped. The few laterals that did occur were well branched. The roots tapered very slowly. They frequently pursued a rather tortuous course, but were mostly poorly branched even to the tips. Some roots ended a horizontal distance of 4 to 5 feet from the base of the crown. Small nodules occurred at depths of 10 to 12 feet, and often throughout the entire extent of the roots, which were sometimes 16.5 feet long. Roots are similar to those of licorice, except the taproot is not so pronounced (Fig. 40).

RUSH-LIKE LYGODESMIA

Lygodesmia juncea, shown in figure 39, is common in many prairies on crests of hills and other dry places. This composite had the deepest root of any species examined. A taproot 2 to 6 mm. in diameter penetrated almost vertically downward in moist mellow soil. The very brittle roots were fleshy and exuded a white latex if broken. Branching occurred not at all, except for tiny laterals less than an inch in length at intervals of 6 to 12 inches. Numerous roots occurred at 18 feet in depth, and one was traced to a distance of 20 feet and 7 inches, when it seemed expedient to abandon the trench because of caving soil.

SOME SHALLOWLY ROOTED SPECIES

Quite in contrast to the moderately and deeply rooted prairie plants, a few have relatively shallow roots. Among these are prairie cat's-foot (*Antennaria neglecta*), scarlet strawberry (*Fragaria virginiana*), blue-eyed grass (*Sisyrinchium campestre*), and spiderwort (*Tradescantia bracteata*).

OTHER UNDERGROUND PARTS

Tubers, corms, and bulbs are found on many species of prairie plants. These are excellent organs for food accumulation and protection of growing points during cold or drought. But they are much inferior to rhizomes as organs of propagation because of their slight elongation and consequent lack of migration (Fig. 13).

STUDIES IN ILLINOIS PRAIRIE AND LOESS HILLS

Root systems of 28 species of prairie plants, including several grasses, were excavated in fragments of prairie along the railroads in Illinois and described by Sperry (1935). Ten of these had previously been studied in western true prairie where all of the root systems were longer and better developed than those in Illinois. In Illinois, the growth of shoots always equaled and often exceeded those produced in Nebraska.

Previous studies led the writer to believe that in mellow loess soils of moderately low water content, roots of the same species would penetrate even deeper than those described. Preliminary studies in the eastern edge of mixed prairie, near Kearney, Nebraska, with a precipitation of only 23 inches, confirmed this belief (Weaver and Bruner, 1948). The longest roots of buffalo grass (*Buchloe dactyloides*) reached a little more than 6 feet in depth, and those of blue grama (*Bouteloua gracilis*) were almost as deep. The tops of these grasses were only 4 to 8 inches high. Roots of western wheatgrass (*Agropyron smithii*) were traced to their ends in the eleventh foot of soil. More extensive work by Hopkins (1951) showed that the short-grass roots were sometimes 6 to 7 feet deep. Roots of little bluestem (*Andropogon scoparius*) penetrated the moist soil to 8 feet in depth and big bluestem (*A. gerardi*) to 10 feet. Even the usually shallow-rooted Junegrass (*Koeleria cristata*) exceeded its depth of about 18 inches in more compact soils by extending downward to 2.5 feet. In adjacent "hard lands" the root systems of all these plants are much less extensive (Weaver, 1919; 1920).

LAYERING UNDERGROUND

"The roots of prairie species are grouped into about three more or less definite absorbing layers, many of the deeper-seated species having few or no absorbing roots in the first few feet of soil. The layering of the roots reduces competition, and, since available moisture is present throughout the subsoil, permits the growth of a larger number of species. However, no relation between layering and seasonal activity is apparent. The period of most active growth and flower production of plants rooted at various levels occurs synchronously, and, like the successive development of aerial parts of different species in time and space above ground (which results in seasonal aspects) probably equalizes the demands upon the habitat, distributing them throughout the growing season" (Weaver, 1920).

Of 43 species of prairie plants examined, 14 per cent were so shallowly rooted that they seldom extended beyond the first 2 feet of soil. The second group, 21 per cent, was composed of plants with roots extending well below the second foot but seldom deeper than 5 feet. They may be designated as intermediate in root depth. The last and largest list, made up of plants whose roots extend beyond a depth of 5 feet (some to 12 or even 20 feet) includes 65 per cent of the species selected as typical of the prairie flora.

Relatively few of the deeper-rooted species (only about one-fifth) rely to any marked degree upon the shallow soils for their water and solutes, while many carry on relatively little absorption in the first, second, or third foot. This root habit is in marked contrast to that of the majority of plants of the mixed prairie, where surface rootlets are often extremely well developed. This appears to result from the true prairie's rather uniformly greater moisture in the deeper soil. Even blue grama and buffalo grass, with notably widely spreading surface roots, under the true-prairie environment showed only a small lateral spread. The true-prairie species as a community emphasize depth of penetration and widely spreading, deep laterals.

AN INDICATOR OF CROP PRODUCTION

"The presence of a continuous cover of tall, deeply rooted grasses indicates conditions favorable for the production of cultivated plants of similar habit, a fact fully substantiated by the excellent yields of wheat, oats and corn. The continued growth of the grasses throughout the season, with the late period of flowering and seed production among most of them, indicates a long favorable growing season uninterrupted by a deficiency of soil moisture. The abundance of water in soil and subsoil is further attested by the presence of an abundance of forbs, many of which extend much deeper than the grasses and absorb water that percolates downward through the surface soil. There water is enough for both grasses and legumes, as well as composites, etc. The possibility of so many plants growing in a given area, often 200 to 250 individuals in a single square yard, is due largely to the fact that the roots absorb at different soil levels, the tops making their development at different heights and at different seasons of the year" (Weaver, 1926).

The deeply rooted species have modified the soil to great depths, enriching it with nitrogen, adding humus by root decay, as well as by making it more porous. As a result of absorption, vast stores of nutrients have been brought from the deeper soils and, upon the death of the tops, deposited in the surface soil. Thus, the prairie furnishes the most productive region for agriculture.

CHAPTER 8

Stability, Seasonal Aspects, and other Studies in Prairie

THE PRAIRIE presents so many problems concerning its way of life that only a few of these have been carefully studied. Some of much importance are presented in this chapter.

STABILITY OF PRAIRIE

Continued study of the great mid-continental grasslands of North America impresses one with their high degree of stability.[1] Deterioration of the prairie under the impact of excessive grazing further emphasizes the stabilizing influence of a cover of grassland. Their former subjection to grazing by herds of bison, antelope, and other native animals has been replaced by annual mowing, usually after the vegetation has completed its growth. The fires started by lightning or deliberately set by the Indians to make travel easier and more secure, to furnish earlier grazing and better conditions for hunting, and to cover their retreat from an enemy, have practically disappeared. What minor changes the annual mowing, absence of grazing, etc., have brought about are known only in part. With few exceptions they have been too small to impress greatly the pioneers. The prairies as they were found in the first quarter of this century represented a climax condition and afforded impressive lessons as regards stability.

Stability denotes a high degree of equilibrium between the vegetation and its habitat under the control of the existing climate. It does not preclude minor changes in the abundance of the constituent species. This regularly occurs from year to year as a response to the extremely irregular variations in the factors of the habitat-complex. The phenomenon, how-

[1] Adapted from Weaver and Flory, Ecology 15, 1934, "Stability of climax prairie and some environmental changes resulting from breaking."

ever, is often more apparent than real. The more important species are long-lived and continuously present. They may be either less or more conspicuous because of their lack or abundance of flowering and fruiting, depending upon locally unfavorable or favorable conditions. Conspicuous fluctuations occur mostly among annuals or other relatively short-lived plants. Although the details of the pattern of the prairie mosaic may change, the shiftings are of minor importance. There are no great waves of emigrations; neither are there immigrations, for the prairie is a closed community and invaders, with rare exceptions, are excluded.

Large tracts of prairie are practically 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. Small subseres are frequently initiated as a result of the occupancy of local areas by stacks of hay. Gopher mounds may temporarily cover the vegetation; the burrows of badgers and other animals likewise cause disturbance. Here invading weeds temporarily find a home from which their offspring are soon expelled as the prairie species reclaim the soil. It is indeed impressive to find these relic areas of prairie entirely uninvaded, although surrounded on all sides by cultivated crops with their accompanying annual weeds or by pastures with their usually longer-lived weedy flora. They are free from invasion although the kinds of invaders are numerous and their methods of competition diverse. In fact the number of possible invaders is quite as large as the more important prairie species themselves. A list of the immigrant flora of Iowa alone contains 263 species (Cratty, 1929). Shimek (1931) states that 265 species make up the bulk of the prairie flora of Iowa. Steiger (1930) found 237 species of prairie plants on a single section (640 acres) of land near Lincoln.

Small tracts of prairie, if undisturbed, are also remarkably free from invasion. Frequently strips of native prairie 10 to 20 feet wide, but miles in length, are found along railways. "In many cases these prairie strips have been preserved without appreciable deviation from the pure prairie type even where bordered on the one side by the roadbed with its ever-present belt of weeds, and on the other by farm lands which have been under cultivation from 30 to 60 years" (Shimek, 1931).

Control in grassland does not require complete occupancy. It is exerted partly through competition for light and especially for the water supply. In upland, the light values near the soil surface, such as are met by invading seedlings, often range from 10 to 30 per cent on days of full sunshine; under the dense cover of taller lowland vegetation, they are 1 to 5 per cent. One needs only to examine a trench dug in the prairie soil to fully comprehend how every cubic inch is permeated with the fine absorbing rootlets of the grasses to a depth of several feet. Masses of roots thoroughly occupy the soil continuously from year to year.

Prairie plants frequently exhaust all the available water in the surface 6 inches of soil—the layer upon which the roots of seedlings must largely depend. The well established vegetation each year develops rapidly from accumulated food supplies, the taller grasses often growing a half-inch per day. During years of drought, practically the entire available water supply is used. If water is abundant, as in years most favorable to growth, the invading seedlings may share the supply only to be deprived of sunshine by the rank foliage of the native flora. Seedlings may appear, but few become established (Blake, 1935).

Stability is increased by the long span of life of many prairie species. Only about 5 per cent are annuals. The dominant grasses and most forbs, once established, retain their vitality over periods of many years. When viewed from above, the grassland cover usually conceals from 60 to 100 per cent of the soil. This cover is very effective in absorbing the radiant energy, since it usually consists of plants varying in leaf pattern and height, the foliage of which more or less overlaps. An acre of bluestem prairie may present 5 to 8 acres of leaf surface.

Even after mowing, the ground is not bare. The bases of the mowed plants extend 2.5 to 3 inches high before new growth begins in autumn. A mulch of fallen leaves, fragments of stems, flowers and fruits, etc., forms a more or less continuous cover of varying thickness.

The stabilizing influence of prairie on temperature, as compared to cultivated field, is marked. On a cloudless day, June 10, 1933, during a period of intense heat and prolonged drought, temperatures were measured in a field of corn and in prairie 500 feet distant, both on a north-facing slope. Air temperature in prairie was 11° cooler (100° F.) at a height of 4 inches than in the field; it was 21° lower (103°) at the soil surface, 38° lower (98°) in the soil surface, and 20° lower (94°) at a depth of three inches. Even at 12 inches depth the prairie soil was 3° cooler (81°) than that in the field of corn.

The marked differences in air temperatures reflect themselves both in greatly decreased humidity and increased transpiration. The increase in soil temperatures has a profound effect not only upon promoting water loss from the soil, and directly upon root functions, but also upon the activities of microorganisms. While nitrate production, for example, proceeds at a maximum rate in the moist prairie soil at 94° F., it becomes slower at higher temperatures and may cease altogether at 131° (Russel *et al.,* 1925). Differences in humidity between field and prairie are often surprisingly great. During the day cited, which was typical for a twenty-day period in June, the relative humidity at a height of 4 inches in the prairie was 31 per cent. It was only 12 per cent 4 inches above the hot, nearly bare soil in the field of corn.

Except on extremely windy days, air movement beneath the dense foliage of the grasses and forbs was not marked. Frequently there was none. A breeze of 9 miles per hour three feet above the prairie vegetation was reduced to 3.7 miles at the height of the foliage and to 0.1 mile at one-half this height.

The demands of prairie vegetation for water are gradual. The various plants, rooted throughout several feet of soil, begin growth early in spring. The field for corn, on the contrary, lies fallow. Planting time occurs in May, and the new crop may absorb only in the surface foot until well into June. The prairie continues growth notwithstanding drought in the surface soil, drought that may be so severe as to check greatly the growth of the new corn. With the progress of the season, the need for more and more water by the developing foliage in the prairie increases. This is in accord with the annual rainfall which usually reaches a maximum in June or July. These demands do not all occur at the same soil level. They are met in part by direct absorption from the soil even far below 5 feet. By midsummer a maximum transpiring area has been attained by the dominant grasses; the increase of water demands by the still growing autumnal forbs are probably largely offset by the waning or disappearance of vernal or estival species. Not so in the field of corn. The need for water constantly increases until flowering and fruiting. Roots are rapidly extended into the deeper soil—into the third, fourth, and fifth foot, which heretofore has furnished little or none of the supply. The demands for water are great and urgent. Actually these deeper soil layers were more nearly depleted of their moisture early in autumn than were the corresponding ones in prairie.

Water relations in a field of winter wheat are quite different from those in either cornfield or prairie. Beginning growth in the surface layer in early fall, the wheat roots often reach a depth of 3 or 3.5 feet before growth is retarded or ceases because of low temperatures (Weaver, Kramer, and Reed, 1924). In spring, resumption of growth precedes that in the prairie, and the maximum demands for water—by all plants at the same levels—precede that in the grassland. By midsummer it ceases abruptly at harvest.

A thorough study of Nature's crops and Nature's way of making the most of a sometimes adverse environment is of scientific importance. It is also fundamental to an understanding of the effect of prairie upon stabilizing such factors as temperature and humidity, and its effect upon stabilizing the soil. It furnishes a basis for measuring the degree of departure of cultural environments from the one approved by Nature as best adapted to the climate and soil. The excessive demands of certain crops upon prairie environment have only recently been realized. In native prairies, the deeply rooted legumes and species of similar habit are usually widely spaced. Under cropping practices, however, the deeply rooted alfalfa is grown in dense stands. Frequently, in the extreme western prairie, it so thoroughly depletes the upland subsoil of its moisture that it is difficult or impossible again to grow alfalfa, even after a lapse of a score of years, on soils thus depleted of their water.

The prairie crop is a mixed stand. Various legumes are blooming or ripening fruit from April until October. The same is true of the different species of grasses. There is a time for flax, another for mints, and still another for roses. Not all of these crops are bountiful every year. Some may form no viable seed. Indeed there is no pressing need among the perennials for fruiting each year. Only in wet years does little bluestem normally fruit abundantly on dry uplands. How unlike the more delicate, annual crops of man. Neither is there a critical time for drought as in wheat, or corn, or clover, where a few days of adverse conditions may prove disastrous. Height and density of cover vary annually, as does also the tonnage of hay. If drought comes early, growth is resumed upon the advent of wet weather. If it comes later, the earlier yielding prairie components have had a good year. Nature's crops are adjusted to fit into periods of dry cycles as well as wetter ones. These have recurred again and again throughout the centuries. Reserves of food of native plants are extensive, and their resources for obtaining water are excellent.

A comparison of the environment and some physiological responses of prairie vegetation and cultivated maize have been made by Flory (1936), and comparison of the environment and certain physiological activities of alfalfa and prairie vegetation by Fredricksen (1938). Similar studies were made on winter wheat and prairie during extreme drought (Noll, 1939), and R. J. Weaver (1941) ascertained the water usage of certain native grasses in prairie and pasture. The water content and osmotic relations of prairie vegetation were ascertained by Stoddart (1935) during a year of extreme drought, and by Marsh (1940) during a year favorable to plant growth. All of these investigations were made near Lincoln, Nebraska.

SEASONAL ASPECTS

Forbs have accommodated themselves to the presence of grasses, as is shown by their seasonal activities and height growth. The kinds of groups of forbs or societies and the degree of development of the grasses lend to each season a distinctly different appearance or aspect. The prairie presents four of these, besides the more somber one of winter. The orderly succession of changes in the conspicuous features of the landscape proceeds with marked regularity.[2]

Prevernal Aspect

The earliest prevernal bloomers appear in the warmer situations late in March or early in April. Among the most important are Pennsylvania sedge, prairie cat's-foot, pasque flower, dogtooth violet, anemone, and white-flowered parsley. The patches of sedges, with their numerous yellow and purple spikes, and those of the white, wooly, prairie cat's-foot are conspicuous on the brown background of dry grasses and herbs (Fig. 42). Carolina anemone develops rapidly from food accumulated in a tuber, and dogtooth violet from a deep solid corm. Eastward and northward, carpets of pasque flower lend a bluish cast to the reddish-brown of bluestems (Fig. 43). There are both yellow and white parsley on the dry ridges; the buttercup (*Ranunculus rhomboideus*) is also an early bloomer.

All of these prevernal species are of low stature; some are short-lived above ground, and none ever reaches the midsummer level of the grasses.

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[2] Originally appearing in Ecological Monographs 4, 1934, this paper, condensed and simplified, was used in Nebraska Conservation and Survey Division Bul. 21, 1939. It appears here with somewhat further change.

After a few weeks of vigorous activity, unshaded by other plants in early spring, they disappear or persist in the understory throughout the remainder of the growing season. There are only about a dozen species of much importance in the prevernal aspect.

Needlegrass, Junegrass, and nodding wild-rye, all of northern extraction, are the only dominant grasses that have made considerable growth, but this is exceeded by the rapid development of bluegrass.

FIG. 42. Carolina anemone (*Anemone caroliniana*) (upper left), and dogtooth violet (*Erythronium albidum*). (Below, left) Prairie violet (*Viola pedatifida*) and a large bunch of blue-eyed grass (*Sisyrinchium campestre*).

Vernal Aspect

Late April introduces the vernal or spring aspect. The drab tone of winter is replaced by the greenish tinge of the new growth of grasses. The bluestems, of southern origin, appear about the middle of April, but on low ground and north slopes the colors of the dried vegetation of the preceding year are not entirely obscured until the first week of May. Bluegrass is then so far advanced that production of flower stalks has begun.

This period initiates rapid growth of plants of summer and autumn as well as those of spring. In the ravines and moist soil the tall-growing sawtooth sunflower, rosinweeds, tall goldenrod, and other late bloomers far outstrip the grasses in rate of growth. Strawberries, violet sheep sorrel, and prairie and meadow violets rapidly develop both foliage and flowers before the light is too much obscured by the growth of the grasses. The new

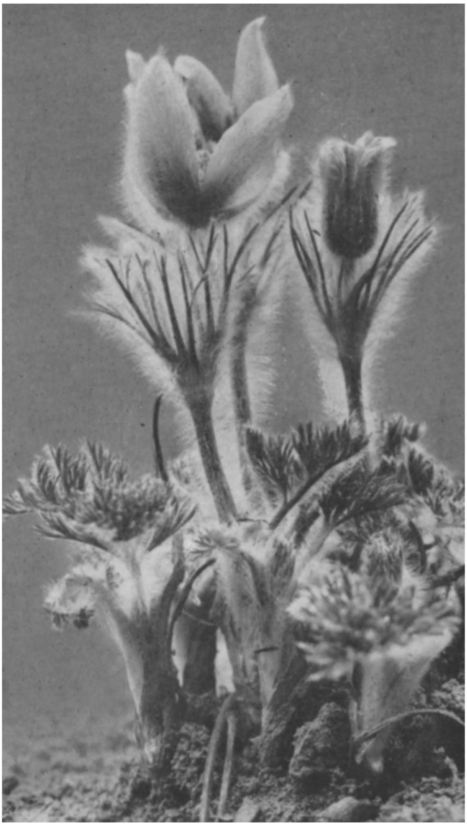

FIG. 43. "In the early days of spring when the last snowbank has melted away from the reddish-brown grassland, myriads of lavender pasque flowers (*Anemone patens*) lend a bluish cast to the gravelly knolls of the northern prairies." Ada Hayden.

shoots of button snakeroot, blazing stars, goldenrods, sunflowers, and sage add tone to the landscape. Winter has gone, spring has come, and the prairies pulse with life.

From the background of green show forth the gems of nature, manifold in variety, radiant in beauty, endless in recurrence—the societies of the vernal aspect. Among these are found blue-eyed grass, yellow star grass, puccoons, ragwort, wild onions, vetch, false indigo, and many others, all enhancing the beauty of prairie in spring (Fig. 44). The yellow of the meadow parsnip, the white masses of flowers of redroot, and the ground plum with its abundance of violet-purple flowers were all familiar sights

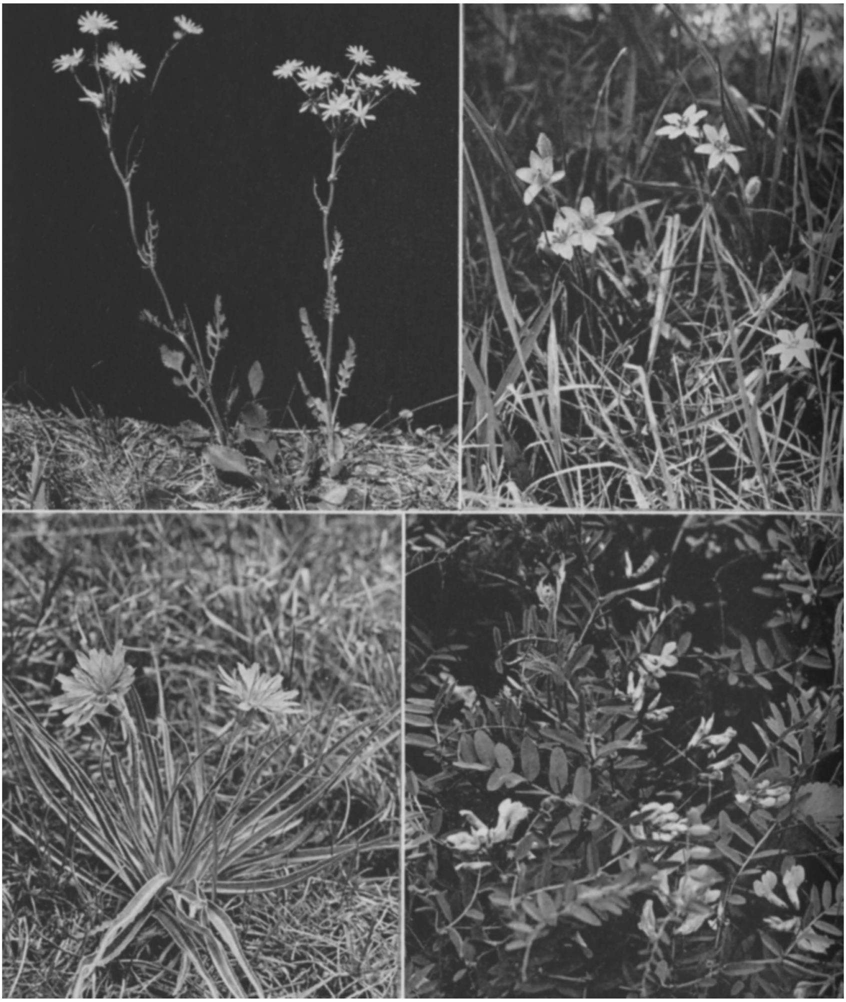

FIG. 44. Prairie ragwort (*Senecio plattensis*) (upper left), and star grass (*Hypoxis hirsuta*). (Below) Prairie false dandelion (*Microseris cuspidata*) and purple vetch (*Vicia americana*).

to the pioneers of the midwest. The large cream-colored racemes of false indigo are conspicuous even at a distance, and masses of purplish flowers reveal the patches of the vetch. The large white flowers of Canada anemone, a late vernal bloomer, decorate the landscape on moist soil, where dense societies of this windflower grow. On flood plains and moist hillsides, the pink or purple of the prairie phlox and patches of violets may be seen. Tiny white flowers of the bedstraw, on plants densely aggregated, are found beneath the grasses of lowlands, and spiderworts present their purple tone to the landscape. The spring flowers of prairie are wonderful to behold.

There are a total of about 40 species of considerable importance in the vernal aspect. Approximately 70 per cent of them are of low stature, as illustrated by violets, strawberry, ground plum, and bedstraw. Nearly all of these may be found in the understory throughout the growing season. Of the remaining species only a few, such as phlox and redroot, are conspicuous above the height of the grasses. The remainder are submerged by midsummer to the general level of the grasses. Thus, during April and most of May nearly all species of this aspect attain not only their maximum flowering but also their maximum rate of growth and other physiological activity. The grasses have not yet so completely overshadowed them as to form a material handicap in the relation to light. But their maximum physiological activities have now been reached, and their life processes are on the decline.

During the vernal aspect all of the species which blossom in summer and autumn have made a vigorous development. The vernal species have in their development forged ahead of the ever increasing wave of summer and autumnal bloomers. Week by week during spring and early summer the struggle for light becomes more and more severe. While most plants that will blossom in midsummer attain only a moderate height in relation to the grasses, autumnal bloomers continue to grow until they are nearly all in the sunshine quite above the level of dominant grasses. This relationship is attained not only on upland but on lowland prairie as well. It is an important fact that species of the spring, summer, and autumnal aspect begin growth at about the same time. By midsummer the physiological activities of the maturing estival species are lessened, but the need for light, water, and nutrients by the autumnal bloomers has increased.

Estival Aspect

The estival or summer aspect begins during the last week of May.[3] By this time bluegrass has blossomed, the spikes of Junegrass are beginning to open, and needlegrass is often in full bloom. The bluestems and other dominant grasses now cover the uplands with a deep foliage of green, attaining on the lowlands a height of 12 to 18 inches. Many spring flowers are gone. Although several vernal species continue to bloom, these too are soon to wane and are rapidly being replaced by an increasing wave of estival bloomers. There is a distinct transition from spring to summer. The landscape is rapidly becoming redecorated with extensive societies of daisies, legumes, and the rose. Many-flowered psoralea and silver-leaf psoralea, where at all abundant, give a distinctive tone to the landscape. Milfoil, daisy fleabane, penstemons, larkspur, wild flax, tooth-leaved primrose, and pale purple coneflower adorn the landscape. The stately plants and showy flowers of several species of wild lily add further variety to nature's varicolored garden.

Myriads of flowers now contribute to the great wealth of midsummer beauty. Among the most distinctive and widely spread societies of upland is that of lead plant. Even before the abundant dark purple or indigo flowers begin to appear in June, the leaden-colored leaves give tone to the prairie. Profuse blossoming continues for several weeks. The white and purple prairie clovers, black-eyed Susan, tick trefoil, licorice, wild bergamot, and rosinweeds adorn the rolling hills and lowlands (Fig. 45). The large white wild indigo with tree-like spreading branches holds high its cream-colored flowers, often two or three feet above the grasses. The white larkspurs stand far above the surrounding vegetation as sentinels of the prairie (Figs. 25, 29). The flowers of wild onions, the pale yellow, bell-like flowers and bladder-like fruits of ground cherries, the blue- or scarlet-flowered lobelias, the delicately painted blossoms of beardtongues, and the large yellow ones of the tooth-leaved primrose are all now to be seen in nature's prairie garden. On low or wet ground one finds the meadow rue, water hemlock, purple-tinged umbels of Sullivant's milkweed, pale-red flowers of swamp milkweed, and orange-yellow to brick-red blossoms of the bush-like butterfly weed.

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[3] The approximate dates given for each aspect apply particularly to the lattitude of Lincoln, Nebraska. They begin 10 to 14 days earlier in northern Kansas and 7 to 13 days later in southern Minnesota.

Many other flowers adorn the rolling hills and lowlands. The patterns are endlessly variable in detail. Each week new elements appear and others gradually decline as the season advances. The advent of severe drought, however, at some period during the growing season, may seriously handi-

FIG. 45. Beardtongue (*Penstemon cobaea*), and (below) a society of black-eyed Susan (*Rudbeckia hirta*).

cap the usual wealth of blossoms, and indeed many flowers may become rather rare.

In July certain coarse composites begin to bloom. The large yellow flowers of entire-leaved rosinweed, stiff sunflower, and the oxeye add further color to the prairie. The very numerous yellow ray flowers of the clustered heads of the compassplant are indeed a conspicuous feature of the prairie. The blooming of the sunflower and the yellowing of the inflorescence of the goldenrod portend the coming of fall. Once more the scenes are shifted as the summer aspect gives way to the oncoming autumnal one.

Species of considerable abundance composing the estival aspect are 70 in number. Plants of the estival aspect reveal a greater height-growth than those of preceding ones. Perhaps only 10 per cent are hidden by the grasses. Forty per cent are approximately as tall as the grasses. The remaining half overtop the grasses and form a distinct upper layer.

Autumnal Aspect

About the middle of July the prairie begins to change gradually in appearance. The graceful flower stalks and flowers of side-oats grama, which have been developing slowly, now appear in abundance for the first time. The spikes of nodding wild-rye are nearing their height of blossoming. Soon the panicles of switchgrass on low ground begin to unfold, and isolated stalks of the bluestems overtop here and there the vegetative growth which has now nearly completed its development. The deep cover of grasses, although still green and vigorous, has passed from a stage of active development to one of approaching fruition and maturity.

Most of the estival plants have finished blooming; others are distinctly on the wane; but many continue into the autumnal aspect for a time. On low ground, water hemlock, wild bergamot, American germander and others are in their prime. Water hoarhound and loosestrife show forth from wet areas, as do also the white and pinkish flowers of water smartweed.

Now the yellow and gold of the sunflower and the oxeye intermingle with the purple of the button snakeroots and blazing stars. Many species of goldenrods occur, sometimes in great masses, and all add much beauty to the autumnal landscape. Various rosinweeds dot the prairie where moisture is plentiful. Pleasing variety is added to the wealth of autumnal colors by the grayish-white flowers of the false boneset, the gray color of the sage, and the black, fruiting heads of bush clover. Ironweeds, gentians, tooth-leaved primrose, and many others are found. Numerous asters blossom from August until late fall, their colors varying from white or lavender to blue or purple. The great stems of the cup plant, each often

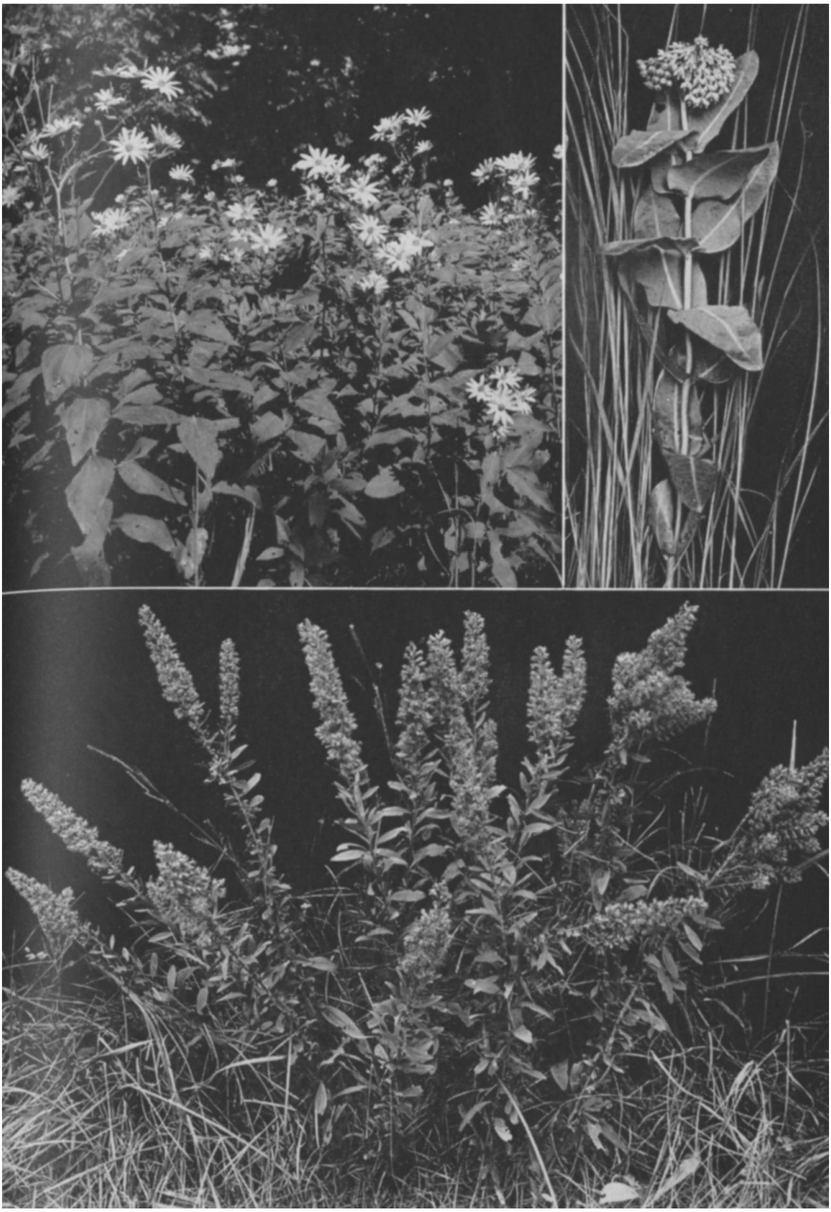


FIG. 46. Society of Jerusalem artichoke (*Helianthus tuberosus*), and (right) Sullivant's milkweed (*Asclepias sullivantii*). (Below) Showy goldenrod (*Solidago speciosa*).

with a score of large yellow flowers, stand 3 to 6 feet high. The compass-plant is quite as conspicuous and often far more abundant. On the upland, societies of stiff sunflowers are conspicuous. Saw-tooth sunflower is a conspicuous bloomer of late fall, as are also Jerusalem artichoke and Maximilian's sunflower and certain others of moist soil (Fig. 46). But nature presents her most gorgeous colors where societies of the various button snake-roots and blazing stars cover the landscape. Indeed such beauty is rarely surpassed. Quite in contrast, the tall Pitcher's sage presents a wealth of large blue flowers during August and September, and the deep blue blossoms of the gentian may be found here and there hidden among the grasses.

Among the autumnal bloomers the gentian almost alone is found in the understory. All others are conspicuous at or above the general level of the grasses. They are of large size and many reach a height of 3 to more than 6 feet. The autumnal aspect is characterized by about the same number of species (40) as the vernal aspect.

During September and late 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 every square yard. The golden panicles of Indian grass glisten in the sun. The dried heads of nodding wild-rye stand thickly in the ravines, while on uplands the open panicles of prairie drop-seed are held aloft above the level of the foliage.

About the first week in September, or earlier if the season is dry, many prairie grasses 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. Late October or November witnesses the waning and finally the death of the aerial parts of the forbs and grasses.

Hiemal Aspect

Mid-September and October witnesses the culmination of fruition and maturity of the late-blooming forbs as well as grasses (Fig. 47). There is then a gradual deterioration of the vegetation, which is hastened by repeated frosts. Although the dried flowers and fruits of some species are still conspicuous, most of them have fallen to earth. The dry or drying leaves may fall to the ground or cling as withered things to the bare stems.

The leaves of the grasses dry in place on the erect stems without much change in outward appearance except that the wonderful shades of bronzes, reds, and golds, gradually fade with the passing of the weeks to the various tints of gray or somber reddish browns. The dead stems of grasses and forbs may remain intact for a long time and often intermix with the green ones of the next summer. As a result of natural deterioration, augmented by the work of the wind and assisted by the weight of ice

FIG. 47. False boneset (*Kuhnia eupatorioides*) in fruit in late autumn, and (right) tooth-leaved primrose (*Oenothera serrulata*) of the summer aspect.

and snow, the once great cover of standing vegetation gradually returns to the surface of mother earth. Here it forms a protecting blanket for the living parts within and beneath the surface of the soil. Unless removed by fire, it decays but slowly throughout the coming seasons. Thus, in winter, life in prairie (except for fruits and seeds) is found almost entirely within the protecting soil. But the prairie is still a living thing—though underground and dormant—awaiting only another summer to build anew the parts above the soil.

The role of lichens and mosses, although they are sometimes abundant in late winter and spring, is a very minor one in prairie. It is only with the appearance of new leaves and shoots from the perennials that the beginning of a new season—a period filled with many wonderful activities—is initiated. Again the prevernal aspect is at hand.

RELATIVE EFFICIENCY OF ROOTS AND TOPS OF PLANTS IN PREVENTING EROSION

Preventing or controlling the wastage of land through soil erosion is one of the major economic problems in America. Plant cover is the main controllable factor. In prairie the force of the rain is broken by the foliage of the grass and forbs and by the litter of fallen leaves and stems beneath. Hence, the rain does not beat directly upon the soil. The lodgement of the undecayed materials among the stems of the grasses forms an intricate series of minute dams and terraces which tend to hold the water until it can percolate into the soil. Abundant humus creates a sponge-like condition in the topsoil which increases its capacity to absorb and hold water. Hence, runoff in prairie is usually slight unless the rains are heavy. Even during heavy rainfall the water that does run off is usually clear.

The living plant materials form a wonderfully efficient anchorage system for the soil, especially the surface layer. This living framework, which holds the soil in place, often constitutes about one-tenth of the total organic matter in the surface 6 inches (Weaver, Hougen, and Weldon, 1935). Because of the wide distribution into thousands of cable-like structures with which the soil is everywhere threaded, and because of the intimate contact of the absorbing roots with the soil particles, the binding efficiency of these threads of great tensile strength is enormously increased. Their combined length in the surface 4 inches of prairie soil is almost unbelievable. This was ascertained by Pavlychenko (1942) from sods at Lincoln, Nebraska, 0.5 square meter in area, as follows: big bluestem 12.9 miles, little bluestem 23.2, needlegrass 11.0, and Kentucky bluegrass 106.0 miles.

A series of experiments were made to ascertain the relative values of tops of prairie plants and their underground parts alone in protecting the soil from erosion (Weaver and Harmon, 1935, Kramer and Weaver, 1936). Since it was not expedient to haul the necessary large quantities of water into the various prairies, large samples of undisturbed sod were brought into the greenhouse where water could be applied under controlled conditions.

Stout frames one meter long and one-half meter wide inside, and ten centimeters deep, were made of planed cypress lumber about one inch thick. The frames were taken to the field and placed over the samples carefully selected as representative of the area. Pairs of samples were taken only a few inches to a few feet apart. Great care was taken that the tops of all plants rooted inside the frames were included and those rooted outside excluded. Tops of plants immediately surrounding the frames were then removed; care was exercised not to damage the plants within one frame. The tops from the second sample were removed close to the soil by clipping either at once or after the sample was excavated.

A spade with a sharp, straight blade was used in cutting the core of soil to a depth of 4 inches around the frame in such a manner that the frame could be forced to this depth in the soil, holding firmly the enclosed one-half square-meter sample. The sample was next undermined by digging the soil from the ends and, especially, from both sides in such a manner that a blunt wedge was formed from the soil block protruding beneath the frame. The frame was then tipped on its side, excess soil was removed, and the bottom was nailed in place.

Upon reaching the greenhouse, the soil was thoroughly watered until no dry soil remained. The frame was then placed lengthwise on a washing rack with a slope of 10°. A second frame of the same size but 12 inches deep was placed upon the first. It was held by a number of iron braces fitting over the frame beneath. A meter strip of wood, 1.25 inches wide and $^3/_{16}$ inch thick, was permanently fastened within the frame, on the lower side of each wall, so that its edge protected the soil in the lower frame. Thus in eroding the soil no water came directly in contact with the sides of the lower frame until at least the upper 2 or 3 inches of soil were removed. A strip one inch wide had been removed from the lower end of the upper frame to permit surface soil to escape during this process, and 4 one-inch holes were bored in the lower end of the lower frame to furnish an exit for the water and eroded soil after the top of the soil had been worn away.

Water was always applied from the same hydrant with the same hose and nozzle and at a distance of 2.5 feet from the sample. Care was taken to move the hose slowly back and forth in a regular manner so that the stream played for only an instant on any one spot. On every sample the first hour of washing was done without a nozzle and the second with the nozzle set so as to throw an approximately uniformly circular stream 4 inches in diameter. Washing was then continued until all the soil had been removed with a stream only three-eighths inch in diameter and, consequently, with greatly increased force.

At first 12.73 gallons of water were delivered per minute under a total force of approximately 1.0 pound. The second condition delivered 4.80 gallons of water per minute which struck the soil with a total force of 1.95 pounds. Finally the volume of water was reduced to 3.42 gallons per minute, and the force of 1.39 pounds was concentrated within an area of only about 0.11 square inch and consequently had a great erosive effect.

When water was applied to the sample of big bluestem with tops removed it became muddy for a period of 5 to 8 minutes, after which it remained clear throughout the first hour. This phenomenon resulted from the fact that the surface 0.5 to 1 inch of soil has few roots and rhizomes. Once this loosely held earth is removed, the soil resists this simple flooding

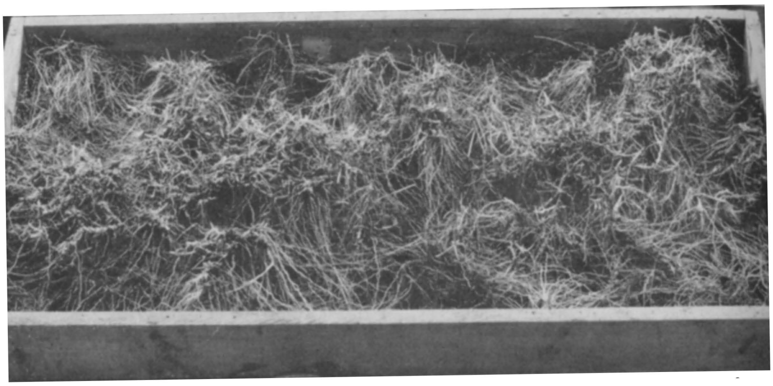


FIG. 48. One-half square meter of sod of big bluestem rhizomes and roots to a depth of 4 inches. Note that they are rigid enough to maintain approximately their original position. Their air-dry weight was 4.1 tons per acre.

for very long periods of time. Even by the end of the second hour the mass of soil had not been greatly reduced. The compacted rhizomes and tough wiry roots maintained their position and formed an effective barrier between the force of the water and the soil. Only after 2 hours and 40 minutes with the small stream of water were the underground parts freed from the soil (Fig. 48).

Unclipped big bluestem soon lodged, leaving only the coarser stems erect. By the end of an hour practically no soil had been removed, the water running clear, but the tops had been compacted into a rather dense layer only 3 to 4 inches thick. The half-erect stems aided in breaking the force of the water. No visible erosion occurred the second hour, but with the application of the finer stream the clear water became slightly turbid.

After another hour the plant mass was beaten so thoroughly that it formed a compact cover only 1.5 to 2 inches thick. The hour following, some of the root-crowns became visible. The cover was somewhat frayed and was beginning to lose its continuity. The runoff water became more turbid. After 7 hours, about ⅜ of the soil had been removed, and after 9 hours only about ⅓ was left. The process of erosion continued at an increasing rate, but only after 12 hours and 57 minutes of applying water, under the impact of 1.4 pounds per 0.11 square inch of surface, was erosion complete.

A pair of samples of sloughgrass was secured from an area where each stem had 5 or 6 green leaves 4 to 5.5 feet long and one-third to nearly one-half inch wide. The basal leaves on the partially lodged grass were no longer green but still clung to the coarse stems. The unconsolidated surface half-inch of soil was soon washed away from the bared sample. The network of rhizomes and roots held the soil tightly. Total erosion time was 4 hours and 18 minutes.

The lodged plant cover afforded almost complete protection from erosion to the second sample. During the first 10 hours, the water was entirely clear. In fact, the efficiency of the thatched cover was so great that after a total of 22 hours not more than ⅛ inch of the soil had been carried away.

Samples of little bluestem sod were obtained for uniformity of ground cover, in silt loam. One had never been grazed but had been mowed annually; the second had been closely grazed for two years. The ungrazed sample was entirely eroded only after 3 hours and 32 minutes, but the grazed one in 2 hours and 40 minutes.

In the following summary of results only the time for complete erosion after the preliminary 2 hour treatment is given. Also data on erosion without the presence of the tops are given first. All samples were taken from silt loam soils.

Big bluestem	2 hrs.	40 min.	Sloughgrass	2 hrs.	18 min.
	12	57		22+	—
Bluegrass	—	45	Little bluestem ...	1	32
	3	35	grazed	—	40
Needlegrass	1	20	(Both with tops)		
(Without tops)					

A direct comparison of the relative resistance to erosion may be had, if one considers the first two treatments as a preliminary conditioning which all samples underwent. Thus, big bluestem and bluegrass both held the soil nearly 5 times as long when tops were intact, compared with underground parts alone. Likewise roots and rhizomes of ungrazed little bluestem held the soil 2.3 times as long as the same species when weakened by two years of grazing. Results with ungrazed and grazed big bluestem were practically the same. In the ungrazed samples there was an almost continuous mat of sod; in the grazed ones openings occurred in which few or no roots were present. It was here that the soil washed away readily and permitted the undermining of the sod. In comparison, bare soil in worn-out, native pastures withstood erosion only during 18 minutes of preliminary treatment, and when clothed with annual weedy grasses it eroded in a total of 41 minutes. When the prairie cover is thus removed by overgrazing, or by the breaking plow, the soil is laid open to accelerated erosion. In a generation or two of careless farming, the topsoil may be nearly or entirely washed or blown away. But its original level may be seen one, two, or even three feet higher in adjacent prairie where the slopes remain protected by the original carpet of grass.

From these experiments it may be concluded that the most formidable line of defence by prairie grasses against erosion is above ground, although the soil is also held in a remarkable manner by roots and rhizomes. The foliage of sloughgrass is especially adapted to protect the soil even against rushing flood water.

Similar studies with field crops (Kramer and Weaver, 1936) have led to the same conclusions. Winter wheat with mature tops intact, for example, held the soil seven times as long against erosion as samples with tops removed. The more nearly a crop approaches the native prairie grasses in its form, manner of growth, and length of life, the greater is its efficiency in resisting the forces of erosion. Hence the excellent manner in which smooth bromegrass (*Bromus inermis*) binds and holds the soil in hilly pastures and especially on recently graded roadsides is readily understandable.

INTERCEPTION OF RAINFALL

Prairie vegetation during rains holds a considerable portion of the rainfall upon its surface until it evaporates. Consequently it does not reach the soil. Water is held on grass and forb as thin films or drops which form

FIG. 49. Rainwater held on the leaves of big bluestem. This sometimes amounted to 53 tons of water per acre. (Lower left) Blocks of sod of big bluestem 3 months after transplanting. Plants on the left have been repeatedly clipped. Blocks of sod of switchgrass 42 days after transplanting in spring. Tops of the plants, with only a few roots, were removed weekly at a height of 2 inches.

on the surface, at the tips, and along the margins of the leaves, and, in addition, it also adheres to the stems (Fig. 49). Total interception is very great, since this native vegetation presents a surface of foliage 5 to 20 times larger than the soil surface beneath it. Leaves occur at many levels from top to base of stem.

Clark (1937, 1940) placed meter-long pans, 4 cm. wide and 5 cm. deep, on the soil under pure stands of various grasses. When necessary, stems were cut and placed in the pans without disturbing the cover. The pans covered one-fifth of the soil. Big bluestem withheld about 66 per cent of the precipitation during a heavy rain and 97 per cent during a very light shower. Interception of rainfall by prairie cordgrass varied from 67 to 80 per cent in hard to light showers. Needlegrass and prairie dropseed withheld 50 per cent or more of a quarter-inch artificial rain applied during a half hour. Lowland forbs intercepted nearly half of the water during heavy showers and about two-thirds during lighter ones. Clark (1937) states: "When an inch of water falls during an hour, buffalo grass intercepts over 28 tons per acre, while prairie composed chiefly of big bluestem may intercept as much as 53 tons per acre."

The prairie cover checks the force of the raindrops and causes them to fall gently upon the mulch-covered soil beneath. Also, by interception, it prevents much water from reaching the soil; but once in the soil loss by evaporation is decreased by shading. The total effect is to retard runoff and soil erosion.

EFFECTS OF REMOVAL OF PLANT COVER

Prairie plants are eminently adapted to grazing, and moderate grazing is little or no more harmful than complete protection. Moderate grazing is grazing to a degree that will permit the more desirable forage plants to maintain or increase their abundance and yet be used from year to year. Under natural conditions the annual forage crop was partially removed by the many types of grazing animals or trampled by them; and prairie fires were common.

In native prairie there are many kinds of plants from which grazing animals may choose. Often the preference for certain species is very marked. Where there are many animals in a circumscribed area it usually happens that the foliage of plants for which the stock shows a high preference may be removed too often and too closely, and these plants begin to lose their vigor and may finally wane and die. They are then replaced by species less disturbed by grazing. Forage from these is usually smaller in amount and often less palatable than from those that have been grazed out. This loss of vigor of both roots and tops is such an important and wide-spread phenomenon that it has been studied rather thoroughly.

Transplanting and Clipping

Representative bunches or sods of several native species of grasses were selected in duplicate and removed from the prairie at Lincoln late in June (Biswell and Weaver, 1933). The tops were clipped at a height of 1.5 inches and the soil cut into blocks 5 by 5 inches in area and 4 inches deep. The blocks were transplanted into galvanized iron containers, a square foot in surface area and 2 to 2.5 feet deep, which were filled with a rich loam soil. Good aeration and proper drainage were provided by an opening in the side, near the bottom, of each container. Containers were placed in a trench in a bluegrass lawn and soil was packed around them. The soil was kept at an approximate optimum water-content for growth by frequent watering. Growth of tops was resumed immediately, as well as after each clipping from July to October.

After the plants had become well established, one lot of each species was clipped at a height of 1.5 inches every 14 days; the other one was left undisturbed. The foliage produced at each clipping was oven-dried and the dry weight ascertained. The weight of tops increased from the first three to five clippings, after which it decreased. The grasses were permitted to grow until early October when all the tops were clipped, dried and weighed. Then the containers were cut open and the soil was carefully washed from the roots.

The unclipped big bluestem made a luxuriant growth throughout the summer; 45 flower stalks were produced. Foliage of switchgrass was 18 inches high, and 40 flower stalks had developed. Little bluestem formed a very thick, heavy tuft of foliage and a few flower stalks. Differences in root development were striking (Fig. 49). The total dry weight of forage produced by the clipped plants compared with controls was only 15, 30, and 13 per cent as great in big bluestem, little bluestem, and switchgrass, respectively. Dry weight of roots, in the same order, was 5.3, 7.9, and 3.6 per cent of that of the unclipped plants. Clipped plants failed to produce new rhizomes and many of the old ones died. Length of roots was greatly decreased and the relative production of roots was more greatly reduced than that of tops.

At the end of the experiment the blocks of sod were buried in soil and frozen at $-12°$ to $-15°$ C., slowly thawed, and again frozen for a second week. The unclipped plants made a good growth, but plants weakened by repeated clipping renewed growth very slowly if at all. No new roots were produced during the 35 days for growth by plants that survived. Clearly, grasses greatly weakened by frequent removal of tops are in poor condition to withstand drought, winter-killing, and competition with other plants (Biswell and Weaver, 1933).

Clipping or grazing of seedling grasses is even more harmful, since their food reserves, for a time, are indeed small. Robertson (1933), who experimented with six prairie and pasture grasses grown in soil, concluded: "Removal of the aerial parts of grass seedlings had an immediately injurious effect which was measurable both above and below ground. Extent of injury depended largely upon the nature of the species and the frequency of the treatment."

Clipping in Prairie

The effect of frequent clipping on big bluestem was determined by a four-year experiment (Weaver and Hansen, 1941). An excellent lowland prairie near Greenwood, in eastern Nebraska, mowed once each year for hay, consisted of 95 per cent big bluestem. A few square rods were set aside and the grass was cut four times each season with hand clippers at a height of 1.5 inches, to simulate grazing. Each of the clippings during the first year was followed by a prompt renewal of growth, the height attained depending largely upon the length of the interval between clippings. Decrease in height of one-third to more than one-half occurred the second year. Thereafter the grass never regained its vigorous former development. Total yield of the clipped plants was only 61 per cent as great as that of the unclipped ones the first year and 41 per cent as great the second. Moreover, the percentage of total annual yield produced before June 1 decreased from 42 the first year to 26 the third. The later beginning and slower growth seemed due to the depletion of food accumulated in the rhizomes.

By August 5 of the first year, bluegrass had made great increases throughout the clipped plot. The following spring the soil was almost completely covered with bluegrass, although very little was found in the control where the shade was dense. A continuous cover was established by the third summer. In appearance it was almost identical with that of a thriving bluegrass pasture. Bluegrass furnished 80 per cent of the spring yield of the fourth year; the relic bluestem was sparse and greatly weakened.

Large areas on uplands of practically pure bluestem were clipped to simulate close grazing by cattle and horses confined to a portion of the same prairie, which had just been fenced for pasturing (Weaver and

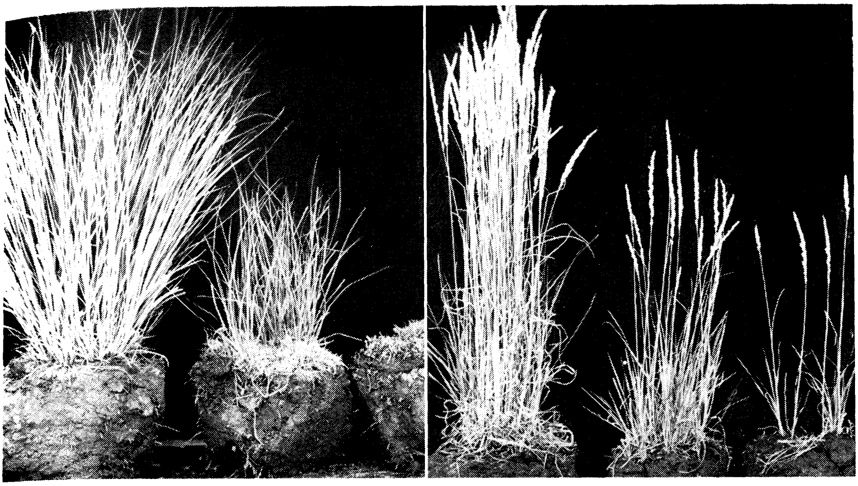


FIG. 50. Unclipped bunch of prairie dropseed (left); typical bunch clipped 3 times the preceding year at 1.5 inches height (center); and one of the many bunches which died during the second year of close clipping. (Right) Control bunch of Junegrass 16 inches tall; (center) bunch clipped twice during the preceding season, and one clipped twice during each of the two preceding years. Both photos on June 20, 1939.

Hougen, 1939). Six clippings were made. After each clipping the plants renewed growth in a few days. They were only about 3 inches high when cut early in May, but 5 inches at the second clipping late in May. Later heights were 7 and 9 inches. The manner in which the grass renewed growth after each of the six cuttings the first year was remarkable. Moreover, the yield totaled 11 per cent greater than that of the unclipped controls. That this growth was made at the expense of reserve foods was clearly revealed by the reduced vigor and yield as well as by the high death rate (also in the pasture) the second year.

In mid-May of the second and drier year the clipped grasses were only half as tall as the controls. The clipped bunches were not filled with shoots as were the unclipped ones. Frequently, they had living stems only around their borders. Since it was a dry year, only four clippings were made. The yield from these grasses exhausted by frequent clipping was only half as great as that of the controls, which had been harvested only once during the preceding year.

The third year summer rainfall averaged above normal. But so much of the little bluestem had died and the remainder was so weakened that the yield from the three seasonal cuttings was only one-third as great as that of the controls. Other experiments verified these results. That two-thirds of the possible forage yield may be lost and the plants so greatly weakened by overgrazing for only three years is alarming. Yet the phenomenon has occurred in thousands of pastures throughout the area of true prairie (Fig. 50).

Clipping Selected Grasses

An investigation was made (Darland, 1947) to ascertain the proper height of grazing various species of grasses in true prairie without effects harmful to the plant. The plan was to clip each of several species of grass at heights at which they are normally removed under moderate and close grazing. Among species employed were little bluestem, big bluestem, needlegrass, prairie dropseed, and side-oats grama. Data on average heights of grazing had been accumulated over a period of years including those with plentiful rainfall and those with light precipitation. Averages were 2 inches for close and 4 inches for moderate grazing for most species, but 3 and 5 or 6 inches for needlegrass and prairie dropseed. Many bunches of each species were permanently located and numbered where they occurred in upland prairie. They were clipped early in May and about six times thereafter, each time when they had reached a height at which they would have been grazed. Recovery, of course, was most rapid early in the season, when environmental conditions were most favorable for growth. It was slower after several harvests, when the grasses were losing their vigor as a result of the frequent removal of foliage. At each clipping the tops from each species cut at each height were collected, air-dried and weighed.

The harmful effects of close clipping, even the first year, were shown in the greater decrease of yield when compared with a moderate height of clipping. Not only was there more forage throughout the season from plants clipped high, but the stand of grass was better maintained, since more forage was left on the ground. The outstanding finding, when the same bunches were clipped the second year, was also the much greater yield from the high clippings. The effects of the previous year's clipping were apparent in all species early in the second season. Plants clipped high were taller and usually showed considerably more vigor. Yield was not much reduced in any grass clipped high the preceding year. Decrease in yield, despite this better year for growth, as was shown by unclipped plants, was much greater under low clipping. The excellent growth of unclipped plants the second season emphasizes the fact that the reduction in yield of all clipped grasses was a result of reduced vigor due to clipping. Even the high clippings were too low for sustained production.

These experiments illustrate why prairie may degenerate into weedy pastures in only a few years under overstocking. But many remain in good condition even after a quarter or half century of moderate grazing which permits the plants to maintain their vigor and replenish the great underground storehouse of food year by year, as they have done throughout the millennia. In grazing prairie we must regard the grass as the chief capital asset. It should be treated with as much care as we give other crops. Grasses flourish or wane according to the treatment they receive. Too close removal of the plant cover is distinctly detrimental.

Method of Measuring Vigor

The degeneration of excellent or good native pastures and ranges into medium or poor ones is always preceded by a decrease in vigor of the most nutritious and best-liked grasses. These are nearly always the climax species. Decreased vigor may result from overgrazing or from drought. If this sign of range deterioration is observed and stocking rate is decreased, or grazing deferred, or the pasture completely rested, the range will usually recover and often improve.

An excellent test of vigor under conditions favorable for development is that of prompt renewal of growth in spring, after grazing, or after transplanting. The last permits exact measurements of heights, production of forage, and the rate of development and amount of new roots.

Blocks of sod of vigorous grasses were obtained from native prairie in spring before resumption of growth. They were transplanted in sandy loam soil in boxes 10 by 10 inches and 24 inches deep, lined with galvanized iron, and with one removable side. Bunches or blocks of sod were selected for transplanting from overgrazed and moderately grazed pastures. The tops were removed and new tops and roots were grown during periods of 4 to 6 weeks. Sand dropseed, side-oats grama, Scribner's panic grass, buffalo grass, blue grama, big bluestem, tall dropseed, and little bluestem were tested, often in duplicate or triplicate, and from widely distant stations.

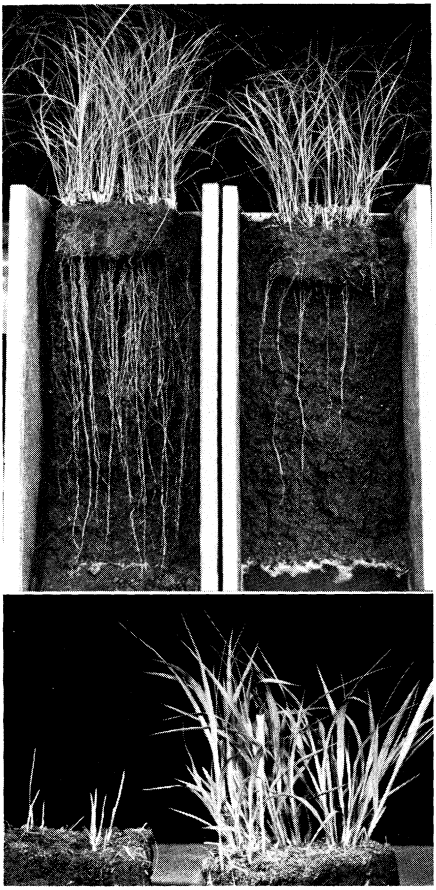


FIG. 51. Transplanted blocks of tall dropseed. One side of each box has been removed and two-thirds of the root systems exposed by washing away the soil. Plant on right has been clipped several times at a height of 2 inches. (Below) Development of big bluestem on May 22; (left) where a thick natural mulch had been left intact, and (right) where the mulch had been removed early in spring. (Courtesy of Botanical Gazette and University of Chicago Press).

Dry weight of tops of weakened plants was 32 to 84 per cent less than that of plants which had good to fair vigor. New roots were always shorter and less branched, and dry weight was 28 to 94 per cent less than that of the controls (Figs. 51, 52).

Leaves of non-vigorous new tops of 6 species averaged 15 to 41 per cent narrower, and average diameter of new roots was 13 to 39 per cent less. Moreover, it was ascertained by banding new roots of vigorous plants that death of roots accompanied frequent removal of tops, as in close grazing.

This test of vigor requires only 4 to 6 weeks. The new roots can be washed free of soil in 30 minutes. These data are from Weaver and Darland (1947).

FIG. 52. Plants of little bluestem grown from sods of similar size taken from an excellent, a good, and a poor pasture. This is the new growth after six weeks. Weight of tops was 30.22, 12.89, and 1.87 gm., although there do not appear to be such great differences. Weight of roots was 4.70, 1.72, and 0.33 grams. Roots were progressively more slender with decrease in vigor.

EFFECTS OF ACCUMULATION OF COVER

Since the time of settlement, the yearly production in prairie has been removed by domesticated animals or mowed and used as hay in winter. Thus, the prairie has been kept free from accumulation of much debris. But where it is completely protected from grazing, mowing, and fire for a number of years, an enormous amount of debris accumulates and the vegetation undergoes much change. Sampson (1921), working in the prairies of Illinois states: "Occasionally local areas may be found that are seldom disturbed by man. It is in these least disturbed tracts where the dead grass remains from year to year that the dominant plants retain their purest stand. The secondary species become insignificant, being represented only as scattered individuals here and there. . . ."

Dyksterhuis and Schmutz (1947) compared the accumulated organic mulch and current yield in climax true prairie, "unmowed and ungrazed for decades," with similar prairie which had been mowed annually. The amount of mulch was more than 4.5 tons and slightly less than 1 ton per acre, respectively. The detrimental effect of the mulch was clearly revealed in yield of hay, which was, in the same sequence, 621 and 1,033 pounds per acre. Thus, a decrease in forage production was associated with the heavier mulch.

Weaver and Rowland (1952) studied a prairie in eastern Nebraska which had been undisturbed by mowing, grazing, or burning for 15 years.[4] "About 80 per cent was covered with nearly a pure stand of big bluestem. Similar stands of switchgrass and prairie dropseed each occupied about 9 per cent. A dense natural mulch, 4.5 to 8 inches deep and weighing 6-9 tons per acre, covered the deep loam soil. . . . It increased the organic matter of the surface soil 1.5-2 per cent and nitrogen content 0.1 per cent of its oven-dry weight. Roots and rhizomes grew thickly below the mulch and mellowed the surface soil. . . . Soil temperatures, 22°-28° F. lower under the mulch in May, delayed growth about 3 weeks compared with plots where the mulch had been removed [Fig. 51]. . . . Yields in June, July, and August [each from separate plots] were 53, 26, and 29 per cent less from mulched stands of *Andropogon,* and 57, 55, and 26 per cent less in *Panicum* than those from unmulched stands. Consequences of the effects of the mulch upon the environment were the production of a nearly pure, but somewhat thinner than normal, stand of *Andropogon*. The understory characteristic of upland prairie had all but disappeared. The usual mid grasses of upland were few or none. Only a few of the taller forbs remained. . . . Between the large bunches of prairie dropseed the deeply mulched soil was usually free of vegetation."

[4] Quotation from Botanical Gazette 114:18, 19, by courtesy of University of Chicago Press.

CHAPTER 9

Some Plant-Soil Relationships

THE FORMATION of soil involves first of all the accumulation of mineral soil material. But as pointed out by the writer (1944) "the constructional processes of soil development are due largely to the incorporation of plant parts and microorganisms among the mineral particles. Upon the fall of leaves and stems the organic matter of the plant, which has resulted from synthetic activity, is incorporated into the soil. These residues of grassland vegetation have returned more to the soil than the green plants have absorbed from it. Throughout their lives plants have synthesized many organic substances—sugars, starches, celluloses, fats, and proteins. Most of these materials return to the soil when the plant dies. This added organic matter produced by vegetation introduces a fundamental change. The substrate is no longer the former one of mineral matter alone, but now contains stored energy in the form of organic material, and a microflora of bacteria, fungi, and other organisms."

Thorp (1948) points out: "As soon as the vegetation is established, many kinds of animals take up their abode in the soil to take advantage of the food provided by plants or to prey on one another. Insects (especially ants), millipedes, earthworms, gophers, prairie dogs, and many other animals live interdependent lives in the soil. Their burrowing operations stir the soil, mix it with fresh minerals, kill some roots, and hasten the process of humification. The soil becomes a community of teeming activity." Thus, there are many relationships, both important and complex, between Prairie Soils and Chernozem and the cover of grasses and forbs which they support (Thorp, 1949). Some of these plant-soil relationships will be described.

QUANTITY OF LIVING PLANT MATERIALS IN PRAIRIE SOILS

The grassland sod is a great conserver of rainfall; the amount of runoff water is relatively small, and the soil is firmly held against the forces of erosion. In fact, the menace of soil erosion did not appear in the midwest until much of the prairie was broken for cropping or weakened by continuous grazing.

A quantitative study was made of the amounts of living plant materials in prairies and pastures of eastern Nebraska. The grasses were cut at the soil surface and discarded. Then samples of soil a meter long and one-half meter wide were taken to depths of 0 to 4 and 4 to 12 inches, respectively. The underground plant materials were obtained by washing away the soil. The plant materials thus obtained were not all living. Undoubtedly some rhizomes were dead and perhaps not a few roots. It was not expedient to separate the dead from the living plant parts; in fact as long as they were undecomposed and not lost by washing, the part they played in holding the soil against erosion was similar to that of living materials. Six representative samples were secured from each kind of vegetation (Weaver and Harmon, 1935).

Big bluestem type is the most important of lowland prairie. Here *Andropogon gerardi* alone constituted about 78 per cent of the vegetation. Big bluestem prairie yielded the greatest dry weight of underground plant parts—4.1 tons per acre in the first 4 inches and 1.3 tons in the 4 to 12 inch depth. The coarse root-rhizome system formed a continuous framework throughout the soil (Fig. 48).

Little bluestem type is the most extensive one of upland prairie. Here little bluestem exceeded in abundance all other upland species combined. This grass ranked second in yield of underground materials. This was 3.3 tons per acre in the surface 4 inches of soil and 1.1 tons in the 4- to 12-inch level. The entire soil mass was threaded by roots which firmly anchored it in place.

Needlegrass dominates a second, drier type of upland of smaller extent. Bunches of this grass are rather widely spaced, so that the basal area is only 11 per cent. Underground materials were less in the drier soil, but well distributed throughout. They averaged 1.87 and 0.89 tons per acre, respectively, in the 0 to 4 and the 4- to 12-inch samples. It has been ascertained that the total length of all the main roots and their branches in a representative 0.5 square-meter sample 4 inches deep was over 11 miles (Pavlychenko, 1942).

From these data it may be seen that the amount of plant material per acre in the surface 4 inches alone far exceeds the tonnage of hay produced.

In little bluestem and needlegrass prairies the annual yield of hay usually ranges between 0.75 and 1.5 tons per acre, depending upon the conditions for growth; in big bluestem of lowlands it usually varies from 1.5 to more than 2 tons per acre.

QUANTITY OF ROOTS, ORGANIC MATTER AND NITROGEN IN RELATION TO CLIMATE

The enormous importance of vegetation in soil formation has been recognized only recently. Its fundamental significance is now understood both by the pedologist and plant ecologist. In fact, the role of vegetation in soil genesis is of such far-reaching effect that it is generally conceded that without vegetation there could be no soil. With increasing emphasis on soil conservation, a natural sequence has been a study of the amount of underground plant parts in various grassland types, and particularly in the portion of the soil—the surface 4 inches—which is most subject to erosion. The purpose of this study was to determine the correlation, if any, between amounts of underground plant materials and an increase in aridity (Shively and Weaver, 1939).

The portion of true prairie studied extends from Guthrie Center, Anita, and Creston, Iowa, approximately 75 miles east of the Missouri River, to Nelson, Nebraska, and Montrose, Kansas, about 200 miles southwestward. Mean annual precipitation varied from 33 inches at the eastern stations to only 26 at those near the western border of true prairie. Moreover, wind movement and evaporation are increasingly greater from east to west, and water-content of soil gradually decreases.

A central group of stations—the Lincoln area—with precipitation of 28 to 30.8 inches and with other factors of growth, except during severe drought, those of moderately mesophytic grassland, was selected in eastern Nebraska. They are on the western edge of prairie soils. This border is clearly delimited by the "lime line" which separates Prairie soils from the Chernozems. Prairie soils are dark in color, rich in humus, very deep, and of high fertility.

The southwestern group of stations in Kansas and southern Nebraska—the Nelson area—with mean precipitation of only 25 to 27.3 inches, is located entirely on the Chernozem soils, a zonal group occupying the most humid part of the drier regions having soils with a calcium carbonate horizon. These black soils are, owing to the luxuriant growth of grasses, high in content of organic matter and even more fertile than the prairie soils, but productivity is less because of the decreased precipitation. This area is distinctly more xerophytic than either of the preceding.

Underground samples were also taken from an area in the mixed prairie. This area which included Phillipsburg and Hays, Kansas, and Holdrege and Oxford, Nebraska, is located in the extreme western portion of the Chernozem soils. Here the precipitation is approximately 23 inches, a decrease of 10 inches from that at the most mesophytic stations. Other conditions for plant development are also decidedly less favorable.

In each area samples were taken at 3 to 6 stations which were often 20 to 40 miles apart. All samples, which were 0.5 square meter in area and 4 inches deep, were taken in silt loam soil. As in previous work, underground plant materials were secured by washing away the soil.

Samples of little bluestem were obtained where this grass alone formed 88 to 98 per cent of the vegetation. The large size of the sample contributed to uniformity in yield. A series of 22 samples of underground plant parts from the Anita, Lincoln, and Nelson areas yielded 3.15, 2.60, and 2.34 tons per acre, respectively.

Samples of big bluestem were secured from 18 prairies. This tall grass often formed nearly pure stands, and always composed at least 95 per cent of the sample. Underground parts decreased from 4.54 tons per acre in the Anita area to 3.54 in the one near Lincoln and then to 3.17 tons in the area westward.

Correlation between the average dry weight and the mean annual precipitation at each station was found to be very significant. The coefficient of correlation of the little bluestem series was .642 and of the big bluestem series .673. In a similar lot of mixed bluestems it was .827.

Upland grasses, unlike those of certain lowland species, depend entirely upon precipitation for their water supply. Hence, a comparison of the yields of all samples from upland in the several areas with the percipitation in those areas is of especial interest. This includes 67 samples of little bluestem, mixed little and big bluestems, blue grama, buffalo grass, prairie dropseed, and mixed grasses. Both volumes (determined by displacement of water) and weights showed a consistent decrease with decreasing precipitation westward. Weight in tons per acre was 3.35, 2.69, 2.43, and 2.19, respectively.

Area	Average Precipitation inches	No. Samples	Volume		Dry weight	
			cc.	%	gm.	%
Anita	32.2	17	1,221	100	375	100
Lincoln	29.1	23	1,027	84	301	80
Nelson	26.2	14	963	79	272	73
Phillipsburg	23.3	13	892	73	241	64

Coefficients of correlation between volume and weight in the sequence of station groups are .812, .695, .847, and .958, respectively. Differences between station groups were again very significant.

The tops and roots of prairie plants produce the large amount of organic matter found in the soil. The virgin grassland soils are rich in both organic matter and nitrogen. Unlike forest soils, where most of this material is found in the upper portion, in grassland soils this enriching material is distributed from the surface to a depth of several feet. The virgin dark-colored Prairie and Chernozem soils are the most fertile soils known.

Soil samples for the determination of organic matter were secured to a depth of 4 inches after cutting the vegetation at the soil surface and removing it and all organic mulch. Each sample consisted of a mixture of 10 individual cylindrical soil cores about 2 inches in diameter. The cores were taken at random in a circular area with a radius of 3 feet. Samples were taken at four widely separated stations in each area, all in soils with a silt-loam texture. Average percentage of organic matter decreased from east to west from 7.14 (Anita area) to 6.08 (Lincoln area), 5.41 (Nelson area), and 4.42 (Phillipsburg area). At no station in any group was the percentage of organic matter as high as that in any group occurring east of it. Statistical treatment of the data showed that the mean for each area was significantly different from the mean of any other area. Per cent of nitrogen decreased from .308 to .271, .248, and .198.

Comparison with preceding data shows a striking correlation between decrease in weight of underground plant parts and organic matter. That the more arid soil contains less organic matter is due partly to the smaller amount of vegetation from which it is formed and partly to the fact that it is rapidly oxidized. Both phenomena are a result of the more arid climate westward. The factor of differences of temperature at the several stations probably had little effect on organic matter, since average mean annual temperatures in the several areas varied only from 48.6° to 52.9° F. This is an important consideration, since Jenny (1930) found, as summarized by Thorp (1948), "within regions of equivalent effective moisture, the nitrogen and organic matter content of soils of medium texture increases 2 to 3 times with every 18° F. fall in average annual temperature, from south to north in the United States."

RATE OF GROWTH OF GRASSES AND FORBS

The early root development of grasses and forbs has a very direct relation to their establishment in a prairie climate. Drought, at least near the soil surface, is nearly always imminent in prairie. The necessity for the

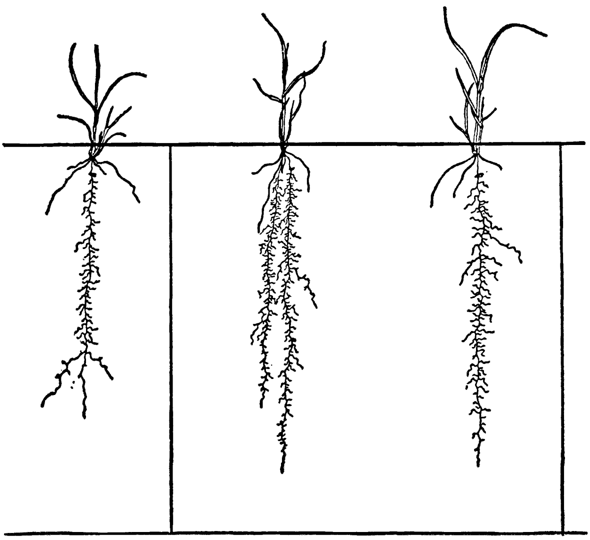


FIG. 53. Seedlings of blue grama, hairy grama, and tall dropseed 44 days old; scale, 1 foot. Note development of tillers and a secondary root system.

seedling to make immediate and extensive contact with the deeper, moister soil is apparent. The success or failure of the seedling depends largely upon its ability to develop rapidly an extensive and efficient absorbing system. Moreover, the functions of the root play such an important part in competition in nature's overcrowded prairie garden that careful consideration has been given to root development of the dominant grasses and certain forbs.

The development of seedlings of blue grama, hairy grama, and tall dropseed 44 days after the seed was planted, on April 20, is shown in figure 53. The plants were 3 to 4 inches tall, in the fifth-leaf stage, and most of them were beginning to tiller. The position of the seed—nearly all prairie grasses must be planted shallowly to insure vigorous seedlings—and the pronounced branching of the primary root are evident. Depths of 7 to 11 inches had been attained in the plot at this early age. Tillering occurred simultaneously with the growth of the unbranched secondary roots. The period of tillering, before the new roots have become well established in the moist soil below the surface, is a critical one for the plant. Drought at this time often causes a high mortality. Conversely, if only a little soil is washed away by dashing rains, it may leave the seedlings lying on the ground, connected to the soil by a single thread-like root.

After 3 months for growth the foliage of blue grama was 8 inches tall, and flower stalks twice this height bore flowers almost in bloom. Some roots extended into the second and third foot of soil. The root system of buffalo grass made a similar development. In fact the ability of seedlings to strike roots deeply, before much transpiring surface above ground is exposed, is marked. Under competition with other grasses such rapid growth, of course, does not occur.

Little bluestem, under optimum conditions for growth, extended a primary root 2 to 2.5 inches downward before the shoot appeared above ground. The root was much branched by the end of 3 days, and, after two weeks, a depth of 6 inches and a lateral spread of 2 to 3 inches were attained. The shoot was scarcely an inch high. Seedling forbs often showed a similar vigorous growth. False boneset 14 days after its appearance above ground was an inch tall, but the much branched taproot was 8 inches deep.

Seedling grasses develop rapidly when conditions are favorable to growth. Development of the following has been studied in root-free experimental gardens and in bared areas in prairie: big bluestem, Indian grass, sloughgrass, switchgrass, Canada wild-rye, side-oats grama, little bluestem, and needlegrass. After three to four months, seedlings of each species had reached heights varying from a minimum of 6 to 12 inches to a maximum of 13 to 30. The seedlings tillered promptly, some in 4 to 5 weeks after seed germination. By midsummer nearly all seedlings had produced 3 tillers and the sod-formers had 1 to 5 rhizomes each. Side-oats grama was especially prolific; by July 30 each dominant seedling had developed 7 to 8 tillers, 1 to 2 short rhizomes, and about 15 main roots. This

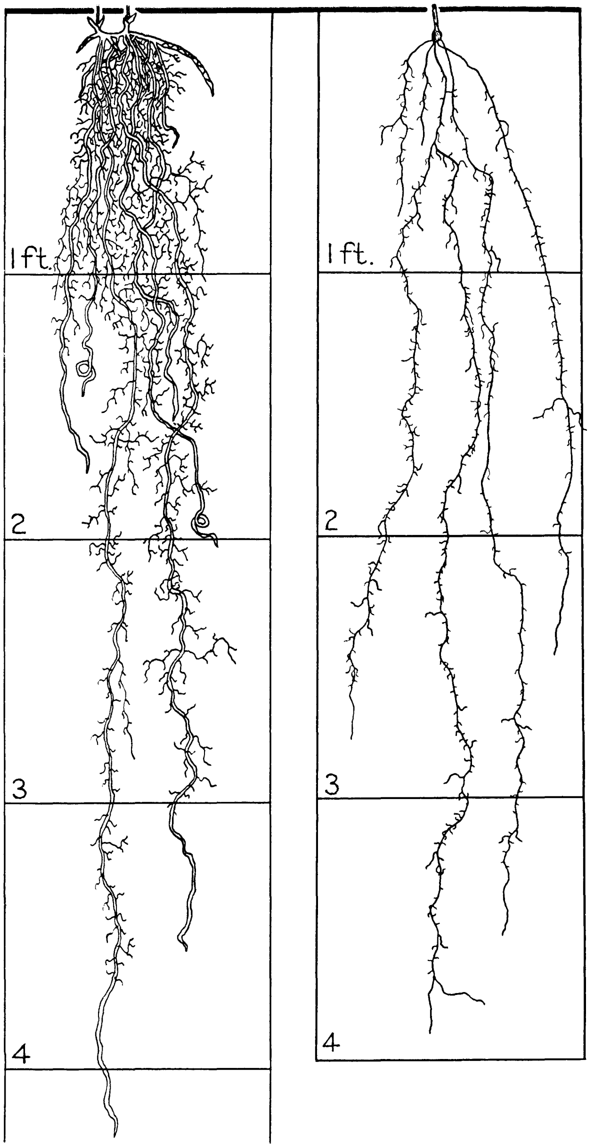


FIG. 54. Roots and rhizomes of prairie cordgrass, and corm and roots of large button snakeroot near the end of the first summer of growth.

species and big bluestem also produced an occasional flower stalk, a process which ordinarily requires at least two years in most grasses in prairie. The root systems penetrated from 12 to 18 inches deep in little bluestem and 18 to 48 in side-oats grama and sloughgrass. Other grasses were intermediate. In sloughgrass the primary root lengthened at an average rate of nearly 0.5 inch per day. In several species roots often spread 6 to 12 inches laterally at various depths (Fig. 54).

Development of shoots from the perennial sod is rapid. Sloughgrass, which grows more rapidly than other prairie grasses, reaches a foliage height of 2 to 3 feet by June 1 and often 5 to 7 feet or more by midsummer. The following are average heights of mature plants in mid-July when full foliage has been attained: big bluestem and Indian grass 2.5 to 3 feet, switchgrass 3 to 6 feet or more, Canada wild-rye 2.5 to 3.5 feet; and side-oats grama about 2 to 2.5 feet. The upland little bluestem is only 10 to 20 inches high and needlegrass from 14 to 36 inches. All add somewhat to their stature upon the development of flower stalks. Variations in height result from differences in amount of water, light, and nutrients. The preceding measurements are averages for the western prairies.

Forbs show rates of growth not unlike those of grasses. Dotted button snakeroot (*Liatris punctata*), although only 3 inches tall and with two leaves at the end of its first season's growth, developed a root system all out of proportion to the top. It was over 3 feet in depth. A considerable supply of reserve food had been stored in the enlarged portion of the taproot, which was 5 mm. thick. Mature plants may reach a depth of 15 feet and the life span is believed to exceed 30 years. *Liatris scariosa* develops with equal rapidity, and reserve food is accumulated in a corm (Fig. 54).

The taproot of *Gaura biennis* during its first season of growth may reach a depth of 4 feet and develop many widely spreading laterals. False boneset, *Kuhnia eupatorioides,* produced a taproot 2 to 3 feet deep by the first midsummer, when the shoot was 12 inches tall. Seedlings of white prairie clover (*Petalostemum candidum*) reached a height of 8 inches by midsummer, and the taproots were 15 to 22 inches deep. Similar development of the seedlings of prairie coneflower (*Echinacea pallida*) was ascertained (Blake, 1935).

ANNUAL INCREASE IN UNDERGROUND MATERIAL

How much root material is produced annually by various perennial grasses, how many growing seasons are necessary for maximum production, and what is the rate of decay after the land is broken by the plow, are fundamental questions to which a review of the literature of prairie grasses gives almost no answer. In such experiments it is obvious that the plant must be grown in soil initially free of roots and provision must be made to keep out roots from other than the experimental plants. The following data are from "Ecology" 27 (Weaver and Zink, 1946).

Separate lots of a tall grass (big bluestem), a mid grass (little bluestem), and a short grass (blue grama) were grown in large steel drums about 3 feet deep and 58 gallons capacity. Nine drums, with perforated bottoms, were placed in a trench, and soil was packed around them. They were then filled with good quality, screened, silt-loam prairie soil which had been brought to an optimum water content for good growth and thoroughly

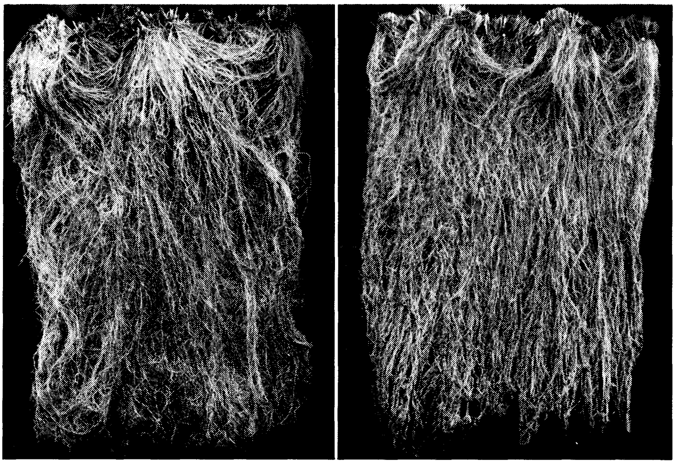


FIG. 55. Roots of big bluestem (left) and little bluestem (right) at the end of the first season of growth. Length is about 32 inches and dry weight 152 and 89 grams, respectively.

mixed. Seeding was done late in April and the seedlings were later thinned to 50 in each container with bluestems but to 100 in each with blue grama. The plants were watered from time to time, and growth each summer was vigorous and continuous. As regards height, flowering, and root extent, the first season's growth was similar to that of plants of each species grown in fertile field soil at Lincoln, Nebraska (Clements and Weaver 1924). At the end of each growing season the roots of one lot of each species were washed free of soil and photographed, and the air-dry weights obtained (Fig. 55).

Roots of big bluestem produced 152 grams of dry weight the first year, but this increased 72 per cent the second summer and 23 per cent the third. Roots of little bluestem yielded 89 grams the first summer; the amount increased 86 per cent the second summer, after which the root weight did not increase. Blue grama produced 76 grams of roots the first year, but this increased 56 per cent the second summer when it reached its maximum development. Big bluestem reached approximately its maximum development the third summer, a year after both little bluestem and blue grama attained maximum root development.

The underground materials produced during the experiment were very similar in amounts to those ascertained earlier in typical mature stands in native prairie. They were also very nearly the same in the surface 4 inches and especially in the surface 12 inches as the average amounts ascertained by extensive sampling in climax prairie dominated by each species (Weaver and Harmon 1935).

Underground parts alone yielded approximately 5.5 tons per acre after 3 years in big bluestem, 2.7 tons in little bluestem, and 1.6 tons in blue grama. Of these amounts 43, 36, and 49 per cent, respectively, occurred in the surface 4 inches, and 78, 69, and 80 per cent in the first 12 inches. The preceding data are from Weaver and Zink (1946).

LONGEVITY OF ROOTS OF GRASSES

Grasses possess two distinct root systems. The primary or seminal root system begins development immediately upon the germination of the seed and consists of one to several main roots and their branches, the number varying with the species. The young plant is entirely dependent upon this primary root system for water and soil nutrients. Later, especially during the period of tiller production, a secondary or nodal root system develops from the lower nodes of the parent culm or from the tillers. The seminal roots are often erroneously designated as temporary.

Fourteen species of native and introduced perennial grasses were studied at four stages of growth. Several plants of each grass were grown in boxes 2 to 4 feet deep with one side removable for root examination. A tiny band of pliable aluminum was placed around each seminal root before the nodal roots had appeared, to insure its identification throughout the summer. Seminal roots were 6 to 10 inches deep three weeks after planting. There were 1 to 4 nodal roots but rarely a tiller. Twenty days later, when the plants were 8 to 10 inches tall and well tillered, seminal root depth was

7.5 to 27 inches, and nodal roots were often equally deep. Although the banded roots were mostly 0.3 mm. or less in diameter, nearly all were profusely branched. After 3 to 4 months, when the grasses were 9 to 19 inches tall and those of two species had blossomed, the seminal roots, despite 6 to 60 nodal roots, extended deeply and frequently to 24 inches depth. The thread-like seminal roots were still alive in all 14 species. Plants of three species from which all nodal roots were continuously excised, tillered freely and remained alive 4 months. One plant with a single, hair-like seminal root, developed 20 square inches of leaf surface in 60 days (Weaver and Zink, 1945).

It is well known that death of tops of practically all prairie grasses occurs each autumn in temperate grasslands where the soil is regularly frozen. Year after year new shoots replace the old ones in this vegetation of long-lived perennials. But as to what portion of the root system of prairie grass is retained and over what period of time, we are almost without information.

To ascertain the length of life, seeds of 8 species of perennial prairie grasses were planted in triplicate lots in loam soil in containers large enough for ample root development (Weaver and Zink, 1946a). They were 24 inches tall and 18 inches in diameter. A removable extension at the top of each container added 4 inches to this height. Each container was filled with a fertile loam soil with adequate provision for good drainage. The extension contained a sandy loam soil easily washed away when the extension was removed, thus exposing the roots for examination. In order to ascertain with certainty the longevity of the roots, small bands of very thin, pliable sheet tin 2 to 3 mm. wide were placed around individual roots. These bands remained bright and unrusted even after 3 years in the soil. The plants were about 2 months old at the first banding. A second banding was made, involving new roots of the same plants that developed in the following 3 or 4 weeks (Fig. 56). A total of 3,424 roots of 181 plants were banded to obtain their longevity. The roots were kept moist while exposed and then covered with dry soil which was immediately moistened. Some were examined at the end of the first and second year, respectively, and the remainder at the end of each of three growing seasons.

Survival on switchgrass and western wheatgrass, after the second summer, was 100 and 42 per cent respectively. After three growing seasons, 81 per cent of the roots of big bluestem survived, but none on nodding

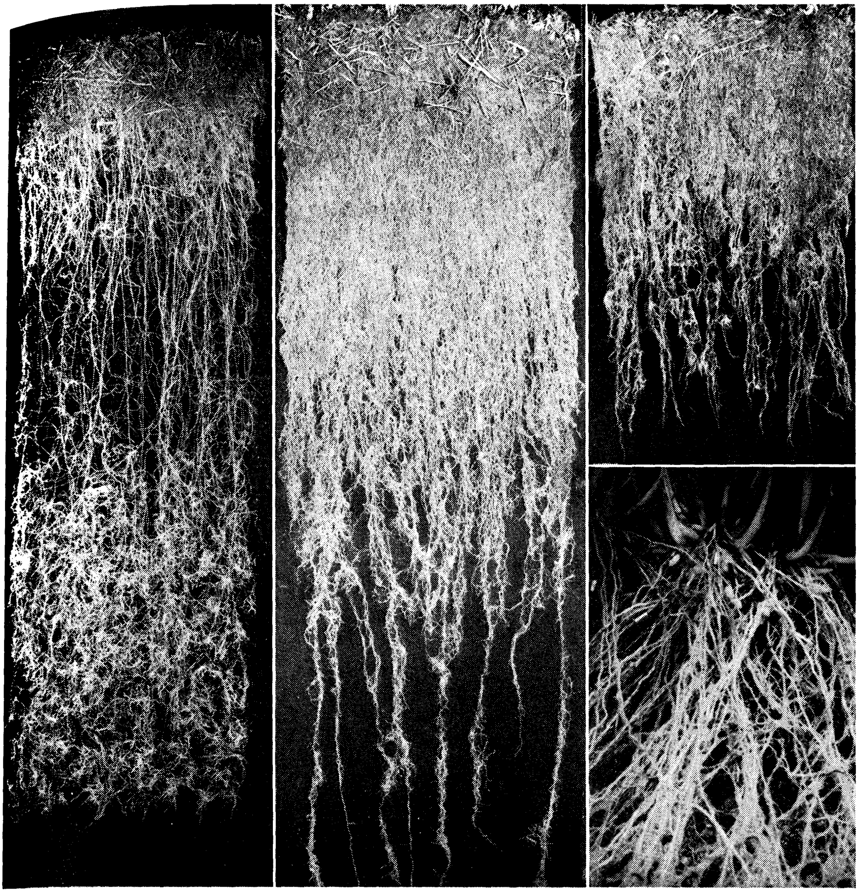


FIG. 56. (Left) Roots of western wheatgrass from a 3-foot monolith of clay pan soil near Carleton, Nebraska. (Center) Roots of Kentucky bluegrass from a 3-foot monolith of a deep, moist, well drained silt-loam. (Right) Roots of Kentucky bluegrass only 22 inches deep from a poor silty clay-loam; each monolith was 12 inches wide. (Below) Switchgrass about 3 months old with roots exposed for banding. Three glistening tin bands may be seen at upper left.

wild-rye. Losses in all species were gradual. After three growing seasons, survival of roots of blue grama was 45 per cent, side-oats grama 14 per cent, and little bluestem and needlegrass 10 per cent each.

The average number of roots produced by individual plants varied from 175 to 882 at the end of the third summer. Compared with the total number of roots, losses among the banded roots were small to negligible. They often amounted to only 2 to 8 per cent of the total number of living roots.

Nearly all of the species studied have a long life and show great permanency of occupation, characteristics which aid greatly in adaptation of grass to semiarid and arid climates. They likewise are important characters of grasses well adapted to soil binding and prevention of erosion.

Such permanency of roots is possible only when the above-ground parts of grasses are vigorous. Established seedlings of smooth bromegrass (*Bromus inermis*) and crested wheatgrass (*Agropyron cristatum*) with banded roots were clipped at 2 inches height at 10-day intervals. There was no loss from unclipped control plants of the first species and only 3 per cent from the second. But roots of clipped bromegrass suffered a loss of 15 per cent and those of crested wheatgrass 73 per cent.

New roots from vigorous, transplanted blocks of sod of big bluestem and little bluestem were banded on May 17, and the tops of one lot of each were clipped at intervals of 10 to 14 days. After five clippings losses of roots were 45 and 64 per cent, respectively. The unclipped controls lost only 3 per cent each. Thus, when prairie grasses are mowed or grazed too early, too often, or too closely, they lose their vigor both above and below ground and may become so weakened that they die.

ROOT DISTRIBUTION THROUGHOUT SOIL HORIZONS

The monolith method furnishes a means of ascertaining the entire weight, and the percentage of weight, of each portion of the root system that occurs in each six inches or foot of soil. Roots were not separated from other plant parts in the surface soil principally because the rhizomes and bases of stems function as roots in the processes of modifying soil structure, adding organic matter to the soil, and preventing erosion. They are produced at about the same general rate as roots and are neither more nor less resistant to decay than are the absorbing organs. The following data are from "Ecological Monographs" (Weaver and Darland, 1949).

It is of interest, however, that the roots alone often constitute the minor part of underground materials in the surface 4 inches of soil. This was ascertained by separating the roots from other underground parts in 3 square feet of sod formed by each of three species. The roots of big bluestem composed 49.5 per cent of the weight of plant material, but those of little bluestem and blue grama only 28 per cent.

The rather usual distribution of six species of grasses expressed in percentages of the total weight of underground parts are given.

Depth ft.	Big bluestem	Little bluestem	Side-oats grama	Blue grama	Western wheatgrass
0 –0.5	68.5	85.8	85.0	87.7	50.9
0.5–1	13.9	5.3	7.8	6.7	14.1
1 –2	10.5	5.0	5.8	3.9	13.5
2 –3	4.4	2.3	1.4	1.3	12.1
3 –4	1.7	1.4	—	.4	9.4
4 –5	1.0	.2	—	—	—
Total Wt. Gm.	49.3	52.0	39.0	35.7	19.3

Little bluestem was taken from a silty clay-loam, wheatgrass from a more compact silty clay-loam, but the remainder from silt-loam. A gradual decrease in the percentage of weight of roots below the 6-inch level with increase in soil depth is apparent. These are all root weights, since the stem bases and rhizomes occurred above this level. Without exception the actual root weight decreased from the second 6-inch level, foot by foot, to maximum root depth.

It should be noted that the percentage of root weight of big bluestem in the surface 6 inches was less than that of the mid grasses, except western wheatgrass. This lower weight is common for big bluestem and also for switchgrass, which is also a tall grass of lowland. Prairie dropseed, needlegrass, and certain other upland mid grasses also exhibit, like little bluestem, a high percentage of weight in the surface 6 inches. Western wheatgrass, examined in six different soil types, had only 50 to 64 per cent of its underground weight in the surface 0 to 6 inches, but 9 to 17 per cent in the 6 to 12 inches of soil.

It is worthy of note that an oven dry weight of more than 300 pounds per acre of grass roots alone has been found in the fourth foot of bluestem prairie. In addition large amounts of roots of legumes, with abundant nodules, as well as roots of numerous other prairie forbs, were also present.

Percentage of roots of big bluestem in the A horizon of several soil types varied almost directly with its depth, from 78 in a 7-inch horizon to 90 in one 20 inches deep. A similar relationship was found in both little bluestem and side-oats grama. In bluegrass the percentages were 82, 92, and 97, in A horizons 7, 13, and 20 inches deep, respectively. The preceding general relationships were found among all of the other prairie grasses examined.

Each soil horizon presents a somewhat different environment for root development. There may be differences in water content, variations in size of pores and total pore space which greatly affect aeration, and differences in the amounts of available nutrients (Weaver and Clements, 1938; Kramer, 1949; Shaw, 1952).

A root system of western wheatgrass was taken from Butler silt-loam near Carleton, Nebraska, 65 miles southwest of Lincoln. There was a good stand of this grass about 3 feet tall. The A horizon was only 7.5 inches deep. Soil in the B horizon (7.5 to 28 in.) was so compact, especially to 20.5 inches, that it was removed with difficulty by means of a pick. Root penetration in this layer, except in cracks, was poor and probably occurred only when the soil was moist. At 28 inches depth, the less compact, lime-flecked parent material of the C horizon was encountered. Here, as in the lower portion of the B horizon, branching of roots was pronounced (Fig. 56). This heavy branching began near the bottom third of the B horizon at 20.5 inches in depth. The air-dry weight of the roots at 20.5 to 33.5 inches depth was 36.5 per cent greater than that in the 13 inches of soil above the 20.5 inch level.[1]

Associated with the reduced branching (8 to 20 inches) was a greatly reduced phosphorus supply and restricted pore space. Increased branching of roots in the lower B horizon (20 to 28 inches) was associated with an increased pore space and with a soluble phosphorus content of nearly 2.5 times that present in the region of restricted development.

Figure 56 shows a root system of Kentucky bluegrass from a deep, rich, Judson silt-loam. Here also is presented another root system also of this bluegrass but taken from a highly weathered, compact, glacial drift, Carrington silty clay-loam. The topsoils (A horizons) are 20 and 7 inches deep, respectively; maximum root depth was 40 and 22 inches in the same order. Weights of the root systems were 27.7 and 8.9 grams, respectively.

Total pore space and clay content of the two soils were not greatly different, at least below 4 inches depth. The Judson soil was well supplied with mineral nutrients at all depths. Total nitrogen content was high. Phosphorus and exchangeable potassium were sufficient throughout the profile to promote excellent root development at all depths. In the Carrington soil only the levels of calcium and magnesium appeared to be

[1] These data and the photos of root systems were published in "Ecological Monographs" (Weaver and Darland, 1949).

optimum for root growth. Phosphorus content was extremely low; at the depth of maximum root penetration, the level of phosphorus was only one-tenth that from the same depth in the Judson soil. Exchangeable potassium was also very low, and only the levels of calcium and magnesium appeared to be optimum for root growth.[2]

RATE OF DECOMPOSITION OF UNDERGROUND PLANT PARTS

Grass is an excellent preventive of soil depletion and, in temperate climates, the best means of soil improvement. It is also man's most useful weapon against soil erosion. The rate of decomposition of plant materials when incorporated with soil has been the subject of numerous investigations. These have dealt almost entirely with the aerial portions of plants and furnish little or no information pertaining to the decomposition of roots. Where the roots have been studied, portions of them have been removed from the soil, and almost invariably ground or at least cut into small pieces to which soil and nutrients were added. They were then kept undei optimum conditions of moisture, aeration, and temperature to promote rapid decomposition. Although such procedure yields valuable information for certain purposes, it does not reveal the rate of decay of the roots under the usual environment in the field.

A study was made which included observations and measurements on the rate of decay of the underground parts of twelve prairie and pasture grasses (Weaver, Ecology 28, 1947). A tall grass, a mid grass, and a short grass were selected for the most extended research. They were big bluestem, little bluestem, and blue grama, respectively. The rate of decomposition of rhizomes and roots was ascertained when the plants were killed and left undisturbed in the natural soil horizons. It was also studied when the underground parts were disturbed as in breaking the sod and left to decay in the furrow slice, and finally when samples of underground parts were placed in prairie soil out-of-doors and permitted to decay. This work was done at Lincoln, Nebraska.

Probably little reduction in the weight of the underground parts occurred the first year. The second year little bluestem and blue grama lost 53 and 54 per cent, respectively, of their dry weight compared with the amounts present in the samples examined at the end of the first year.

[2] These data are from the "Agronomy Journal" (Fox, Weaver and Lipps, 1953).

After 3 years the decreases in weight from the preceding year were 59 and 28 per cent. Total decreases in amounts of residues from the end of the first to the end of the third year were: big bluestem 83 per cent, little bluestem 81 per cent, and blue grama 67 per cent.

Relative resistance to decay varied with the species. Materials of Kentucky bluegrass, June grass, needlegrass, and switchgrass decayed most rapidly. Only small fragments, if any, were found after 3 years. The bluestems, Indian grass, and western wheatgrass decayed somewhat less rapidly. A few roots retained some tensile strength for 3 years. The most resistant to decay were blue grama, side-oats grama, and buffalo grass. Much undecayed material remained and some roots of each of the three grasses retained moderate tensile strength after 3 years. Complete decomposition of the roots, to a condition in which no particles could be distinguished by the naked eye from soil, required 3 to 5 years.

The growing of perennial grasses actually decreases the tendency of soil to erode even after the soil is again cultivated. For a time this may be due in part to the undecayed roots, and in part to the effects of the decaying roots upon promoting soil aggregation or retaining the soil aggregates already formed.

CHAPTER 10

Settlement and Studies in Eastern Prairies

IN VIRGIN prairie big bluestem formed a dense sod, and under conditions favorable for its best development it reached a height of 10 to 12 feet. Early settlers repeatedly state that cattle grazing on such prairies could be located by one on horseback only by standing up in the saddle, or by climbing some elevation and observing the waving of the grass as the cattle moved about in grazing.

EARLY DESCRIPTIONS OF PRAIRIE

A botanical report by Short (1845) of a trip across the prairies of Illinois is an outstanding early contribution. He pointed out that Illinois is naturally divided into three regions. "First—The heavily timbered tracts which for the most part occupy the southern portion of the State, bordering on the Ohio river, and which, extending into the middle and northern portions, are found in detached bodies surrounded by prairies, and in these situations are called 'Groves.' These groves are, for the most part, contiguous to, and often bounded by watercourses, which have preserved them from the action of fire. Secondly—The open prairies, of from one to twenty miles in diameter, entirely destitute of trees, and indeed of all other woody plants, except along the margin of water courses which occasionally pervade them. Thirdly—'The Barrens,' or tracts somewhat intermediate between the two former, being sparsely covered with oak trees of several different kinds, and of considerable size, with a dense undergrowth of various shrubs and annual plants.

"Twenty miles west of the Wabash . . . we met with the first prairie in a state of nature; and from this, extending northward to the Lakes, and westward to the Mississippi, they continue, increasing in magnitude, and interrupted only by occasional groves of timber, so as to occupy by far the largest portion of the central, eastern, western, and northern portions of the State of Illinois.

"On fairly entering the prairie region, and reaching the centre of one of these immense natural meadows, the view presented to the eye of a novice in such scenery, is one of the most pleasing sort." After describing the flora and listing many species of grasses he remarked: "All these grasses in their young and tender states are eagerly devoured by cattle: as they become harder and less succulent by age, the coarser are rejected and the more tender are sought for. . . . All of them, however, are cut promiscuously for this purpose, and when they occur, as frequently they do, in large natural meadows, occupying the ground to the almost entire exclusion of other vegetables, they yield a productive return to the labor of the mower; and when well cured make excellent hay. Our horses, which had never before been accustomed to any other than the cultivated grasses, ate this natural hay with great avidity. The quality of these grasses, both for pasturage and mowing, is much improved by the burning of the prairies during the winter, which, destroying the dead and dry stems, affords a better and earlier bite in the spring, as well as a cleaner swath for the scythes; and by protecting certain portions of the prairie from the action of fire until the spring or early summer, vegetation is then so much retarded by a 'late burn', as the settlers call it, as to afford good pasturage throughout the latter part of the season."

Atwater (1818) in his essay "On the prairies and barrens of the West", which was then western Ohio, states: "To the traveller, who for several days traverses these prairies and barrens, their appearance is quite uninviting, and even disagreeable. He may travel from morning until night, and make good speed, but on looking around him, he fancies himself at the very spot whence he started. No pleasant variety of hill and dale, no rapidly running brook delights the eye, and no sound of woodland music strikes the ear; but, in their stead, a dull uniformity of prospect 'spread out immense'."

Gerhard (1857) in his interesting book "Illinois as it is" states: "Immense prairies of grass, interlaced with groves and stretching, principally along the water courses, cover two-thirds of the entire state in the north.... Some extend in immense level plains, others are rolling, others again broken by hills. . . . On the lower, humid prairies, where the clayey stratum lies close to the surface, the middle or principal stalk of grass, bearing the seed, grows very thick, having long and coarse leaves, and attaining a height of 9 feet, so that the traveller on horseback will frequently find it higher than his head. . . . On the undulating prairies the grass is finer, and exhibits more leaves, its roots are interlaced so as to form a compact mass, and its leaves spread in a dense sod, which rarely exceeds the height of 18 inches, until late in the season, when the seed-stalk shoots up." Clearly he is describing the lowland and upland communities of grass as we know them westward today.

"Let it not be supposed, that life on these boundless regions is monotonous and dreary, for nowhere does nature sit more majestically enthroned, overawing man by the terrible grandeur of her phenomena, than on these immense prairies. What can be more beautiful and charming than a summer's day—what more sublime and terrific than a thunderstorm, on these plains? . . . And even when stern winter has thrown her snow-white mantle over the earth, and the silence of death seems to reign over the far-reaching waste, . . . then the prairie presents a truly magnificent aspect."

A description of Iowa prairie is given by Quick (1922). "We reached a point from which I could see the Iowa prairie sweeping away as far as the eye could see. . . . It was like a great green sea. The old growth had been burned the fall before, and the spring grass scarcely concealed the brown sod on the uplands; but all the swales were coated thick with an emerald growth . . . and in the deeper, wetter hollows grew cowslips, already showing their glossy, golden flowers. The hillsides were thick with the woolly [pasque flowers]. . . . On the warmer southern slopes a few of the splendid bird's-foot violets of the prairie were showing the azure color which would soon make some of the hillsides as blue as the sky; and standing higher than the peering grass rose the rough-leafed stalks of green which would soon show us the yellow puccoons and sweet-williams and scarlet lilies and shooting stars, and later the yellow rosin-weeds, Indian dye-flower and goldenrod."

In Plumbe's "Sketches" (1839), a description of Iowa prairies is given by Judge James Hall. "The scenery of the prairie is striking, and never fails to cause an exclamation of surprise. The extent of the prospect is exhilarating. The outline of the landscape is sloping and graceful. The verdure and the flowers are beautiful; the absence of shade, and consequent appearance of profusion of light, produce a gaiety which animates the beholder. . . . These plains, although preserving a general level in respect to the whole country, are yet in themselves not flat, but exhibit a gracefully waving surface, swelling and sinking with an easy slope, and full, rounded outline, equally avoiding the unmeaning horizontal surface, and the interruption of abrupt angular elevation. It is that surface which, in the expressive language of the country, is called rolling, and which has been said to resemble the long, heavy swell of the ocean, when its waves are subsiding to rest after the agitation of a storm. . . . The whole of the surface of these beautiful plains is clad throughout the season of verdure, with every imaginable variety of color, from grave to gay. It is impossible to conceive a more infinite diversity, or a richer profusion of hues or to detect the predominating tint, except the green, which forms the beautiful ground, and relieves the exquisite brilliancy of all the others."

SETTLEMENT OF PRAIRIE

"To the dweller of forests, the prairie pioneer, the landscape of the treeless grassland seemed extremely monotonous. There was an innate longing for the companionship of trees. His immediate ancestors were from the eastern deciduous forest, and theirs were from the forested continent of Europe. Forest groves were man's first temples and . . . trees have always been a part of man's aesthetic and social life" (Albertson and Weaver, 1945). The pioneers at first did not move from forest directly into prairie. They sought out grassland areas characterized by groves of trees or those near the forest or woodland along streams.

"Prairies and 'barrens' were encountered by the first settlers of the great [Mississippi] valley . . . but it was not until the white man crossed the Wabash river in his westward advance that he beheld the prairies in all their splendor, and all their monotonous magnitude. These prairies presented varying aspects. The early settler avoided them at first in part for the reason that he thought them not fertile because treeless, and in part because they did not furnish the much needed building materials, fuel and water; but as his experience increased, there were added to these reasons the menace of prairie fires and the terror of winter storms. Both of these dangers have practically disappeared with the settlement of the prairies and the development of shelter-belts, but neither will be forgotten by those who witnessed their mad fury" (Shimek, 1911).

Other reasons for avoiding the eastern prairies were the breaking of the tough sod which required two or three years to rot and become readily tillable. Much of the flat lands was low and swampy and poorly drained;

prairie trails were practically impassable in spring because of the mud. Moreover, the prairie did not provide a proper water supply until wells were dug. Many settlers suffered from fever and ague on these wet prairies. Little wonder many pioneers "looked out upon the prairies as vast wastes to be dreaded and avoided. . . . The forests and upland prairies were first changed. Then the fertile wet prairie was drained" (Adams, 1915).

When the early settlers came to Ohio they found in the west-central part of the state, areas of grassland scattered through a dozen or more counties. These big bluestem, Indian grass, and little bluestem prairies were the eastern outliers of the vast grasslands of Illinois and westward.

The prairies of northwestern Indiana (Benton County), an extension of the Grand Prairie of Illinois, were settled in 1830–31, but land hunters had seen them by horse in 1824. This ocean-like prairie region with the island-like groves of forest covering nearly level land, except for swells or ridges which separated the drainage systems, has been described by Welch (1929): "In 1870 there were a great many sloughs scattered through the county. The cultivated land was along the ridges and these were seepy and wet. About 1875 or 1876 the first ditches were plowed through the waste land and the swamps were eliminated. . . . The tile industry began about 1881 and during the next 20 years thousands of acres were prepared for cultivation."

"By 1840 the westward movement was confronted with the true prairies of what came to be known as the Middle West. Many of the smaller prairies of Ohio and Indiana adjacent to rivers and timber had already been occupied. . . . The oak openings and the small prairies of Michigan, Indiana, Wisconsin, Illinois and Missouri then were being settled. But the pioneers hesitated on the edge of the large prairies with their seemingly endless expanse of thick grass. There was a sense of vastness about them that seemed overpowering, an impression of a greatness that could not be subdued" (Edwards, 1948).

Illinois forms a part of the Great Central Plain of North America. The total relief from the lowest point, where the Ohio river enters the Mississippi in the southwest, to the highest point in the northwest is less than 1,000 feet. The distance is approximately 400 miles. The land is flat, and over most of it drainage was poor. The primitive, flat prairie land of Illinois was poorly drained to the extent that water stood in ponds and lakes for weeks or months in the spring and early summer (Turner, 1934). It was first settled in the southern wooded area and northward along the streams. Poggi (1934) states: "The discovery that the prairie was good crop land, about 1830, initiated a flood of immigration, and by 1840 less than 4 per cent of the province remained unsettled. . . . Environmental conditions determined the fact that the prairie province should be the last section of Illinois to be settled. Not until the railroad was built across the east-central part of the state did the settlers leave the river banks for the prairies, which they then discovered to be of great fertility." One great reason for being near watercourses was that they provided avenues for transportation.

"It was soon demonstrated that the cast-iron plows brought from the East would not scour when used to break the prairie sod. Large plows with wooden moldboards plated with iron strips would turn furrows, but it took as many as six yoke of oxen to pull them. . . . The development of the steel plow [by John Deere in 1837–40] provided a satisfactory means of turning over the sod (Fig. 56a). The building of railroads across the prairie region connected the farmers with better markets and brought them fuel and building material" (Edwards, 1948).

Permission of the Federal Government to settle in Iowa was first granted in 1833, but white settlers did not reach Palo Alto and Clay counties in the northwest until 1855–56. In Iowa, according to Shimek (1911), "A little more than seven-eighths of the surface was prairie, leaving less than one-eighth for the forest area, which, however, included the thickets bordering streams, and the scrub-oak thickets in various parts of the state, which should scarcely be dignified by being called forests." This is the only state that lies entirely in the region of the prairie. In the eastern two-thirds, deciduous forest followed the rivers and streams from the southeast. Only fringing forest occurred towards their upper limits, and in northern and western Iowa many of the streams were treeless through the prairie.

Woodland and edge-of-the-woods settlement usually preceded the general occupation of the prairie. As the settlers became more numerous along the timber, they began to crowd out onto the prairie. According to Hewes (1950), "nearness to woods continued to be a considerable advantage as late as 1900 when stream-side woodlots were still retained by many farmers on the prairies of Story county [in central Iowa]. First, the well-drained prairie and, later, the wet prairie were occupied." According to Parker

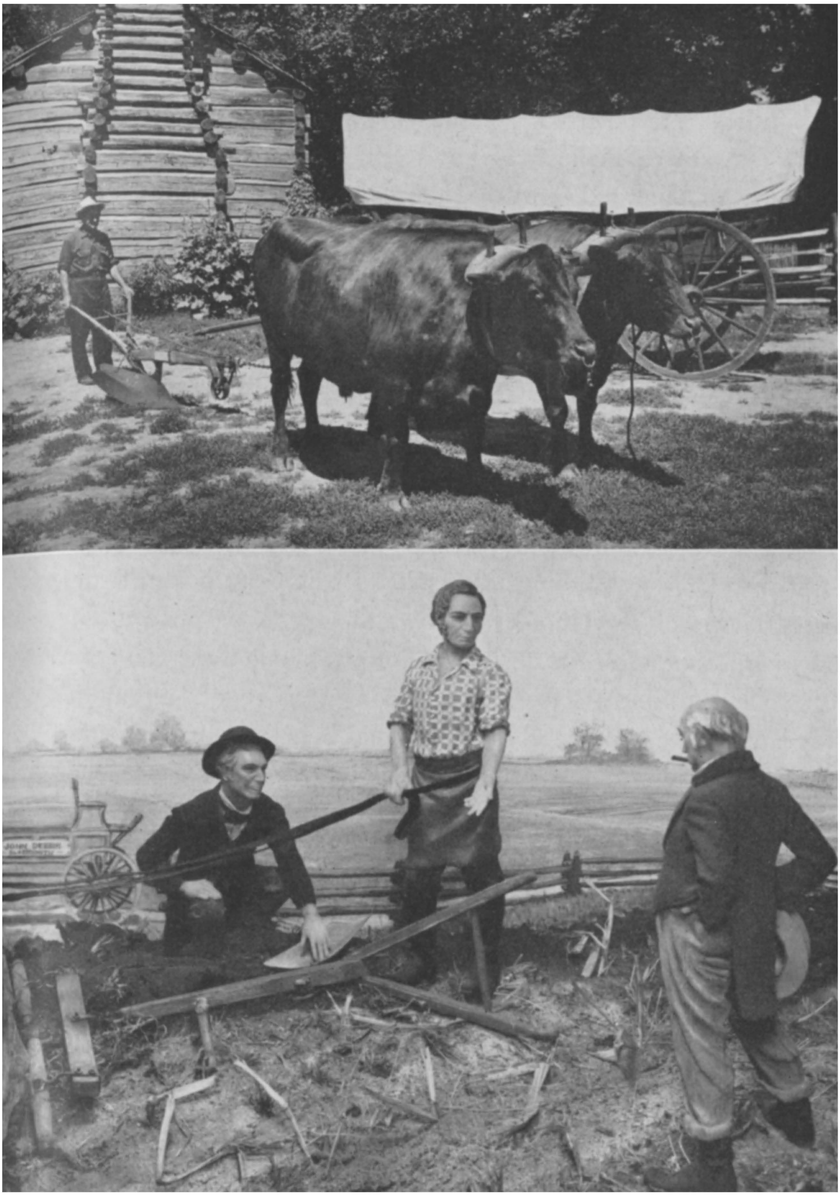


FIG. 56a. (Upper) Oxen hitched to an original prairie sod-breaking plow. Photo at Lincoln's New Salem, by Herbert Georg studio. (Lower) Photo of part of a museum diorama, showing John Deere demonstrating the pioneer sod-breaking plow. (Courtesy of the Illinois State Museum)

(1856) "For the sum of $2.50 per acre, the prairie is broken [by a paid sod-breaker], and often corn is planted the first year, by striking the axe into the turf and dropping the corn, which yields 15 to 25 bushels per acre. This is called sod-corn. The second year the turf is rotten, the ground easily tilled." He describes the breaking plow as 10 feet long, cutting a furrow 22 to 24 inches wide, and pulled by some five yoke of oxen. Breaking the tough sod constituted a problem previously unknown to the pioneers in the prairie.

STUDIES IN EASTERN PRAIRIES

The eastern portion of the great prairie region has received much less study than that of the western part. This fact has long been recognized by students of grassland (Fig. 57). As pointed out by Gleason (1909): "Unfortunately for the ecologist, the prairies of Illinois were converted into cornfields long before the development of ecology and phytogeography in America, thus forever prohibiting satisfactory investigation on some questions of most absorbing interest. . . . The older botanists neglected [the structure of vegetation] entirely, although it was open to direct observation." Sampson (1921) states: "Unfortunately these pioneer writers, accustomed to life in a forested region, were generally unfamiliar with the plants of the prairie and failed to leave us an adequate account of the natural prairie flora. Furthermore, the importance of a knowledge of the relationship of plants to the environment in which they live was not recognized until a later date. According to Transeau (1935) "In the Peninsula the dry prairie knolls (as well as the forested uplands) became the home and village sites and their obliteration was completed many years ago. The wet prairies remained for a longer time, but the digging of thousands of miles of drainage ditches, and the laying of hundreds of thousands of miles of tile have long since completely altered the soil water relations. On most of the prairie farms from Illinois to Ohio the present (1930–35) drought has led to the third general deepening of wells in order to secure an adequate water supply. . . . The present growth of trees on wet prairie soil cannot be used as evidence that trees could have lived there a hundred years ago. Then during a part of nearly every year it was under water, and during another part it was desiccated, with cracks and fissures extending three feet or more into the subsoil."

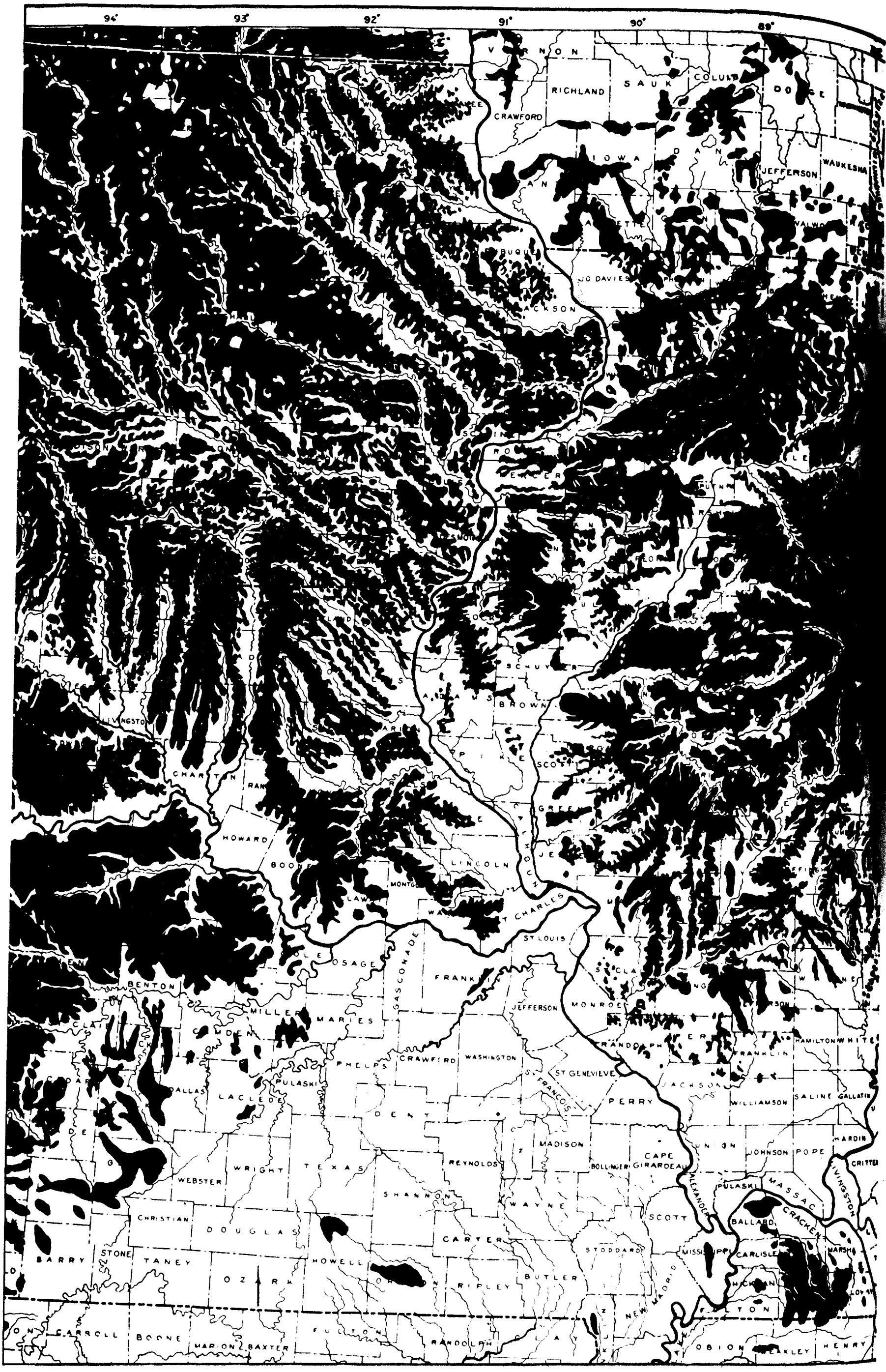
Studies in Ohio

By the use of nontechnical contemporary descriptions, Sears (1926) attempted to reconstruct the physiognomy of the original prairies of Ohio. "Apart from the bog meadows most of them were wet, displaying variously *Juncus, Scirpus, Typha, Phragmites, Spartina, Calamagrostis* and *Andropogon furcatus,* as well as numerous dicotyledonous herbs. Sometimes elm, ash, and willow were conspicuous invaders. In other cases there was a dryer herbaceous border dominated by *Andropogon scoparius* with various composites, etc. Between this and the oak-covered uplands was frequently a shrub zone of plum, hazel, and wild rose. Still higher were open groves of oak and hickory."

Jones (1944) in his analysis of the relative abundance of species within relic prairie areas in Ohio concluded that all of the major grassland types, except needlegrass and prairie dropseed, were well represented at the time of settlement. "Poorly drained sites within these areas, such as sloughs and swales were dominated by *Spartina Michauxiana,* and sand ridges and moraines were covered with *Andropogon scoparius*. The over-drained and over-exposed 'meadow and glade' areas within and at the edge of the plateau [of eastern Ohio] were dominated by *Andropogon scoparius* and *Sorghastrum nutans,* which frequently grew as bunch grass instead of forming closed associations as did the *Andropogon furcatus* on the flat areas in the central part of the state." He lists plants believed to be representative of the species characteristic of Ohio's prairies.

Shanks (1939), working in northwestern Ohio, states: "Prairie vegetation occupied about one-tenth of the area of Wood county. The tall bluestem (*Andropogon furcatus*) was the principal dominant, but the drier prairies were locally dominated by *A. scoparius,* marshy areas by *Calamagrostis,* species of *Carex* and *Phragmites,* and sloughs by *Spartina.* The most constant prairie indicators in this area at present are: Tall bluestem . . . Indian grass (*Sorghastrum nutans*), tall smooth panic grass (*Panicum virgatum*), prairie dock (*Silphium terebinthinaceum*), sawtooth sunflower (*Helianthus grosse-serratus*), Sullivant's milkweed (*Asclepias sullivantii*), large blazing-star (*Laciniaria scariosa*), and stiff goldenrod (*Solidago rigida*)." Even in areas where there was a good stand

FIG. 57. Distribution of grassland (black) in the prairie peninsula. (Courtesy of E. N. Transeau and Plant Ecology)


94°
93°
92°
91°
90°
89°
VERNON
RICHLAND
SAUK
CRAWFORD
IOWA
JEFFERSON
WAUKESHA
JO DAVIES
SCHUYLER
BROWN
PIKE
SCOTT
HOWARD
BOONE
LINCOLN
ST CHARLES
ST LOUIS
CHARITON
OSAGE
GASCONADE
BENTON
MILLER
MARIES
CAMDEN
JEFFERSON
MONROE
PHELPS
CRAWFORD
WASHINGTON
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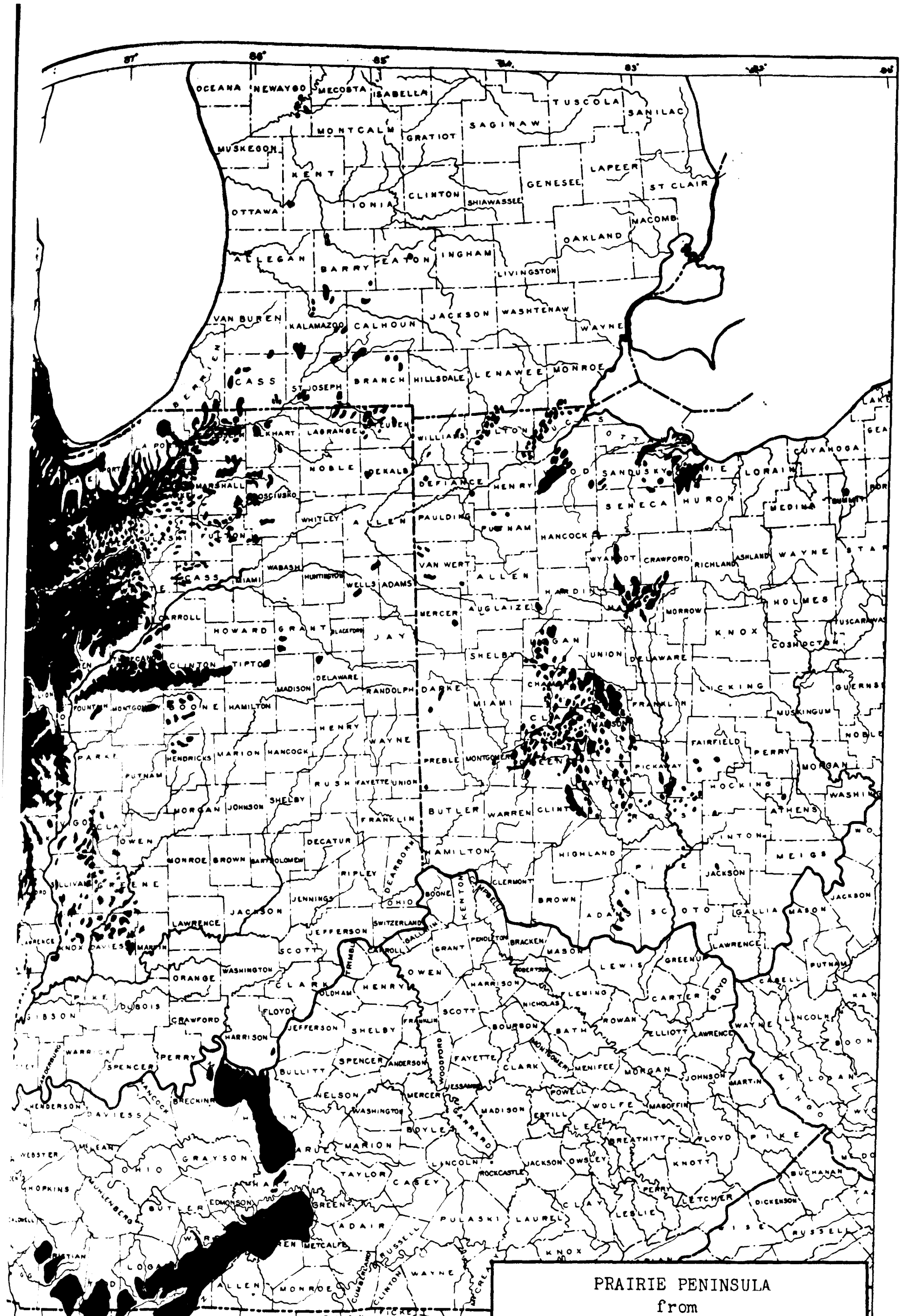
PULASKI
LACLEDE
DALLAS
DENT
PERRY
JACKSON
FRANKLIN
HAMILTON
WHITE
WILLIAMSON
SALINE
GALLATIN
MADISON
UNION
JOHNSON
POPE
HARDIN
WEBSTER
WRIGHT
TEXAS
REYNOLDS
BOLLINGER
CAPE GIRARDEAU
ALEXANDER
PULASKI
MASSAC
LIVINGSTON
CRITTENDEN
SHANNON
WAYNE
SCOTT
BALLARD
CRACKEN
CHRISTIAN
DOUGLAS
CARTER
STODDARD
MISSISSIPPI
CARLISLE
MARSHALL
BARRY
STONE
TANEY
OZARK
HOWELL
RIPLEY
BUTLER
NEW MADRID
HICKMAN
FULTON
CARROLL
BOONE
MARION
BAXTER
FULTON
RANDOLPH
CLAY
OBION
WEAKLEY
HENRY



PRAIRIE PENINSULA
from
Transeau, E. N. Ecology 16: 423.
1935

of oaks, the prairie vegetation made up the bulk of the ground cover. For the locations of prairie areas in the eastern prairies, see Transeau's map (Fig. 57).

Studies in Michigan and Indiana

Veatch (1927) points out that the Michigan prairies were restricted to the southwestern part of the state. They occurred on level or nearly level land as small, separate bodies, varying in size from about 80 acres to a maximum of about 25 square miles in a region with 32 to 36 inches of precipitation. These are dry prairies as distinguished from marshes. A total of 39 had been located and their location mapped. There were a few bur oaks on nearly all of the prairies and some hazel brush, particularly on the forest border. "The land was broken up for farming at an early period and it is fairly certain that no virgin prairie land exists at present."

In a study of the flora of Indiana, Parker (1936) states: "At present the prairie communities of Indiana are restricted largely to the western portion of the central and northern part of the state with small isolated communities to the east and northeast. . . . The former more widespread extent of grassland is indicated by communities which appear in habitats comparable to those in the western prairies and in which the species bear the same relationship to each other (as to relative importance and dominance) as they do in the prairie region."

According to Rohr and Potzger (1951), the prairie in Indiana no doubt had scattered trees even in areas of its best expression, and the open forest very likely had prairie grasses as understory vegetation—for crown cover of the trees must have been very open. The vegetation pattern in the three northwestern counties is quite clearly defined. A grassland vegetation yields to an ecotone of oak-grass vegetation, and this in turn merges into a definite oak or oak-hickory forest community.

Studies in Illinois

Sampson, in 1921, made an outstanding contribution to the vegetation of Illinois. He attempted to include all the prairie habitats, classify the communities, and point out the successional relations. His studies were chiefly on lowland vegetation, since upland prairies were limited to small tracts, fence rows, and railway rights-of-way. His description of the hydrosere in the development of prairie is abstracted. "The shallow postglacial lakes did not become forested but supported a luxuriant growth of herbaceous water plants which decayed, but slowly, beneath the surface water and gradually filled the lakes. In this way enormous sloughs arose and a deep deposit of humus accumulated. The depth and area of these postglacial lakes are attested today by the depth and extent of the rich humus soils which accumulated in them. . . . The series of this succession of plants leading to the gradual filling of the sloughs may be seen today in areas little disturbed by man. At first the bulrushes are most abundant and prominent. . . . They are replaced by sedges which dominate during a second stage of deposition. The sedges are followed by slough grass (*Spartina Michauxiana*). Sometimes the slough grass follows the bulrushes directly without an intervening sedge stage. . . . The slough grass is followed in order by blue jointgrass (*Calamagrostis canadensis*) and tall Panicum (*Panicum virgatum*) or by Panicum alone, which, in turn, is finally replaced by tall bluestem. Tall bluestem remains as the dominant grass of true prairie.

"Where the upland clay soils become covered with a prairie vegetation instead of a forest, the first abundant grass to appear upon them is short bluestem (*Andropogon scoparius*). This grass, in time, becomes crowded out and is replaced by tall bluestem."

Sampson studied the succession of plant communities on the flood plain of the Mississippi River in northwestern Illinois. The plants representing the various associations usually occupied 85 to 95 per cent of the area in which they were dominant. "The areas of the individual associations vary from a few square rods to tens of acres. . . . One *Panicum virgatum* association was found occupying nearly 100 acres and similar areas of *Spartina Michauxiana* are not infrequent."

The chief communities of the hydrosere on the river flood plain were: *Scirpus fluviatilis, Spartina Michauxiana, Panicum virgatum,* and *Andropogon furcatus.* But sometimes there was an intermediate sedge stage (*Carex vesicaria*) between the bulrush and slough grass. Also at times slough grass was followed by a bluejoint (*Calamagrostis canadensis*) stage before the tall panic grass community developed. A very similar sequence of communities was found on the old lakebed of Lake Chicago, as well as in more than twenty morainal depressions in other parts of Illinois.

A large number of the characteristic species of each community is listed by Sampson. The *Spartina Michauxiana* association of grasses, including

Elymus virginicus, sedges (*Carex*), rushes (*Juncus*), and spike rushes (*Eleocharis*), was similar to that found in the sloughgrass habitat throughout true prairie. A considerable group of mesic forbs occurred. *Stachys palustris, Lycopus americanus* and *Iris versicolor* were representative.

Several species of *Panicum,* with *Elymus canadensis* and *E. virginicus,* were the chief grasses in the *Panicum virgatum* association. Such forbs of lowland prairie occurred here, as *Ranunculus septentrionalis, Anemone canadensis, Cicuta maculata,* and *Rudbeckia hirta.* Most of the species listed occur in similar moist areas westward. *Calamagrostis canadensis* and *C. inexpansa* are grasses of wet lands which sometimes formed a separate community between the typical sloughgrass and tall panic grass habitats.

Grasses and the many forbs listed in the *Andropogon furcatus* association were much, but not entirely, the same as those of this community in western Iowa and Nebraska. In the *Andropogon scoparius* community *Stipa spartea, Panicum scribnerianum,* and *Sporobolus heterolepis* were some of the most important grasses. In fact all of the grasses and the long list of forbs were also common to western true prairie.

"The data obtained from early settlers and a careful study of the prairie relics seem sufficient to reconstruct rather accurately the original prairies of the southern Illinoisan glaciation. . . . On the exposed clay *Andropogon scoparius* was abundant, and associated with it were many coarse herbs. A mixed association consisting of the two Andropogons, *Sorghastrum nutans,* and *Sporobolus heterolepis* may have occurred in transition zones on some of these clay areas." Of the Wisconsin glaciation Sampson states: "The xerophytic grass association dominated by *Andropogon scoparius* is the characteristic association of these shallow soils [as on morainal ridges]. Relic patches of this grass are most frequently found on the broken topography near woodlands where the subsoil has been exposed by erosion. As in the southern part of the state, *Sorghastrum nutans, Sporobolus heterolepis,* and coarse herbs are also more conspicuous in these areas.

"To sum up, both the historical data and the data obtained from relic prairie areas lead to the conclusion that *Andropogon furcatus* is the climax grass of the whole upland prairie region of the state, and that in the successions leading to this climax from the more xerophytic uplands and exposed clay soils *Andropogon scoparius* is the most important species" (Sampson, 1921).

The prairie station described by Vestal (1914) is an example of perhaps the most luxuriant type of true prairie. "The county line station, a half-hour's ride west of Chicago, contains areas of prairie, forest, and forest border in still fairly good condition. . . . This type is of three appearances: The *Andropogon furcatus* prairie, the mixed grass prairie, and the *Silphium terebinthinaceum* prairie. . . . It will perhaps be helpful to regard the mean and the two extreme conditions of this series as constituting distinct plant associations, which may be called xerophytic prairie-grass, mesophytic prairie-grass and the hydrophytic or swamp prairie." These intergrade gradually, and many species tolerate a wide range of soil moisture and other environmental conditions, so that some species are found abundantly in more than one association.

Chief grasses of the xerophytic grass association were *Andropogon scoparius, A. furcatus, Sorghastrum nutans, Panicum virgatum, Stipa spartea, Sporobolus heterolepis,* and *Koeleria cristata.* A few characteristic forbs were *Silphium laciniatum, S. integrifolium, Solidago canadensis, S. rigida, Amorpha canescens, Aster multiflorus* and *Euphorbia corollata.*

"There are several well-defined representatives of the mesophytic association. One is dominated by the tall grass, *Andropogon furcatus,* often with hardly any other species present; one is dominated by a number of grass species (the mixed consocies of mesophytic prairie-grass); and one is dominated by the large rosinweed *Silphium terebinthinaceum* and by grasses." Typical grasses of the mesophytic prairies were, in addition to those listed above, *Panicum scribnerianum* and other species of *Panicum,* and *Elymus canadensis.* There were also species of sedges and rushes. A few characteristic forbs were *Allium cernuum, Fragaria virginiana, Viola pedatifida, Eryngium yuccifolium, Phlox glaberrima, Pedicularis canadensis, Lobelia spicata, Rudbeckia hirta, Rosa humilis, Euphorbia corollata,* and *Parthenium integrifolium.* The hydrophytic prairie passes insensibly or with a conspicuous zonation into swamp prairie.

Gleason (1910) made an extensive study of the vegetation of the inland sand deposits of Illinois, and briefer studies of sand vegetation in prairie have been reported by Shimek in Iowa (1917), Schaffner in Kansas (1926), Bruner in Oklahoma (1931), and elsewhere.

Prairies on Flood Plains

On the wide alluvial bottomlands of the larger rivers, of both eastern and western prairies, the forests were often limited to relatively narrow strips along the channel and the abandoned oxbows, alternating with strips of prairie. According to Bradbury (1809) "The flat valley of the Missouri river [near Omaha], about 6 or 7 miles in breadth, is partly prairie, but interspersed with clumps of the finest trees, through the intervals of which one could see the majestic but muddy Missouri." Brendel (1887) in discussing the flora of the Peoria, Illinois region states: "We distinguish wet and dry prairies. The former in the river bottoms or in depressions of the dry prairies which occupy the high and undulating plain." A much earlier observation of an explorer, Patrick Kennedy, (Imlay, 1797) is cited by Gleason (1910). "We encamped on the southeastern side of the Illinois River, opposite to a large savanna, belonging to, and called the Demi-Quian swamp [the Spoon River, joining the Illinois river opposite Havana (Turner, 1934)]. The lands on the southeastern side are high and thinly timbered; but at the place of our encampment are fine meadows, extending farther than the eye can reach, and affording a delightful prospect."

Sampson (1921) lists thirteen flood plain, grassland areas in Illinois along the Mississippi and Illinois rivers. Turner (1934) states: "The observed conditions occurring in the Mississippi and Illinois river valleys seem to be as follows: the customary floodplain forest is confined to a belt or zone from a few hundred yards to a half mile in width paralleling the river channel or surrounding ponds and lakes. The landward side of this forest type merges into a grassland association, at first on the hydric side of mesophytism, but giving way in turn, as the elevation of the floodplain increases, to a mesic grass association."

Schaffner has been intimately acquainted with the prairies of Kansas since 1871, at a time when the original conditions still prevailed. He states (1926): "The first bottom of river flood plain, where a normal soil had developed, was largely occupied by a typical *Andropogon furcatus* prairie, due to the action of prairie fire which was continually destroying the forest belts developed in the river bends and confining them to narrow strips. . . . The advance of flood plain forest after the cessation of prairie fires, even in competition with the Andropogon, was, therefore, very rapid—about a third of a mile in thirty years." The second bottom was ordinarily too dry to permit of tree growth. Only the low flood plain, deep ravines, and steep protected slopes are potential forest habitats in the absence of fire.

At the time of settlement of southern Wisconsin, in about 1830, the area was characterized by large tracts of prairie, openings [prairies] in the deciduous forest of from less than one to more than one hundred square miles in extent (Fig. 57). Of these, less than one per cent remains (Gould, 1941). Bur oak openings were the principal timbered lands over a large portion of the southern part of the state. Lapham (1846) states that "there are no considerable portions that can be called timber land, it being almost entirely oak openings or prairie."

In describing one of the few remaining openings, Stout (1944) states: "These [bur] oaks are all broad-topped and so spaced that seldom are the branches of two trees interlocked. Also they are rather uniform in size. There are no young trees or shrub growth anywhere in this [pastured] grove nor has there been such growth here for at least one hundred years. Between the trees there is the firm turf of native grasses that have never been disturbed by cultivation." These groves occurred on both level or undulating uplands. Former prairie land lay adjacent to this grove. "It is known that 'prairie fires' burned over this area both before and some time after the arrival of the early settlers. Storms have broken down or uprooted some of the trees; but except for the removal of such trees no wood has been cut in the grove." The age of most of the trees was at least 200 years. Quoting from the "History of Dane County," Stout states: "The entire town[ship] was covered with a sweet and nutritious grass called blue joint [big bluestem]. As this grass was burned every fall, and there was no underbrush or timber, a two-horse wagon could be driven through the openings with ease. As the annual fires prevented the roots of the timber from growing near the surface, the land was broken for the same price for breaking prairie. . . . This [Rock] county is about equally divided between prairie and oak openings. The trees are so scattering that men frequently make farms without felling—only girdling them—besides the openings are annually burnt over, like the prairies. . . . Groves are interspersed through the prairies at intervals . . . in fact few men on the prairie live more than three miles from timber." Stout continued: "The bur oak openings comprise almost pure stands of the one species, *Quercus macrocarpa* (with a sprinkling of *Q. alba* especially on the higher lands) and they constitute the most characteristic arboreal association that was in direct contact with the prairie. The belt of oak openings extended between the prairies and the denser deciduous forest."

Cottam (1949) stated: "The oak woods in southwestern Wisconsin have been transformed from widely spaced oak openings to dense woods in the last one hundred years. These oak openings contained scattered, broad crowned trees. The herbs and shrubs were mostly prairie plants. Some of the old, open-grown trees remain in the present woods, but are now surrounded by tall, relatively unbranched forest-grown trees. The present understory is mostly forest shrubs and herbs.

Small prairie areas of Central Wisconsin, on the border between the prairie and deciduous forest, have been studied by Thompson (1940). These areas were among those first cultivated in this region (in the 1850's) as there was no difficulty in clearing the land. Of about 20 areas examined, each had from 9 to 32 species of true prairie grasses and forbs.

Curtis and Green (1949) studied a total of 65 prairie relics in Wisconsin. Of a total of 237 species only 19 occurred in 50 per cent or more of the stands. The most common were *Andropogon furcatus, Euphorbia corollata, Amorpha canescens, Solidago rigida,* and *Coreopsis palmata.*

PRAIRIE INCLUSIONS AND FOREST BORDER

In the deciduous forests of the central states, small fragments of prairie frequently occur.[1] They are usually found on hillsides exposed to the south, southeast, or southwest, and are present in all of the western prairie states. In size they vary from a few square feet to several acres. According to Shimek (1911): "The prairie ridges appear in all the forested rougher parts of the state, but are most striking in the heavily timbered eastern parts where they have been known as 'oak openings' because the surrounding forest, consisting largely of oaks, encroached upon them. These prairie openings are sometimes mere tongues of greater prairie areas which extend into the forest, but they are frequently surrounded by forest and may be several miles from larger prairie tracts.

"The rugged bluffs along the upper Mississippi river, particularly those which border that part of the river flowing between Iowa and Wisconsin, display irregular treeless tracts on their slopes. . . . Very few of these treeless areas on the more rugged bluffs are artificial clearings. The great majority are natural openings, and there is no evidence to show that

[1] For convenience, this section includes the entire prairie.

they were ever covered with forest. On the contrary, their location indicates that the absence of trees is due to natural causes, and that they are of long standing. . . . It is clear that these treeless areas are simply prairie tracts distributed irregularly on the most exposed portions of the bluffs, or dominating on larger exposed surfaces" Shimek (1924). He made extensive collections in these areas, and states: "As illustrated and suggested by these lists, every feature of the treeless bluff areas simply duplicates the conditions which exist upon the broader prairies, and we must consider these areas simply as outliers or detached fragments of the general prairie" (Fig. 58).

Irwin (1929) described a typical prairie opening of about one-third of an acre in the Cincinnati region of Ohio. Most important species were *Andropogon scoparius, Sorghastrum nutans* and *Silphium terebinthinaceum*. One-half of the plants and five-sixths of the important species were prairie plants.

Hill prairies in Illinois occur on the more exposed upper slopes of the bluffs, on the east side of the larger stream valleys. Their presence is not restricted to any one section of the state, as they can be found from northern to southern Illinois, according to Evers (1952). He studied sixty hill prairies with a combined area of almost 200 acres. The vegetation was the bunch-grass type, with little bluestem the usual dominant. Side-oats grama and big bluestem also occurred in nearly all of them.

Other studies in Illinois were made by Vestal (1918), and in southeastern Nebraska by Pool, Weaver, and Jean (1918), and by Hanson (1922). There have been many others.

From Indiana to eastern Kansas the prairie is bordered by a forest of oak or oak-hickory. The bur oak extends along the bluffs and hillsides of rivers and streams to the western edge of true prairie. According to Transeau (1935), "The forests bordering and to some extent penetrating the prairie peninsula are regularly oak, oak-hickory, and oak-maple-linden, and these borders are often miles in width, even in Indiana and Ohio, where much of the upland is otherwise occupied by beech-maple." The prairie-forest relationship along the eastern margin was that of a mosaic of prairie and forest communities. Here the transition from grassland to forest was abrupt. At most, according to Transeau, it was only a few rods in width.

Vestal (1914) described the species of the border zone between prairie

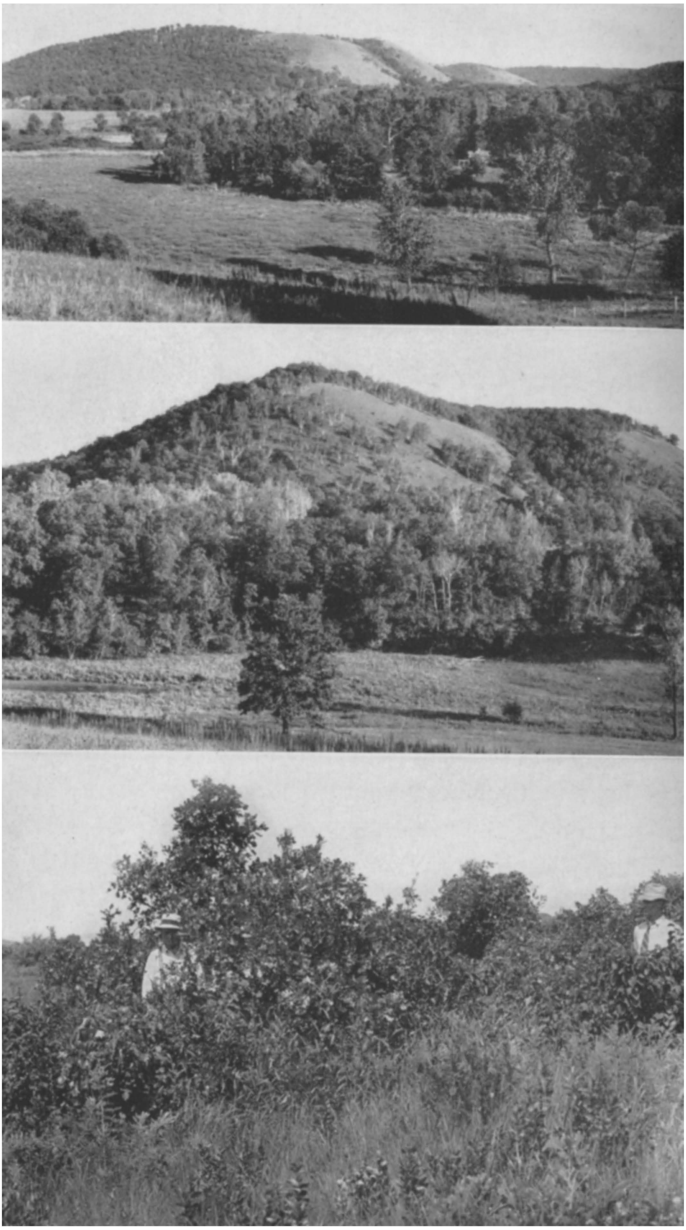


FIG. 58. Oak opening in northeastern Iowa on the west-facing bluffs along the Upper Iowa River. Photo by W. L. Tolstead. (Lower) Forest-prairie border near Guthrie Center, Iowa. Hazel (*Corylus americana*) is the chief shrub.

and forest, still in good condition, near Chicago on the western edge of Cook county. "The exposed borders show very distinct zonation. In some places a low-tree zone is seen at the edge of the forest proper. This is composed of wild crab (*Pyrus coronaria*) or of plum (*Prunus americana*) or of thorn-apple (*Crataegus* sp.). These trees are usually from nine to fourteen feet in height, and form a zone of varying width. A shrub zone is seen just outside the trees. A dogwood (*Cornus Amomum*) dominates; hazel (*Corylus americana*) and elder (*Sambucus canadensis*) are locally abundant. The dogwood is usually three and a half feet high, the hazel is about seven feet high; the shrub zone is four to ten feet wide. Grape-vines (*Vitis vulpina*) cover some of the outer shrubs and trees. The outermost zone is almost a pure growth of sunflowers (*Helianthus decapetalus* and *H. divaricatus*), locally replaced by a species of *Verbesina*. The height of the sunflowers is two to four feet; the zone is two to eight feet in width. The prairie just outside the sunflower zone is strikingly uniform with that farther from the forest."

Shimek (1911) observed that "prairie plants are rarely found in the woods and that rarely except as isolated individuals and then only on edges of openings or where there is exposure to sun and wind." Conversely, not only forest trees but also herbs of the forest fail to appear on the open prairie. There is very little mingling of the two floras except rarely in border belts.

"In Iowa, along the borders of the prairie and forest contacts, and in prairie openings, forest plants frequently invaded the prairie during cycles of favorable seasons, only to retreat again before the advancing prairie flora with the return of drier seasons" (Shimek, 1948).

In Iowa the forests were found chiefly in the northeastern, southeastern, and south central parts of the state and usually adjacent to the larger streams. Groves were found at points remote from streams and many streams were entirely destitute of a forest border, especially in their upper courses. Where there is a flat plain into which the larger streams have cut narrow valleys, trees may be absent. Thickets may border swamps and lakes. Bur oak is the dominant forest type in all these border portions of the natural groves.

In describing the western boundary of the Big Woods in Minnesota, Winchell (1875) says: "It is not well marked, the trees gradually becoming thinner and smaller, and more and more restricted to the valleys of the streams, till the country is changed to a treeless prairie. Around the outskirts of the woods small oaks and aspens constitute almost the only arboreal vegetation."

Moyer (1910) lists the following shrubs as common along the borders of the bur oak savannah in Minnesota, which extends northwesterly as a narrow band of forest to Canada.

Wild plum (*Prunus americana*)
Wild red cherry (*P. pennsylvanica*)
Choke cherry (*P. virginiana*)
Sheepberry (*Viburnum lentago*)
Downy arrow wood (*Viburnum pubescens*)
Burning bush (*Euonymus atropurpureus*)
Red osier dogwood (*Cornus stolonifera*)
June berry (*Amelanchier oblongifolia*)
Smooth rose (*Rosa blanda*)
Hawthorne (*Crataegus* sp.)
Willows (*Salix* spp.)
Buffalo berry (*Shepherdia argentea*)
Wolf berry (*Symphoricarpos occidentalis*)
Snow berry (*S. orbiculatus*)

The vegetation at the shrub station at Minneapolis, where studies of the environment in forest, shrub, and prairie were conducted, consisted chiefly of *Corylus americana*. Intermixed were prickly ash (*Zanthoxylum americanum*), poison ivy (*Rhus radicans*), species of *Rubus* and *Viburnum,* and smooth rose (*Rosa blanda*). Bittersweet (*Celastrus scandens*), gooseberry (*Ribes cynosbati*), and dogwood (*Cornus*) were also present (Weaver and Thiel, 1917).

In the central portion of the western prairie the extreme outposts of the forest are represented by relatively few species of trees and shrubs along the creeks and sheltered ravines which more or less dissect the rolling portions of the prairie. The Missouri River and many of its tributaries have belts of forest fringing the bluffs and sometimes extending somewhat over the adjacent hills. In addition, in southwestern Iowa and northwestern Missouri some natural prairie groves occur.

Protected ravines of the prairie, especially near the forest, may contain one of more species of shrubs that constitute the forest border. Near the forest margin, these shrubby plants increase not only in number of species but also in stature. They migrate up the slopes and over the hilltops and often form a shrub border a few rods to a mile or more in width between prairie and oak woodland. The most abundant species are smooth sumac (*Rhus glabra*), coralberry (*Symphoricarpos orbiculatus*), and hazel (*Corylus americana*).

Sumac spreads into grassland by means of very long underground parts, which give rise to new shoots sometimes 25 to 30 feet from the parent plant. They usually occur at depths of 3 to 12 inches. Coralberry grows in clumps to a height of 2 to 5 feet and casts a dense shade. Hazel spreads by means of large, woody, underground parts in the surface 6 inches of soil. They give rise to new shoots a foot or two beyond the parent plant.

Where shrubs extend into prairie it is by mass invasion. The leaf mulch produced and held by them against the wind is almost as detrimental to the prairie grasses as the shade of the shrubs. Studies have revealed that an advance of only 2 to 3 feet may require 3 to 5 years (Clements, Weaver and Hanson, 1929). Extension of forest into prairie, such as occurred in a limited manner following settlement and the cessation of prairie fires, is often attained as a result of changes in habitat brought about by the shrubs. But in many places bur oak invaded without the aid of shrubs. Shrubs are abundant at the forest edge. Here are found hazel (*Corylus americana*), prickly ash (*Zanthoxylum americanum*), buckthorn (*Rhamnus lanceolatus*), raspberries (*Rubus strigosus* and *R. occidentalis*), dogwoods (*Cornus drummondi* and *C. amomum*), and burning bush (*Euonymus atropurpureus*). Virginia creeper (*Parthenocissus quinquefolia*), wild grape (*Vitis vulpina*), bittersweet (*Celastrus scandens*), and poison ivy (*Rhus radicans*) are the chief climbing vines. Gooseberry (*Ribes missouriense*), coralberry (*Symphoricarpos orbiculatus*), and the western snowberry (*S. occidentalis*), wild plum (*Prunus americana*), and smooth sumac (*Rhus glabra*) are very common. Although the shrub community has fewer species in northern than southern Nebraska, it is more extensive northward. The more xeric shrubs are found commonly along streams or in pockets in ravines. The wild plum and smooth sumac form thickets far from the woodland, and coralberry occurs where trees fail to grow (Fig. 59).

The ground oak (*Quercus prinoides*), with its top of many stems and extensive underground parts, was rarely seen in the western prairies, although it was common eastward. A fuller account of the shrubs bordering grassland is given by Aikman (1929) for Nebraska and Aikman and Gilley (1948) for central Iowa.

Environmental conditions from prairie to the shrub ecotone and woodland have been measured and the mechanism of invasion studied in Minnesota and Nebraska (Weaver and Thiel, 1917; Pool *et al.*, 1918; Clements *et al.*, 1929). Over most of the territory, it seems probable that shrubs and woodland could not extend their areas greatly even if unhandicapped by mowing and prairie fires.

Competition between shrubs, trees, and grasses was studied at Weeping Water, Nebraska, over a period of three years (Clements *et al.*, 1929). "The fascinating problem of the relation of the forest edge to grassland has been much debated on the basis of general observations, but has never before been attacked in a comprehensive and quantitative manner, or with the experimental procedures focused upon the essential functions of competition, reaction, and ecesis." Environment in air and soil was measured at several stations, and exclosures to livestock were established. Water relations at the margin of a thicket were secondary to the effect of light. "Practically all of the evidence from the several studies described points to the slow encroachment of thicket and woodland at the edge of the prairie, though under a rainfall of 30 inches, this is due to some degree to the modifying influence of stream and valley. . . . A much longer period of experiment is needed, however, to yield a complete understanding of the marginal relation of forest and prairie, and a fairly accurate evaluation of the control exerted by climatic cycles. . . . The slow advance of chaparral and forest will be hastened by the wet phase, retarded by the dry, or even converted into a retreat. It appears fairly certain that there can be no final victory for either, only periods of varying duration in which one or the other holds the ground won by the favor of the changing cycle." The widespread damage of drought to the shrubs and trees of this woodland and to trees throughout the western prairie has been described by Albertson and Weaver (1945).

The occupation of grassland by forest through changes in habitat brought about by invading shrubs is easily understood, but the establishment of bur oak in grassland without such aid is less readily comprehended. Planting of the large acorns might be done by timber squirrels or perhaps by downward migration on slopes. During germination a taproot is extended about 7 to 9 inches deep before the leaves are unfolded.

Holch (1931) ascertained that in cultivated prairie soil in southeastern Nebraska, the strong taproot reached a depth of 4 to 5 feet during the first summer. Lateral roots were very abundant from the soil surface to maximum depth, but the lateral spread was only about 15 inches. This root system supported a leafy shoot only 12 inches tall. After the second summer both taproot and a few major branches were more than 6 feet deep. The next year the branches were so wide-spread that a column of soil 4 by 4 feet in surface area and 6 feet deep was well occupied by the roots of bur oak saplings 3 feet high. Such a root system could compete well against both grass and forb.

Roots of mature bur oaks, 50 to 65 years old, 35 to 40 feet tall, and 12 to 18 inches in basal diameter, were examined. They were growing on the edge of prairie in eastern Nebraska (Weaver and Kramer, 1932). The taproots were about 14 feet deep (Fig. 59). One gave rise to 30 large main branches, mostly in the surface 2 feet of soil. These spread widely, extending 20 to 60 feet laterally before turning downward. They and some of their numerous branches reached depths as great as or greater than that of the taproot. The weight of this magnificent root system equaled that of the top.

These findings help to explain how low water content of prairie soil is compensated by the excellent root system of this xeric oak. Bur oak was one of the few trees in Nebraska and Kansas that endured especially well the terrible drought of 1933–40 (Albertson and Weaver, 1945).

In Oklahoma the chaparral which forms an ecotone between forest and prairie is a low, woody growth and occurs in habitats that are too dry for the development of trees. "It consists of fringing belts of shrubs and tongues of shrubby growth which extend into the grassland along the streams and ravines. [It] is best developed and richest in species where it occurs at the margins of the deciduous forest but is most extensive westward in the general savannah region, although the component species are fewer. . . . The chaparral fringe between the flood-plain forest and the [eastern] prairie consists of the following species: *Cornus asperifolia, C. amomum, Rhus glabra, R. copallina, Cephalanthus occidentalis,* and *Diospyros virginiana.* All are true shrubs except the last which frequently becomes a small tree 6 to 8 inches in diameter and 25 feet or more high. It forms dense thickets in ravines as well as along flood plains and frequently occurs in pure stands" (Bruner, 1931).

He states further: "The chaparral is represented in the central part of western Oklahoma by communities of 'shin oak.' Here *Quercus mohriana, Q. stellata palmeri, Q. s. rufescens,* and *Q. vaseyana* occupy sandy areas and are especially abundant in overgrazed pastures and abandoned fields.

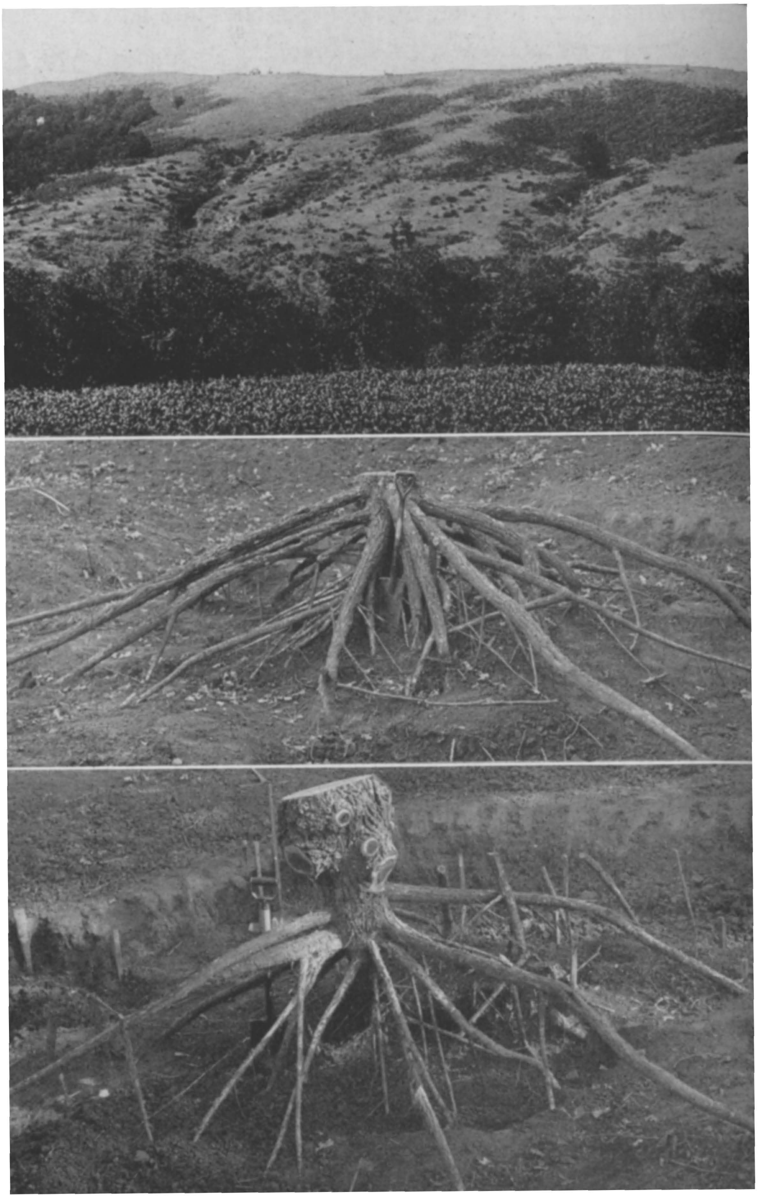


FIG. 59. View of south-facing bluffs bordering the Missouri River opposite Yankton, South Dakota. Principal shrubs are coralberry and wolfberry (*Symphoricarpos*), smooth sumac (*Rhus glabra*), and dogwood (*Cornus*). (Center) Partially excavated root system of bur oak (*Quercus macrocarpa*). (Below) the same tree with portions of the upper roots removed. (Courtesy of Botanical Gazette and University of Chicago Press)

Great circles of zones indicate that the oaks have spread throughout a period of many years.

"The transition from oak-hickory forest to [western] true prairie is most commonly made by various mixtures of *Symphoricarpos symphoricarpos, Rhus copallina, R. glabra, Quercus stellata margaretta, Q. marilandica,* and *Q. prinoides.* Frequently *Symphoricarpos* is absent and also, not uncommonly, the sumacs. The ecotone then consists of a low growth of *Q. prinoides* intermingled with the grasses at the margin. Nearer the forest proper, *Q. stellata margaretta* and dwarfed specimens of *Q. marilandica* form low clumps which give way to the typical tree-forms. All of the oaks sprout vigorously and dense stands of more or less alternating areas quickly occupy cleared places or advance slowly into the grassland where the latter is not stabilized. . . . Ravines in the prairie frequently support chaparral communities in which the oaks are absent."

CHAPTER 11

Studies in Central and Western Prairies

THE WESTERN prairies were the last to be settled. Here very extensive areas of grassland may still be seen. Studies of this grassland began later than those eastward and, with the rapid development of ecological methods, they have been continued to the present time. However, much early work was done in the great prairie state of Iowa.

STUDIES IN IOWA

The prairies of Iowa have been investigated by Shimek throughout a long period of years. He knew conditions in Iowa before much of the vegetation was disturbed by settlement. He studied the flora of about 60 localities, chiefly in Iowa, during a period of 20 years previous to 1911. In his major paper (1911), details of the floristic composition of the prairies of Iowa are discussed and the physical and biotic factors which were thought to cause or control them. Here one finds a comparison from 12 stations of the several types of prairie areas, namely flat, rolling, ridges, prairie openings, alluvial, and sand dunes. About 275 species of the typical plants of Iowa prairies were compared by means of tables. The abundance and relative distribution of the species were roughly indicated. From this comparison he concluded: "The major part of the flora of all these types is the same, and constitutes one of the most distinctive characteristics of prairie." Comparison of the tables with those from the prairies westward (Chapters 3 and 5) bears out this statement.

Most of Shimek's paper (1911) is concerned with exposure of prairie to evaporation and why the prairies are without trees. He concluded in part: "Exposure to evaporation as determined by temperature, wind, and topography is the primary cause of the treelessness of the prairies. The prairie flora persists on the exposed areas because it is xerophytic. Prairie fires were an effect rather than a cause [of prairie], and where acting as a cause were local." He states (1931) that among 265 species composing the bulk of the prairie flora of Iowa, 67.5 per cent are ordinarily dispersed by wind, 24.5 per cent by animals, chiefly birds, and 8 per cent by hygroscopic properties.

Shimek's study of the prairie region about Lake Okoboji in northern Iowa (1915) consisted largely of lists of species found in different localities with numbers indicating abundance.

The rapid disappearance of the prairie in eastern and central Iowa was indicated by Shimek (1925) in his paper "Persistence of the Prairie." "The purest remnants of the prairie are often found along the right of way of the older railways which entered the territory before the original prairie was broken." He described such an area in southeastern Iowa and one in the north-central part.

Many broad flat plains in Iowa contained large undrained areas, the marshes, swamps, ponds and lakes of which possessed a rich flora of hydrophytes. These are well represented in Palo Alto and Clay counties of northwestern Iowa in the Wisconsin drift area where extensive botanical studies were made by Hayden (1943). Stages in the succession from hydrophytic vegetation of the lakes, ponds, and rivers, through swamp, marsh, and fen, as represented there, were discussed and beautifully illustrated. The scant shrub and tree stage was described and an account was given of the vegetation of wet meadow. Though the native prairie is quite generally destroyed, some areas of natural vegetation yet remain in the state-owned refuges. "Plants from southerly floras are less common in northern Iowa than in southern Iowa. . . . Nearly 200 species of the prairie flora are plants indigenous to northern regions. They are thought to represent remnants of northern floras which probably occupied the region after the ice retreated." These include species of fens and swamps, many of which are sedges and grasses.

In an earlier paper, Hayden (1919) reported extensive studies on the ecological subterranean anatomy of many plants of prairie as well as those of sedge meadow and reed swamp.

STUDIES IN MINNESOTA AND DAKOTA

The prairie in Minnesota, except for identification of species and collecting for the herbarium, was studied but little before the sod was all broken. An interesting exception is the work of Moyer (1910). He described the prairie flora of southwestern Minnesota, a part of the great grass-covered plain which characterized the western part of the state. Here the prairie remained mostly unbroken or unfenced until about 1870. The high rolling prairie, the valley and prairie meadow, and the prairie sloughs were each given separate attention, as well as the flora of bluff and rock outcrops. Grasses were recognized as the most important constituents of the flora but the writer felt "incompetent to write accurately about . . . the prairie grasses. With the exception of narrow strips along the streams or on the north slopes of protected bluffs, or in ravines, such as the coulees cut by streams in the slopes of the Coteau, the region . . . is all prairie." (Fig. 60).

The principal grasses and forbs of Minnesota prairie were listed by Rosendahl (1926) under high rolling grassland flora, prairie meadow, and grassland of steppe. "For a short distance east of the western border, especially in the southwest over what is known as the Coteau des prairies and to a lesser extent on dry slopes and along the bluffs of river valleys, the flora assumes a more typical western aspect since it was in these habitats that many of the representatives of the Great Plains flora found congenial surroundings."

Ewing (1924) investigated a region in northwestern Minnesota which forms part of the watershed between the headwaters of the Mississippi and the eastern tributaries of the Red River of the North. Here a brush-prairie complex had developed on the wet flats after the recession of the glacial Lake Agassiz. It was a transitional community lying between the deciduous forest belt and the western prairie, destined to develop into a mesophytic deciduous forest. He described briefly the intermixed grassland dominated by *Koeleria cristata, Andropogon scoparius* and *Sporobolus heterolepis,* but with *Stipa spartea* and *Bouteloua curtipendula* and many other grasses common to both upland and lowland intermixed. A list of forbs common to prairie is presented. The brush-prairie passed very gradually into the great expanse of prairie westward, the amount of brush decreasing uniformly as the flatness of the land became more marked.

In northern Minnesota along the Red River Valley the vegetation was much the same as that to be described in North Dakota. Throughout the Minnesota prairie, needlegrass and slender wheatgrass (*Agropyron trachycaulum*) were species of much greater importance than they are southward.

Shantz (1924) gave a short account of the prairie grassland. In 1923, in his study on the vegetation of the Great Plains region, he considered only the western portion of true prairie. His needlegrass and slender

FIG. 60. Nearly pure stand of needlegrass in northwestern Iowa, and (below) grazed prairie in western Minnesota. The dark patches are sloughgrass or prairie cordgrass and the light-colored vegetation in the foreground is blue grama.

wheatgrass community occupied most of eastern South Dakota and eastern and northern North Dakota west of the 97° west longitude. "In this association the plants start growth early in spring, as soon as temperature conditions are favorable, and continue usually until late in July, when drought occurs. This grassland characterizes a relatively heavy [Chernozem] soil. The soil is black and 3 feet or more in depth to the layer of carbonate accumulation. During the early part of the growing season the soil may hold in storage an available moisture the equivalent of 5 inches of rainfall. The region as a whole has a relatively short frost-free period, ranging from 100 to 170 days. The growth period, even in this section, is usually terminated by drought, the total soil-moisture supply being consumed by the grass cover. There is consequently no storage of moisture in the soil and no drainage through the subsoil to the water table below. The evaporation in this region is relatively low." Rainfall at the western edge of true prairie is about 23 inches in southern South Dakota and 21 near the Canadian border. The Chernozem soil is highly productive.

The rich, black soils of the Red River Valley and eastward were developed under a cover of tall grasses. This vegetation now remains only as small relic patches—old cemeteries, railroad right-of-ways and other relatively undisturbed plots. It formerly covered a strip of territory 35 to 45 miles in width in eastern North Dakota and extended far southward. Whitman *et al.* (1941) listed the most important grasses, all tall or mid grasses, as follows: big bluestem, needlegrass, side-oats grama, feather bunch grass (*Stipa viridula*), slender wheatgrass (*Agropyron pauciflorum*), western wheatgrass, prairie Junegrass, and Kentucky bluegrass. These made up the bulk of the vegetation.

Feather bunch grass or green needlegrass is a tall, perennial, tufted plant 1.5 to more than 3 feet high. The leaves, of good forage value, are 4 to 12 inches long, and usually are partially rolled. A growth of short hairs occurs on the upper end of the leaf sheath which clasps the stem. Slender wheatgrass is a short-lived, perennial bunch grass. It is 1.5 to 2.5 feet tall and forms rather large and very leafy bunches. The spikes are very narrow, but they are 6 inches or more in length.

On the drier ridges and knolls in this community and in the more xeric one westward, little bluestem was one of the major species. In sloughs, ditches and other wet places prairie cordgrass, reed canary grass, and other hydric grasses occurred. In less wet areas switchgrass, fowl bluegrass (*Poa palustris*), foxtail barley (*Hordeum jubatum*), and Macoun wild-rye (*Elymus macounii*) were found. Prairie dropseed was likewise an important species.

The true prairie extended northward into Manitoba. An early list of the flora of the region was published by Christy (1887), who made his observations in 1883 and 1884 when this province in its primitive prairie condition was just being settled. Shimek (1925a) in 1920 found only a few remaining tracts of prairie, so completely had the sod been broken. He listed approximately 175 species collected about 100 miles west of Winnipeg and compared them with those of a fertile prairie in northeastern Iowa. A study of the lists of grasses and forbs reveals that the flora of Manitoba was very similar to that of Iowa in identity of species.

Bird (1927) listed species of a prairie climax typical of the plains of southwestern Manitoba, although somewhat more arid due to the sandy nature of the soil. With a few others, the commonest species were big bluestem, little bluestem, switchgrass, Scribner's panic grass, needle-and-thread, needlegrass, prairie dropseed, Junegrass, blue grama, and Kentucky bluegrass. He considered the aspen parkland northward as an association of the tall grass of the eastern Great Plains which extends by finger-like projections and isolated areas throughout the parkland. Western wheatgrass is a dominant species.

As one travels westward from the Red River Valley in North Dakota, "the taller grasses gradually drop out and the mid and short grasses become more important. Needle-and-thread, feather bunchgrass, western wheatgrass, slender wheatgrass, blue grama, prairie Junegrass and Kentucky bluegrass are the dominant species. . . . Other important species include Macoun wild-rye, cordgrass, wild barley, prairie dropseed, marsh muhly [*Muhlenbergia racemosa*], sweetgrass [*Hierochloe odorata*], switchgrass, and several sedge species" Whitman *et al.* (1941).

The area of true prairie in the Dakotas, according to Clements and Shelford (1939), includes the eastern one-third of these states. The part occupied by the bluestem type in South Dakota is not unlike the one in North Dakota in width and is a westward extension of the prairies of Iowa and southern Minnesota. Westward it gives way to Shantz' needlegrass and wheatgrass community with dominant grasses already described.

Except in the southeastern portion of the state, few ecological studies have been made (Fig. 61). Harvey (1908) traced the seasonal development of the various societies in the prairies at Yankton, South Dakota.

STUDIES IN NEBRASKA

Pound and Clements (1900) in their "Phytogeography of Nebraska" dealt in a very general way with the eastern Nebraska prairies. Thornber (1901) studied a large prairie near Nebraska City over a period of 3 years.

Factors of the environment were measured, the species (188 in number) were listed, and special attention was given to the most characteristic species of each seasonal aspect. The number of forbs in each of a large group of quadrats was recorded and an excellent phenological table was made.

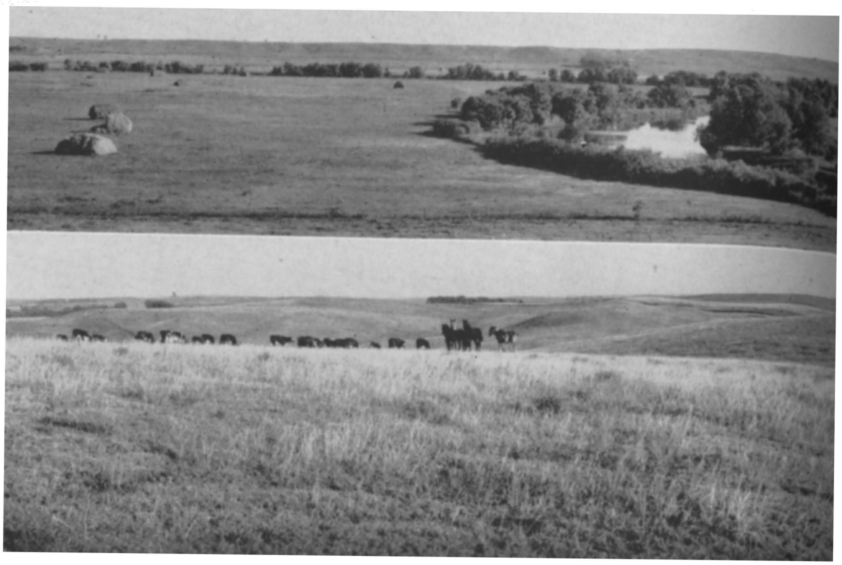


FIG. 61. Hay meadow along the James river in eastern South Dakota. The chief grass is big bluestem. (Below) Typical rolling land in southeastern South Dakota where native prairie is used for grazing.

Clements (1920) in "Plant Indicators" gave an excellent general account of True Prairie, its extent, factor relations, sequence of dominants, societies, and seasonal aspects. He discussed the eastern "belt of prairie more or less interrupted by woodland" under the heading "The Subclimax Prairie." This is the most complete condensed description that has been made. A brief description was also included by Clements and Shelford, "Bio-ecology" (1939), where both plants and animals of prairie are taken into account.

Clements and Weaver, as described in "Experimental Vegetation" (1924) maintained stations in prairie at Nebraska City and in various habitats from upland through lowland to marsh at Lincoln, as well as in mixed prairie. Seeds of grasses and forbs were sown on the soil surface, in small trenches cut in the surface sod but refilled with soil freed of roots, and in square-meter areas denuded in a similar manner. Seeds of trees and shrubs from bordering woodland, and also rhizomes, were employed. Blocks of sod of many grasses were excavated and some reset in place for controls while others were transplanted into different habitats. Germination in relation to depth of planting the seed, establishment, and development of both shoots and roots were studied. While the results over the four-year period can not be recorded here, this study gave a far better understanding of life in the prairie.

Most of the study on "Plant Competition," by Clements, Weaver and Hanson (1929) was concerned with grassland. Transplant cultures of grasses or grasses and forbs were placed in true prairie; quadrats were partially denuded by the removal of various species; and competition between seedling trees and prairie grasses was studied.

Flats 14 by 14 inches in area and 4 inches deep, with removable bottoms, were employed. After a suitable excavation was made in mowed or burned prairie in spring, the contents of each flat was transplanted as a unit in the surrounding sod. Plantings were made so that in the cultures dominant species competed with other dominants (e.g. big bluestem with switchgrass on low prairie and little bluestem with needlegrass on upland), tall or mid grass with short grass (as wheatgrass with buffalo grass), grass with forb, forb with forb, and grass with weeds. Root relations of the competing species as well as top growth were studied. A waxed-cord grid placed over the culture at the time of transplanting divided the area permanently into square-inch units so that an accurate record of numbers, tillering, and loss of seedlings by death, could be recorded. Each transplanted area, examined three times yearly, gave its own interesting story. Many findings thus obtained have been given elsewhere in dealing with these species.

That conditions of life are severe in the overcrowded prairie was shown conclusively by the removal of all but one species from a single square meter, or all but a central clump of grass. The remaining sunflowers or goldenrods or grass, profiting from an increased supply of water, light and nutrients, increased in vigor, size, and production of flowers and seeds. The elimination of competition led to an increase in stature and volume, ranging from 30 to 100 per cent, and produced more or less striking changes in form. Increases became more marked during a second growing season.

The third study, competition between seedling trees and prairie grasses at Lincoln, has been summarized by Albertson and Weaver (1945) as follows.

"In extensive experimental work on competition of seedling trees with grasses, seedlings of soft maple, honey locust, American elm, boxelder, and green ash were grown under four degrees of competition. Four, long, parallel trenches 4 inches wide and 4 inches deep were made in prairie on low, level land by removing the native sod. They were filled with loose prairie soil free from roots and the seed sown, water being added from time to time to insure germination and establishment. Four degrees of competition were obtained as follows:

1. In the first trench, the sod was overturned to a depth of 4 inches to a distance of 6 inches on both sides, and was then thoroughly pulverized to constitute a mulch. Frequent shallow hoeing kept this area free from all vegetation during the following seasons. The overhanging grasses along the edges were kept clipped to insure good lighting and thus confine the competition to the soil.

2. The grass along the second trench was kept clipped to the ground to a distance of 6 inches on both sides. There was practically no competition for light, the demands of the clipped cover for water and nutrients were moderate, and the corresponding competition was not severe.

3. Along the third trench the grasses were watered rather freely from time to time during the first year, and especially in periods of drought. They were not trampled and since sufficient water was present at all times, the competition in this row was chiefly for light and to some extent for nutrients.

4. Trees in the fourth trench were flanked by the grasses of the prairie and were entirely unaided in competition with them.

"As a whole, the mortality among the trees increased with the degree of competition. Figure 62 is representative of the relative development; watering caused the grasses to grow more vigorously, with the consequence that the trees received even less light than in the unaided row. Some deaths occurred each year. At the end of the third year the average loss of all trees in the mulched row was 31 percent, in the clipped 62, while it was 79 and 92 percent, respectively, in the watered and unaided rows.

Development of the root systems in the third year was directly in proportion to the tops."

Structure of vegetation was studied on an 800-acre prairie near Lincoln by Steiger (1930). "The presence of coyotes, rattlesnakes, etc., gives evidence of the slight disturbance caused by man, the annual removal of the matured vegetation being comparable in some respects to its former removal by prairie fires." Environmental factors of upland and lowland were studied. "The water content of soil showed the greatest and most consistent variation, and is the most important factor determining the differences in the structure of vegetation." Habitats varied from high prairie, ravines, and low prairie to wet meadow. A total of 237 prairie species was found. By extensive quadratting it was ascertained that *Andropogon scoparius* was dominant in uplands, covering 26 per cent of the area occupied by grasses and sedges. Six other most abundant grasses, each covering 7 to 17 per cent, respectively, were *Bouteloua oligostachya* (*B. gracilis*) and *B. hirsuta, Sporobolus heterolepis, Poa pratensis, Andropogon furcatus* (*A. gerardi*), *Bouteloua curtipendula* and *Koeleria cristata. Andropogon furcatus* (34 per cent), *Poa pratensis* (30 per cent) and *Andropogon scoparius* (25 per cent) were dominants of lower ground. Much attention was given to seasonal aspects and the period of anthesis for each species of the several habitats. Upland prairie reached its climax of flowering earlier in summer due to limited soil moisture. The individual ecology of many prairie plants was considered. (Fig. 63).

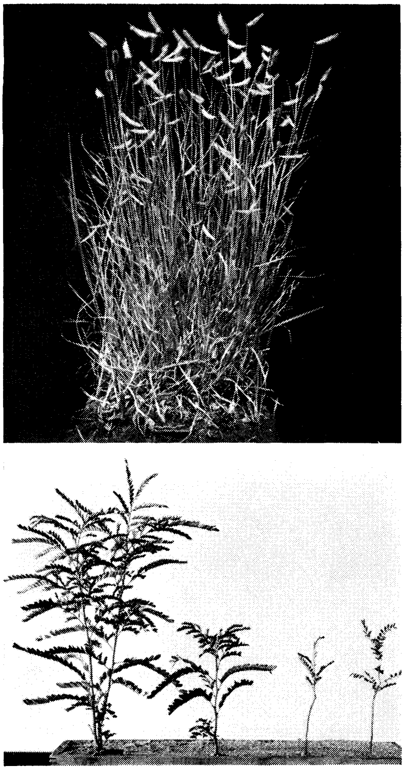


FIG. 62. Large bunch of hairy grama (*Bouteloua hirsuta*), a common and excellent forage grass in the Flint and Osage Hills. (Below) Growth of seedling honey locust (*Gleditsia triacanthos*) in mulched, clipped, watered and unaided rows in prairie. Photo at end of first growing season.

Blake (1935) studied the viability and germination of seeds and early life history of prairie plants near Lincoln. "The seeds of most prairie plants are subject to deep dormancy during the greater part of the year. . . . The seeds of 4 [autumnal] harvests were tested for 13 grasses and 18 forbs. . . . The percentage of germination [in a greenhouse] varied considerably for any species from year to year and often from season to season. Germination of the seeds of most of the important grasses . . . ranged between 10 and 20 per cent; a few yielded over 40 per cent. That of most forbs . . . was below 15 per cent, although in some species it was regularly at least 50 per cent. . . . Relatively few of the viable seeds which fall on the prairie germinate under natural conditions. . . . Relatively few seedlings were found [in prairie], although during the 4 years [seedlings of] 42 species of forbs and 6 grasses were observed."

The transition of prairie vegetation to that of the plains, that is from true prairie to mixed prairie, is not due to physiographic changes or barriers. The limiting factors are entirely climatic. The area of transition is approximately 50 miles wide. The gradual change westward seems to be due almost entirely to the decrease in precipitation and increased evaporation combined with more severe intermittent periods of drought. The true prairie has often been described as occupying (in its central portion) the eastern half of Nebraska and Kansas (Clements, 1920; Clements and Shelford, 1939). But a careful, long-time study of the vegetation shows this boundary to be quite too far west.

Changes in the vegetation on the western edge of prairie are reduction in height, decrease in density, and a distinctly more xeric impress. These are accompanied by changes in composition of plant cover, and finally in the replacement of the dominants of prairie by those of the plains. Changes in population of forbs are also marked.

The grass cover on the western edge of true prairie south of the Platte River has been described by Weaver and Bruner (1954). "On the nearly level land little bluestem usually dominated but it was commonly intermixed with 5 to 15 per cent of big bluestem. These percentages were ascertained by extensive sampling by meter quadrats more than a quarter of a century ago. Little bluestem remained dominant over much of the terrain where ordinarily one would expect to find big bluestem. Where the land locally was slightly lower and received run-in water the percentage of big bluestem increased accordingly until finally rather pure open

FIG. 63. Excellent pasture condition in a large range, studied for many years, near Lincoln, Nebraska. This area has been grazed for a half century. (Below) Bluestem prairie near Carleton, Nebraska, that was taken over by wheatgrass during the drought of 1934-41. It was broken for cultivation in 1951.

stands occurred. Its turning reddish brown and often drying in summer, sometimes over considerable areas, revealed the rather unstable water supply. Many poorly drained uplands supported big bluestem where small depressions occurred. Conversely, a slight rise in the topography often resulted in nearly pure little bluestem, the bunches becoming more pronounced and more widely spaced. Westward, blue grama and buffalo grass gradually appeared between the bunches and later became intermingled as an understory." The usual prairie species accompanying little bluestem, such as prairie dropseed and needlegrass, need not be listed. "Where an additional water supply was afforded, as in depressions on hillsides or on protected north slopes and in ravines, the bluestem grasses, switchgrass, and nodding wild-rye formed limited areas of vegetation. Western wheatgrass scattered sparingly through the prairie, often occupied considerable areas on compact soils, especially those with clay pans, sometimes to the exclusion of nearly all other vegetation.

"At stations bordering the transition zone on the west [70 miles west of the area just described] the dominance of grasses had rather completely changed. Blue grama and buffalo grass were the most important and occurred in continuous and sometimes nearly pure stands. Elsewhere they were found as an understory to side-oats grama, wheatgrass, needle-and-thread, Junegrass and sand dropseed. Little bluestem frequently remained as a principal species. Associated species were red three-awn (*Aristida longiseta*), purple three-awn (*A. purpurea*), squirreltail (*Sitanion hystrix*), and various carices—penn sedge (*Carex pennsylvanica*), involute-leaf sedge (*C. eleocharis*) and thread-leaf sedge (*C. filifolia*). Little barley (*Hordeum pusillum*), six-weeks fescue (*Festuca octoflora*) and false buffalo grass (*Munroa squarrosa*) were also characteristic species. Big bluestem, Indian grass, tall dropseed and other tall grasses were often found in deep, moist ravines. Thus the dominant mid grasses were of a more xeric type and the prominent understory of short grass, not found in true prairie, extended over much of the soil without the presence of a well developed overstory of mid grasses."

Many of the taller and more conspicuous forbs found eastward did not occur or were much less frequent; conversely, western species which were rarely seen eastward occurred in and westward from the transitional area. Conspicuous among these were *Chrysopsis villosa, Sideranthus spinu-*

losus, Astragalus plattensis, Cirsium ochrocentrum, Malvastrum coccineum and *Gaura coccinea.*

In the loess hills north of the Platte, the transition occurs somewhat differently. In eastern Nebraska there is a continuous cover of prairie vegetation on hills and valleys. But west of the prairie boundary the hilltops are clothed with short grasses, blue grama alone often composing 90 per cent of the cover. The hillsides support a cover of about half blue grama and half side-oats grama, sedges, western wheatgrass, and some bluestems—vegetation very typical of plains grassland. Together these types occupy two-thirds of the area. Only in ravines, on terraces, and on the best protected lower slopes did big bluestem and other grasses characteristic of its type occur (Weaver and Bruner, 1948; Hopkins, 1951). This westward extension of the big bluestem type along valleys into the plains region is a common phenomenon. Often it is confined to narrow ribbons a few feet or a few yards wide in the very bottom of the ravine. Clearly it is here postclimax in nature, depending upon an additional supply of water beyond the actual precipitation.

If the boundary between Plains and Prairie vegetation were to be indicated by a line, 98° 30′ W longitude would be representative (Weaver and Bruner, 1954).

STUDIES IN KANSAS AND MISSOURI

Schaffner (1926) states that he has been intimately acquainted with the prairies of Kansas since 1871, and has herded cattle there in big bluestem so high that "even from the back of a pony, a stray cow could only be located by the waving of the grass." This was true even on the richer uplands (Schaffner, 1913). He states that both Sampson's and Shimek's observations—in Illinois and Iowa, respectively—are in substantial agreement with his own, and, by letter, that he is "in 100 per cent agreement" with the findings of Weaver and Fitzpatrick in "The Prairie" (1934). He compared lists of species of a prairie in south-central Illinois with those in eastern Kansas and found them to be practically identical. A vivid description was given of vegetation in Clay County, which was settled in great numbers in 1869–71. It is about 70 miles east of the line of transition to plains vegetation. "The true prairie . . . occupies the better and moister soils of the valleys, second bottoms, ravines, and the moister ordinary levels. . . . Enormous development of organic matter which became dry in autumn was the cause of the very great and destructive prairie fires which burned every plant down to the surface of the ground. In the absence of fire for several years the surface becomes matted with a thick mulch and shrubs like *Amorpha canescens, Ceanothus ovatus,* and *Meriolix serrulata* develop their perennial woody stems, while with annual fires the aerial shoots are mostly annual. Absence of fire and grazing for a number of years shows an important effect on the character of the vegetation, but it does not prepare the soils for a forest, except in special edaphic habitats, as low river flood plains and steep bluffs."

Zonations from sedge meadow to upland prairie were outlined with the principal species concerned. Salt marshes he regarded as edaphic, halophytic islands in the sea of grasses. The sandy areas were also "isolated islands in prairie." Brief description of the mixed little and big bluestem areas of the drier habitats and lighter soils is given. Chief grasses and typical forbs associated with the grasses are listed. Clay county is in the area described in "The Prairie," and Schaffner's list need not be repeated. "Many of the plants . . . have brilliant flowers of many hues and produce a gorgeous spectacle at various seasons of the year. Aside from the composition of the grass vegetation, . . . the most characteristic thing about the mixed Andropogon prairie, therefore, is the abundance of deep-rooted and large-rooted perennials and the brilliant floral display at various seasons, one wave of anthesis following another from early spring to late autumn. The grasses are usually not so tall as to obscure the other vegetation as is generally the case in the true *Andropogon furcatus* prairie." The transition from Prairie to Plains is discussed.

In Kansas, the largest remaining tract of true prairie occupies the western half of the eastern one-third of the state. This is the Flint Hills region, so called from the cherty or flinty limestone over which many of the soils have developed. From the excellent cover of its bluestem grass it is often called the Bluestem Hills. According to Fly (1946), it has an area of 3,800,000 acres. This enormous prairie extends from near the Nebraska state line entirely across Kansas and into Oklahoma, where it is known as the Osage Hills. The hilly topography is most pronounced adjacent to streams and rivers, where steep breaks and escarpments occur. Over much of the area the topography is rolling, and many nearly level areas occur. "Most of the soils of this region are very dark to nearly black, highly granular silt loams or silty clay loams with chert fragments throughout and on the surface. They rest on fragmental beds of chert or flint, are readily permeable, with enough clay and silt interspersed with the rock fragments to furnish good water storage capacity. Roots penetrate deeply. The soils are well supplied with mineral nutrients" (Fly, 1946). On flat hilltops and ridges shallow soils overlying compact clay may occur. These, as the vegetation indicates, have less favorable water relations. Mean annual precipitation varies from 30 to 36 inches. In only relatively small areas has the sod been broken for cultivation (Figs. 1, 64).

The writer studied this grassland in 1952 and 1953. While most of the prairie is pastured, numerous areas are used only for the production of hay. Many of these widely distributed mowed prairies were examined, and in some the composition of the vegetation was ascertained by numerous square-foot samples taken at random along predetermined lines. In the tables each station is indicated by a number and the number of samples taken is in parenthesis. In table 4, the first station was on level to north-sloping upland about 40 miles east of Newton. The second was on level to rolling land between Augusta and Winfield. Numbers 3 to 5 inclusive were in the Osage Hills: 3 on a gentle north slope near Grainola, 4 on gently rolling land with outcropping limestone, near Foraker, and 5 in the same prairie on a north slope below the outcrop. Number 6 was on gently sloping lowland near Cedarvale, and 7 was on rolling land south of Cassoday. Only the species that composed 5 per cent of the vegetation in any sample were included in this survey.

Examination of table 4 reveals that big and little bluestem composed 73 per cent of the vegetation, and that they were nearly always evenly distributed. Big bluestem occurred in quantity of 5 per cent or more in 71 per cent of the 275 samples, and little bluestem in 67 per cent. Next most important grasses were, in order, side-oats grama, blue grama, Indian grass, switchgrass, buffalo grass, and tall dropseed. Species that averaged less than 1 per cent but composed at least 5 per cent of the vegetation in one or more samples were hairy grama, Junegrass, Scribner's and Wilcox' panic grasses, Canada wild-rye, prairie three-awn (*Aristida oligantha*), purple lovegrass (*Eragrostis spectabilis*), sedges (*Carex* spp.), witchgrass (*Panicum capillare*), plains muhly (*Muhlenbergia cuspidata*), and eastern gamagrass (*Tripsacum dactyloides*). The eight species in the table plus forbs composed 87 to 97 per cent of the cover. Usually the others occurred in relatively few of the samples.

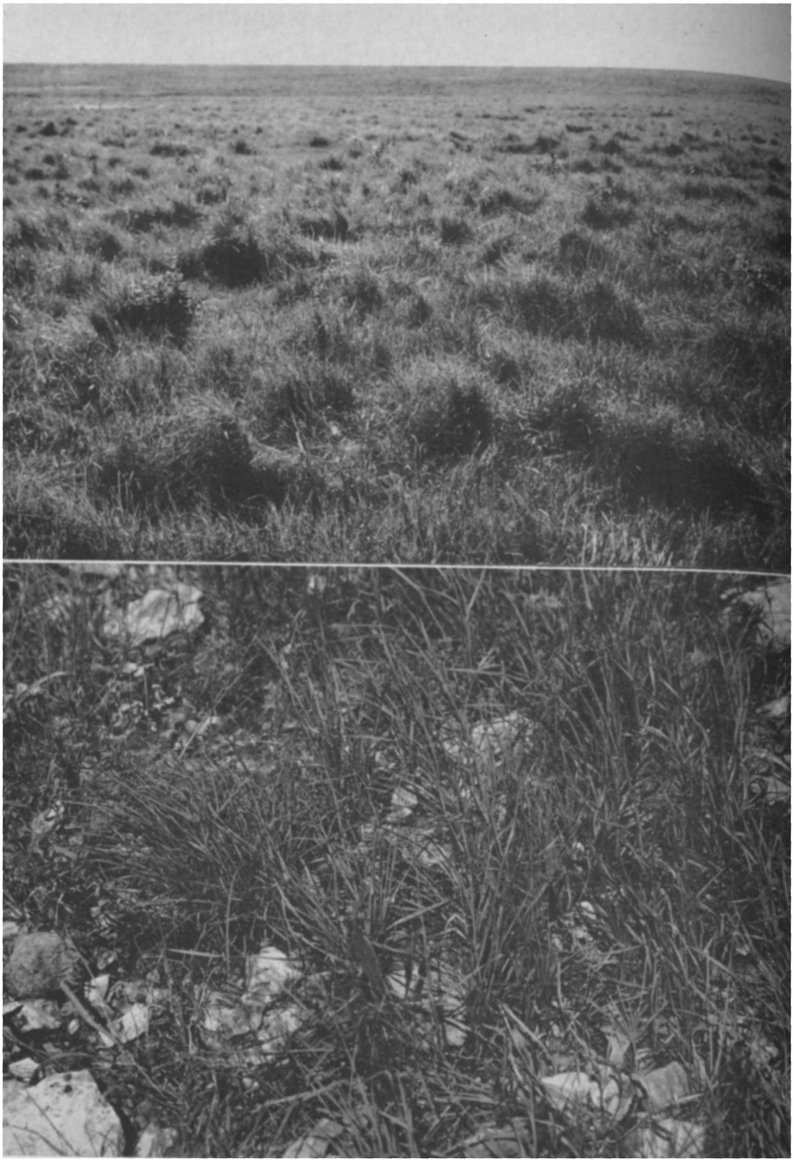


FIG. 64. Typical grassland near Cassoday in the Bluestem Hills of eastern Kansas. This native prairie is not heavily grazed. The bunches are mostly Indian grass and little bluestem. About a third of the vegetation is big bluestem. (Below) Typical view in the Flint Hills south of Manhattan, Kansas, showing the excellent production of bluestems despite the flint rocks which are of normal occurrence in the thin soils.

The average basal area in the prairie ranged from 14 to 19.6 per cent, with an average of 16.8 per cent. This is somewhat greater than the average (13.3 to 15.3 per cent) in little bluestem and big bluestem prairies of Iowa, Nebraska, and northeastern Kansas.

TABLE 4. Composition in percentage of prairie vegetation in the Bluestem Hills. Figures in parentheses show number of square-foot samples taken.

	1	2	3	4	5	6	7	Ave.
	(50)	(40)	(50)	(40)	(30)	(40)	(25)	(275)
Big bluestem	36.7	24.5	29.2	29.2	73.7	57.1	22.2	38.9
Little bluestem	45.8	38.0	41.3	22.0	7.5	32.8	53.6	34.4
Side-oats grama	5.0	.9	3.3	23.5	1.0	—	3.6	5.3
Blue grama	.6	16.1	1.1	8.5	—	.8	2.2	4.2
Indian grass	2.0	2.2	.7	2.6	10.5	2.6	—	2.9
Switchgrass	2.9	8.8	3.3	—	.1	2.1	2.5	2.8
Buffalo grass	—	—	10.0	3.5	—	.1	—	1.9
Tall dropseed	.5	4.0	7.1	.6	—	—	—	1.7
Forbs	2.2	1.0	1.6	2.8	3.8	.9	3.0	2.2
Total	95.7	95.5	97.6	92.7	96.6	96.4	87.1	94.5
Basal Area	15.1	19.5	16.8	14.0	19.6	17.3	15.3	16.8

Many pastures were also examined. Nine, in good to excellent range condition, were sampled (Table 5). They were located as follows: 1 and 2 were on gently rolling land north of Eldorado and north of Cassoday, respectively; 3 and 4 were on hilly land south of Cottonwood Falls; 5 was on a long south slope and 6 on a similar northeast slope, both north of Strong City; 7 was on a long north slope in the same vicinity; 8 was on very hilly land 14 miles southeast of Manhattan, Kansas (Fig. 1); and 9 was farther northward on bluffs near Garrison.

Although these pastures had been moderately grazed for many years, the percentage of bluestems was practically the same (74) as in the mowed prairies. Little bluestem, however, was more abundant than big bluestem in 7 of the pastures, and averaged twice as abundant as big bluestem. This may have resulted from selective grazing of big bluestem, but probably was a result of their natural distribution over the hilly land, little bluestem usually being more abundant on upper slopes. For example, on a long north-facing hillside near Strong City in the central Flint Hills, 60 samples, well spaced from hilltop to lower slope, gave the following percentage composition: big bluestem 37 per cent and little bluestem 46 per cent. Ten samples on the hilltop revealed 25 and 39 per cent, respectively, of these grasses and 21 per cent of hairy grama. On the upper slope 20 samples averaged 34 and 51 per cent of big and little bluestem, but on the mid and lower slope, 30 samples gave, in the same sequence, 41 and 17 per cent. Thus, big bluestem increased from 25 to 41 per cent and little bluestem decreased from 51 to 17 per cent from hilltop to lower north slope. On the hilltop, bare places on large rocks or shallow soil were frequently 0.5 to 1 square yard in area. On the upper slope several rock ledges reduced the area for plant growth, but on the lower slope, rocks were infrequent and the soil was relatively deep. On the opposite, south-facing slope, rock outcrops occurred at three levels with a level bench above each. Here the composition of the vegetation varied greatly not with slope but with depth of soil.

TABLE 5. Composition in percentage of high-grade pasture vegetation in the Bluestem Hills. Figures in parentheses show number of square-foot samples taken.

	1	2	3	4	5	6	7	8	9	Ave
	(25)	(25)	(25)	(25)	(25)	(35)	(60)	(40)	(30)	(290)
Big bluestem	22.4	18.4	30.4	32.4	32.2	19.4	37.1	23.9	8.4	25.0
Little bluestem	57.0	48.0	26.1	31.1	46.4	60.0	45.6	58.6	70.1	49.3
Side-oats grama	2.7	19.9	17.3	5.0	3.8	3.2	3.9	1.9	.2	6.4
Blue grama	3.6	—	—	—	.2	—	.1	.1	8.6	1.4
Indian grass	7.2	.4	1.6	4.8	7.0	7.2	.6	2.0	3.7	3.8
Switchgrass	1.6	—	—	1.0	1.4	1.4	.8	—	1.4	.8
Buffalo grass	—	2.6	9.6	2.0	—	1.2	—	—	.2	1.7
Tall dropseed	.4	1.5	1.6	1.6	.8	—	1.3	.7	.2	.9
Hairy grama	.1	8.6	7.0	4.2	1.0	2.4	3.6	6.4	—	3.7
Sedges	.1	—	2.6	.8	1.4	2.0	1.3	3.4	—	1.3
Forbs	2.8	.6	3.8	1.3	1.6	1.2	5.7	2.4	.8	2.2
Total	97.9	100.0	100.0	84.2	95.8	98.6	100.0	99.4	93.6	96.6
Basal area	16.5	17.6	15.4	17.5	17.2	19.5	18.0	14.3	21.0	17.4

Big bluestem occurred in quantity of 5 per cent or more in 78 per cent of the 290 pasture samples; little bluestem in 85 per cent. Thus, in pasture both grasses had a much higher frequency (in amounts exceeding 5 per cent) than in prairie, where, in the same order, the percentages were 71 and 67.

Despite increases in side-oats grama, Indian grass, and hairy grama, these high grade pastures had essentially the same composition as ungrazed prairie. Of the species that attained an average of less than 1 per cent but composed at least 5 per cent of the vegetation in one or more samples, all but windmill grass (*Chloris verticillata*) appears in the prairie list. The basal area was also practically the same as in prairie. The absence or scarcity of weedy invaders was marked.

According to Anderson (1953), "The Flint Hills have been used intensively for grazing since the early 1880's when southwestern cattlemen discovered that animals could be fattened to market conditions on them in a single summer season." They were rapidly fenced at this time and, therefore, "have practically no history of intensive use as open range. . . . The major objective has been to obtain rapid steer gains during the early part of the growing season. . . . For this reason the cattlemen have demanded adequate acreage allowances. This, together with the fact that many animals attain market condition during midsummer and are then removed for sale, has left these pastures understocked in the last half of the growing period, thus a large volume of growth and relatively adequate carbohydrate food reserves have been allowed to accumulate each season." Consequently, despite annual burning in spring, the large, well managed ranges—some over 10,000 acres in extent—are still in good to excellent condition. Fair to poor pastures occur mostly where both farming and stock raising are practiced and the smaller ranges are more or less continuously overstocked.

A study of a total of 30 prairies and pastures was made by the writer. In a lowland prairie near Eldorado, Kansas, big bluestem in August was 12 to 16 inches high and composed 85 per cent of the vegetation. There was 1 to 4 per cent Indian grass, a similar amount of little bluestem, and most of the remainder was eastern gamagrass (*Tripsacum dactyloides*), and needlegrass (*Stipa spartea*). Conversely, on upper slopes of hills little bluestem often composed two-thirds or more of the vegetation.

The following indicates degeneration. On some hillsides in ranges in fair condition, big bluestem intermixed with clumps and small patches of Indian grass clothed the lower slopes. On thinner soil, where drought damage had been severe, tall dropseed formed streaks and patches. On spots with clay pan, buffalo grass and western wheatgrass grew in dense stands. Belts of big bluestem below rock outcrops alternated with blue and hairy grama and patches of buffalo grass on and above them. On the nearly level, rocky upland, Indian grass covered a third of the area, little and big bluestem were intermixed, and some switchgrass also occurred. This illustrates the complexity of the vegetation, which varied greatly with depth of soil and degree of grazing.

On the thin soils of outcrops and ridges and on "tight soils" on many hilltops, hairy grama, blue grama, side-oats grama, buffalo grass, and June-grass were the chief species. In many prairies various shrubs grew on the rocky hilltops and limestone ledges. Chief among these were smooth sumac (*Rhus glabra*) and skunk brush (*R. trilobata*), which varied from scattered plants to rather dense stands. Redroot occurred here and on the hillsides, and coralberry (*Symphoricarpos orbiculatus*) in the ravines, but sometimes on the hills as well. Dogwood (*Cornus*) was found mostly in grassland adjacent to streams. Lead plant occurred thickly in most pastures—sometimes it was impossible to walk through the grass without constantly touching this legume—but in others it was almost absent.

In these grasslands, drought and fire had left practically no Kentucky bluegrass; needlegrass and prairie dropseed south of the Kansas river were almost rare. Indian grass and switchgrass were usually more abundant than northward, but there are few suitable habitats for sloughgrass. Eastern gamagrass is commonly found on low ground and springy places on hillsides. Silver beardgrass (*Andropogon saccharoides*) is an occasional invader near the Oklahoma boundary, but it was rarely found in undisturbed prairie.

In experimental pastures in typical Flint-Hills range near Manhattan, Anderson (1953) ascertained the following percentage composition of the vegetation: little bluestem 24, big bluestem 18, Indian grass and side-oats grama each 8, blue grama and hairy grama together 6, buffalo grass nearly 5, and introduced Kentucky bluegrass 8. Perennial grasses composed 84 per cent of the vegetation and perennial forbs about 5 per cent. Basal area was 21 per cent.

Beyond the Flint Hills, the bluestem prairies spread westward. Excellent hay fields and extensive pastures once prevailed. A gradual decrease in stature, thinning of stand, and increased dominance of the less mesic grasses occur as the climate becomes progressively more arid. In the transition to mixed prairie, the local effect of topography was often beautifully illustrated. In certain long, gently sloping ravines, water supply in the shallow ditch was sufficient to support sloughgrass and a border of switchgrass with nodding wild-rye. Where heavy rains occasionally caused the water to spread two or three rods laterally, bluestems and Indian grass occurred. Then abruptly, where the slope gently ascended, a carpet of short grasses and side-oats grama was spread, with bunches of bluestems scattered through it only on the lower slope. Typical Mixed Prairie covered the hillsides and hilltops.

Study of prairies of northeast Kansas southward to the Kansas River was included in the survey of prairies of Iowa and Nebraska (Weaver and Fitzpatrick, 1934). Few detailed studies have been reported on the area southward (Hetzer and McGregor, 1951). Many of these grassland areas have been examined, but not in detail, by the writer. Everywhere areas of bluestem prairie may be found as hay meadows or pasture land. In the southeast, as in western Missouri, the planosols are droughty, a soil condition which helped to maintain the prairie sod unbroken. Big and little bluestem are the chief dominants; on low flat land big bluestem prevails. Indian grass is often abundant, and, like eastern gamagrass, frequently composes 8 to 10 per cent of the vegetation. Tall dropseed is often plentiful. Communities of switchgrass and sloughgrass are frequently well developed. Lists of forbs are composed mostly of species common northward but there is, as in all of southern Kansas, a distinctly southern element. This has little effect either upon the general appearance or the structure of the vegetation. These prairies extend into eastern Oklahoma, where they have been described by Bruner (1931). It is unfortunate that more study, aside from floristic, has not been made either here or in Missouri.

Palmer and Steyermark (1935) in "An Annotated Catalogue of the Flowering Plants of Missouri" separate the prairie region of the state into the glaciated and unglaciated parts. The first occupies most of the area north of the Missouri River. It had practically the same composition as adjacent prairies in Iowa. "A typical prairie flora, consisting largely of grasses and perennial herbs in which legumes and composites played a conspicuous part, covered the uplands before they were brought under agriculture. Only a few traces of this now remain, the best examples being along the fenced right-of-way of the railroads. Most of the species of this flora are also found in the unglaciated areas farther south." The unglaciated part that was covered with prairie occupies much of the western third of the state south of the Missouri River. "The true prairie flora of the uplands is quite similar to that of the glaciated sub-division, . . . but with an increasing proportion of southwestern species towards the south."

Certain northern species, found north of the Missouri River, are absent here. Large tracts of this area have been kept for hayland and for pastures. One of the best prairie areas occurs in the three counties bordering southeastern Kansas.

Drew (1947), working near Columbia, Missouri, compared scattered relics mostly along railroad right-of-ways with native prairie that had been pastured, mowed, or burned over a period of 125 years. Lists of species of dominants and other plants show the characteristic composition of bluestem prairie.

STUDIES IN OKLAHOMA AND TEXAS

Bruner (1931) made extensive studies of Oklahoma prairies. The following is from his "Vegetation of Oklahoma." True prairie lies west of the oak-hickory deciduous forest and extends westward approximately three-fourths of the distance across the state, excluding the panhandle. Precipitation is about 25 inches on its western border. Prairie does not occur throughout this region, however, since more than a third of its central area is occupied by oak-hickory savannah. "Savannah is bounded on the west by a line extending southwestward through Osage county [96° 45′] and then only slightly westward to Jefferson county [97° 45′ west longitude]. It is separated very sharply from true prairie on the west by the transition from sandstone soils to the heavier soils originating from clays and shales. The eastern boundary is the climax deciduous forest, but the area is not continuous since a large lobe of true prairie occurs on the fine textured soils of the northeast. Thus, the savannah forms a belt usually 50 or more miles in width extending across the state." Many islands of savannah woodland occurred in the prairie at considerable distances from the margin of the community.

"The savannah is characterized by a scrubby growth of oaks usually associated with hickory [chiefly blackjack oak, *Quercus marilandica,* post oak, *Q. stellata,* and hickory, *Hicoria buckleyi*]. Grassland alternating with limited areas of open woodland is characteristic of the northern and southern extremities, but throughout the central part the woodland dominates and grassy areas occur only locally. Here the forests frequently characterize the landscape for many miles . . . . Climatically the area should be dominated by grasses but the open, porous soil permits the growth of trees and, in places, turns the balance decidedly in their favor." Characteristic grasses of savannah are mostly different from those of prairie, and the forbs fell into two groups, those associated with the wooded areas and those associated with grassland.

The prairie west of the savannah passes gradually into mixed prairie; the transition is entirely climatic. It was characterized by the *Andropogon scoparius* type with *Andropogon saccharoides* (silver beardgrass) second in importance. "Little bluestem is the principal sod-forming grass of the region and occurs over large tracts in almost pure stands. On the drier ridges of the true prairie or where heavily grazed, it . . . assumes the bunch habit. Thus, under natural conditions, the appearance of short grass in the sod of true prairie indicates thin soil or other areas unusually low in water content; otherwise it is a reliable indicator of overgrazing. . . . *Andropogon furcatus* is common throughout the prairie. It is an indicator of unusually high water content being largely confined to depressions and protected slopes. *A. chrysocomus* [a form of *A. hallii*] not only indicates a deep moist soil but one containing considerable sand . . . . *A. saccharoides* occurs especially in the southern part of true prairie. Its ecological requirements approach those of *A. scoparius* more closely than do those of either of the preceding grasses. . . . It is found, as a rule, in habitats much too dry for *A. furcatus*." *Koeleria cristata* and *Stipa spartea* occur only in scattered bunches. *Agropyron smithii* is of common occurrence and is a local dominant in low, broad valleys or on gently rolling areas especially in the north-central portion of the state. *Bouteloua gracilis,* and *B. hirsuta* on sandy soils, clothe rather extensive areas where the tall grasses have been suppressed by grazing. *Sporobolus asper, Poa arida* and *Tridens flava* are common but less important grasses.

Lists of societies of each of the seasonal aspects are given and some are described. "The spring beauty (*Claytonia virginica*) is a low-growing, bulbous, perennial which blooms four or five weeks in early spring and then, like many other prevernal plants, entirely disappears. The least bluets (*Houstonia minima*) is the smallest as well as one of the earliest plants of the prairie. In favorable seasons extensive carpets of green plants only an inch or two high are given a purple cast by their tiny but abundant purple-blue flowers. . . . Wild onions form extensive societies. Early in spring *Allium nuttallii* appears and soon extensive communities characterize the drier, prairie soils. The societies are frequently so dense that other vegetation is obscured. After a brief period of blooming the plants rapidly mature and soon disappear completely except for their subterranean bulbs. . . . The asters mark the beginning of the serotinal aspect and are the last to disappear in fall. In favorable seasons, they may be found blooming in November long after the goldenrods, blazing stars, and most other species have matured and died." Similarity of the forbs to those described in the western section of true prairie northward is very great. But there is also a considerable element of southern species which reach their northern limit here or in southern Kansas.

In the less extensive prairie east of the savannah the precipitation is 35 to 40 inches, and the vegetation is much like that of lowland prairie northward. The luxuriant vegetation is composed of many species, mostly of tall grasses.

"The most typical expression of the . . . prairie of eastern Oklahoma is found in alternations and mictia of *Andropogon furcatus, A. nutans, A. scoparius,* and *Bouteloua racemosa.* The big bluestem (*Andropogon furcatus*) is found in slight depressions or on more moist slopes where it is frequently associated with *Andropogon nutans.* . . . Slightly drier slopes and areas which are more exposed or better drained are occupied by *Andropogon scoparius* which is usually accompanied by *Bouteloua racemosa.* Where the soil is still more moist than that occupied by the big bluestem, *Panicum virgatum* is usually dominant. In ravines or depressions or areas where the soils have a slightly coarse texture, *Panicum* dominates or alternates with the big bluestem. *Elymus canadensis* has much the same requirements as *Panicum* and is found especially where the soil has been disturbed. Areas with a very high water content are characterized by sloughgrass, *Spartina michauxiana.* Sloughgrass occurs only where the soil is saturated at intervals."

The lists of forbs in each of the four seasonal aspects contain numerous species that are common to more northerly lowland prairies and that do not occur in the lists for the western Oklahoma true prairie. A considerable number of more southerly distributed forbs are also found here.

Carpenter (1940) presented a considerable amount of information on true prairie in his study of "The Grassland Biome," and an excellent list of references on studies in grassland by both botanists and zoologists. Data presented by Smith (1940) apply to true prairie, and the paper presents an excellent bibliography on the effects of overgrazing on certain birds, prairie insects and rodents.

Rice (1950) studied the growth and floral development of five species of range grasses in central Oklahoma. He found that the number of leaves with blades expanded on a given culm was a fairly accurate index of the time of floral initiation. In big bluestem, for example, the number was 9 to 11 but only 5 or 6 in switchgrass.

A southern extension of true prairie located between the Eastern and Western Cross Timbers of northern Texas has been studied by Dyksterhuis (1946). The following is an abstract. This body of grassland, the Fort Worth Prairie, approximately 10 to 30 miles wide and about 110 miles in length, lies between the Red River on the north and the Brazos River on the south. "The principal soils are intrazonal Rendzinas with immature profiles resting upon soft limestone parent materials. These calcareous clays have the dark color and high organic content characteristic of the prairie. . . ." Average annual precipitation is approximately 32 inches. Settlement swept across this prairie in the single decade of 1850 to 1860. Cattle raising was at first the chief industry. Real settlement began in 1870. Barbed wire became generally available in the 1870's and by 1883 most progressive ranchers and most farmers had fenced with barbed wire. In 1939–1944, when this study was made, the eastern portion of the prairie was nearly all under cultivation and the western part was mostly range land. Eleven areas of relic climax vegetation were selected for detailed analyses. These were fairly well distributed throughout the length of the prairie. None had been grazed or burned for at least 5 years nor had they ever been cultivated or subjected to other types of severe disturbance. They included large hay fields surrounded by range land, unmowed areas within such fields, and a cemetery with hay land or range on three sides.

"The most conspicuous feature of the relict vegetation . . . is the overwhelming dominance of *Andropogon scoparius* which constitutes nearly two-thirds of the total plant cover. Observational studies from one end of the prairie to the other support the tabular evidence that *Andropogon scoparius* is the principal climax dominant. *Bouteloua curtipendula* with a [high total] coverage of 8.11 per cent is ranked as the second most important species though far less important than the former." Other species which furnished 2 to 5 per cent of the total plant cover were *Sorghastrum nutans, Sporobolus asper,* and *Bouteloua hirsuta.* Perennial forbs furnished 8.2 per cent. Moreover, all of these grasses had a high frequency. The major climax grasses begin active aerial growth near the first of March and produce a ton or more of forage per acre by the first of June.

His study of seasonal development of the vegetation is also of great value. Numerous species resumed or accelerated vegetative growth late in January and in February. By March 1 prairies from which old growth had been removed by fire or grazing presented a general greenish appearance. On March 15 leaves of little bluestem averaged 2 inches in height. Both grasses and forbs had made considerable growth. By October 1 species in bloom generally included *Andropogon furcatus, A scoparius, A. saccharoides, Sorghastrum nutans* and *Sporobolus asper.* No frost had occurred by November 15, but the prairie landscape suggested autumn because of the general absence of blossoms, the reddish cast of the Andropogons, and the dead stems of numerous species of forbs. Blossoms of a few forbs were found in December and early January.

The present community is a grazing disclimax in which *Stipa leucotricha* and *Andropogon saccharoides* are the major dominants. These grasses had an average coverage of 20.3 and 7.8 per cent, respectively, and both had a frequency of 62.4 per cent. The same data for *Andropogon scoparius* were 4.7 and 38.5 per cent. Thus, "Increase in coverage of *A. scoparius* affords a measure of the rate and extent of ecological succession on rangeland; while increase in *Stipa leucotricha* indicates ecological retrogression."

In a study of the postclimax Western Cross Timbers, Dyksterhuis (1948) ascertained the original vegetation beneath the sparse overstory of post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*) was also dominated by *Andropogon scoparius.* Associated with it were the two tall grasses, *Sorghastrum nutans* and *A. furcatus* as lesser dominants.

The characteristics of the composition of plant communities of grasslands in general (i.e. their floristics, structure, and resulting physiognomy) and methods of measuring them, have been thoroughly discussed by Hanson (1938, 1950).

CHAPTER 12

Beginning of Drought

PRECIPITATION had been somewhat deficient and drought periods occurred in 1931 and 1933 when moisture was not available to the roots of plants in the surface foot of soil. This, however, had little effect upon the vegetation. Then came the summer of 1934 when drought was the greatest ever recorded in true prairie. This offered an exceptional opportunity to study the response of the native plants to extremely adverse water relations. Because of an intimate knowledge of their habits during normal years, this complex and difficult task was much more readily and accurately performed. The early studies were made near Lincoln, Nebraska, but similar conditions prevailed in general throughout the true prairie west of the Missouri River. A better understanding of the severity of drought may be had, if the usual or predrought environment is understood.

PREDROUGHT ENVIRONMENT IN PRAIRIE

Physical factors of the environment of prairie were measured at Lincoln, Nebraska, during each growing season for a period of 13 years (1915–1928) preceding the great drought of the thirties (Weaver and Himmel 1931). Continuously recording instruments were operated in an extensive area of unbroken upland prairie. Lincoln is centrally located in the midst of the western true prairie, and conditions at this station were, in general, those prevailing over wide areas.

The mean annual precipitation for a period of 50 years preceding the great drought was 28 inches. Nearly 80 per cent of the precipitation falls during the growing season and 14 inches during the three months of May, June, and July, a seasonal distribution of moisture favorable to the growth of grasses.

The Prairie soil is rich, deep, and fertile. The mellow, granular, dark-colored topsoil, enriched by thousands of generations of grasses, extends usually to depths of 12 to 18 inches. Beneath is a zone of higher clay content and lighter color, which extends to a depth of about 3 to 4 feet. Underlying this soil (solum) is the parent material. It is often yellowish or at least lighter in color than the solum, partly because of its lower content of organic matter and partly because it is rich in lime. The parent material extends many feet in depth. Although lime has been eluviated from the A and much of the B horizon, the soil is neutral or only slightly acid, since a constant supply of lime is brought to the surface by the grasses and deposited there when they die.

The water content in the surface 6 inches of upland soil varied widely and rapidly, often 10 per cent or more during a single week. Only twice during the 13-year period was the water content reduced to the nonavailable condition. At no time was the water available for plant growth entirely exhausted in the 6- to 12-inch layer. In the second, third, and fourth foot the available supply ranged between 5 and 21 per cent, except for a few times when the minimum fell to 1 to 3 per cent. The soil below four feet had been found fairly moist and a total water content of 20 per cent or more was not unusual. It is believed that under the grassland cover the deeper subsoil was constantly moist to great depths.

Average day air temperatures in the cover of vegetation sometimes reached 90° F. but were more usually between 75° and 85°. Maximum daily temperature sometimes reached or even exceeded 100° F. Average day relative humidity varied between 50 and 80 per cent during years of greater rainfall but fell frequently to 40 to 50 per cent during drier years. Only rarely was the humidity less than 20 per cent.

Partly due to the increasing demands of growing vegetation for water and partly to seasonal distribution of rainfall, impending drought is, in general, more imminent with the advance of the growing season.

DROUGHT IN SPRING

After an unusually warm winter with light snowfall, the spring of 1934 began very dry.[1] March had practically no efficient rainfall, and April and May each had less than half an inch. The arid conditions were accentuated by high winds with an average mean daily velocity of about 12 miles per hour. Frequently these carried great quantities of dust which lodged among the grasses but readily rose again into the air. Drought in the mixed prairie westward had already prevailed for a year, and the source of dust was

[1] This story of the first year of great drought is an adaptation from the article by Weaver, Stoddart, and Noll, Ecology 16, 1935, and from Weaver and Albertson, Ecology 17, 1936. Four of the 49 figures in the second article are reproduced.

the fields and denuded ranges of Oklahoma, Kansas, and adjacent areas. Temperatures were often abnormally high and much clear weather prevailed. The available water content of the upper foot of soil was sufficient, however, for certain early grasses and prevernal bloomers to develop vegetatively. Their period of blooming was considerably shortened, however, and flowers were reduced both in size and number. Hence, even this earliest aspect was rather poorly developed in the wind-swept, dust-covered, and dried vegetation of the previous year.

Many species of the vernal aspect developed only poorly. Not infrequently the flowers withered and dried without producing seed. Many of these—violet, strawberry, prairie cat's-foot, and oxalis—are shallowly rooted. Conversely the deeply rooted ground plum, false indigo, and a few others dominated the aspect. Bluegrass in the understory remained in a half-wilted condition until it dried late in May. In fact, the drying bluegrass gave the prairie its early dead appearance. Estival and autumnal forbs developed slowly under the great evaporation stress resulting from the hot, dry, windy weather.

The flower stalks of the shallowly rooted Junegrass were only a fourth the normal length and the plants dried in mid-May. The usual 3-foot stature of needlegrass was reduced to 12 inches, and was scarcely exceeded by the flower stalks; the leaves rolled and the plants dried.

EARLY SUMMER DROUGHT

The severe drought of late May was accentuated in June. Water content of the soil was greatly reduced, and drought made a deep impress upon the uplands. The normal deep-green of the foliage was now a yellow-green, a condition undoubtedly caused by a decreasing nitrogen-fixing bacterial activity in the dry soil. The foliage level was only 5 to 7 inches high, instead of the normal 8 to 14 inches. Various shallowly rooted plants had dried. Temporary amelioration of the arid conditions occurred on June 8 and 14, when light rains wet the upper 3 to 4 inches of the parched soil. The July rainfall of 0.4 inch was dissipated in light showers. Deeply rooted plants were drawing heavily upon the moisture supply below 3 feet. Repeated soil sampling showed that less than 2 per cent of water was available even at this depth.

Early in June the leaves of little bluestem were tightly folded, the tips had dried, and some leaves had a reddish tinge as in October. Water content within the plant decreased from 77 per cent in April to 36 per cent in midsummer, when the plants died. Soon the leaves of the more deeply rooted big bluestem began to wilt. In the driest places both species of bluestems had withered and turned brown as if visited by an early frost. Side-oats grama was wilted and Indian grass was clearly in great distress. It appeared to have migrated too far up the slopes during years of abundant moisture. The tendency to blossom early was marked in many species. Smooth goldenrod blossomed in mid-June instead of late July. Also the period of flowering was short. In general, the prairies were only scantily decorated with flowers in early June, and there were almost none after June 15. Indeed, many summer bloomers had wilted and dried. Conversely a few species with roots extending 12 to 20 feet into the cool, moist earth produced flowers in extraordinary abundance. Among these were tooth-leaved primrose, many-flowered psoralea, and prairie rose. Water content of the rose decreased only a little, from 55 per cent early in June to 50 per cent at the end of July. This slight decrease was also ascertained in other very deeply rooted plants. But even the rose, which normally continues to blossom well into July, had ceased blooming by the middle of June. Various other deeply rooted species blossomed very early and for only a short time.

On low ground the grasslands showed little effect of drought; they were withstanding desiccation in a remarkable manner. But the thinner soils and drier areas on hilltops and upper slopes were clearly delimited by the drying vegetation. The unreplenished moisture was decreased daily by vigorous absorption by half-wilted plants. The level of available water sank daily, to 3 feet in depth in July and 4 feet in August, with only a modicum available to 6 feet. As drought began its steady and unhindered march down the slopes, responses of the various species to water deficit, as shown by wilting and drying or unarrested development became clearly apparent.

DEPTH OF ROOTING AND REMOVAL OF TOPS IN RELATION TO DRYING

Among the upland grasses, big bluestem was the last to succumb, since its roots extended deepest. A remarkable phenomenon in early drought was the brighter green of the scattered tufts of big bluestem contrasting with the reddish-brown bunches of little bluestem, whose roots were less extensive. Big bluestem remained green long after little bluestem, prairie dropseed, and side-oats grama were apparently dried beyond recovery and after needlegrass had gone into a condition of drought-dormancy.

In experimental areas where the grasses had been clipped and the leaf surface for transpiration had thereby been repeatedly reduced, big bluestem remained turgid above ground many days after the unclipped plants had wilted. This phenomenon also was clearly evident in many half-deteriorated native pastures where, although the soil was moist at a depth of four feet, the more shallowly rooted dominant bluegrass had dried but the big bluestem and other deeply rooted species continued to absorb the precious water. Lead plant developed vegetatively as if there were no drought. Its roots extend 12 to 15 feet into the cool moist earth. These plants appeared exceptionally robust because of the low stature of the grasses. Numerous deeply rooted forbs behaved in a similar manner.

That the wilting and drying of the prairie plants was not due to high temperatures and low humidities alone, but primarily to low water content of soil, was shown in many ways. Stiff sunflower, for example, was often completely wilted and the leaves dried even in sod where big bluestem flourished, while a foot or two distant in cultivated land, the same species was 3 or more feet tall, abundantly supplied with flower heads and continuously turgid. Moreover, where local areas in the prairie were heavily watered, not only the revived grasses but all of the forbs as well continued throughout the hottest and driest period without noticeable wilting. Forbs that could not be found elsewhere reappeared. Some that had ceased blossoming burst forth in full bloom.

MIDSUMMER DROUGHT

The most trying period began about June 20. The half-cured little bluestem on hilltops and xeric slopes crunched like snow when one tread upon it. Even the accompanying big bluestem was half dried. Then followed a period of most intensive drought. A terrific heat wave swept over the prairie. It continued until the last week in July. During this time the scorching sun seared the prairie as if by fire, and life in all but the most deeply rooted species retreated underground. The average daily maximum temperature increased week by week from 88° to 111° F., and average day temperatures ranged upward from 77° to over 100°. The average day minimum humidity over a period of six weeks did not exceed 22 per cent, and it was as low as 15 per cent. Minimum humidities of 3 to 5 per cent were recorded on certain afternoons. Wind movement was frequently high. The rate of evaporation was often twice and sometimes nearly three times as great as that recorded in prairie during the three preceding years. The small amount of water in the subsoil was soon exhausted. These are the factors that intensified the drought.

No rain fell; clouds were rare—in fact during the latter half of the period they seldom formed. The light was intense; the dust-filled, yellow, western sky in evening portended another day of drought. The hot southerly winds blew as from a desert; drought that had bleached the green hilltops to patches of brown alternating with white, now crept down the slopes. Late in July the area of dried grasses had extended to the lower slopes.

The persistence of the grasses and forbs was remarkable. Unlike a field of maize, wheat, or clover which can sometimes be ruined by a few days of drought, the native forbs yielded only a little each day. Neither were their leaves torn and frayed by the wind as were those of cultivated crops. There were no blossoms to tell the seasonal aspect, for the oven-like heat and dryness prevented flowering. Only after days of wilting and rolling or folding of the leaves, weeks of battling the intense heat, high winds, and low humidities under the cloudless skies, did life finally retreat underground to wait the advent of rain. The bronzes, yellows, and golds, colors normally appearing late in autumn, were of short duration. For soon the blazing sun had scorched the withered grasses until the prairie had the bleached appearance common to the late winter aspect.

DROUGHT IN LOWLAND

As the weeks passed without rain, the lowlands began to reveal the impact of drought. Early in August big bluestem on the lowest slopes lost its green color, wilted, and dried. This indicated that the water supply within reach of the roots was practically exhausted even on the low ground. With the drying of the bluestem, switchgrass, nodding wild-rye and even sloughgrass showed great distress. The leaves were bleached to a yellowish green. Many species of forbs, as tick trefoil and saw-tooth sunflower, at home in the ravines and on lowlands, were succumbing to the drought. In one ravine the water table had been lowered from very near the soil surface to a depth of 5.5 feet.

Scattered showers and periods of cool weather ameliorated the drought after the first week in August. But greening and growth were not continuous nor did they occur generally. Growth had scarcely commenced before the surface water supply was again exhausted. One had to observe closely to perceive the new development—the general bleached aspect of the prairie remained unchanged. On lowlands along the Missouri river, entire meadows of big bluestem dried. Cattails and rice cutgrass in the marshes became dry and brown. Clearly the prairie suffered a great catastrophe during this year of terrible heat and drought.

It is believed that the great loss of vegetation was due to drought and not directly to high temperature. Grasses in experimental plots that were watered did not die. Increased temperature decreases the relative humidity, which results in increased water losses by transpiration, as well as by evaporation from the soil. It is usual for high temperatures and drought to work together in the destruction of vegetation, but drought is nearly always the direct cause of death, a fact which was later shown experimentally (Mueller and Weaver, 1942). The severe conditions of drought were aggravated by high winds and often by dust storms.

EFFECTS OF THE FIRST YEAR OF DROUGHT

Supply of moisture the following spring and early summer was replaced to a depth of several feet. It was adequate to promote excellent growth. Thus, the dead vegetation was readily distinguishable from the living. Where the basal cover had previously been ascertained, it was now clear that the loss ranged from a third to half of the vegetation. The major damage was in the nature of openings as if burned in the prairie carpet. Because of the unusually good development of the foliage in early summer, superficially the cover appeared normal. To appreciate the losses one had to penetrate the foliage cover and examine the soil surface.

In areas moderately affected by drought, spaces bare of living plants were more or less isolated. But even these bore their toll of dead crowns of grasses. Where drought had been more severe, the open spaces were plentiful and formed an irregular network of unoccupied soil surface. Openings of moderate size graded imperceptibly into larger ones a square yard or more in extent (Fig. 65). Elsewhere, the cover was so decimated that the terrain appeared almost bare throughout the summer with only remnants of a former population. Where losses were only 10 to 25 per cent, a good matrix of native grasses remained. In some areas the more mesic bluestem, Indian grass, and bluegrass had disappeared and only blue grama, side-oats grama, and certain xeric forbs were found. Truly the prairie had suffered a major catastrophe. This is a review of destruction wrought in a single prairie in eastern Nebraska.

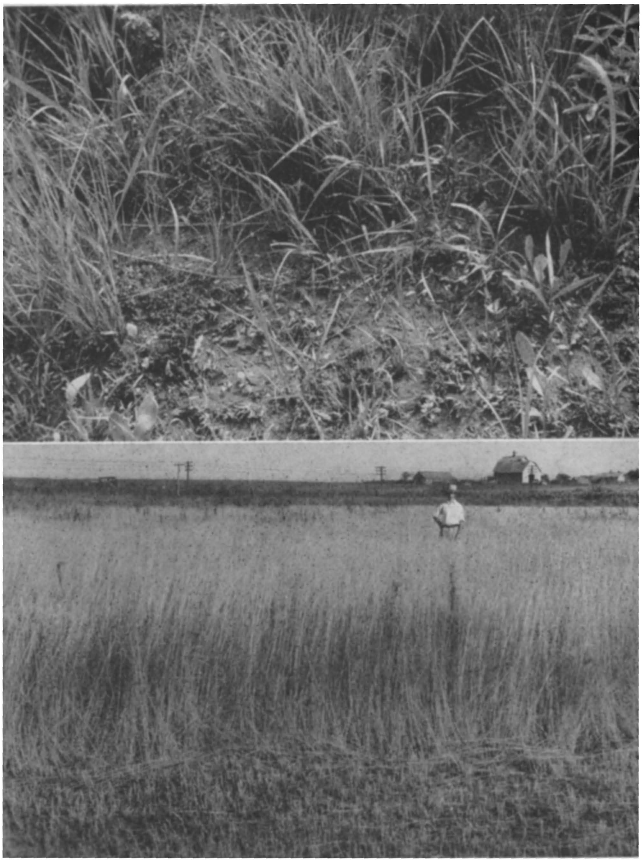


FIG. 65. Typical bared space in little bluestem prairie resulting from drought. June 7, 1935. (Below) Lowland formerly dominated by big bluestem which has been entirely replaced, as a result of drought, by a thick stand of western wheatgrass.

Thirty large prairies were examined in Iowa, Nebraska, and east-central Kansas. These were the same grasslands repeatedly studied preceding the drought. At that time each prairie was investigated and fully described as a unit. Thus changes wrought by the drought were readily ascertained.

Some prairies on the deep loess soils of southwestern Iowa as well as some northeastward on the glacial soils had not been greatly harmed. Others had suffered a loss of 20 to 50 per cent of certain grasses on the more exposed slopes. Death by drought increased southwestward, varying from 20 to 50 per cent on thinner soils of exposed ridges to as much as 80 to 95 per cent losses farther west on nearly level land. Great destruction had also occurred even on low ground, sometimes resulting in an entire change in plant population. In many western prairies, for example, patches of wheatgrass, from a few to many square yards in area, grew where bluestems had died (Fig. 65).

All of the native grasses suffered some loss, but death was greater among those with relatively shorter roots, such as little bluestem, Junegrass, young needlegrass, and Kentucky bluegrass. This occurred everywhere but was especially pronounced where they occupied the drier soils. In some prairies where little bluestem alone formed 60 to 80 per cent of the predrought cover, all but 5 per cent of the bunches had died. Prairie dropseed also sustained losses, which, like those of Indian grass, often amounted to 80 or more per cent. Big bluestem, because of its deeper root system, was usually injured least, but over considerable areas of certain prairies it failed to grow (Fig. 66).

Loss of Ground Layer

With the wilting of the grasses on uplands and their death over great areas, plants of the ground layer were not afforded the usual protection from insolation at this most critical time of great drought. Most of the understory species suffered heavy losses and in the drier, western true prairies practically all succumbed.

Prairie cat's-foot, one of the seven most important prairie forbs, was all but swept away from the more western prairies and suffered enormous losses elsewhere. Kentucky bluegrass was almost completely killed except in a very few unusually wet spots in these prairies. Eastward it died on hilltops and exposed slopes and even on lower ones where debris had been removed by fire. In many nearly level areas it remained only in the bottom of ravines.

Scribner's and Wilcox' panic grasses and other low-growing species were affected to an extent similar to that of bluegrass, and were rarely found. Long-fruited anemone and rosettes of hawkweed practically dis-

FIG. 66. An open stand of big bluestem resulting from the death by drought of the more shallowly rooted little bluestem at Carleton, Nebraska. (Below) Dense stand of six-weeks fescue (*Festuca octoflora*) in prairie near Belleville, Kansas, on soil formerly occupied by little bluestem.

appeared. Strawberry, species of violets, and blue-eyed grass were further examples of plants that sustained great losses. Stiff bedstraw and Canada anemone and many other species of lowland were greatly depleted or failed to grow.

Increase of Certain Prairie Grasses

Western wheatgrass made the greatest increase of any native grass. Formerly it occurred only sparsely in the eastern prairies and was confined mostly to the thinner soils and especially to roadsides, soils with clay pans, and greatly disturbed places. It was now entrenched, at least in small areas, in practically all of the drought-stricken prairies and was taking possession of extensive areas in others. Especially westward, it had caused profound change. It thrived in places where the bluestems had died, and it promptly claimed areas overwhelmed by dust, which was very destructive to the bluestems. From these vantage points it rapidly extended its territory. Only deeply rooted forbs remained in the dense sod of this mid grass. Its early growth in spring and migration by long, slender rhizomes were distinct assets.

In grasslands bordering the mixed prairie, buffalo grass, profiting by the death of its taller competitors, was increasing its holdings, often very rapidly. Blue grama was behaving similarly, although without stolons its spreading was much slower. Eastward it remained almost unharmed in the same local areas where little bluestem had died. Here it was spreading.

Six-weeks fescue had become abundant in bared areas of eastern Nebraska prairies. Westward it was locally in complete possession of hilltops and slopes where the dominant grasses had died. Bunches of 20 to 30 stems of this annual were found regularly growing in the dead crowns of little bluestem. In a single square meter, 200 bunches were not uncommon. The abundant and very light seed ripens in July and is broadcast by the wind (Fig. 66).

Spreading of Forbs

Of the native forbs, many-flowered aster had become an important weed in most of the prairies, but not in all, being almost absent in some that were greatly disturbed. It ranged from great local abundance to complete temporary control over one-fifth to one-half of certain large prairies. The thick stand of somewhat woody, tangled stems, 18 to 26 inches tall, formed almost thicket-like growths.

Daisy fleabane had become a widely spread weed in about half of the drought-damaged prairies. This winter annual seeded so thickly that frequently 20 to 30 plants per square decimeter clothed the bare soil where the grasses had died (Fig. 26). Extensive societies, sometimes covering continuously a third of a large prairie, were visible at long distances. Sleepy catchfly and Venus' looking-glass, both species with minute seeds easily carried by the wind, were also often extremely abundant.

Many plants with bulbs, corms, or tubers, such as wild onion, dogtooth violet, and Carolina anemone, occurred in unusual abundance. Most plentiful of all was violet sheep sorrel. It was common to abundant in most of the drought-injured prairies, often occurring in great numbers in places where the dead grass left the soil bare. Rough pennyroyal and Pursh's plantain, which had formerly occurred almost solely in association with the short grasses westward, were now scattered more or less abundantly over the bared and semibared places in nearly all of the prairies. Smooth goldenrod, sage, and milfoil were sometimes practically the only species surviving over considerable tracts.

Invasion of Ruderals

Certain ruderals normally not found in prairies were now widely distributed. Peppergrass was common to abundant in nearly all of the prairies where death by drought resulted in enough light for establishment. This weed was often a good indicator of the amount of bared space. Seeds were borne in such abundance that they literally covered the soil beneath the densely aggregated plants. But this and certain other annual weeds remained abundant for only one or two summers.

Horseweed was common in the prairies of the eastern half of the area and in some more westerly ones as well. The plants were frequently 2.5 to 3.5 feet tall. Russian thistle was confined largely to more westerly prairies, where annual sunflower, buffalo bur, and little barley were also plentiful. But pigweed and wild lettuce were usually more abundant in eastern Nebraska prairies than westward.

Hairy chess occurred in very great abundance in the western part of the area, where it frequently covered entire hillsides in the drought-thinned vegetation. Downy brome was common in the grassland eastward.

Summarizing, during the first summer after the drought portions of the grassland most seriously damaged were clothed with aggressive native forbs and ruderals in such abundance as to give the appearance of abandoned fields, or more often, that of weedy pastures.

CHAPTER 13

Vegetation and Soil at the End of Drought

DROUGHT prevailed in the prairie over a period of seven years. Its varying intensities and the appalling destruction of vegetation were measured and recorded each growing season.[1] But the parched prairie soil was wet in 1941 to a depth of several feet. The hot, dry air was now warm and moist. The terrible dust storms had ceased. A changed environment had come at last, for this was the end of the drought. The long delayed recovery of vegetation had begun. A resurvey of the vegetation was made both above and below ground. It concluded the phase of deterioration and at the same time provided a clear and definite background from which the processes of recovery to a new dynamic stabilization might be traced.

CONDITION OF GRASSES

Little bluestem suffered the greatest losses. It was now outranked in abundance by six other species. Most of this loss occurred in 1934. Any early recovery brought about by precipitation was only temporary. Minor losses of weakened plants continued throughout subsequent years. The stands of this formerly most important dominant were terribly depleted. In numerous prairies not a trace remained, at least above ground. In others, small amounts occurred only in the most favorable habitats. The thinned stands were usually invaded by needlegrass, prairie dropseed, blue grama, or western wheatgrass, or partially repopulated by a spreading of big bluestem and side-oats grama which formerly accompanied little bluestem. In Iowa it had nearly always persisted but sometimes with a shifting in abundance from first to third place, being outranked by big bluestem and prairie dropseed.

Big bluestem, although suffering great losses, withstood the ravages of drought in a most remarkable manner. It frequently persisted, even if

[1] This chapter is a condensation, to about 10 percent, of a very long paper, Weaver and Albertson, Ecological Monographs 13:63-117. Five of the 70 figures are reproduced.

in small amounts, in mixtures where little bluestem succumbed. Despite this it decreased greatly in 1936 and 1937. Over large areas, now occupied by needlegrass or other xeric species, it had largely vanished from the upland. But never entirely routed, this vigorous species made a remarkable development during the moderate rainfall of 1938. Having much moist, rich soil and little competition, it reached a height and thickness of stem otherwise attained only on lowland, flowered profusely, and spread by means of strong rhizomes. In this way it claimed much territory formerly occupied by little bluestem, with which it was so regularly intermixed. In many prairies big bluestem was a chief dominant, although confined to certain areas; in others it remained in only a few small patches, entirely surrounded by more drought-resisting and aggressive xeric grasses. Areas of this tall grass in ravines and extending up lower slopes shrunk greatly in width, often remaining as narrow belts. On both lowland and upland it had frequently been replaced by western wheatgrass. On certain hilltops and xeric slopes, big bluestem was replaced by blue grama after the death of little bluestem. At the end of the drought it had lost greatly in area compared with that which it formerly occupied.

Kentucky bluegrass, widely and uniformly scattered throughout the prairie before the drought, also dominated many native pastures. It had, with rare exceptions, entirely disappeared from pastures west of the Missouri River as well as in western Iowa, and also from portions of prairies where the general cover was greatly damaged. But the shade provided by grasses and forbs enabled it to survive in small amounts. By very early growth in spring, dormancy during midsummer, and vigorous development during autumn, bluegrass had been able to profit from the early spring and often late autumnal rainfall even during dry years and had thereby recovered in part, especially in ravines. It was never found with western wheatgrass or blue grama. Only in the relic bluestem areas was its normal state of an adopted interstitial species maintained.

Needlegrass at first suffered greatly from the drought. Both the oldest and the youngest, and more poorly rooted, plants were killed. Perhaps half of its population died. But once the survivors extended their roots into the new territory made available by the thinning of the stand, their resistance to drought was greatly increased. Almost every year some seed ripened, and during years of least drought seed was produced in abundance. It profited greatly by the death of the bluestems and other neighboring grasses. Its spread had been increased enormously, and many new centers had been established. The bunches were mostly young, small, and widely spaced, and year-old seedlings were everywhere in the bared soil. A continuous spreading of this species had taken place into bared or semibared areas regardless of slope and even onto low ground. The new stands occupied 5 to 10 times the area of those of predrought which were still extant.

Early losses of prairie dropseed from drought were even greater than those of needlegrass, sometimes exceeding 85 per cent. It seems probable that this late-blooming bunch grass had been greatly handicapped throughout the years by mowing during September before the seed had ripened. During several of the years of drought, yield of grasses was so light that the prairies were unmowed. Then the large seeds were frequently produced in great quantity. Much soil, bare or only scantily covered with short-lived annual grasses and forbs, was available for occupation. Here prairie dropseed spread rapidly and became fully established in nearly pure stands. Increase had amounted in some prairies to 10 or more times the original area occupied, but elsewhere a heterogeneous mixture of widely spaced bunches of this species with those of needlegrass, big bluestem, or mats of blue grama, and clumps of tall dropseed occurred.

Tall dropseed was frequently a constituent of prairie vegetation, the plants or small bunches usually occurring as scattered individuals. It is a xeric grass which readily spreads even in dry soil. It was now present at least sparingly in all of the prairies and abundantly in some. Despite this increase, it was still among the least important of the 10 grasses of highest rank.

Side-oats grama is highly drought-resistant; it often persisted where all other mid grasses succumbed. Its abundant rhizomes enabled it to spread rapidly. Moreover, it is a prolific seeder, and its range of habitat from moist to dry sites is very wide. Only a grass with such characteristics could increase so rapidly, even if widely and uniformly distributed, from its predrought abundance of only about 0.5 per cent of the basal cover to a species of the first rank. Approximately one-fifth to one-third of the vegetation in most of the prairies consisted of this species, except in the portions dominated by western wheatgrass, and even in wheatgrass it was prominent during years with at least moderately good rainfall. It was fully as abundant as needlegrass.

Blue grama, formerly very limited and of local occurrence in true prairie, was the least harmed by desiccation. Its increasing abundance in the understory of undisturbed prairie was an indication of the proximity of the mixed prairie. Little wonder that with the death or thinning of its mid-grass competitors and the impact of the dry mixed prairie climate for a period of years, this dry-land species flourished. It was more widely and more consistently represented by seedlings, and especially seedlings that survived, than any other species. Wind and surface water carried the seeds down the slopes and by intermixing them with soil aided in their planting. In this way new centers of distribution were started. By means of peripheral growth from old and new clumps, territory was gained even during years so dry that most grasses merely survived. Hence in the grasslands patches of blue grama both large and small were to be found anywhere except where the original cover of mid grasses prevailed (Fig. 67).

Buffalo grass formerly occurred even less frequently than blue grama, but it had made good gains in all grassland areas where it occurred. Both short grasses had commonly intermixed with western wheatgrass. In native pastures half bared by trampling, it spread widely and now often clothed the soil with nearly pure stands, thus extending the vegetation of the Great Plains far into true prairie.

Junegrass is less stable and of shorter life span than any of the preceding species. The root system is relatively shallow, and its marked predrought occurrence on uplands resulted in great loss. It re-established itself quickly from seed after the early drought. Hence certain prairies which lost heavily were repopulated with Junegrass only to be bared once more when extreme drought struck again. It is a drought evader profiting by early growth, summer dormancy, and autumnal development, as well as by decreased competition. After the drought it was found mostly where vegetation was very open. There was less Junegrass at the end of the drought than at its outset.

Other grasses that lost heavily were the low-growing Scribner's panic grass and Wilcox' panic grass. These common grasses of the understory almost disappeared. For several years they were seen rarely, and even in 1940 in the few prairies where they occurred they were far less abundant than formerly. Conversely, plains muhly (*Muhlenbergia cuspidata*), a drought-resistant western species, gradually migrated eastward and increased in prairie and pasture to form small pure stands on many dry hills and xeric slopes.

FIG. 67. View in wheatgrass prairie near Carleton, Nebraska, where the bluestems were replaced during the great drought. (Upper right) Hilltop prairie in eastern Nebraska (Valparaiso) where blue grama spread very widely and replaced many species of prairie. Photo in early spring. (Below) Relic big bluestem in Carleton prairie before it was entirely replaced by western wheatgrass.

Sand dropseed, following the early years of drought and consequent widespread losses of pasture grasses, increased rapidly in pastures from the status of an occasional invader to a species of major importance. Invasion of the bared areas in prairie took place only slowly and only during the later years of drought.

Switchgrass, nodding wild-rye, and slough grass had retained their former abundance on lowlands with a rather constant supply of ground water or water from runoff. Such places, however, were relatively few. In general, there had been a great shrinking of the territory in ravines and lowlands occupied by these species. Frequently they had been replaced by big bluestem, as soil aeration was improved, or by western wheatgrass. Clearly, all three of these grasses had greatly decreased.

A striking feature of the drastic modifications of the grassland was the great and continued spreading of western wheatgrass. During the drought years it continued to spread over all types of terrain to cover one-half to three-fourths of the area of many former bluestem prairies. Long narrow belts of wheatgrass around the brows of hills indicated where drought first laid bare the soil. Often whole hillsides were covered with pure stands of this grass, and many lowlands were a continuous sea of its undulating culms (Fig. 67). Wheatgrass, however, never invaded true prairie until the former occupants were greatly thinned.

Wheatgrass was so successful a competitor for the meager supply of soil moisture that it often caused the death of more mesic grasses and forbs. It renewed growth in early spring and produced abundant foliage in May and June, and flower stalks 2 to 3.5 feet tall. Seed was produced in abundance, and migration was rapid by means of long, slender, much branched rhizomes.

The early luxuriant growth, when water was available, resulted in greatly reducing the amount of soil moisture for use by other species, most of which began development four or more weeks later. Lack of much debris under western wheatgrass permitted rain to loosen the surface soil and roil the water that entered it. This resulted in decreased infiltration and greater runoff than on soil covered with bluestems. Sometimes amount of infiltration was decreased one-half or more from that under the bluestems. The amount of water transpired from a normal stand of western wheatgrass or evaporated from the soil it covered was found by experiment to be more than twice as great, from March 25 to May 20, as that from little bluestem prairie. Soil sampling revealed that there was always a lower water content under wheatgrass than under bluestems only a few feet distant.

The normal root depth of wheatgrass in moist soil is about 8 feet, but during the drought the depth corresponded with the depth of moist soil, which was about 2 to 2.5 feet. A few feet distant, higher water content and much deeper penetration of both water and roots of other grasses were recorded.

Summarizing, according to their abundance and control over the habitat at the end of the drought, the grasses were easily separated into four groups. In each group the species were arranged, so far as possible, in sequence of decreasing abundance. Species of greatest abundance were western wheatgrass, side-oats grama, big bluestem, and needlegrass. Those of considerable abundance were blue grama and prairie dropseed. Little bluestem, Junegrass, tall dropseed, buffalo grass, and Kentucky bluegrass were of lesser abundance. Three species of least abundance were plains muhly, Scribner's panic grass, and Indian grass. Thus, the bared and semibared areas had been largely reclaimed by perennial grasses or by certain native forbs. Annual grasses, where present, chiefly occupied the interspaces and, with rare exceptions, were not found in large belts or patches as formerly.

The prairie pattern had thus changed in a remarkable manner. Certain communities had disappeared or were represented by relic patches; others were rapidly enlarging their holdings. New communities were developing and dominating vast areas. These changes were occurring in the true prairie wherever the cover had been opened by drought. Basal area was only one-half to one-third its normal amount. The lower layer of grass and forbs had almost been destroyed.

CONDITION OF FORBS

Decrease in numbers of forbs was not gradual but sporadic, corresponding with severity of drought. Deeply rooted plants such as prairie rose, lead plant, and false boneset had frequently held out against drought and competition with western wheatgrass until the last two or three years. Some still persisted. In many prairies they were about the only forbs that remained, except for drought-evading species which grew only in spring. Many shallowly rooted plants were nearly all killed at the first great impact of the drought. Others like stiff sunflower and prairie coneflower lingered a second year; plants of most species persisted a little longer and were continuously depleted in numbers with recurring periods of drought.

Ground plum, many-flowered psoralea, and false boneset were examples of species which succumbed much more gradually and considerably later than the shallowly rooted forbs which died during the first year of desiccation.

By 1940 most species of forbs had decreased greatly, some almost to the point of extinction, as a consequence of the continued recurrence of dry years. This pertains to forbs that root deeply as well as to those of moderate and shallower rooting habits. Loss of legumes was especially noticeable. West of the Missouri River, losses were approximately one-half to two-thirds of the forb population; only small losses occurred in Iowa.

Even at the beginning of drought, available soil moisture below the solum, although extending deeply, was small in amount. Throughout the years of drought, precipitation did not augment this supply, and even deeply rooted plants were forced to depend upon water largely from current precipitation. Thus, as years of severe drought alternated with those of more moderate soil moisture deficiencies, loss of forbs was progressive. By 1939 forbs were only one-half to one-third their former abundance, and thereafter there were further marked decreases in a weakened plant population.

Drought occurred during various periods of the year. Wilting, drying, and more or less complete defoliation of tops by grasshoppers were common phenomena later in the drought cycle among even the most deeply rooted species. Dwarfed stature was characteristic of the more drought-resistant species which continued to grow slowly, even if intermittently. Lack of mulch on the soil with little or no cover of grasses and lack of the usual shade accentuated the drought. Failure to complete vegetative growth or to blossom or ripen seed was usual. Little or no replacement of the forb population occurred over a period of 6 or 7 years.

Development of only a few stems from crowns of perennial species that normally supported many revealed at once the severe environment and the weakened condition of the vegetation. In early years of drought the forbs were often robbed of the meager water supply in spring by the growth of a host of annual grasses.

A few species of native forbs profited by the death of their competitors. Many-flowered aster, propagating both by seeds and very efficient rhizomes, became so extremely abundant as to ruin many of the prairies or large portions of them for the production of hay. In the early years of drought it appeared that this forb might completely dominate some grasslands, and much native sod was broken because of the seriousness of this pest. But as xeric grasses increased their territory, there was a great decrease in both size and abundance of this forb. Daisy fleabane was almost equally widespread. Blossoming was so profuse that at a distance the prairie had the appearance of a field of newly fallen snow. Smooth goldenrod had become extermely abundant in many prairies. One could readily estimate the degree to which the grasses had been destroyed by observing the density of its stand. There was a remarkable increase of species with corms and bulbs as well as those with thickened roots or other storage organs.

The average number of species of long-lived native forbs found before the drought in bluestem prairies in Iowa was 85, in Nebraska and Kansas 50, and in wheatgrass prairies in Nebraska and Kansas 38. At the end of the drought the numbers were, in the same order, 82, 41, and 21.

The same species of forbs decreased considerably in stature even before the drought as its habitat became drier westward, but during and near the end of the dry years, differences in stature were greatly increased, since drought was not so severe in the Iowa prairies. Hundreds of measurements have been made, but only a few will be used to illustrate a general condition. Lead plant decreased in height from 19 inches to 7 and then to 5 inches, and prairie rose from 30 to 18 and finally to 6 inches.

The number of stems of forbs in two circles, 50 feet in diameter, was ascertained at each of 12 stations. Average number of stems at the Iowa stations was 27,875, at the Nebraska-Kansas bluestem stations 7,109, and at the wheatgrass stations only 1,083.

CHANGES UNDERGROUND

Root penetration during drought has been directly correlated with depth of moist soil. The grasses and forbs died in 1934–1936 only after they had exhausted the available water in the surface few feet of soil. The light showers of drought years or even scattered heavy rains were inadequate to moisten again the third, fourth, and fifth foot, or at least all parts of this dry layer. Consequently, plants with roots not already established in the deep, moist subsoil were barred from entering it (in many areas) by 2 or more feet of permanently dry soil. Dependence upon current precipitation became much greater. But with the profound disturbance of the plant cover and its disappearance in places, the rate of entry of water into the soil was greatly decreased. This decrease in rate of infiltration profoundly affected root distribution.

Bared soil greatly retarded water infiltration; any type of cover, living or dead, promoted it; soil under the native prairie grasses absorbed water much more rapidly than soil covered with the great invader, western wheatgrass.

INFILTRATION OF WATER

The rate at which water entered the dry prairie soil was ascertained by sprinkling it on the soil surface as rapidly as it was absorbed. This was done over a small area for a period of 30 to 60 minutes. Some water was intercepted by the foliage and evaporated without reaching the soil. But on the level areas selected, only a very small amount was lost by runoff. The drought-bared areas had all lost some soil by wind and water erosion and were often depressed an inch below the general soil surface. In one prairie where the granular, silt-loam topsoil was 12 inches deep and very dry, experiments were performed with results shown in figure 68. The depths of water penetration, which were determined by digging a small trench through the watered soil immediately, averaged 9 and 2 inches, respectively, under the grass and bare soil after 30 minutes of sprinkling. Where sprinkling continued for 60 minutes the respective average depths of moist soil were 20.5 and 11.5 inches.

This experiment is representative of many others which gave similar results, infiltration into bare soil being least and into big bluestem sod greatest. Under western wheatgrass, the rate of infiltration was intermediate, averaging 5.5 inches compared with 7 inches under blue grama and 9 inches under big bluestem. In other experiments steel cylinders, sharpened at one end and well lubricated, were forced into the soil. Water was then added as rapidly as it could be absorbed until an amount equalling 1.6 inches of rainfall had been applied. The time for the infiltration of the water was recorded. Data were obtained from eight widely separated prairies; six were in southeastern Nebraska and two in north-central Kansas. All were on soil of silt-loam texture but variable, of course, in proportions of sand, silt, and clay. The pairs of experimental areas were never more than 9 feet apart and sometimes only 6 feet. If the average time for infiltration under bluestem and other prairie grasses is considered as 1, those under wheatgrass and into bare soil were 2.3 and 2.8, respectively.

Differences in depth of soil moisture penetration at Lincoln, after a rain of 1.1 inches in August when the soil was very dry, were ascertained by a series of 16 measurements in the prairie. Moisture in bare places averaged

FIG. 68. Depth of penetration of water in dry soil (black); (upper) where 1.4 inches of water were sprinkled on blue grama and bare soil in 30 minutes. In the lower figure 1.4 inches of water were sprinkled on big bluestem and bare soil in 30 minutes. In each picture a ruler is lying on the bare soil. Dark streak in lower figure is a shadow.

3.7 inches deep, that under western wheatgrass 4.0 inches, and that under bluestems 6.8 inches. These differences are representative of numerous other measurements made throughout the drought years.

Weaver and Noll (1935) measured the amount of runoff water from three similar erosion plots on the same slope and only a few yards distant. In one 2.5-inch rain loss of water from prairie was nil, from overgrazed prairie 29 per cent, and from prairie soil almost bared by grazing 50 per cent. Penetration of water after 5 days was, in the same order, 42, 22, and 19 inches.

The reason for these differences seems clear. On soil without a cover of vegetation or debris, the impact of raindrops or of water sprinkled on the surface loosens the soil particles, which are then suspended in the water. This water on entering the soil pores carries the fine, suspended particles with it. The pores are more or less completely clogged on the surface, and a compacted layer of soil formed. This layer greatly decreases absorption and increases water loss by runoff. Western wheatgrass had invaded many areas upon which wind-blown dust had been deposited and through which water infiltrated only slowly. But even where the soil was not dust-covered, this grass had furnished little debris during the drought years, and much bare ground was exposed.

Studies by Duley (1939) and Duley and Kelly (1939) with mulches on cultivated soil have shown that this clogging of the soil pores and "the development of a condensed layer on the surface of cultivated bare soil has far greater effect on the intake of water than differences in soil type, degree of slope, previous moisture content of the soil, or the rate of rainfall. In fact, . . . it seemed to have a greater effect than all the other factors combined." Thus conditions on the soil surface greatly influence water content of soil, and this in turn is a controlling factor in distribution of roots of the grasses and forbs.

EFFECTS ON ROOT DEPTH

A study of the root systems at the end of the drought showed that root development was normal in relic grasslands where the original plant population was little affected above ground. In badly denuded areas where only widely scattered relic or invading grasses occurred, much space between the plants was almost free of living roots. But in half-bared places where relic grasses or invading species had increased, depth of roots corresponded with that of current rainfall penetration, about 2 to 2.5 feet. This last condition occurred most frequently.

In one examination a deep trench, 16 feet long, was dug on a level hilltop near Lincoln, Nebraska, in an area typical of the usual depth of moist soil and roots during the late years of the drought. This was done late in July, 1940. Figure 69 shows that the roots of western wheatgrass, which a few years earlier had invaded the left half of the area, are only 2 feet deep. The deeply rooted forbs that remained alive were much dwarfed above ground but unwilted. This was also true of the dotted button snakeroot growing in the big bluestem sod. The roots of this grass, which was also a recent invader, were, owing to greater water penetration, deeper than those of wheatgrass. That roots of little bluestem, big bluestem, and other grasses were formerly abundant to 4 to 7 feet was shown by their dead remains, still only partially decayed, in the deeper soil.

Rain in the spring of 1941 moistened the soil more deeply and enabled western wheatgrass to penetrate to 3.5 to 4 feet in the area shown in figure 69. Big bluestem extended downward even farther into the newly moistened soil, which in July, 1941 was separated from the moist soil below by a layer of dry soil only 6 to 12 inches thick. By May, 1942, soil moisture in the upper layer was in contact with that in the deep subsoil, and the roots of both seedling grasses and young forbs were growing deeply in the cool moist earth. This condition was quite general.

In ravines where additional water was supplied by runoff so that the soil was moistened very deeply, the roots of surviving species often grew deeper with increase in drought. Big bluestem, western wheatgrass, and certain other grasses increased 12 to 15 inches in root depth and branched more profusely than normally. Certain forbs, such as ironweed, nearly doubled their root length.

REPLACEMENT OF TRUE PRAIRIE BY MIXED PRAIRIE

One of the most outstanding phenomena of the dry climatic cycle was the destruction of a portion of one plant association and its replacement by a more xeric one. This change occurred very gradually between 1934 and 1941, a period of only seven years. The scene of action was the broad area on the western edge of true prairie in central Kansas, eastern Nebraska, and eastern South Dakota. It was distinctly east of the mixed prairie. The replacement occurred, as a result of drought, in an area over 100 miles in width. This phenomenon was general over hundreds of square miles of grassland. It was studied in detail from year to year in carefully selected representative places.

Upland true prairie is characterized by a continuous stand of certain dominant mid and tall grasses. Although there is an under layer of forbs with a few low-growing grasses, these form open stands, are not contin-

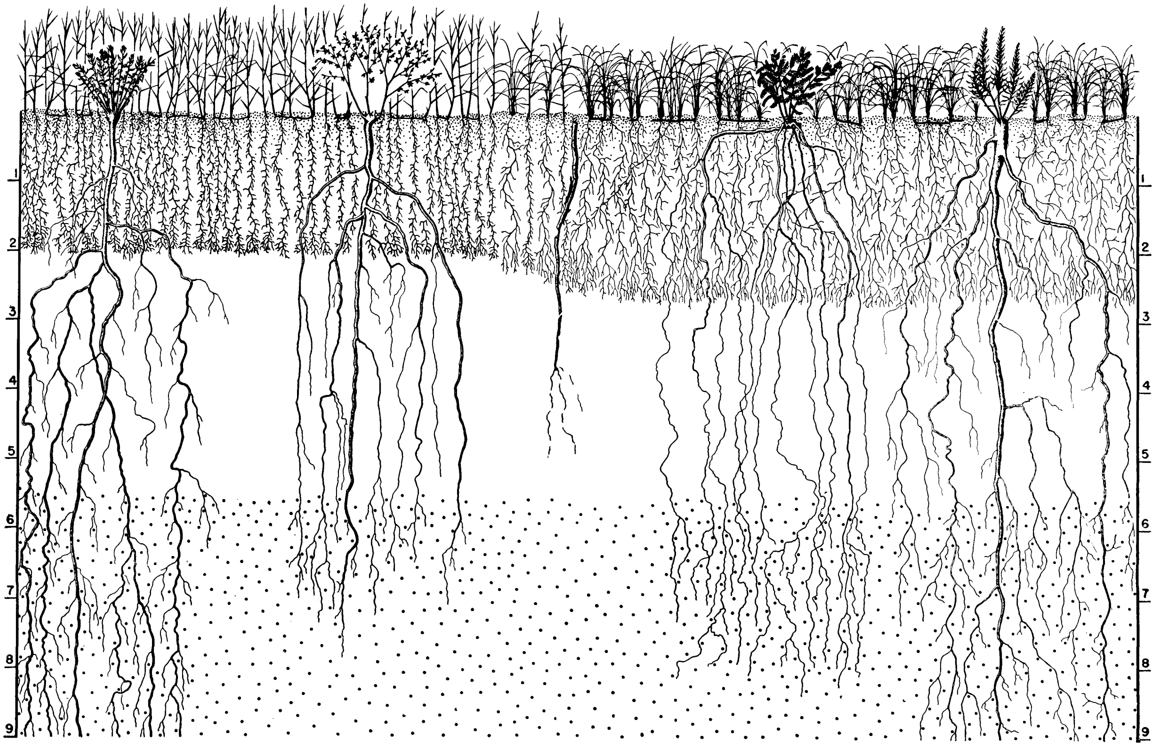


FIG. 69. Relation of roots to soil moisture near the end of the drought. The roots of western wheatgrass (left) and big bluestem (right) penetrated only to the depth of currently moist soil. The dry layer between 2 or 2.5 to 5.5 feet was the result of complete exhaustion of available soil moisture by the original plant cover before plants died of drought. The deeply rooted false boneset (*extreme left*) and dotted button snakeroot (*right*) survived because many of their roots were in moderately moist soil beween 5.5 and 16 feet depth.

uous, and are distinctly subdominant. Hence, true prairie is readily distinguishable both in physiognomy, or general appearance, and structure from mixed prairie with its dominant mid grasses and dominant short grasses. These typically form an upper story and a lower layer, respectively, or short grasses of the drier places may alternate with the mid grasses of less xeric sites.

In addition, certain dominants which characterize each association are different. Even the dominant grasses which occur as such in both associations exhibit differences in appearance, in size, and often in habits of growth in the two associations.

The three prairies selected for illustration had been studied at two periods just before the drought and intensively summer after summer following 1934. They were located, respectively, 65 miles southwest of Lincoln near Carleton, Nebraska, 30 miles northwest of Carleton near Clay Center, and 45 miles southwest of Carleton near Montrose, Kansas. These bluestem prairies were ungrazed but had been mowed in the fall for the crop of hay. They were entirely representative of the area as a whole, considerable parts of which were still unbroken prairie and pasture land. They are in the Chernozem soil group.

Vegetation in all three prairies responded to the drought in a very similar manner (Weaver, 1943). An outline of change in the Carleton prairie follows. In 1932 little bluestem furnished 50 to 85 per cent of the cover; big bluestem, 50 per cent on lowlands but 15 to 20 per cent elsewhere. There were a few small areas of blue grama and buffalo grass. Wheatgrass was nearly confined to ravines, forming a fourth to a third of the cover locally.

In 1934–1935 little bluestem suffered 95 per cent loss; big bluestem lost 10 to 15 per cent. Less than a fourth of the prairie was covered with a greatly thinned stand of bluestem; one-fourth was mixed (mostly big) bluestems and wheatgrass; half was dominated by alternes of a nearly pure but open sod of wheatgrass. Both short grasses had increased.

In 1936 and 1937 big bluestem lost heavily and was dominant only in local but clearly defined patches (Fig. 67). Wheatgrass greatly extended its territory. Side-oats grama increased in abundance. Short grasses extended their local areas and started new ones.

By 1938 big bluestem remained uninvaded in patches 2 by 3 rods or less in area; one lot in a ravine was 5 by 8 rods. It had become less important in the fourth of the prairie where it was intermixed with wheatgrass. Death of bluestems resulted in more extensive areas of wheatgrass, which had spread over nine-tenths of the prairie. Blue grama increased greatly; it occurred in patches 1 to 225 square yards in area.

In 1939 side-oats grama thrived as wheatgrass waned; it had invaded wheatgrass over nearly the whole prairie. Blue grama and buffalo grass were still increasing. Pure wheatgrass stands were greatly thinned by invasion of side-oats grama and short grasses, or wheatgrass was thinly invading short grasses and thus forming mixed prairie. Pure short-grass stands were common. Many equal mixtures of big bluestem and side-oats grama occurred. Pure big bluestem had thickened its stand, but the size of areas had decreased.

In 1940 nearly all big bluestem had died. Many former mixed patches were now all wheatgrass. All but 1 per cent of side-oats grama had died. Wheatgrass increased greatly and occupied three-fourths of prairie. Blue grama and buffalo grass increased greatly.

In 1941 and 1942 a good mixed prairie of wheatgrass and short grass was fully established (Fig. 67). Precipitation in spring was often sufficient to promote a good growth of wheatgrass, but conditions of growth were extremely detrimental to later developing grasses. Robertson (1939), who worked with drought vegetation two years, describes conditions at Carleton as follows: "Four days spent on this prairie in the middle of July, 1936, served to impress one with the severity of physical and biotic factors so extreme that even native vegetation could not endure them uninjured. Daily maximum temperatures ranging from 104° to 111° F. accompanied by relative humidities of 19 to 24 per cent, continuous strong winds, glaring sunlight, and subnormal precipitation combined to make the grasses crackle underfoot like wheat stubble. Only false boneset (*Kuhnia glutinosa*) and blazing star (*Liatris punctata*) appeared unhampered by drought, and they were borne down and partly eaten by hordes of grasshoppers."

These were conditions frequently encountered by the writer during the seven-year study of drought. Prairie fires sometimes occurred in midsummer.

CHAPTER 14

Recovery and Development Toward Stability

FOLLOWING the long period of drought, nature was promptly at work repairing the damage of a great catastrophe.[1] Similar destruction had probably occurred many times in the long history of grassland, but of this there is no written record. Years of nearly normal or above normal precipitation kept the soil almost constantly moist. Rain also moistened the deep subsoil, most of which had been permanently dry for several years. Vegetation made a good recovery, and the subsere of weedy grasses and forbs gradually gave way to several communities of perennial grasses. It seems clear that the methods and sequence of recovery in this large midcontinental grassland were in general, and often in particular, the same as in areas far northward and southward as well.

DEVELOPMENT OF GRASSLAND COMMUNITIES

At first the processes of development were slow, since deep dormancy often follows great drought, but later they became greatly accelerated. When the weedy native forbs had been subdued, when the annual grasses and weeds had been mostly replaced by perennial grasses, and when the dominant species had replaced the former interstitial ones, there crystallized out of the heterogeneous drought populations several very definite grassland communities or types.[2] In fact, the western wheatgrass type had grown steadily, year by year almost from the beginning of drought. Likewise, the short grasses had migrated into new territory and gradually claimed it for themselves. Other types were less clearly defined, since

[1] Condensed from Weaver and Albertson, Ecological Monographs 14:393-479, 1944, and Weaver, Ecological Monographs 20; 251-270, 1950. Nine of the 152 figures have been re-used.

[2] These developing communities of upland became well defined between 1940 and 1945. They are tabulated on page 259.

dominants were much intermingled and subdominant species at times played a leading role in repopulating the bared soil.

The only places where a complete subsere from bare soil to perennial grass occurred were in portions of prairies so deeply covered with dust as to smother all vegetation. Here annual weeds were soon replaced by western wheatgrass. Nearly all other areas had some relic climax grasses, or at least some that recovered from dormancy.

The spread of needlegrass during the dry cycle had been so great, from hilltop to lower slope and on flood plains, that it was now surpassed in area only by western wheatgrass and big bluestem. On lower slopes and even on low ground formerly covered by big bluestem, it found during the drought a dry warm soil, similar to its usual predrought home on uplands. The large size and deep burial of the fruit, due to the twisting awn, insured germination even when the surface soil was dry.

In 1941 the great production of foliage, even of widely spaced plants, resulted in partially shading the soil. Enormous seed crops were produced and also myriads of seedlings, sometimes as many as 20 per square foot (Fig. 70). The stand thickened as the plants matured. The soil mulch had been restored, and species of the understory were gradually appearing.

Prairie dropseed was thinned even more greatly than needlegrass. But it recovered without loss of territory and benefited greatly by the death of its competitors and the consequent opening of new territory for invasion. Cessation of mowing, because of very little forage production during the driest years, permitted this late-blooming bunch grass to ripen abundant seed. Seedlings became established over many acres adjacent to old stands and developed into new bunches. This enormously increased the territory occupied by this type.

When drought laid bare much prairie soil and great storms filled the air with dust, these high winds undoubtedly carried the wheatgrass seed along the bared surfaces. Almost always where layers and drifts of dust were formed, wheatgrass was the early occupant. Spreading of wheatgrass was well advanced during the early years of drought. When good rains came in 1938, it extended outward rapidly along the periphery of its established communities as well as into neighboring areas not yet stabilized (Fig. 70). There was little competition for light, since even under a good stand of wheatgrass about 80 per cent of full sunshine reached the soil surface. Few seedlings of any kind were ever found in established wheatgrass. Any ruderals in an invaded area were soon suppressed and died. Exceptions were *Hordeum pusillum* and weedy species of *Bromus*. *Festuca octoflora* and *Erigeron strigosus* are likewise annuals with periods of growth similar

FIG. 70. Seedlings of needlegrass near established bunches. They are of various ages. Photo in June, 1943. (Below) Area bared of big bluestem by drought is being invaded by linear migration of western wheatgrass.

to those of wheatgrass. They shared the late fall and early spring moisture with the wheatgrass.

Relic forbs were almost entirely those with deeply penetrating root systems—characteristically lead plant, dotted button snakeroot, prairie rose, and false boneset. These were dwarfed immediately after the wheatgrass invasion. With a gradual depletion of subsoil moisture, which was not replaced by current rainfall, they became successively fewer and nearly disappeared. This occurred even on low ground.

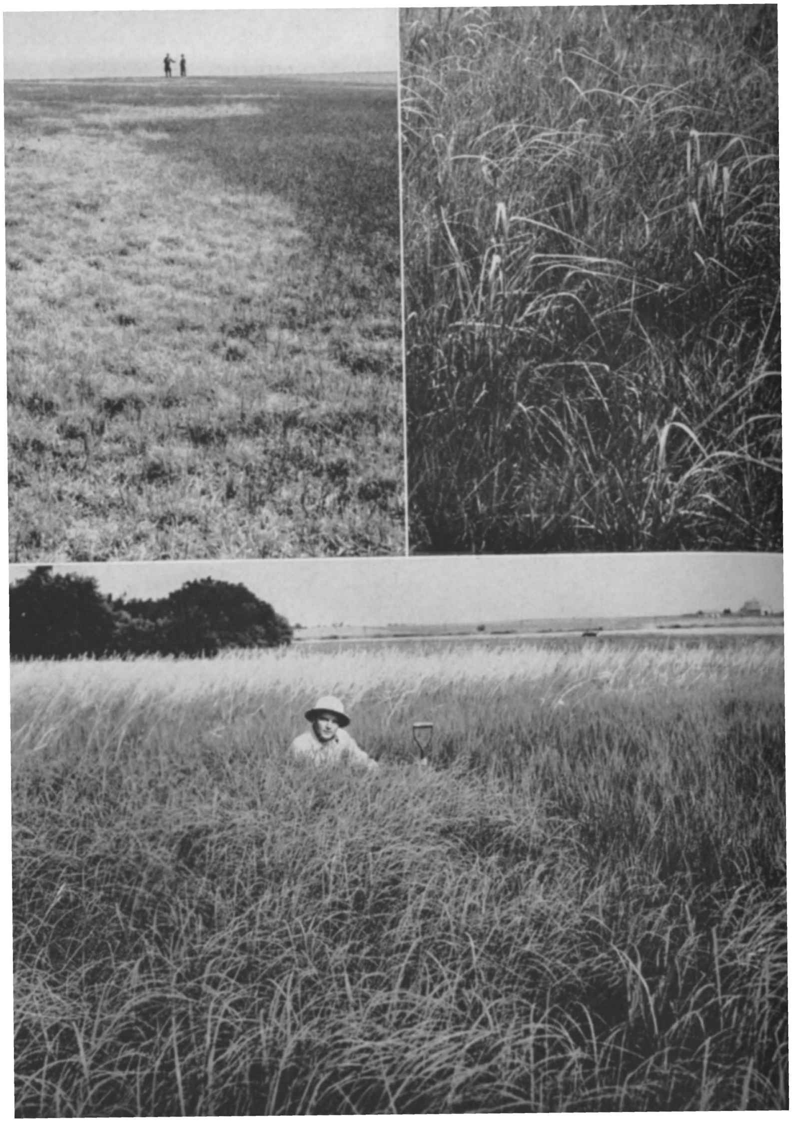


FIG. 71. Dust-covered bluestem prairie reseeded to blue grama (light) and western wheatgrass (dark) during the great drought. (Right) Recovery of scattered plants of big bluestem in 1943 in area taken over by western wheatgrass during drought. (Below) Lowland prairie near Lincoln, Nebraska, which was damaged by drought. Big bluestem remained in left foreground, western wheatgrass at right, and needlegrass (light color) in fruit in the background.

Relic little bluestem was easily overcome by wheatgrass, and during all of the years with severe summer drought any relic big bluestem was dwarfed and usually dried by midsummer. It was repeatedly found that change from big bluestem to wheatgrass was accompanied by a decrease in yield of nearly one-half on upland and two-thirds on low ground.

Blue grama is the most drought resistant of all the native grasses not only of true prairie but of mixed prairie as well (Mueller and Weaver, 1942). It not only had enlarged most of its original small patches until they now covered many acres of uplands but had also established thousands of new outposts (Fig. 71). It occurred everywhere from hilltops to the lowest slopes. In 1940, when drought in June bleached white the wheatgrass, which did not revive with the July rains, the green understory of blue grama made a striking contrast. Big bluestem was often entirely dried above ground while beside it blue grama was still green.

When good rains finally came, blue grama seedlings occurred so thickly in bare interspaces or on other unpopulated soil that they gave the appearance of a newly made lawn. Thus, the history of blue grama has been one of constant gains. Only after two or more years of good rainfall was its possession disputed by the bluestems. Buffalo grass, less abundant and more greatly harmed by drought than blue grama, also increased greatly.

The formation of the mixed prairie community became clearly apparent in some grasslands in 1938 when an intermixing of wheatgrass and short grasses along their numerous borders became pronounced. Mutual invasions by mid grasses and short grass had resulted as early as 1938 in very large areas of mixed prairie.

Blue grama also established seedlings in places that had been invaded by wheatgrass. In fact, its seedlings (and those of buffalo grass over the limited region where it occurred) were practically the only ones, except side-oats grama, that became widely established. They produced vigorous bunches which later often aggregated into an open sod. And they withstood competition for water, which suppressed or killed nearly all other plants, both weeds and native species. Hence, mixed prairie consisted almost entirely of the pure layer of wheatgrass above and the short grass or grasses below. The mixed prairie type occurred in the western edge of true prairie throughout a belt 100 miles or more in width.

The period of invasion of both wheatgrass and short grasses was completed in 1941, since practically all of the remaining prairie area was then occupied by other types of vegetation. The intermixing of short grasses and wheatgrass, however, had not terminated. Under certain local conditions wheatgrass was almost replaced by blue grama.

The big bluestem type on upland resulted from the survival of this grass wherever the former little bluestem type had lost its chief component, *Andropogon scoparius*. After heavy initial losses, big bluestem survived the drought in the bunch habit, but later, unless overwhelmed by wheatgrass, spread to form a sod. With the coming of a series of good years, big bluestem sometimes increased from a 10 per cent stand to form a cover that became 80 to 95 per cent as dense as that on low ground before the drought.

Quite in contrast to this outcome were the hundreds of places where the open stands of big bluestem were early invaded by wheatgrass. Then the bluestem was nearly always dwarfed, later suppressed and ultimately exterminated in its former home, mostly on uplands, but sometimes on lowlands as well. Many dry years were characterized by a moist early spring. This promoted the growth of wheatgrass which used so much of the available water that even the early growth of big bluestem was sparse.

The original upland cover of mixed little and big bluestem remained after the terrible drought only in small areas. The total amount of this type did not exceed 10 per cent of the area in any prairie examined. It is designated as the big bluestem—little bluestem type, since in most of these areas big bluestem was more abundant at the end of the drought. Only in a few places did little bluestem comprise more than half of the vegetation, although formerly it often composed 80 per cent. These relic areas were sometimes scarcely disturbed. The bluestem grasses were only thinned and not destroyed. They maintained themselves as a community throughout the drought.

These communities varied greatly in size and distribution. They occupied the parts of the grassland least disturbed by invasion, and places where other species had never become dominant. These remnants of undisturbed or little modified grassland were found in all situations. They remained clearly demarked from other types of prairie. They retained a good soil mulch, an understory of low growing grasses and forbs, and plants of many other species that died elsewhere.

Over considerable areas, widely scattered plants of various species recovered, reseeded, or invaded at about the same time. This gave rise to a mixed grass community of variable composition. It was here that the battle for dominance was waged fiercely and continued for a long time. Soil originally clothed with the little bluestem type was now supporting as dense a population of perennial (and mostly climax) grasses as current water content would permit. Here prairie dropseed, tall dropseed, side-oats grama, blue grama, big bluestem, and needlegrass occurred in mixtures of greatly varying proportions. In later years revived little bluestem and various other grasses were also admixed. In this type one found mixtures of species that were not seen in prairies before the drought.

The preceding communities were often so distinct that mapping along ecotones only a few feet in width was possible, as shown in figure 71 (Weaver and Darland, 1944). This mosaic cover of the prairie after three years of nearly normal precipitation even where complete was not climax. Only the period of occupation of all of the territory by a number of different types of vegetation had been reached. A condition of stabilization had not been established and return to the predrought dynamic equilibrium of climax types necessitated many changes.

GENERAL RECOVERY

Recovery from dormancy sometimes did not occur until one or more years after heavy rains. Vegetation was usually slow and conservative in its changes. The degree of recovery varied with the amount of depletion, the type of vegetation, and the amount and seasonal distribution of soil moisture. But in two or three years the prairie cover again became almost complete, even though it differed greatly from the former one.

Grasses recovered by increase in size of relics, by tillering, by production of rhizomes and stolons, by development of old rootcrowns and underground parts following deep dormancy, and by production of an abundance of seedlings.

The great abundance of big bluestem, which was second only to wheatgrass, was due at first to drought survival because of its very deep root system, but thereafter to its rapid spreading everywhere by rhizomes. Occurrence of stems singly or in groups of twos or threes was frequently common along a line indicating the position of the advancing rhizomes. The great increase and wide spreading of penn sedge may be partly attributed to its rhizomes. Although rootstocks are absent or poorly developed in blue grama, buffalo grass which intermingles with it freely and forms a denser cover than blue grama alone, is equipped with stolons.

The breaking of a long period of dormancy in crowns and rhizomes of grasses was observed in some prairies after a single year of good rainfall and in nearly all after two or three years. Little bluestem began to break its long dormancy and rejuvenate from old crowns only after one year of good rainfall. In some prairies such rejuvenation was not pronounced until a year later. Survival of little bluestem in a dormant state usually occurred only in restricted places. But occasionally, dormant bunches were scattered thinly over an entire slope. In 1943 it revived in certain places on dry south slopes where it had not been seen since 1934. At first only a few stems appeared even from large bunches. Often the remainder of the crown was dead. In 1943 some revived plants had only 4 to 10 stems and 1 or 2 flower stalks (Fig. 72). On the margins of the relic bluestem type, revived bunches were common. These drought relics had produced some foliage each year but no seed. But in 1942 and 1943 seed was ripened in abundance. Big bluestem likewise survived long periods of dormancy. On some north-facing slopes where little and big bluestem had early disappeared, blue grama formed extensive open stands. Smaller and younger bunches filled much of the interspace between the mats of blue grama and portended a dense cover. In 1942, a fine open stand of big bluestem appeared from old rootcrowns and rhizomes which had been dormant for several years. It occurred mostly in the interspaces between the bunches and sods of blue grama, but its vertical stems sometimes penetrated through them as well.

In one large prairie near Lincoln, 20 sampling plots were selected in the wheatgrass community, which had been well established since 1935. Care was taken to select them where the wheatgrass was pure, since they were to be used to determine production of this grass compared with that of big bluestem. No big bluestem was found in any of them at this time or when the grass was clipped in May and again late in June. Neither was it observed in closely adjacent prairie where other plots were selected for later clipping when the grasses had matured. But in August, when a third cutting was made, considerable big bluestem had appeared in several of these plots. It was 5 to 15 inches tall, and was scattered lightly to rather thickly and occurred widely in places where in May and June no bluestem grew (Fig 71). When the tops were cut and the soaked soil was slowly and carefully washed away, the skeletons of extensive rootcrowns and rhizomes were found. The roots had practically all decayed, but the rhizomes were

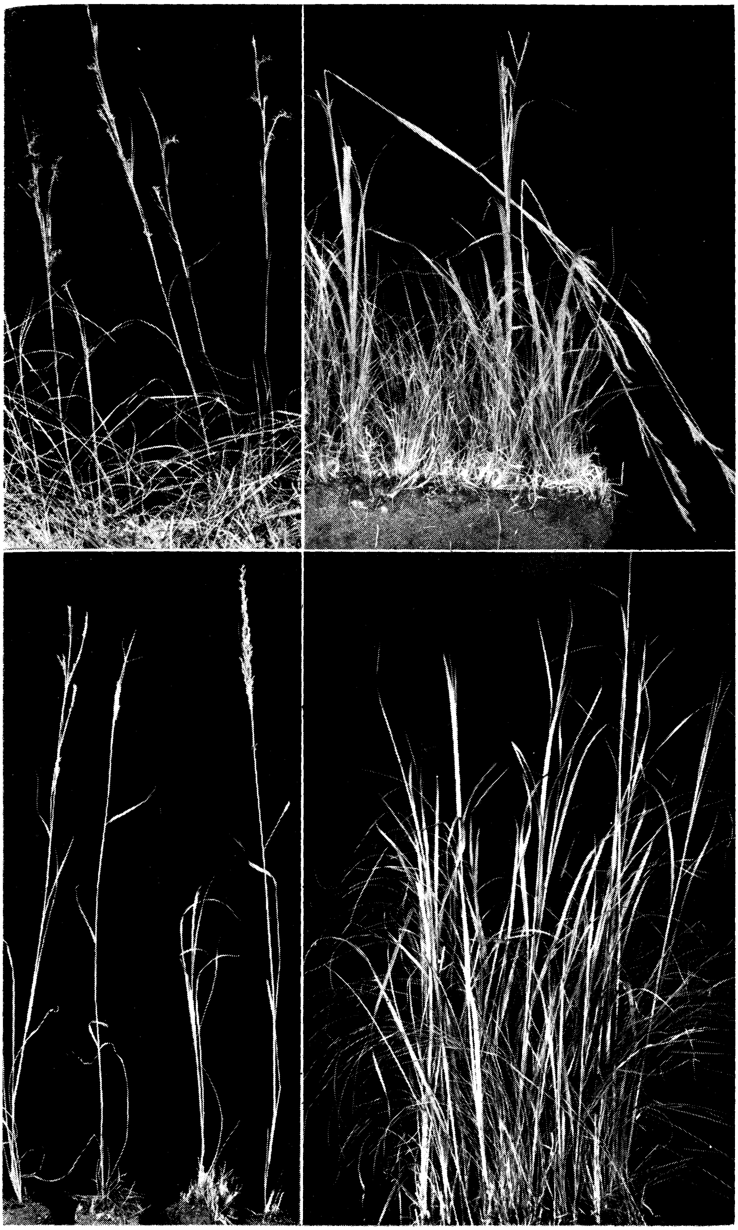


FIG. 72. (Upper left) Recovery of little bluestem from relic bunches of sod. (Lower left) Similar recovery of big bluestem and Indian grass. (Right) Big bluestem growing up through blue grama sod (above), and (below) through a bunch of prairie dropseed which invaded during dormancy of big bluestem.

distinct, not as continuous stems but as dead, cork-like pieces .25 to 1 inch long but still in place throughout the 4- to 12-inch interspaces between living stems. The new shoots were not from seeds but from the largest and best preserved rhizomes.

Sloughgrass reappeared in certain ravines where during drought a dense stand of wheatgrass prevailed. Its large coarse rhizomes had remained dormant. Other species that behaved similarly in less moist portions of ravines were switchgrass, Canada wild-rye, and big bluestem. After the mass invasion of wheatgrass and its absorption of the soil moisture in early spring, they remained dormant.

In the spring and early summer of 1941 there was an almost continuous supply of moisture available to promote germination and establishment of seedlings. Conditions for growth of seedlings in both 1942 and 1943 were excellent. In 1942, for example, the surface soil under the rapidly developing grasses was damp practically all spring and mostly throughout June, not only because of rain and heavy dew but also because of much cloudy weather. Moreover, after 1941 vegetation had thickened and furnished the seedlings considerable protection from direct insolation, thus aiding their early development. Very large crops of seedlings were produced. All of the dominant species within the area were usually represented except those of the bluestems, especially little bluestem, seed of which was still rare.

By midsummer the young plants of blue grama were 4 to 5 inches tall, and those of side-oats grama and Junegrass 7 to 9 inches. They were producing new tillers and new roots in great numbers. Often no bare soil was seen but instead there was a sod of seedlings so dense that it seemed that the seed had been sown by hand. Success of seedlings in most places was assured by the presence of a recently developed soil mulch, a condition usually lacking during drought but a powerful deterrent to the rapid loss of surface soil moisture.

In 1943 one was impressed by a new phenomenon, that of different stages of development of the several species, from seedlings to small bunches. By midsummer, seedlings of the previous year were rooted 1.5 to over 2 feet deep, and older bunches even more deeply. The oldest were beginning to produce flower stalks, which indicated both successful establishment and a permanency of the cover.

Recovery of vegetation was demonstrated by an increase in the number of plants, an increase in vigor and stature, the resultant thickening of the stand, and the exclusion of ruderals. It was also shown by accumulation of debris, reappearance of societies of forbs, reconstruction of a layered vegetation, and finally by an increased yield.

The number of plants increased very rapidly once adequate soil moisture was continuously available. Lead plant, for example, put forth two to four times as many stems from its widely spreading underground parts as it did during years of water deficiency. Nearly all species with rhizomes increased the number of plants far beyond that of drought. The breaking of dormancy added new individuals from rootcrowns, rhizomes, and roots, where few or none had appeared in previous years. Stiff sunflower, normally about 2.5 feet tall and with only one or two flower heads, attained a height on the hilltop of 42 inches, and the plants produced an average of 5 heads. Big bluestem reached a height on upland previously found only in ravines. The increased vigor was clearly due in part to an excellent water content in the soil and aerial conditions favorable to growth, and probably also to the release of unusual amounts of nitrates (always low in prairie) and other nutrients from the rapid decomposition of dead underground parts long stored in a dry soil. Possibly the rest period itself may have had a stimulating effect on some plants.

The greater vigor and increased stature of plants in drought-disturbed places were very evident when the plants were compared with those in adjacent undisturbed, sod-bound prairie. Thickening of the stand was pronounced everywhere. Bunches that before had been only sparsely filled with stems now produced them in great abundance. One of the most impressive features of prairie in 1943 was the density of the foliage. Where much bare ground had formerly been exposed, there was now sufficient cover almost to conceal the soil. There was a scarcity of most forbs, and an unusual prevalence of grasses. The increased cover reduced the light and excluded weeds. This added greatly to returning the prairie to a more normal appearance.

With the increase in plant population and amount of foliage, there was also an increase of mulch. In most places enough plant parts had accumulated to cover the soil with a thin mulch, which was quite in contrast to the bare, black soil even in 1940 and 1941.

Little replacement of the native forb population occurred during the 7 years of drought. Seasonal aspects, if any, were poorly marked. Seedlings of forbs were rare until 1941 and 1942. Many forbs which had vanished from all but relic patches of little and big bluestem prairie returned after a year or two of good precipitation. Blue-eyed grass, which had not been seen anywhere after 1934, occurred in great numbers in 1943. It must have sprung from seed widely scattered, even in the driest places, since practically all plants had only one or two stems. On some hillsides they grew more thickly than if the stands of 7 normal years had been combined. Prairie violet, hawkweed, and prairie cat's-foot are examples of forbs that became rare during drought and returned very slowly. Seedlings and young plants of false boneset have been found in considerable numbers since 1942 about the relatively few old plants that survived the drought probably because of their extremely long taproots. Purple vetch, which had decreased almost to the point of vanishing, appeared again in considerable abundance. Pitcher's sage was represented widely by seedlings and young plants over many lower slopes. Only rarely did a mature plant survive the drought.

Seasonal aspects were almost absent, so scarce were the forbs. Although the flora of forbs had distinctly increased in both species and abundance in some prairies, in others scarcely more than a dozen perennial species occurred. They were always fewest in a cover of western wheatgrass. To appreciate their scarcity, compared with predrought abundance, one had only to find a broad ravine in which little bluestem still persisted. Accompanying it were species, often 25 or more, which had entirely vanished elsewhere.

Many-flowered psoralea was represented by many seedlings during the three years of recovery. The new, single-stemmed plants ranged from 5 to 10 inches in height. But exactly similar plants were found arising from large roots or rootcrowns, often much decayed, which had been dormant during the long drought. The prairie clovers reappeared from rootcrowns, as did also an occasional pale purple coneflower.

Stiff sunflower again appeared in something of normal abundance in parts of some prairies for the first time since 1934. All plants examined were from rhizomes or rootcrowns.

The final evidence of recovery was the great increase in yield. Dry weight has long been considered the best measure of growth. Air-dry weight of forage harvested from numerous sample plots was obtained from three stations in Nebraska and Kansas. Total plant production in

1941 was 2.3 times that in 1940, and yield in 1943 was 2.7 times as great. This increase in yield resulted from the very great thickening of the plant cover.

FURTHER DEVELOPMENT TOWARD STABLE PRAIRIE

Three or four years after the great drought had ended, most of the bared soil had been repopulated. But the vegetation was still quite different from that of the former climax. Many species characteristic of the years of drought were still present. Drought-depleted forbs did not yet occur in their usual abundance, and they did not form the characteristic societies of prairie. Height-growth of grasses was very irregular, varying greatly with the degree of competition. The understory was far from complete, and the vegetal mulch was not yet continuous. The predrought communities of lowland—sloughgrass, big bluestem, and switchgrass with wild-rye—retained their identity. But the three upland communities had been increased to eight in number, as is shown in table 6.

TABLE 6. Major communities of upland true prairie, before (left) and after the great drought.

Original Types		Old or Modified Types	Rank
Little bluestem	1	Relic big bluestem-little bluestem	4
		Big bluestem	6
	2	Mixed grasses	7
Needle grass	4	Needlegrass	3
Prairie dropseed	5	Prairie dropseed	8
		Newly Developed Types	
	6	Western wheatgrass	2
	7	Blue grama	5
	8	Mixed prairie	1

By way of a summary, each community warrants a separate statement. A relic big bluestem—little bluestem type resulted from the modification of a part of the predrought little bluestem community, but it covered relatively small areas and ranked fourth in size.

The big bluestem type on upland resulted from the survival of big bluestem wherever the former little bluestem type had lost its chief component, little bluestem. After heavy initial losses, big bluestem survived the drought in the bunch form, but later, unless overwhelmed by western wheatgrass, it spread to form a sod.

Mixed grasses formed a community of variable composition over considerable areas formerly clothed with the little bluestem type, where widely scattered plants of different species recovered, reseeded, or invaded at about the same time. These species had merely completed the occupation of bared soil where no other type had gained control. The resultant community is not climax.

Needlegrass, in addition to holding all of its original territory, had spread widely. It had not only claimed much land formerly held by the little bluestem type, but had also repopulated much low ground where big bluestem formerly flourished.

The stands of prairie dropseed were thinned following the first impact of drought even more greatly than those of needlegrass. But this species recovered without loss of territory. Seedlings became established over many acres adjacent to old stands and developed into new bunches. Thus the area occupied by this type increased enormously.

Western wheatgrass spread by seed and appeared over a wide territory immediately following 1934. It often utilized all available moisture and thus caused dwarfing or death of most other vegetation. Relic bluestems were usually replaced by pure stands of western wheatgrass.

Blue grama often survived where all other grasses died. It spread almost without interruption from 1935 to 1942, and promptly thickened its stand. Buffalo grass, less abundant and more greatly harmed by drought than blue grama, increased rapidly.

A mixed prairie type was formed by the replacement of bluestems by western wheatgrass and short grasses and their later intermingling. This began in 1938 and was completed in 1941. Invasion had ceased, since the remaining area was occupied by other vegetation, but not the intermixing of short grasses and western wheatgrass.

PERSISTENCE AND EFFECT OF WESTERN WHEATGRASS

The persistence of communities of wheatgrass and their marked effect in modifying the water relations of the soil were most impressive phenomena. Wheatgrass had not extended its area since the bared soil was reclaimed by other perennial dominants. Only rarely had it surrendered its control over very extensive areas occupied during drought. Replacement of wheatgrass by more mesic species was taking place very slowly and only over a long period of time. It may persist indefinitely where clay pans are present.

Further inquiry into the comparative effects of wheatgrass and other prairie grasses on the amount of soil moisture involved soil sampling. Soil under other prairie grasses contained a higher percentage of moisture than did the same soil, a few feet distant, under wheatgrass. The difference ranged between 1 and 13 per cent, and there was a greater amount of moisture in each of 36 samples from prairie.

Six years after the drought, most prairie forbs had increased greatly in number and size, many exceeding predrought conditions in both of these respects. But in wheatgrass sod, forbs were few or often almost absent. They had only a few stems per plant, and these were much reduced in size. For example, lead plant and many-flowered psoralea were often 2 to 4 times as tall and proportionately larger in prairie than in wheatgrass. A few seedlings were found in certain years, but very few compared with the numbers in adjacent grassland. Moreover they were dwarfed and their success in attaining maturity seemed doubtful.

Dwarfing of the forbs, which still persisted in 1946, and also the difficulty of establishment of seedlings of either perennial forbs or grasses were due to the great amounts of water absorbed and transpired by wheatgrass. The production of a new crop of shoots in autumn and the growth in early spring while most other vegetation was still dormant greatly depleted the soil of its moisture.

Studies on the kinds and numbers of forbs found in large patches of wheatgrass on upland prairie were made in August, 1946. Five pairs of circular areas, each with a diameter of 30 feet, were examined. Each pair consisted of one area in wheatgrass and one only a few feet distant in big bluestem or bluestem intermixed with other perennial grasses. Twenty species of perennial forbs were found in the prairie plots, but only 7 in those of wheatgrass. The total numbers of stems were 4,029 and 403, respectively. Thus, in wheatgrass there were only 35 per cent as many species and 10 per cent as many stems as in bluestem prairie. The average heights of representative species were often twice as great outside the areas of wheatgrass.

Where wheatgrass invaded lowlands, as in the bottoms of ravines, and temporarily replaced the taller grasses such as big bluestem and switchgrass and sometimes also sloughgrass, the dormant tall grasses have usually reclaimed the area. But the recovery does not indicate that the rhizomes of wheatgrass have died. With drought, wheatgrass vegetation may once more appear. In some prairies where wheatgrass completely replaced the bluestems, at least above ground, the area has been regained by the dormant bluestems. Potentially there are two possible crops. Which will develop depends upon the climatic cycle.

NEEDLEGRASS, PRAIRIE DROPSEED, AND PERSISTENT FORBS

There had been little or no extension of the communities of needlegrass since 1943. Neither had the Stipa-covered areas decreased perceptibly as a result of invasion. The chief changes had been a further thickening of the stands, both by an increase in the basal area of the established bunches and by an enormous increase in the number of seedlings and small clumps of all ages.

The spreading of prairie dropseed into new territory continued in some prairies until 1946. In some extensive prairies it became the most abundant grass. Where it grew in pure stands, the lodged leaves usually formed a more or less complete ground cover. In many places the new stand was invaded even in the bunches, following the general recovery by big bluestem (Fig. 72). This tall grass overtopped the dropseed and by shading, hindered its growth. The roots of big bluestem also penetrated more deeply for water. Thus, some areas of prairie dropseed have been replaced by big bluestem.

An indicator of delay in recovery was the persistence in places of certain species in the marked overabundance they had attained when the soil was otherwise bare. Chief among these were many-flowered aster, daisy fleabane, smooth goldenrod, violet sheep sorrel, and Carolina anemone. Examples among the grasses were side-oats grama and purple lovegrass, and the lingering presence of sand dropseed and hairy chess.

ROLE OF BIG BLUESTEM AND LITTLE BLUESTEM

The great upsurge of vegetative development of practically all prairie plants during and following the very wet year 1944, was pronounced.

Among all the grasses that flourished so remarkably in 1944, the growth of big bluestem was most impressive. That year witnessed the best development of vegetation in a decade. Moreover, by this time the driest slopes were well covered with grasses. By mid-August plants of the uplands and even on the hilltops had produced a great abundance of flower stalks 5 to 5.5 feet high. Each was tipped with a forked inflorescence. Patches and strips of openly spaced bunches spread for many rods over the ridges and upper slopes. Others extended down the slopes and merged with the areas of big bluestem at their bases. The stand almost everywhere was open, because of rapid, widespread propagation by rhizomes. Because of its greater stature, its deep shade overshadowed most other grasses.

A similar upsurge did not occur in undisturbed patches of bluestem prairie. Here the grasses, despite the increased rainfall, were not so rank. They had far fewer flower stalks, and these were conspicuously more slender and shorter even in comparable or better sites. The irregularity in height of the new cover in drought-bared areas, compared with that in undisturbed sod-bound patches which escaped such destruction, was very conspicuous.

Where big bluestem had grown between the bunches of prairie dropseed or had come up in them, it was clear that the dropseed was growing less vigorously. By 1946 big bluestem had spread over many uplands to form open but continuous patches in and between the bunches of this species. It flourished almost as if no other grasses were present. The drought-swept hilltops now often appeared like a lowland meadow, half of the vegetation being big bluestem. Its great height-growth, its deeper roots, and its sod-forming habit placed the bunch-forming prairie dropseed at a disadvantage during wet years. In many places, big bluestem seriously threatened the dominance of this grass.

Big bluestem also successfully invaded the sod of blue grama established during the drought. The short grass was completely ousted even locally only after two or three years of dense shading (Fig. 72). It should be emphasized that by 1947 total foliage almost everywhere was a fourth to even a third denser than during seasons with normal precipitation. The sod had thickened by an unusual development of most species. Hence shade was very dense.

The spreading of big bluestem in the years following 1944 was marked in almost all the prairies except where wheatgrass thrived. Most advanced were single shoots, then small to large bunches, and lastly the closed ranks of this tall grass.

Following the drought, little bluestem was of only intermediate importance and was outranked in abundance by six other dominant species. But flower stalks developed, seed ripened, and seedlings and small tufts were common by 1943. The major return, however, was by the awakening of dormant crowns. This grass occurred often as widely scattered bunches and increased greatly in or near places where its survival was greatest. The bunches became extremely well filled with stems, and seedlings produced many new bunches. It spread considerably and also thickened its stand. Once again certain uplands took on the appearance of climax prairie with little bluestem as the chief dominant. Considerable little bluestem reappeared in upland stands of big bluestem. Mixture of two-thirds little bluestem and a third big bluestem with a few other grasses became common; parts of prairies with a dominance of 90 percent little bluestem could now be found.

Where blue grama had invaded its territory, the old crowns of little bluestem sent forth new shoots without regard to the presence of the invader, a phenomenon that has been noted for nearly all species of dominant prairie grasses as well as forbs (Fig. 72). With the return of little bluestem a cover of organic mulch was rapidly formed.

Conversely, in some former little bluestem prairies little bluestem was still rare or absent. In a few places it revived in local areas taken over by wheatgrass during drought. These it seemed to be reclaiming. Later study showed the dominance of little bluestem and the suppression of wheatgrass. Its return in abundance in many drought-populated places and in relic areas was spectacular.

Bluegrass was practically absent by the end of the drought, though formerly it composed about 5 per cent of the vegetation. Recovering slowly in ravines, it spread upward along them onto the hills. In wetter years it completely covered much bare soil or formed a thin understory to whatever prairie grasses were in possession, except wheatgrass. Among the bluestems, bluegrass had not reached its predrought amount of 4 to 10 per cent of the vegetation in many prairies. Yet it greatly exceeded this amount in some areas where it almost alone had replaced the early postdrought understory of downy brome, hairy chess, and certain other annual grasses.

RECOVERY OF FORBS AND RE-ESTABLISHMENT OF SOCIETIES

By 1944 the forbs had nearly all increased greatly in stature. This was one of the most outstanding features of the prairies, but it was nearly confined to those of the relic bluestem type. Here too they first increased in abundance. Excellent examples are lead plant, many-flowered psoralea, silver-leaf psoralea, and stiff sunflower. These were nearly all old, well established plants. The increase was mostly in height-growth, abundance of foliage, and number of stems. In some prairies a predrought stand was almost attained by many-flowered psoralea; stiff sunflower produced large plants without much increase in numbers. Dwarfed, single-stemmed plants of large-bracted wild indigo now developed 4 to 5 stems of normal size. The very deeply rooted false boneset often produced 20 to 40 vigorous stems where only a few dwarfed ones grew before.

But increase in stature was not apparent in some prairies even in 1944. Societies of forbs were few, highly localized, and almost confined to ravines and other favored sites. The following were becoming more plentiful where their stand had been greatly depleted: tooth-leaved primrose, silvery aster, blue-eyed grass, dotted button snakeroot, smooth goldenrod, prairie sage, entire-leaved rosinweed (locally), and westward, velvety goldenrod. But many of these were not yet present in normal abundance. About 20 other species were again seen occasionally, some for the first time since the drought. Despite these gains the general aspect in the prairie everywhere was that of grass with only occasional forbs; a longer time was necessary for the re-establishment of the societies.

In 1945 forbs were much less localized than before; greatly disturbed areas were being populated as well as relic communities. It was now also clear that some had spread widely and occurred in sites where they were not found before the prairie grasses had been greatly depleted. Silver-leaf psoralea not only had far exceeded its predrought abundance in many prairies but had spread over the driest hilltops as well. Redroot, formerly quite local on upper slopes, had now spread widely, and the stand had thickened greatly.

A remarkable increase in numbers of many species had been attained. Stems of stiff sunflower were sometimes 30 to 60 per square meter. Lead plant was greatly overdeveloped; often 9 to 15 tall and very leafy stems were counted per square meter. Plants of dotted button snakeroot were often 5 to 10 times more abundant than before the disturbance caused by drought. Many-flowered psoralea grew so thickly in some prairies that in early summer the whole area appeared as a single society of this legume. Plants of Indian turnip were especially large, thrifty, and overabundant. Silver-leaf psoralea had increased to 100 to 130 stems per square meter in 1947. Societies of at least 25 species were repeatedly observed, but only 12 in the more western prairies.

The heavy rainfall following the years of drought had now wet the soil many feet in depth, and all plants, including the most deeply rooted, had benefited greatly. All were of unusually large size and many grew more thickly than the writer had ever seen before. While rigid sunflower normally has only 1 to 3 heads when growing in prairies, it now had from 3 to 7, and all were much larger than normal. Prairie rose had greatly increased, and in many places in relic bluestem prairie it formed one-third to one-half of the entire plant cover. In one large prairie, redroot had migrated from the upper slopes downward to the banks of ravines. Small plants were scattered over the entire hillside. The large size and enormous crop of fruit produced by ground plum was remarkable. Seventy-five to 95 unusually large fleshy fruits were counted on single plants. Hawkweed, previously found as isolated individuals, was not infrequently well aggregated, 10 to 20 rosettes occurring in a single square meter. By 1944 seedlings of some forbs were plentiful in places, but they were far more abundant, more varied, and of greater general occurrence in following years. The process of reseeding interspaces among the thickening vegetation and small bare places wherever they occurred continued in 1945 and 1946.

The understory vegetation was returning only slowly and even seven years after the drought the ground layer was far from complete. Thus, despite great increases in numbers of forbs, and even an overabundance of certain species, the total population was still far below that preceding the catastrophe of drought. Moreover, distribution was not so uniform. Thus, the effects of drought were still plainly to be seen by any one who could interpret the prairie landscape.

A good soil mulch occurred everywhere in predrought prairie. Almost none was found on the bare, black soil during the 7 years of drought. By 1944 the denser vegetation had gone far toward re-establishing a protecting cover of debris. Junegrass and prairie dropseed were prominent species in producing this mulch. An excellent type of mulch was furnished by bluegrass, and side-oats grama also furnished much debris.

Hairy chess has gradually disappeared from many prairies and its abundance was greatly reduced in all. But its role in preparing and maintaining a mulch should be emphasized. Thick local stands in small bared places often had 20 to 25 stems per square inch and a height of 10 to 12 inches. Even after it disappeared in areas of true prairie during the years 1945 to 1947, it still persisted in patches of short grass. Sometimes the mulch in blue grama was 2.5 inches thick. In pure stands of needlegrass the mulch was sometimes only partial. Under newly established prairie dropseed, where the plants were not densely aggregated, bare black soil still occurred. In the mixed grass type of somewhat open stand, 20 to 30 per cent of the bare soil was free from any cover of dead vegetable matter.

PRAIRIE IN 1953

On the western margin of true prairie where mixed-prairie species had invaded extensively, recovery was remarkably slow. Western wheatgrass and short grasses spread rapidly here when the former occupants, chiefly bluestems, had succumbed to drought. But bluestems, prairie dropseed, and other species had to regain areas already occupied by a thriving vegetation. Thus, 12 years after the end of drought mixed prairie still prevailed over two-thirds of the land it had invaded during the 7 years of drought. The change from the mixed prairie population to one of true prairie will require a long period of time for its completion. Nature is slow but persistent. Finally she will put back upon these prairies those species that were there in the first place, long before the drought. At least this has happened in the more easterly prairies, wholly or in part.

Eastward one type of vegetation that has almost disappeared is the mixed-grass community. The needlegrass component has usually been reduced to small and often insignificant amounts. Big bluestem has taken over the greater part, and communities of prairie dropseed or little bluestem the remainder.

The mixed-prairie type has been greatly enlarged at the expense of western wheatgrass and blue grama communities, and little of either of these remain with a single dominant in control. Where blue grama occurred in the other communities, it has greatly decreased and mostly succumbed in the shade of taller species. Many areas of western wheatgrass have been slowly invaded by bluestems. Much needlegrass and prairie dropseed have also been replaced by bluestems.

Big bluestem communities on upland are regaining an increasing population of little bluestem. West of the Missouri River, recovery to the predrought climax has not yet been fully attained. But in areas eastward where drought was much less severe, the prairies, as clearly as one can read the landscape, are the same as those described in earlier chapters of this book.

CHAPTER 15

Degeneration of Prairie

CLIMAX prairie is a very stable vegetation. It has endured the catastrophes of fire, flood, freezing and drought throughout untold centuries. Myriad animals, from bison and antelope to ground squirrel and gopher, have fed upon the vegetation above or below ground, trampled it, burrowed in the earth, buried some plants with soil, and wallowed in the wet places. All of this damage was constantly repaired, and the cover of prairie grass and forbs, with a few small shrubs interspersed, continued over the level land, hillsides, and valleys; the ravines were merely folds in this great green carpet of vegetation. But most of the True Prairie has now been destroyed by the slow but certain process of fragmentation. The sod was turned by the breaking plow, first in small patches but soon in larger ones. Then the broken land exceeded the unplowed soil in area. Much of this land degenerated to bluegrass because of excessive grazing, and today, especially in the eastern portions, areas still covered with the native grasses are rare.

EFFECTS OF BURNING

Next to the breaking plow, overgrazing (often followed by breaking) was the chief cause of degeneration. Fires were damaging and destructive. Frequently prairie fires occurred in the fall and left the soil exposed and without protection from dryness, wind, and rapid freezing and thawing. While the fires often resulted in changes in the amount and composition of the prairie vegetation, they probably never caused its disappearance.

Much has been written about prairie fires, but few scientific studies have been made of their effects upon prairie. Shantz (1924) states: "These grassland areas were often burned over in late summer or winter. . . . Aided by high winds, these fires swept with great rapidity across the grasslands of the prairies and plains, and early settlers and travelers could find safety only by starting backfires, since the broad band of burning grass, often 100 to 200 yards across, made it impossible to pass through the flames to the burnt areas of safety behind."

Effects of burning have been thoroughly studied in the Flint Hills of Kansas. Anderson (1946) pointed out that the highly productive bluestem pastures are stocked lightly because under the lease system of management grazing begins so early that at first the pasture cannot support large numbers of animals. Since the cattle are marketed in late summer, there is almost always a surplus of forage during the latter part of the growing season. This forage retains but little of its palatability or nutrient value after maturity. The only practical method of removing it is by fire, and since it interferes with early grazing the following spring, annual burning has been widely practiced over a period of 70 years. Burned pastures can be grazed earlier and grazing is more uniform when the old vegetation is removed. But early grazing is injurious to the vegetation. The early lead in forage yield of burned over unburned vegetation is not maintained; unburned pastures give a greater total seasonal yield than burned ones.

Aldous (1934) after seven years of experimentation ascertained: "The yield of the unburned plot, however, averaged approximately 48 per cent more than that of the plot burned in late spring. The unburned plot also yielded about 54 per cent more than the plot burned in the medium spring, 72 per cent more than the plot burned in early spring, and 88 per cent more than the plot burned in the late fall. The yield of grasses on these plots was approximately in the same proportion as the total yield of vegetation, the check plots being greatest, followed by the late spring, medium spring, early spring, and late fall-burned plots."

The contention that pasture burning reduces pasture weeds cannot, according to Anderson (1946), be supported by any trials yet conducted on bluestem pastures. There is no experimental evidence that burning bluestem pastures reduces soil fertility; no decrease was found after 5 years of burning. "Burning bluestem pastures undoubtedly reduces forage yields, but when the burning is done over wet soil there is little evidence to indicate that this loss of yield is due so much to actual damaging of the grass as it is to reduction in the amounts of soil moisture available to the growing crop." A close relationship has been shown between earliness of burning and reduction in soil moisture. This reduction results from long spring exposure to runoff and from surface evaporation during the period between the time of burning and the beginning of growth of the warm-season prairie grasses. When summer rainfall is below normal, the grass may cease growth on areas burned early but not on adjoining unburned pasture.

Anderson (1953) points out that "Aldous (1934) showed that early spring burning caused an increase in density and favored the finer stemmed species such as little bluestem and prairie dropseed, while burning as late as possible before spring growth started caused a decrease in density and induced a trend toward the taller, coarser species such as big bluestem, Indian grass, and switchgrass." He believes the early burning resulted in conditions more favorable for little bluestem and other prairie dominants of drier sites.

Fire is less destructive to grasses than to woody vegetation and it may sometimes benefit prairie where debris has accumulated over several years. This undoubtedly occurred where fires were set by lightning. The prairie and indeed the entire area of North American Grassland at the time of settlement consisted of a climax vegetation, the extent of which was controlled by climate. Fire was only one of the many environmental factors. The grasses produced large amounts of dead, dry, inflammable material. Lightning often started fires. "Thus the Grassland climates favor fire, just as they favor grass whether there are fires or not. . . . Fire, if not primitive man, himself, would simply have been one part of the ecological complex of a region with the climate of the Grassland. . . . Also, the precipitation pattern of eastern America during major drought years can explain why the influence of fire was restricted to the grassland. The climate of the forests generally did not favor burning" (Borchert, 1950). After extended study of the climate of Central North America, Borchert concludes: "The geographical pattern of postulated post-glacial fluctuation of the Grassland fits the facts of the recorded climate. The pattern of the Grassland at the time of white settlement also fits those facts. The patterns, themselves, suggest very strongly that they were, in the words of an earlier author, dictated by the master hand of climate."

NATURE OF DEGENERATION UNDER GRAZING

Degeneration of prairie under grazing was considered in conjunction with the extensive study of native grasslands of western Iowa, eastern Nebraska, and portions of four adjoining states, to the north and south, respectively (Weaver and Fitzpatrick, 1934). The pastures varied in size usually from 20 to 160 acres, although westward, especially, some ranges

320 acres or more in extent were not infrequent. Scores of pastures were studied year after year and in spring, summer, and autumn.

In the study of the pastures (Weaver and Hansen, 1941), it was observed that the degree of overgrazing was best recognized and measured by three types of plants which were used as indicators. First of these are the preferred or more palatable species that cattle and horses select and eat. Such species as big bluestem, little bluestem, and most legumes are examples. They are grazed so consistently that they gradually weaken and finally die. The degree to which the most palatable plants have decreased is one measure of the stage of degeneration. Species of this kind are called *decreasers*. As these decreasers gradually disappear they render the uneaten plants more conspicuous. Because of more water and light their growth is greatly increased and they may spread widely. Such plants are therefore called *increasers*. Kentucky bluegrass, side-oats grama, and many inedible forbs, such as ironweed and stiff goldenrod, furnish excellent examples. They are enabled to store more food in their propagative organs as well as to produce more seed. The decreasers are correspondingly handicapped in all these respects by the upsurge of the increasers. Thus, during the early stages of degeneration resulting from grazing there is considerable shifting of the plant population, but entirely among the species which are normal components of the native prairie.

As the hold of the native species is weakened, small bare places appear. There are many causes for these. Death of greatly weakened plants may result from drought or winterkilling, since loss of vigor of tops also weakens the roots. Bare spots appear where dung has smothered the grass or where animals have pawed or trampled the earth or slipped on wet soil. These bared areas are colonized by weedy grasses and forbs. Examples are prairie three-awn (*Aristida oligantha*), ragweed (*Ambrosia*), and hoary vervain (*Verbena stricta*) (Fig. 73). They have no place either in prairie or good pasture. They are a third type of plants, designated as *invaders*. Once established, they furnish seed for a new population. Gradually, the native grasses and forbs are partially or entirely replaced by invading species which are better adapted to close grazing and trampling. Nearly all of these are less productive, or less palatable, or both, than the original occupants. Before this stage of deterioration is reached, the livestock is usually forced to graze even the least desirable increasers, unless they are woody, wholly unpalatable, or protected by spines.

FIG. 73. (Upper row) Prairie three-awn (*Aristida oligantha*), hairy chess (*Bromus commutatus*) and little barley (*Hordeum pusillum*). (Lower row) Hoary vervain (*Verbena stricta*), gum plant (*Grindelia squarrosa*), and wavy-leaved thistle (*Cirsium undulatum*).

Although the process of deterioration of prairie is a gradual one, it was ascertained that the intelligent use or careless abuse of these grasslands had resulted in pastures and ranges which could logically be grouped into four classes—excellent, good, fair, and poor. The first consisted almost entirely of climax grasses and an abundance of nutritious forbs, which, as nearly always occurs, were of the highest grazing value. In good pastures many of these persisted, but there was a strong trend toward loss of vigor and decrease in abundance of the best grasses and forbs. About half of the vegetation consisted of the less productive Kentucky bluegrass or of short grasses. In fair pastures climax grasses and the most palatable forbs had all but disappeared. Here bluegrass, blue grama, or buffalo grass were the dominants. Usually bluegrass alone was in control east of the Missouri river and the short grasses westward, but in the transitional area it was not unusual for both types to occur. Poor pastures were characterized by broken cover, more or less isolated patches of bluegrass or short grass, and much bare soil or soil supporting a stand of various species, mostly weedy annuals.

CLASSIFICATION OF PLANTS BASED UPON THEIR RESPONSE TO GRAZING

Plants found in pastures may be classified according to the manner in which they respond to grazing. Lists have been compiled after constantly checking the behavior of the species concerned in many pastures over long periods of years (Weaver and Hansen, 1941). The plants have been observed under varying degrees of grazing and their normal abundance checked in adjacent prairies or in strips of native prairie just over the fence along roadsides. The following types occur:

Prairie grasses that decrease under grazing
Prairie forbs that decrease under grazing
Prairie grasses that increase under grazing
Prairie forbs that increase under grazing
Grasses that invade pastures
Weedy forbs that invade pastures

Prairie Grasses That Decrease

A considerable number of prairie grasses tend to decrease in abundance more or less rapidly when true prairie is grazed. Finally all may disappear.

The most important species, all perennials, are:

Andropogon gerardi Big bluestem	*Panicum virgatum* Switchgrass
Andropogon scoparius Little bluestem	*Stipa spartea* Needlegrass
Sorghastrum nutans Indian grass	*Koeleria cristata* Junegrass
Spartina pectinata Prairie cordgrass	*Sporobolus heterolepis* Prairie dropseed
Elymus canadensis Canada wild-rye	*Sporobolus asper* Tall dropseed

Big bluestem has high palatability or grazing preference, which refers to the taste an animal displays for any plant. It has been found to be most preferred of prairie grasses in all grades of pasture where it occurs. It is selected by livestock even where other forage is abundant (Weaver and Tomanek, 1951). When big bluestem is grazed, many new shoots are produced from the bases of stems and from rhizomes. These give rise to an abundance of foliage just above the soil surface. This grass makes its greatest radial spread in spring while using the food reserves of the previous summer. Hence, early grazing limits normal development, decreasing growth of both rhizomes and new shoots. Since the best stands on rolling land occur in and along ravines, grazing here is soon uniform and intense. With the increase in light, which results from the pasturing of the bluestem, bluegrass spreads rapidly between the stems and tufts of this tall grass. Both grasses are then closely eaten. Year by year bluegrass increases, and finally big bluestem entirely disappears. On uplands it persists longer, the last remnants being found on steep slopes and on the banks of deep ravines. The clumps are gradually weakened with increasingly close grazing. Other grasses, especially bluegrass, migrate in. Soon outlines of the former clumps are scarcely distinguishable, if indeed big bluestem has not entirely disappeared.

Little bluestem, while not of such high grazing preference as big bluestem, is readily eaten in spring and early summer, but often avoided after the rather woody stems are produced. Where moderately or closely grazed it produces palatable and nutritious forage throughout the entire growing season. Probably because of its habit of growing in tufts and bunches, it does not withstand grazing as well as big bluestem, and disappears earlier, lingering longest on the least grazed, roughest land. Once an old bunch is grazed and the dried stems removed, as happens under overstocking or drought, it is regularly grazed thereafter and bluegrass or short grasses exert continuously greater competitive pressure. With overgrazing, the older, central portion usually dies first. Peripheral growth may continue, but stems become progressively sparser. The bunch often breaks up into many fragments which may succumb but slowly or disappear rapidly depending upon the closeness of pasturing.

Sloughgrass or prairie cordgrass is grazed readily in its earlier stages of development, but once the coarse woody stems are formed, only the tops are eaten. But as the stems are broken by trampling, the shade is reduced, and bluegrass and other vegetation invade. Finally sloughgrass disappears.

Switchgrass is palatable when young but practically worthless for forage at maturity when the stems become lignified, except that the leaves and panicles may be eaten. The sod it forms is very open and does not well resist heavy grazing and trampling.

Needlegrass renews growth very early in spring and, like Canada wildrye and Junegrass, is sought out and repeatedly grazed. Like these grasses also, it has a high grazing preference and is very nutritious. It is especially liked by horses. The bunches are grazed rather closely and repeatedly as new foliage appears. Consequently, there is very little reseeding, and the original stand, grazed again late in fall when most other forage is often dry, disappears early.

Prairie dropseed is palatable to all kinds of stock and furnishes considerable forage when it is not allowed to mature. Green shoots in old bunches filled with debris are readily grazed. It withstands close grazing rather poorly. Tall dropseed, which has a much lower grazing preference, decreases in amount much more slowly.

Prairie Forbs that Decrease

Prairie plants other than grasses that decrease and may entirely disappear under continued grazing constitute a long list of important species. All are perennials. Among these, the legumes especially furnish much nutritious forage. For convenience of treatment, they are listed separately from the other representative forbs that are also readily eaten and which decrease in abundance under grazing.

LEGUMES

Amorpha canescens
Lead plant
Astragalus canadensis
Canadian milk vetch
Astragalus crassicarpus
Ground plum
Glycyrrhiza lepidota
Wild licorice
Lespedeza capitata
Bush clover
Desmodium canadense
Showy tick trefoil
Desmodium illinoense
Illinois tick trefoil
Petalostemum candidum
White prairie clover
Petalostemum purpureum
Purple prairie clover
Psoralea argophylla
Silver-leaf psoralea
Psoralea esculenta
Prairie turnip
Psoralea tenuiflora
Many-flowered psoralea

OTHER FORBS

Allium spp.
Onions
Anemone cylindrica
Long-fruited anemone
Aster laevis
Smooth aster
Aster praealtus
Willow aster
Ceanothus ovatus
Redroot
Coreopsis palmata
Tickseed
Echinacea pallida
Pale purple coneflower
Euphorbia corollata
Flowering spurge
Helianthus spp.
Sunflowers
Heliopsis helianthoides
Oxeye
Kuhnia eupatorioides
False boneset
Liatris punctata
Dotted button snakeroot
Liatris scariosa
Large button snakeroot
Oenothera serrulata
Tooth-leaved primrose
Rhus radicans
Poison ivy
Rosa suffulta
Prairie rose
Solidago altissima
Tall goldenrod
Solidago speciosa
Showy goldenrod

Lead-plant, under the practice of mowing or grazing where the top is removed each year, produced each spring 2 to 5 or more stems from the crown. Since it is the most abundant plant of upland, aside from the grasses, it furnishes very palatable forage in considerable quantities. Analysis of four clippings per growing season in a virgin prairie in western Iowa revealed that the seasonal yield of this species alone was 200 pounds of air-dry forage per acre. Stems regenerate from the stores of food in the root-crown and very deep, woody taproot. Hence the plant may persist a long time. But only remnants of this formerly abundant species are usually found in fair and poor pastures.

Ground plum is freely grazed and usually has disappeared by the time the prairie has been reduced to fair pasture. The thick taproot and large root-crown are effective in maintaining life, yet large clumps have been known to be reduced by one year of close grazing to plants with a single weak branch and one small flower cluster. The much coarser Canadian milk vetch (*Astragalus canadensis*) suffers the same fate as the ground plum.

Wild licorice is greedily eaten by livestock, especially when it is young. Despite its great store of food underground in strong taproot and rhizomes, it is practically all dead by the time close grazing results in fair pasture.

Whether the several species of psoralea are eaten depends considerably upon the earliness of grazing. The plants put forth rather thick stems which elongate to 3 to 6 inches before branching. Later, as the stems become woody, only the leaves and tender branches are usually grazed. When the stem is bitten or broken off, renewed growth takes place from the base.

Prairie clovers are readily grazed in their earlier development before they become woody, and they are rarely found in pastures degenerated beyond the good pasture stage.

Among non-legumes, wild onions are closely grazed with the grasses. Their very early appearance and rapid growth in spring aid in their extermination. Even the shrub, redroot, quickly disappears from prairie that is continuously grazed. Horsetails or scouring rushes are grazed with the other vegetation, and although the plants may grow thickly just beyond the fence in prairie, they are rarely found in abundance except in excellent or good pastures.

Stiff sunflower is so readily eaten that it does not long persist in pastures, despite the abundance of food stored in the rhizomes. Even mature plants, except the bases, are eaten when grazing is deferred until midsummer. The fate of Jerusalem artichoke is very similar, as is also that of the saw-tooth sunflower. The several species of button snakeroot and blazing stars, which are abundant in grassland, disappear early when prairie becomes pasture. Usually this occurs in the good pasture stage. The abundant foliage and tender tops of the prairie rose are readily eaten by livestock, and, after the underground food reserves are depleted in producing new shoots, the plant finally succumbs. Poison ivy, common in prairies, also soon disappears from pastures when grazing becomes more or less uniform. The showy goldenrod, which grows in bunches, readily succumbs to grazing. Tall goldenrod is grazed when young, but only the tops are consumed when the plant is half-grown. However, by the time bluegrass has rather completely sodded over the ravines and lower slopes, where this species thrives, grazing and trampling have removed all but the last remnants.

Prairie Grasses that Increase

Although much grazed, certain native grasses profit so much by the changed conditions under pasturing and the waning of other important competing species that they increase greatly. Ten of the most important are listed.

Poa pratensis
Kentucky bluegrass
Agropyron smithii
Western wheatgrass
Bouteloua curtipendula
Side-oats grama
Bouteloua gracilis
Blue grama
Bouteloua hirsuta
Hairy grama
Buchloe dactyloides
Buffalo grass
Panicum scribnerianum
Scribner's panic grass
Panicum wilcoxianum
Wilcox' panic grass
Carex pennsylvanica
Penn sedge
Eragrostis spectabilis
Purple lovegrass

Since the settlement of the Midwest, Kentucky bluegrass has successfully invaded the prairie, as a result of mowing and grazing, and has spread very widely. It is a dense turf- and sod-former, producing large numbers of slender, shallow rhizomes. These give rise to tufts of grass above ground from which arise a profusion of fine, fibrous roots. This grass is not only unusually resistant to grazing but is also able to maintain its hold and actually to increase the stand even where the soil is much trampled and the grass closely grazed. Its productivity decreases during the hot midsummer, but renewed growth begins in the fall and continues until freezing weather prevails. During dormancy it is very resistant to adverse conditions. Early spring growth, when most other species are dormant, greatly favors its spreading. It is also favored by close, selective grazing of big bluestem, and makes its first appearance as a continuous sod in the bottoms of swales and ravines, along paths, and about gates. Although bluegrass is very palatable, aggressive, and persistent, it is rather low-yielding.

Western wheatgrass begins growth very early and develops a good sod. It is drought evading, using available moisture in spring for rapid growth and early seeding. It is semidormant during midsummer, often drying, but resumes growth in fall. In grazing preference and forage value, except when young, it ranks far below most grasses of true prairie. It furnishes early (and late) forage, but often only the tops of older plants are grazed even when other vegetation is not abundant. Once established, it is very persistent; since the beginning of the great drought its importance in western pasture has greatly increased.

Side-oats grama increases slowly but consistently under grazing. This occurs despite the fact that it is well liked by stock because of its leafiness, and is closely cropped. In fact, it compares favorably in feeding qualities with the bluestems, being readily eaten when dry. The flower stalks are relished only when young, although their leaves are eaten. Hence, in low-grade pastures where this species is still present, it is common to find flower stalks and some seed. It is a prolific seeder, and seedlings are commonly found. Although it appears in bunches in prairie, under grazing the rhizomes, 2 to 4 inches long, promote the formation of small areas of sod. It readily invades places bared by the death of other species. In prairie it was most abundant on dry slopes and steep banks. Under grazing it may form a nearly pure cover over such areas and remain as a relic even in poor pastures.

When bluestem pastures are too closely grazed, blue grama may spread throughout the drier places, but it appears prominent only when the seedlings have, by prolific tillering, formed bunches of tufts. From these larger mats a more or less continuous sod may develop locally. This results both from tillering and from spread by short, scaly rhizomes. Very frequently, if the sod is continuous, it is intermixed with buffalo grass. Under moderate grazing, these grasses are cropped closely and uniformly with little apparent harm. Blue grama is a choice species for all classes of stock. The seasonal yield, however, is frequently only about 60 per cent as great as that of good bluestem pasture. Under close grazing the blue grama mat breaks up into more or less isolated tufts between which annuals such as little barley, plantain, peppergrass, and numerous other plants, occur.

Hairy grama is similar in stature and general appearance to blue grama, except that it grows in small bunches. It furnishes forage of good quality. It seeds readily, and the seedlings mature early. Relatively little of this grass occurs in pastures, except on shallow rocky soil. It often forms 5 to 15 per cent of the vegetation on ridges and hill crests in the Flint Hills prairies and pastures in Kansas.

Buffalo grass, like blue grama, is of minor significance in native true prairie, since it cannot endure the shading of its taller competitors. But under grazing it occurs widely, especially over the more arid western portion of true prairie. Its rapid spread results from propagation by stolons which root readily when they come in contact with moist soil. The hard seeds are produced within the grass mat; unless crushed between the teeth

FIG. 74. Stiff goldenrod (*Solidago rigida*), Baldwin's ironweed with western ironweed on right (*Vernonia baldwini* and *V. fasciculata*), and milfoil (*Achillea millefolium*).

of grazing animals, they may pass through the digestive tract unharmed. The plants of buffalo grass are seldom more than 4 to 5 inches tall but, as in blue and hairy grama, the leaves grow so near the soil that much green tissue remains even under very close grazing. This explains in part why this grass can withstand heavy grazing and why it persists where all mid grasses have disappeared. The forage, like that of blue grama, is very palatable and nutritious even when it has cured in fall or as a result of drought in summer. These short grasses renew growth late in spring, much later than bluegrass.

Prairie Forbs That Increase

Numerous forbs are either entirely uneaten by stock or grazed so sparingly that they are not much handicapped. They profit greatly by the release from shade and vigorous competition common in prairie and increase greatly in number and often in stature (Fig. 74). The following list includes the most important species:

Achillea millefolium
Milfoil or yarrow
Antennaria neglecta
Prairie cat's-foot
Artemisia ludoviciana
Sage or mugwort
Asclepias verticillata
Whorled milkweed
Aster ericoides
Many-flowered aster
Baptisia leucophaea
Large-bracted wild indigo
Callirhoe alcaeoides
Poppy mallow
Erigeron annuus
Fleabane
Erigeron strigosus
Daisy fleabane
Lygodesmia juncea
Rush-like lygodesmia
Oxalis stricta
Yellow sheep sorrel
Silphium integrifolium
Entire-leaved rosinweed
Silphium laciniatum
Compassplant
Solidago missouriensis
Smooth goldenrod
Solidago mollis
Velvety goldenrod
Solidago rigida
Stiff goldenrod
Vernonia baldwini
Baldwin's ironweed
Vernonia fasciculata
Western ironweed

One of the worst of these forbs is Baldwin's ironweed. It is usually found only in ravines in eastern Nebraska prairies. The leaves are bitter and the plant is avoided by stock. When the bluestems and other grasses about the plants are eaten, it rapidly increases its area and develops large bush-like clumps 1 to 3 feet in diameter, consisting of 50 to 150 or more woody stems. It gradually migrates out of its home in ravines or on lowlands by means of wind-blown seeds and becomes established in bared spots on uplands, although here the bunches are usually not so large. This forb is thus a reliable indicator of the length of the period of overgrazing and something of the degree as well.

Grasses That Invade Pastures

When the tops of prairie plants are continuously more or less completely removed by grazing, light at the soil surface greatly increases. This, combined with the opening of the sod by the death of certain species, permits a host of weeds, none of which is found in climax prairie, to become established. The change in the light relation is marked. Under a good stand of big bluestem, the light is frequently reduced to 1 to 3 per cent of full sunshine. In upland prairie, light intensities of only 10 to 20 per cent have been regularly recorded. Moreover, with a reduced stand of grass, less water is absorbed by the plants and more is left for invaders (Fig. 73).

The following list includes the more important species, most of which are weeds, that are not a component part of undisturbed true prairie vegetation but which regularly occur only in the lower grade pastures. All except windmill grass, foxtail barley, Canada bluegrass, sand dropseed, and paspalum, are usually annuals in eastern Nebraska (Fig. 73).

Aristida oligantha
Prairie three-awn
Bromus secalinus
Chess
Bromus tectorum
Downy chess
Bromus commutatus
Hairy chess
Chloris verticillata
Windmill grass
Digitaria sanguinalis
Crabgrass
Eragrostis cilianensis
Stinkgrass
Eragrostis pectinacea
A lovegrass
Hordeum jubatum
Foxtail barley
Hordeum pusillum
Little barley
Panicum capillare
Witchgrass
Poa compressa
Canada bluegrass
Paspalum stramineum
Straw-colored paspalum
Schedonnardus paniculatus
Tumblegrass
Sporobolus cryptandrus
Sand dropseed
Sporobolus vaginiflorus
An annual dropseed

Weedy Forbs that Invade Pastures

A host of weedy forbs also enter native pastures when too close grazing, excessive trampling, and other causes result in much bare soil. Examples of the most important are ragweeds (*Ambrosia*), various thistles (*Cirsium*), gum plant (*Grindelia*), plantain (*Plantago*), vervain (*Verbena*), and spurge (*Euphorbia*) (Fig. 73). In extended drought Russian thistle (*Salsola kali*), burning bush (*Kochia scoparia*), and stickseeds (*Lappula*) may become very abundant in the western areas. A census of weedy prairie forbs and other weedy forbs and grasses was taken over a period of years in 41 pastures. All types of pastures were represented. Aside from the prairie grasses, a total of 87 such species entered into the composition of the vegetation. The average number of species occurring in excellent pastures was 9; in good pastures there were 15. The number increased to 18 in fair pastures and 22 in poor ones. Likewise, total number of species, in the same order, was 25, 45, 72, and 59 (Weaver and Hansen, 1941).

DEGENERATION UNDER EXCESSIVE GRAZING

Climax grassland, when grazed lightly, retains essentially its natural composition. It is only when grazing animals are circumscribed in their range by fences and when too large a number are thus confined, that grazing and trampling become so excessive that the normal plant cover can not be maintained. Numerous changes in the vegetation then occur. These changes often take place so gradually over a period of years that until the plant cover has been greatly disturbed or a large proportion of the more valuable species have been actually killed, deterioration may not be recognized. When this stage of depletion has been reached, many seasons of proper management are required to re-establish the original forage cover. Conversely, where prairie is grazed intensively, in only a few years almost unbelievable changes occur.

The task of maintaining grazing lands in a high state of productivity is fundamentally based upon a knowledge of the vegetation; in fact, a knowledge of native plants and forage conditions is vital to the successful management of pasture or range. Conservation of range land can be accomplished only by attention to correct grazing. Native prairie has been the home of grazing animals for untold centuries. Prairie plants are eminently adapted to grazing, and conservative grazing is not inimical to their development. But to maintain production, moderate grazing must be practiced. Forage production from a pasture in good condition may be several times as great as that from one in an advanced degree of degeneration. Poor pastures, like poor crops, are expensive. As the prairie degenerates, the best-liked and most nutritious grasses and forbs wane and disappear. They are replaced by species of lower grazing value. Weeds become abundant. Finally, the farmer or rancher says the prairie has been "grazed out." Often the land is plowed, and thus another tract of prairie forever disappears.

An Example on Lowland

A native bluestem pasture was found in which a part had degenerated into bluegrass sod, other portions were covered with western wheatgrass, and the remainder was typical and excellent prairie.[1] This level or nearly level tract of 50 acres was on well drained lowland near Lincoln, Nebraska. The dark colored, porous, highly productive soil was Wabash silt loam. Into it the roots of bluestem and wheatgrass extended to a depth of 6 to 7 feet, and even the more shallowly rooted bluegrass penetrated to nearly 3 feet.

Formerly the entire area had been covered with typical prairie, mostly big bluestem and little bluestem; but smaller amounts of needlegrass also occurred. Lead plant, silver-leaf psoralea, and ironweed were common prairie forbs. During the great drought it had been pastured for three years; bluegrass had entered along the bottom and banks of a small depression which crossed the pasture, and from here it had spread outward to some extent. It occurred in several parts of the area. The repeatedly grazed bluegrass formed a sod almost free from other grasses and forbs. Invasion and increase of wheatgrass was a direct result of the dry soil and high winds. Large amounts of wind-borne dust from adjacent cultivated fields had been deposited in this prairie. It occurred in layers of varying thickness, sometimes several inches deep. Under the deeper deposits all vegetation had been destroyed and wheatgrass had rapidly invaded. Areas of wheatgrass occurred in many places in the pasture. Wheatgrass and bluegrass each occupied almost exactly one-third of the pasture. Few other plants grew in the dense wheatgrass sod. Vegetation in the bluestem or prairie type, like the bluegrass and wheatgrass, was in a thriving condition.

The pasture was heavily stocked each year with about 45 head of yearold steers (Fig. 75). Grazing began about May 1 and extended well into October. Both precipitation and temperature were so favorable to growth during 1943 to 1945 that even bluegrass remained green and continued growth almost all summer. In 1946 the plant cover had degenerated greatly; moreover the summer was drier, and the number of cattle was considerably decreased.

Strong portable exclosures, each of which kept the cattle from disturbing 30 square feet of vegetation, were set up. Each consisted of a frame of four long steel posts bolted together at the top but spread at the base where they were bolted to wooden strips 2 inches square and 5.5 feet long.

[1] Materials for this section are from Darland and Weaver (1945), Nebraska Conservation Bulletin number 27, and Weaver and Darland (1948), Ecology, January, 1948.

The sides of the pyramidal frame were covered with a heavy grade of woven fencing wire. The purpose of the exclosures, which were moved to a new location each month, was to determine, by clipping, the monthly yield and consumption of forage.

FIG. 75. (Upper) A lowland pasture near Lincoln, Nebraska, in which degeneration under excessive grazing was studied over a period of 4 years. (Lower) Extensive area near Corning, Iowa, where prairie has been replaced by Kentucky bluegrass as a result of continuous grazing.

The amount of each kind of forage produced and consumed each month is of great importance, not only in relation to favorable or unfavorable environment but especially in its relation to changing plant population resulting from overuse of the pasture.

Five or six widely separated sampling areas of about 10 square rods each were selected in each of the three grazing types. In each sampling area one exclosure, with its grazed control of similar size, was located in early spring. It was moved to a new location in the area at the end of each of the 5 or 6 months of the grazing season.

In selecting the original location for an exclosure, two places were chosen within 10 or 15 feet of each other in which the vegetation was as nearly alike as possible. The forage in one was to be clipped after a month of protection; that in the other, which was subjected to grazing, was also to be clipped at the same time. One exclosure was then securely set in place. Since the sides of the exclosure sloped inward from the base, it was not disturbed by the livestock. The control area was also clearly marked. At the end of each month at the time of the clipping, new places for the exclosure and control were selected in the same general area. These were as nearly as possible like the former control area, and were selected before clipping, since both of the former plots were now to be clipped by hand close to the ground, closer than the cattle could graze. By subtracting the air-dry weight of vegetation of the control from that obtained from the exclosure, the monthly consumption from the 30-square-foot area was obtained.

The average yield in any type during the first month was represented by the air-dry forage under that exclosure, since all debris from the previous year was carefully separated from the new vegetation and discarded. During the second month the total yield was the amount that grew on the area newly exclosed less the amount of new vegetation remaining ungrazed in the control area of the preceding month. This may be clearly understood by examining table 7.

The results from all the exclosures in any forage type were averaged and the amount of forage consumed each month has been plotted in a graph. For comparison, graphs of data from the other types are included (Fig. 76).

In figure 76 it may be seen that considerable consumption of wheatgrass (about 325 grams) occurred in May. This cool-season grass made an early growth and was 12 to 24 inches high during this month. Flower stalks were produced by June, and thereafter little wheatgrass was eaten until autumn, when a new crop of shoots and green leaves grew from the rootstocks. Conversely, the warm-season bluestems had begun growth several weeks later than the wheatgrass, and only a small amount of forage was consumed in May, simply because only a little was produced. But while the matured wheatgrass was nearly dormant during the summer, the bluestems gave high yields in June, July, and August. Since the summer was moist and fairly cool, bluegrass did not dry out in midsummer as is usual, and much forage of this lower yielding grass was also eaten.

TABLE 7. Amount of new forage harvested from exclosure number 12 and from its control each month in 1944. The air-dry weights are in grams.

	May	June	July	Aug.	Sept.
Exclosure	962	1338	1494	1520	1782
Control	482	1245	1456	1423	1444
Amt. consumed	480	93	38	97	338
Exclosure	962	1338	1494	1520	1782
Control of preceding month	0	482	1245	1456	1423
Amt. of yield	962	856	249	64	359

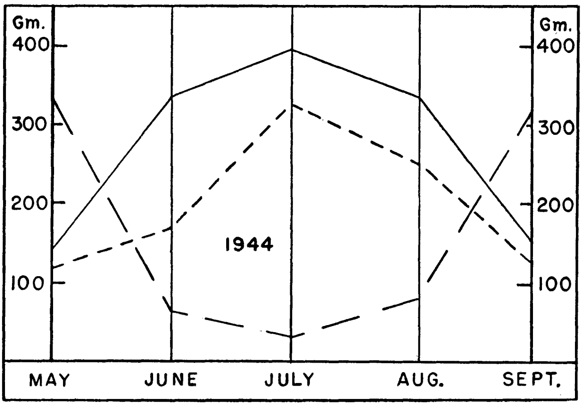


FIG. 76. Average amount of forage in grams consumed per unit area in the prairie type (continuous line), bluegrass type (short broken lines), and wheatgrass type (long broken lines) in 1944.

Relation Between Consumption and Yield

The relation between the monthly consumption of the several types of vegetation is shown by superimposing the graph showing yield on that showing consumption. The average monthly yields (and consumption) may be added and the total in grams calculated in tons per acre. This has been done in figure 77.

Only about a third of the bluegrass which grew in May was consumed, and only slightly more than half in June. Consumption during the remainder of the year somewhat exceeded current growth. This means, of course, that during mid and late summer some of the grass produced earlier in the year was also utilized. The total annual yield was 1.88 tons per acre, nearly all of which (1.65 tons) was consumed. The bluestem prairie produced 39 per cent more forage than bluegrass. The amount of forage consumed was 37 per cent greater. About one-third of the wheatgrass was consumed by the cattle in May. Utilization decreased to about 10 per cent of the yield in June and remained at a low level until new shoots appeared in September. Thus, while the total amount of forage eaten was 1.40 tons per acre, the total amount produced was more than 2.5 times as great, or 3.56 tons. Lower yields of bluestems than of wheatgrass were not due to their yielding qualities but to the fact that production in bluestems had been reduced by four years of grazing. Extensive experiments have shown clearly that the yield of wheatgrass is only 32 to 68 per cent as great as that of adjacent ungrazed bluestem. It seems clear that the tough stems and harsher leaves of wheatgrass, although produced in the largest amounts, were the least preferred of the three types of vegetation. This was well shown by the height at which the forage was grazed.

Height of Grazing

Bluegrass was grazed in spring and early summer to a height of 1.5 to 2 inches, but later, as forage became less plentiful, to 1 to 1.5 inches. Big bluestem and little bluestem were grazed somewhat variably, 1 to 8 inches in early summer but later often to a height of only .5 to 1.5 inches. Grazing of wheatgrass was much higher (6 to 18 inches), even in May, and thereafter at a level of 18 to 20 inches or more until September. Even then the lowest grazing was 14 to 20 inches.

The preference of the livestock for the bluestems and bluegrass resulted

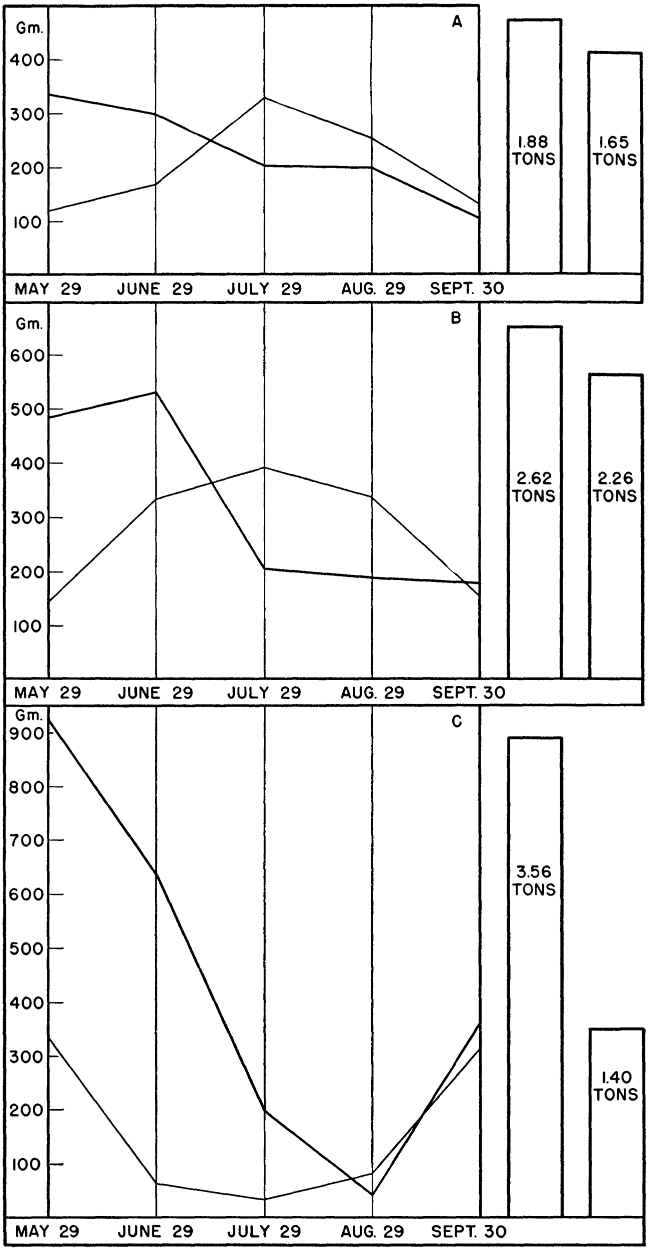


FIG. 77. Graphs showing average yield (heavy line) and average consumption (light line) in grams per unit area in (A) bluegrass, (B) prairie grass, and (C) wheatgrass type in 1944. Seasonal yield and consumption are shown in tons per acre.

in continued close grazing. Ungrazed patches of mature forage in each of the several types were marked early in 1943 and their persistence ascertained. All were grazed closely and repeatedly except those in wheatgrass, which remained essentially intact. A series of marked, well grazed plots revealed that where bluegrass or prairie grasses were once closely grazed such grazing was repeated in subsequent years. Of 100 marked bunches of various prairie grasses 85 per cent were closely grazed or had disappeared by the end of two years. Prairie vegetation is greatly harmed by grazing and trampling in May at a time when the warm-season grasses have not had time to produce much forage. Too early removal and too close utilization of the forage resulted in the rapid replacement of prairie by bluegrass and consequent reduction, at the end of two years, of about 35 per cent in annual yield of forage.

Weakening of Prairie Grasses and Invasion of Bluegrass

The population of prairie grasses became greatly reduced. A weak growth of much depleted bunches or of fragments of bunches of little bluestem could be found only on close examination. No thriving plants were seen; the scattered relics were all of low vigor. Big bluestem was somewhat more persistent. But even in parts of the prairie most recently invaded by bluegrass, big bluestem composed only about a fifth of the normal harvest in the exclosures. Clearly, under this close grazing it was about to disappear. A test of its vigor was made on May 17, 1945, by transplanting blocks of sod of the same size with tops and roots removed into rich soil under very favorable conditions for growth. The first was from an overgrazed area; the second, somewhat protected by bunches of tall dropseed, had been only moderately grazed. The third, with full vigor, was from an adjacent prairie. After six weeks, height of foliage was 10, 16 and 24 inches and dry weight of tops 3.8, 14.3, and 35.3 grams, respectively. Dry weight of roots was, in the same order, 0.85, 3.15 and 10.66 grams. This illustrates the weakened condition of overgrazed plants and the extent to which even moderate grazing affects them. Plants of low vigor cannot successfully compete with either bluegrass or weeds.

In May, 1944, bluegrass dominated only a third of the pasture. But after another year it had increased so rapidly and prairie grasses had been so greatly weakened by the heavy grazing imposed upon them that the bluegrass spread over nearly all of the prairie and formed dense stands.

Bluegrass is well adapted to close grazing; it is persistent and aggressive. First it grew between the bunches and patches of bluestems. Later, rhizomes grew through the crowns of bunches or weakened sod, and shoots of bluegrass appeared in the dead centers and other bare places. The sod-mat continued to spread throughout the entire crown of little bluestem until only a few leaves of this grass were found, if indeed all had not died. This also happened to other heavily grazed bunch grasses and even to the sod-forming big bluestem and switchgrass (Fig. 78).

Each year the prairie grasses were grazed as soon as they were a few inches tall. This early spring grazing

FIG. 78. Invasion of bluegrass into prairie sod. The web of roots and rhizomes occurred between a depth of 0.5 inch and 2 inches. The roots of all other vegetation were removed after the sod was cut at 2 inches in depth and the soil washed away. All are viewed from below. (Upper) Early invasion; the web became somewhat matted as, in washing, the roots sank to one plane. (Middle) Intermediate stage; the openings were occupied by needlegrass and Junegrass. Elsewhere the mat had spread through the sod of weakened big bluestem completely surrounding its roots. Greatest vertical thickness of the mat is 3/16 inch. (Lower) Uniform, dense, pure stand of bluegrass. Note great abundance of white rhizomes and dense masses of dark-brown roots. These formed a rug-like mat rather uniformly 1/3 inch thick. Air-dry weights of the 16- by 18-inch mats above were 8.5, 37, and 137 grams, respectively.

before the vegetation is 4 to 5 inches high is very injurious, since to replace the top, the plant must draw heavily upon its food reserves. Moreover, these grasses were repeatedly and heavily grazed until late fall. By 1945 this had destroyed the prairie type; it had been replaced by bluegrass. This loss imposed much closer grazing on the lower yielding bluegrass. When forage had been plentiful the bluegrass was grazed only in spots or patches in early spring. But now general grazing of bluegrass began earlier. In June of 1946, all of the forage was consumed as soon as it was produced, and this continued throughout summer and fall. Thus, the graph of consumption was also the graph of yield. Loss of the bluestems forced the hungry cattle to graze the wheatgrass. Its consumption increased from 1.40 tons per acre to 2.67 tons in 1945. It was cropped so closely in 1946 that the yield was reduced to much less than half that of the preceding year. Thereafter it almost disappeared as bluegrass invaded.

While these changes in the grass populations were occurring, certain inedible prairie forbs increased greatly, and bared spots became populated with various invading weeds. The tall, woody-stemmed ironweeds often grew so thickly in patches that they hindered grazing even when trampled down. From a single patch of thistle in 1943 many patches now occurred, some with 50 to 100 plants. Some plants had become established in 50 different parts of the pasture. Many other weeds were scattered throughout the bluegrass sod. New paths in fall and the deepening of old ones indicated much trampling, as the hungry cattle searched for food. In the autumn of 1946 no appreciable part of the forage crop remained. The bluegrass had been reduced throughout to a height of 0.5 to 1 inch in securing the 1.35 tons per acre of forage. A further chief expression of the unsatisfactory condition of the pasture was the restlessness and very evident reduced gains of the livestock.

Too early grazing, and too frequent and close removal of the herbage, even late in fall, are both faulty practices that are never economical. They are usually unintentional on the part of the farmer or range operator, simply because he is unfamiliar with the fundamental physiological activities of plants. When prairie hay is fed to stock in winter, the owner realizes that when the stack is gone he must provide more forage. But when the better grasses are grazed in fall to a degree where the remainder should be left and where its removal damages the plants greatly or may even cause their death, the presence of this herbage and of unpalatable weeds often gives the false impression that there is still plenty of forage.

To the ecologist the early signs of degeneration were evident: decreased vigor and waning of prairie grasses, invasion of bluegrass, and increase of weeds. Later indicators of degeneration were disappearance of prairie grasses, loss of native forbs, decrease in yield, closer grazing and decrease in vigor of bluegrass, appearance of bare spots, excessive trampling, and continuous spreading of weeds.

The preceding example of the replacement of prairie grasses by bluegrass began with the incoming of the settlers with their livestock. The writer has observed and studied all stages of this phenomenon from Dakota to Kansas and from Missouri to Minnesota (Fig. 75). Areas of half prairie grass and half bluegrass are common, and all intermediate conditions may be found. If protected, the natural succession, as will be shown, results in reestablishment of prairie; continued grazing—and this is the dominant practice—leads to the disappearance of native species and the development of bluegrass sod. As regards the eastern prairies, Sampson, working in Illinois, in 1921 stated: "Intensive grazing accompanied by the introduction of blue grass and red top destroyed practically all of the native prairie plants of the farms not cultivated. The bluestem prairies became bluegrass pastures, and where drainage accompanied grazing the native plants of the sloughs were also replaced by blue grass. In areas too wet for blue grass, red top became abundant, while in still wetter areas sedges and rushes prevailed."

CHAPTER 16

Process and Causes of Degeneration. Regeneration

THE MOST important phase in regeneration of prairie is the shift from undesirable forage species to the more desirable ones which occur regularly in the climax condition. While this principle is more or less generally understood, few studies that illustrate this phenomenon have been made. Before considering regeneration of prairie from pasture, the specific changes from high grade to low grade pasture and their causes should be thoroughly understood. Then the processes of regeneration and methods of accelerating them may be more easily comprehended (Figs. 79, 80).

COMPOSITION OF VEGETATION IN THE SEVERAL STAGES OF DEGENERATION

Grazing of natural vegetation by wild animals before the settlement of the prairie probably had little effect on the composition of the vegetation, because the grazing was both widespread and intermittent. But when domesticated grazing animals were introduced and limited in their range by barbed wire, conditions rapidly changed. Stages of degeneration of prairie can be distinguished readily by anyone sufficiently acquainted with the plants to recognize the various species of decreasers, increasers, and invaders, and approximately the relative abundance of each class. In such studies the climax vegetation is not only the starting point of the process of degeneration but also the standard of comparison for the ensuing stages.

The ecological classifications of species, based upon response to grazing, were grouped and incorporated in a quantitative system of range classification by Dyksterhuis (1948). This was done by applying percentages of coverage to them and terming them "Decreasers," "Increasers," and "Invaders." In 1949, he showed the range condition classes diagram-

FIG. 79. (Above) View in excellent native pasture in eastern Nebraska. Some of the bunches of little bluestem have been grazed out and bluegrass is increasing in the foreground. But nearly all the vegetation is composed of prairie grasses and forbs. (Below) Good pasture. Nearly all of the bunches of little bluestem and prairie dropseed have been grazed. Big bluestem, though plentiful, has been grazed uniformly. Bluegrass is abundant and almost alone occupies many of the smooth patches where bluestems and other prairie grasses have been grazed out.

FIG. 80. Fair pasture near Anita, Iowa. Prairie grasses have been entirely replaced by bluegrass. Note abundance of dunged patches and weeds where the sod is broken. (Below) Poor pasture with broken bluegrass sod and an abundance of iron-weed. Many of the weedy grasses and forbs shown in preceding figures occurred here. Formerly this was an excellent bluestem prairie.

matically and the trends of decreasers, increasers, and invaders from excellent to poor range.

In one study (Voigt and Weaver, 1951)[1] twelve native pastures were selected near Lincoln, Nebraska, three of each of the four pasture types or range condition classes. These pastures were studied in groups, each group containing an excellent, a good, a fair, and a poor pasture. Although the groups were 5 to 20 miles distant, pastures in any one group were only a mile or two apart. They varied in size from about 50 to 70 acres. Each had one main hill with various slope exposures, level hilltop, and some nearly level lowland. All were nearly square or broadly rectangular in shape. The rolling topography was much the same in each, and the soil type was the same or very similar throughout. Moreover, the distance of any part of a pasture to an abundant supply of water was not great. The original vegetation in each pasture, as judged by adjoining prairie, was, before grazing, almost identical.

The method of sampling the vegetation was simple. Two lines were marked out permanently in such a manner that they crossed the pasture in diagonal directions; one line intersected the other near the center of the pasture, somewhere on the slope of a hill. Random square-foot samples were studied every 15 to 20 paces along these lines. This gave information on the composition of vegetation in all representative sites in each pasture.

In ascertaining percentage composition, the total vegetation in the sample, regardless of its amount, was considered as unity or 100 per cent. Usually two or three grasses formed the bulk of the vegetation, the total of their separate percentages of composition amounting to 80 to 90. The per cent for each species was that part of the total basal area it composed, which was the area of a cross-section of the plant at grazing height—1.5 inches above the soil. A total of 150 samples were taken in each of the 12 pastures. Each individual sample was classified as to its percentage of grass decreasers, increasers, and invaders, and forbs. Statistical treatment of the data showed that the sampling was adequate for all pastures of each class in the three groups.

These data show that each species of decreasers actually became progressively less as the grade of pasture became successively poorer. Similarly most species of increasers gained in abundance from excellent to fair

[1] Data from Ecological Monographs 21:39–60.

pasture. Following the breaking down of the plant cover, each of the four most important increasers became less abundant. Invaders were of small importance in excellent and good pastures. In fair pasture their increase indicated what would happen if the plant cover became more open, as occurred when fair pasture was reduced to poor pasture.

	Grade of Pasture			
Groups and Species	Excellent	Good	Fair	Poor
Decreasers				
Big bluestem	24.8	14.6	2.8	1.7
Little bluestem	25.0	14.2	1.0	0.2
Prairie dropseed	11.7	2.0	—	—
Tall dropseed	4.5	3.0	0.1	—
Other grasses	0.6	0.4	—	—
Total	66.6	34.2	3.9	1.9
Increasers				
Kentucky bluegrass	16.2	40.2	50.6	23.3
Side-oats grama	13.1	14.4	6.2	2.9
Blue grama	0.2	3.1	29.2	1.6
Other grasses	1.0	2.9	2.0	3.9
Total	30.5	60.6	88.0	31.7
Invaders				
Sand dropseed	0.2	1.5	4.2	8.3
Western wheatgrass	0.4	—	0.2	2.1
Weedy bromegrasses	—	0.5	1.0	4.3
Other grasses	1.5	1.1	0.8	22.8
Total	2.1	3.1	6.2	47.5
Forbs	0.8	2.1	1.9	18.9
Grand Total	100	100	100	100

The poor pasture is the last stage in the long story of degeneration of prairie. The best-liked grasses had disappeared and bluegrass had been weakened by excessive grazing and trampling. Even the increasers had been reduced in abundance from 88 to 31.7 per cent. A host of low-grade invading grasses, mostly annuals, had replaced the highly nutritious grasses and now constituted more than a third of the vegetation. With these were intermixed a large number (18.9 per cent) of invading weedy forbs or non-palatable, weedy, native forbs. These included a more or less continuous overstory of gum plant, ragweed, ironweed, and others. These plants not only were almost inedible but actually hindered the grazing animals in searching out the grasses.

Degeneration from excellent to fair pasture is almost entirely due to changes in the abundance of prairie grasses. The decreasers composed two-thirds of the cover in excellent pasture, but only one-third in the good grade. Conversely, increasers made up only about one-third of the cover in excellent range, but nearly two-thirds in good pasture. In fair pasture, where decreasers fell to 3.9 per cent, the loss was almost compensated by the increasers, which were present in 88 per cent abundance. But the change to poor pasture involved a great incoming of invading grasses and forbs which together accounted for about two-thirds of the vegetation.

In the Loess Hills of Nebraska, beyond the western boundary of true prairie but southeast of the Sand Hills, true prairie extends far westward but only as postclimax vegetation in the deep ravines and on low terraces among the hills.[2] The degeneration of this vegetation and its percentage composition has been thoroughly studied for several years.

The percentage of each decreaser (first group), increaser (second group), and the chief invading grass are shown in each grade of pasture:

Species	Excellent	Good	Fair	Poor
Big bluestem	58	29	3	1
Little bluestem	5	1	—	—
Blue grama	6	7	10	9
Side-oats grama	10	16	3	6
Buffalo grass	4	19	72	44
Bluegrass	12	21	6	6
Sand dropseed	—	—	2	15
Total per cent	95	93	96	81

The remainder of the vegetation consisted of other grasses and forbs. Changes in forb populations were from those common to lowland prairie to an abundance of ironweed, hoary vervain, annual sunflower, and annual ragweed. These changes were gradual but distinct. Cover of vegetal mulch decreased in grams per square foot as follows: 89, 40, 14, and 7. Yield of perennial grasses in tons per acre decreased from 2.44 to 0.27 (Branson and Weaver, 1953).

DETERIORATION OF ROOT SYSTEMS

It should be clearly understood that prairie plants under close and continuous grazing also degenerate below ground. For example, one bunch

[2] Data abstracted from the Botanical Gazette 114:397–416 by courtesy of that publication and The University of Chicago Press.

of little bluestem was selected from a large pasture where grazing for several years had been very light. It was in a vigorous condition. A second bunch, grazed closely for two or three years, was selected as representative of a part of the pasture in only fair condition. The individual tufts composing the bunch were abundant but more or less separated by bare spaces. Thus the crown was somewhat open. A third clump was from a part of the

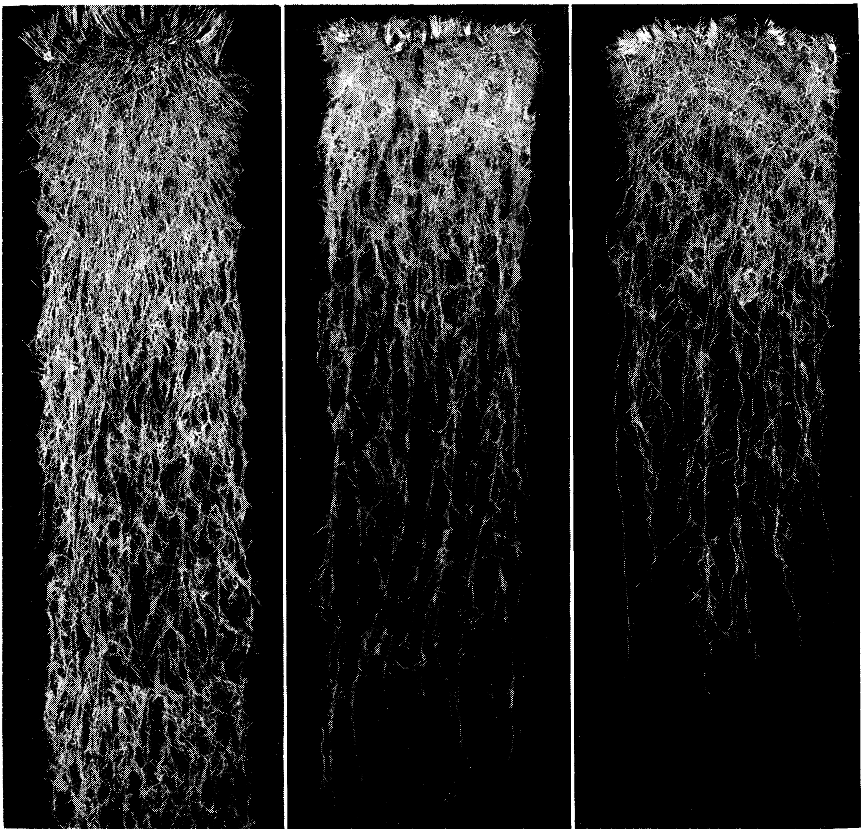


FIG. 81. Roots of representative little bluestem bunches from high-grade, mid-grade, and low-grade pastures. The depth of each monolith was 4 feet; air-dry weight of roots was 52, 23, and 13 grams, respectively. (Courtesy of Journal of Range Management)

range in poor condition; although little bluestem still persisted, the plants were much weakened. The bunch was very open, and the organic mulch was so meager that much bare soil was exposed. The tufts of grass were short and stunted; many fragments of dead plants were present.

A monolith of soil 3 inches thick was taken under each bunch, and the root systems were obtained to a depth of 4 feet (Fig. 81). Decrease in amount of roots at all levels from high-grade to low-grade pasture is clearly evident. Approximate depths of root penetration were 5, 4, and 3 feet, respectively. The percentage decrease in weight at the several depths is shown in table 8, where it may be seen that the total decrease in weight of roots was at first 55 per cent and finally 75. It should also be noted that root deterioration occurred from the tips upward toward the crown. This sequence has been ascertained several times and the actual process of root death and decay of root-ends was observed by the writer on Sudan grass as a result of frequent clipping (Peralta, 1935).

Further studies on big bluestem and other grasses gave similar results, as shown by Weaver in the April, 1950, *Journal of Range Management*, from which the preceding data were abstracted. "A good top that produces much nutritious forage and a good root system that can withstand drought and store much food for growth in early spring go hand in hand. A depleted range of non-vigorous grasses is usually also one in which the root systems are absorbing water and nutrients only in the upper portion of the soil."

TABLE 8. Dry weight of underground plant materials of little bluestem at the several depths in the three grades of pasture and percentage decrease from the high-grade type.

Depth	High-Grade	Mid-Grade	Decrease	Low-Grade	Decrease
ft.	gm.	gm.	%	gm.	%
0 –0.5	44.60	18.99	57	10.17	77
.5–1	2.74	2.21	19	1.63	40
1 –2	2.59	1.61	38	1.07	59
2 –3	1.20	.64	47	.21	83
3 –4	.75	.07	91	—	—
Total	51.88	23.52	55	13.08	75

CAUSES OF DEGENERATION

Common practices resulting in improper utilization of prairie are numerous. Chief of these are grazing too many animals for the productive capacity of the area (grazing too heavily); turning livestock in the pasture before the best-liked or key species have made enough growth to withstand the impact of grazing (grazing too early); and keeping animals on the range so late in the growing season that the plants are unable to store sufficient food reserves to withstand the rigors of winter and renew growth promptly in spring (grazing too long or too late). Moreover, water, salt, shade, and shelter all have a powerful attraction for animals and improper location of these results in certain areas being overused and others underused (improper distribution of livestock).

A clean looking, closely cropped pasture in true prairie is one that is being overgrazed. The proper use of a range cannot be accomplished by utilizing all of the herbage present; to preserve the important species, much material must remain unharvested. When forage is abundant, cattle tend to graze conservatively, but when it becomes scarcer they graze more closely. A properly used bluestem range appears somewhat ragged. While some grass is grazed short, some is only half used, and certain plants escape grazing almost entirely. At the end of the grazing season at least one-third of the forage crop should be left on the soil. One veteran range conservationist stated the facts succinctly as follows: "The annual forage production of range plants must be divided three ways. About half can be harvested by animals as food. The other half serves two purposes. It manufactures food—plant food—that is stored in the bud and root tissues. Thus some leaves and stems provide a shield to the soil against rain and wind. The other purpose is to furnish decaying residue. Mixed with the soil, the residue gives tilth and fertility. When livestock are forced to take more than their share of the forage, the plants suffer, the soil suffers, and eventually the livestock diet is cut down" (Allred, 1946).

Deterioration of prairie is due in a large measure to the preference of livestock for certain individual species. Plants such as bluegrass, blue grama, and other species that develop much foliage near the soil surface, persist and usually increase while many species with foliage on shoots quite above the soil surface, such as the bluestems, switchgrass, and others, will be grazed out. The final result is the weakening and disappearance of the most valuable forage species and their replacement by plants of lower forage value or by worthless weeds.

Grasses differ from forbs in method of growth. Near the base of the leaf there is a transverse intercalary zone of growth. Hence if a portion of the leaf is cut or bitten off, the leaf can continue growth. Indeed, for a long time, as in big bluestem, the shoot, aside from the leaf blades, consists entirely of a clyinder composed of leaf sheaths. The older ones are on the outside, and new ones develop successively within from the growing point, which remains in the surface soil. The expanded leaf blades of a shoot 18 inches high are shown in figure 82, and also a shoot with the several leaves, of which it is composed, separated. This may be more easily seen in a stalk of another grass, maize. When the plant is about 2 feet high and in the seventh-leaf stage, the growing point which produces leaves may be only about 2 to 3 inches above the soil.

FIG. 82. A shoot of big bluestem 20 inches tall on June 30. Similar shoot with leaves separated but in the same position. No stem has developed. (Below) Representative rhizomes of big bluestem with abundant buds (small leaves around a growing point), actual size. Photo in April before growth began.

When growing points occur more than an inch above the soil, they may be removed by grazing and no new leaves can be produced from them. Stems, either sterile or flower-producing, finally develop by growing upward through the cylinder of leaf sheaths (Evans and Grover, 1940; Kiesselbach, 1949). Branson (1953) has shown that Kentucky bluegrass, blue grama, and buffalo grass maintain growing points of sterile shoots at the level of the soil surface. These grasses are all very resistant to grazing. In contrast, switchgrass, needlegrass and Junegrass extend their growing points far above the soil surface in May or June. These grasses are rather readily "grazed out." Portions of stems of grasses as well as leaves are also removed in grazing. Growth then may take place from buds produced in the axils of the sheathing leaf bases at the lower end of the stem. Growth in elongating stems of grasses occurs near the base of the internodes (*i.e.* just above the "joints"). Hence if grasses have been blown down or trampled, they may again turn upright (as does lodged small grain) unless the tissues are already mature.

Disappearance of desirable species of grasses is accompanied by a decrease in vegetal soil mulch, and eventually by soil erosion and deposit. Increased runoff results in drier soils, and this may be a factor contributing to low yields of closely grazed and much trampled pastures. Numerous studies have shown that with a decline in range condition, as from good to fair pasture, there is a corresponding decrease in grazing capacity. Even annual grasses yield less in poor range. In the degeneration from good to poor pastures, total production of preferred forage is reduced. Organic mulch, which increases absorption of moisture, reduces soil temperature, and aids in preventing germination of weed seeds, is decreased. But loss of nutrients and soil by runoff, and damage by soil deposit, are increased.

REGENERATING NATIVE PASTURES

Range restoration means stopping deterioration and bringing an upward trend from an unsatisfactory to a satisfactory condition (Campbell, Ellison, and Renner, 1948). Pasture improvement denotes an increase in abundance of the more palatable species and an increased density of plant cover. Perhaps the most unquestionable evidence of improvement is the appearance of higher (nearer the climax) species in the normal succession and the disappearance of species representing lower stages.

The management of grazing in pastures is generally concerned with utilizing the vegetation to the maximum degree that is compatible with efficient livestock production and the maintenance of forage resources. Protection of the soil should be carefully considered.

The first consideration in improving pasture is the control of livestock, both as to kind and numbers. Scientific studies have shown that it usually requires 3.5 to 5 acres of upland prairie to furnish forage for one animal unit (a mature cow or steer). In large pastures, overuse often occurs in some places because of poor distribution of ponds or wells, and of salt and shelter, while underuse of the forage occurs in other portions of the pasture. Good distribution may also be attained by proper fencing (Weaver and Tomanek, 1951).

The season of grazing is extremely important. Plants utilize a part of their food reserves to produce new foliage. If this is removed by too early grazing, more crown and root reserves must be used. The plant may be weakened and finally die. But if grazing is deferred until the bluestems are 5 to 7 inches tall, they can well withstand moderate grazing. Anderson (1940) restates a fact that is now well known by range technicians: "As a result of spring protection, stands of grass on the deferred [bluestem] pasture have been maintained in better condition in spite of the fact that it has been subjected to much harder use. At the end of each grazing season it has had a better cover of grass to afford protection against runoff and erosion during winter and spring." It has also been ascertained that more forage is produced from pastures that are moderately grazed than from those that are overgrazed.

Sustained production of forage plants and in fact the very existence of good pasture grasses which undergo annual grazing and trampling is largely dependent upon the treatment they receive. Too little grazing results in waste of forage and is also detrimental to certain species, while overuse results in range deterioration.

Mowing or otherwise eradicating competing weeds is, of course, beneficial to the better grasses. Proper fertilizing of the soil may also be helpful. Improvement may be retarded by the absence or scarcity of seed. Scattering hay over the poorer places, especially hay that has been cut from a prairie at the proper time to secure an abundance of seed, furnishes both seed and a protective mulch which will aid in the establishment of seedlings. But the problem of pasture care and improvement—a part of range management—is a highly specialized field which is not a part of this study of prairie.

That excellent development of seedlings occurs in true prairie was demonstrated long ago by Clements and Weaver (1924). Small areas in prairie were bared and the seedlings kept free from weedy competitors. The plants made an excellent growth. Tall and mid grasses planted in experimental gardens completed their life cycle in a single favorable growing season by blossoming and ripening seed. But where the seedlings grew thickly in competition cultures (often 1 to 3 per square inch), development was considerably retarded.

RESEEDING ABANDONED LAND

The return of abandoned land to prairie is often extremely slow. Shimek (1948) studied the restoration of a prairie on an abandoned railroad right-of-way in Iowa. At the end of 10 years the adjoining native prairie had not completed the repopulation of the protected area. Less than half of the prairie species had migrated into this area. Aikman (1930) traced the natural succession of plants on land retired from cultivation in eastern Iowa through an early weed stage of 1 year, a second stage of 2 to 4 years, and a third stage of 3 to 18 years. He found that little bluestem may invade land formerly cultivated, after 16 years of abandonment. Booth (1941) has studied fields abandoned from cultivation for a few years to 30 years, in the true prairie region of Oklahoma. They did not appear to be nearing the fully developed prairie stage.

Cornelius (1950) has worked for many years on cultural practices necessary for seed production of native grasses under cultivation in eastern Kansas, and the establishment of prairie species following reseeding. He states (1946) that "within the last decade, many farmers and ranchers have changed their concept of proper land use. Some fields, formerly cultivated, are being revegetated to perennial grasses to be used for grazing or hay, thereby controlling erosion and improving soil fertility.

"Although abandonment from cultivation would eventually permit native perennial grasses to cover the area, it has been found during the past decade that these species can be successfully seeded, and that productive grassland can thereby be obtained much more quickly than by natural revegetation. These grasses, which have the advantage of being well adapted to the environmental conditions . . . are slower in germination and seedling growth than most cultivated annual and perennial crops.

"It is feasible and practical to plant seed of perennial native tall and mid grasses on land to be retired from cultivation in the true prairie region. The time for the succession from weeds to perennial grasses will require two or three years. Annual weeds and forbs dominate during the first season, and the desirable species are usually inconspicuous. Mowing at least once and preferably twice in the first season is necessary to control the weedy plants which compete for moisture, nutrients, and sunlight.

"One mowing is usually necessary in the second year to reduce growth of the annual weedy forbs. The area may be grazed lightly during the latter part of the second season. By the third season the area supports a good cover of grass. The perennial grasses constituting the climax have suppressed the annuals. The area is now ready for grazing or hay."

By revegetating land to suitable native perennial grasses for grazing and hay, erosion is controlled and soil fertility is improved. Often climatic soil drought or drought resulting from competition of weeds for the available water supply may result in failure in reseeding both pastures and formerly cultivated land.

Only in the last quarter century have native grasses been used to develop new pastures and meadows and for the control of erosion. Harvesting seeds, whether in native prairie or from cultivated grasses, is done by hand, by strippers, by mowing machines, and more recently by combines. How and when to harvest, how to process the seed by removing appendages and hulls, and how and when to plant the seed and care for the crop of seedlings requires trained and experienced men. Grass seed production alone is a highly specialized business. It is not a part of the story of the prairie; neither is grass breeding. These have been recently described by Staten (1952).

RETURN OF BLUESTEM PASTURE TO PRAIRIE

Near Lincoln, Nebraska, prairie which had been grazed for 23 years degenerated into bluestem-bluegrass pasture.[3] The degree of change from

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[3] From an address to the American Society of Range Management, at Omaha, Nebraska, Jan. 27, 1954. Data are from Weaver and Hansen (1941a), Weaver and Bruner (1945), and later research. A much more comprehensive account occurs in the American Journal of Botany (Weaver, 1954).

the original vegetation could readily be seen, since the pasture adjoined a large prairie of which it was formerly a part. At the beginning of the experiment a part of the pasture next to the prairie was fenced, thus keeping out livestock. This area was 31 rods long and 4.5 rods wide—large enough to be representative but small enough so that one could become intimately acquainted with the vegetation and closely observe changes from year to year. In fact, this was done until the pasture regenerated a nearly typical prairie flora. This required a period of 17 years. Both pasture and prairie were mowed late in autumn each year and the hay was removed. The experimental pasture extended northward from the top of a low hill down a gentle slope and included its nearly level, well drained base. The silty clay loam (A horizon) on the hilltop and upper slope was 12 inches deep; the silt loam of lowland was 20 inches deep. Both soils had deep, permeable B horizons. These fertile soils were watered by an average annual precipitation of 28 inches.

The pasture represented a good range condition before the occurrence of great drought in 1934. About half the vegetation consisted of little bluestem and big bluestem, and half of Kentucky bluegrass. Weeds were not abundant. But when the area was fenced, both bluestems occurred very sparingly and bluegrass remained only in small, widely scattered patches. A drought invader, sand dropseed, was sparse in places but abundant in others, as was also the drought-resisting side-oats grama. Other grasses were very scattered. Dense patches of peppergrass and Pursh's plantain occurred. Many-flowered aster and smooth goldenrod were prairie forbs that had become abundant weeds. They, with the annual horseweed, were the chief constituents of the wide-spread weedy flora.

The adjoining prairie had suffered very moderately from drought, except the driest upland part. It recovered rapidly at the end of the drought and each summer produced abundant fruit and seed of both grasses and forbs adjacent to the pasture.

Pasture Populations During Drought

Development of vegetation on the nearly bared soil during the dry years (1937–1940) consisted of repopulation with annual weeds, certain drought-resistant prairie forbs, and xeric grasses (Figs. 83, 84). Together they finally produced a more or less complete cover. Bluegrass at first

(1937) composed more than half of the vegetation, but drought killed all but 3 per cent. The remnants of little and big bluestem, 6 and 4 per cent respectively, fluctuated in amount from year to year but gradually increased. Grasses that increased greatly during drought were sand dropseed and side-oats grama. The dropseed at first composed one-fourth of

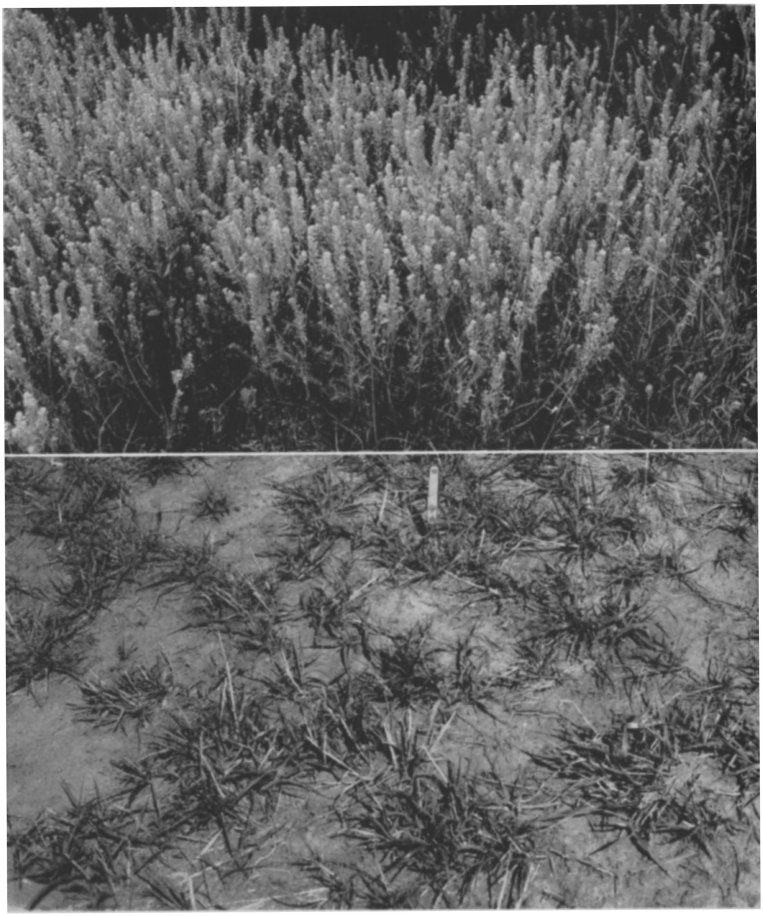

FIG. 83. Dense stand of peppergrass (*Lepidium densiflorum*) and open stand of sand dropseed (*Sporobolus cryptandrus*) following years of grazing the prairie and severe drought.

the total grasses. It continued to spread despite the drought until it furnished 39 per cent. Side-oats grama increased even more rapidly, from 4 to 14 per cent in four years. Four other grasses and sedges composed about 4 per cent of the grass population in 1937, but each of these increased about threefold. They were hairy grama, penn sedge, June-grass, and *Cyperus filiculmis*. Blue grama had become established on both upland and lowland in small patches.

The preceding percentages are based upon a thorough analysis of the very open vegetation by means of stem-counts. The number of stems of each plant in each square decimeter was listed. This method was found best in studying fragments of drought-damaged plants and the scattered individuals of invaders. A total of 43 square-meter quadrats was employed.

FIG. 84. Bunch of sand dropseed in September with panicles expanded; height is about 26 inches. Open growth of smooth goldenrod (*Solidago missouriensis*), remnants of a dense patch which is being thinned by the grasses.

In addition, the more apparent variations in the vegetation of the entire experimental area were observed throughout each summer.

Only 5 of the 26 native forbs which grew in the quadrats were of major importance. Three annuals, rough pennyroyal, daisy fleabane, and Pursh's plantain, were the chief forbs for a time, but by 1940 all had decreased at least 90 per cent. But smooth goldenrod and many-flowered aster increased greatly in numbers and spread widely. Of the 17 species of weeds, only 3 were of outstanding importance. They were horseweed (49 per cent), peppergrass (44 per cent), and little barley (7 per cent). The first two rapidly decreased, but little barley became so abundant that it composed nearly 90 per cent of the weed population.

Conditions of the vegetation near the end of the drought period (1940) were as follows: sand dropseed (39 per cent) dominated in many places and occurred in mixture with side-oats grama (14 per cent) in others. In parts of the area it was well intermixed with little bluestem (18 per cent) and big bluestem (12 per cent). Penn sedge (4 per cent) and Junegrass (3 per cent) were far more common than before. Blue grama occurred in small scattered patches that had increased somewhat in area. Hairy grama, prairie dropseed, and plains muhly were found as occasional bunches. Bluegrass (the remaining 3 per cent) was scattered thinly on the lower ground. Dense patches of aster and goldenrod had been thinned as the grasses increased. The bunches of grass were larger, thicker, and of greater height, and they produced many more stems than earlier in succession. Little barley and other plants of the annual weed stage had practically disappeared, and the impress of the vegetation was distinctly one of grasses.

Succession Following Drought

In the summer of 1941, when the great drought was broken by heavy rain, the bluestems composed 27 per cent of the plant cover. Other prairie grasses were each represented by 1 to 12 per cent. Although most of these grasses were not abundant, yet they did dominate in many scattered local areas and distinctly indicated some progress on the return to prairie. Conditions for growth were good to excellent during the following period of twelve years. Succession probably would have been much more rapid except for the presence of a good stand of two dry-land grasses. These were sand dropseed, which is not a species of climax prairie, and side-oats grama, which is normally represented by only about 3 per cent. They composed 46 and 12 per cent, respectively, of the post-drought plant cover. Moreover, bluegrass, profiting by wet weather, spread very rapidly over the lowland, and finally over the upland as well. Sand dropseed and side-oats grama produced some seed during every year of drought and sometimes seeded abundantly; this was not true of most of the prairie grasses. An abundance of seedlings in grassland, following several years of drought, must be preceded by a good seed crop (Weaver and Mueller, 1942). Lack of seed also delayed the progress of normal succession.

With the occurrence of heavy precipitation and other conditions unusually favorable to growth, there was a great upsurge in the development of the foliage cover, especially in the spring of 1944. The shade thus produced was especially unfavorable to sand dropseed. It had reached its maximum abundance and widest distribution, and it promptly began to decline. In one group of quadrats where it composed 68 per cent of all the grasses, it was reduced to 35 per cent by 1943. Side-oats grama decreased sharply, in some places to a third of its former abundance in three years. As the more mesic bluestems and other prairie grasses regained their vigor and became more abundant, the denser shade produced by them was the greatest cause of the marked decline of both drought dominants. The revival of widely scattered and long-dormant crowns of both big and little bluestem occurred after 1942. The phenomenon of renewed growth after 5 to 7 years' deep dormancy during which no new shoots had been produced occurred throughout the western prairie (Weaver and Albertson, 1944). Seedlings of grasses and forbs were scarce for a year or two following the drought. The rate of succession was retarded, in part, by the small number of seedlings. But established plants increased by tillering, by shoots from rhizomes, and by other methods of vegetative propagation.

Three years after the drought, sand dropseed generally occurred only sparingly, but it was abundant in some places. The chief grasses of upland were side-oats grama and bluegrass, but intermixed were some bluestems. In parts of the lowland, bluegrass and big bluestem each formed a dense sod. Pursh's plantain and other weedy annuals had practically disappeared. Hairy chess still remained in the most open places, commonly intermixed with sand dropseed. Many-flowered aster and smooth goldenrod had been greatly subdued by the grasses. The cover was quite dense, and a mulch, absent during drought, had accumulated. However, several grasses and many forbs at home in the adjoining prairie were still absent in pasture (Fig. 85).

From 1944 to 1948 little bluestem gradually increased, partially by the tillering of established bunches, but largely from seedlings which became abundant. The various stages from single shoots to small tufts were all represented, since each year was a good one for seedling growth and seed production. Clearly a little bluestem type was developing on upland. Big bluestem flourished on the lower ground, where numerous bunches and patches of sod alternated with bluegrass. Later it spread to the upland as well. Patches of blue grama were reduced in size and later disappeared as a result of shading. Well developed plants of sand dropseed were not common, and even remnants of once vigorous plants were becoming progressively fewer. As the former prairie dominants increased, the drought dominants decreased accordingly. But some still prevailed. Although the number and abundance of legumes and other forbs were increasing, the

FIG. 85. (Left) Old fence-line between prairie (right) and pasture (left) in September of 1940. The light color in pasture is due largely to the dried plants of sand dropseed. Same view in September, 1944, after the sand dropseed had been suppressed by returning bluestems.

population was still low, and societies had not yet developed. The basis for rapid return of prairie conditions, however, was well prepared.

As one studied the area each growing season, progress in development was clearly apparent. But to observe and record it adequately one had to keep clearly in mind the several changes in the plant population which were still to occur. These included the increase of former prairie dominants, the suppression of drought dominants under this wetter phase of the climatic cycle, and the disappearance or reduction to normal numbers of other relics of drought populations. They also included the return of a normal population of forbs and a new development of societies, the re-establishment of the understory in the vegetation, and the building of a soil mulch. The adjacent prairie furnished an excellent standard for comparison. It was also a source of seed for the regenerating prairie, in addition to whatever may have been present when it was closed to grazing.

A careful comparison of regenerating and climax prairie was made in 1948–49 (Mentzer, 1951). A series of 12 plots, each 6 by 12 feet in area, were placed at random throughout the length of the subsere just opposite a similar lot in the prairie. The distribution and approximate abundance of all of the more important grasses and forbs in each square foot of each plot were mapped. Comparison of the maps revealed the following:

"A little bluestem type occupied the upper third of the north-facing slope; a big bluestem type had developed on the mid-portion; and a big bluestem-Kentucky bluegrass type was found on the deeper and richer soil of the nearly level lower third of the subsere.

"Little bluestem was sparse throughout, but it was more than three times as abundant in prairie as in pasture. Big bluestem in the little bluestem pasture type occurred sparingly and mostly in small bunches. Elsewhere, there was almost as much of this grass in pasture as in prairie. Bluegrass was abundant and widely scattered in pasture, and always present but sparse in prairie. Blue grama occurred only in pasture and side-oats grama was more abundant there. Tall dropseed was abundant in prairie but rare in pasture. Sand dropseed occurred throughout the pasture where it invaded during the drought. It was not found in prairie. Forbs were not abundant in the subsere, even eight years after the drought, despite their large variety and abundance in the prairie."

Mentzer (1951) found that the average air-dry yield of prairie grasses and forbs was 24 and 120 per cent, respectively, greater in climax prairie than in regenerating prairie. But the combined weight of bluegrass and invading, mostly weedy grasses, was 60 per cent less in the prairie than in the subsere.

A steady increase of the percentage yields of prairie grasses in the vegetation of old pasture compared with that in prairie (considered as 100 per cent) had been previously obtained. At the end of one, two, and four years of succession the yields were 8, 18, and 67 per cent, respectively (Weaver and Hansen, 1941a). But eight years later Mentzer ascertained that 77 per cent of the subsere vegetation was composed of prairie grasses. This indicated a closer approach to the climax.

Favorable moisture conditions continued during the twelve years following the drought, or until late summer of 1953. Continued observation

FIG. 86. Normal plant of sand dropseed (upper left), and suppressed plants in the shade of developing bluestems. Small relic on right was found in the bunch of big bluestem. (Below) Development of stand of big bluestem and (left) little bluestem in lowland pasture (Photo 1951).

revealed that on upland the small bunches were developing into large ones which furnished seed to repopulate the interspaces. The small tufts of big bluestem developed bunches and small patches of sod. Bluegrass, side-oats grama, sand dropseed, and hairy chess all decreased year after year, as did also smooth goldenrod and many-flowered aster (Figs. 84, 86). Only traces of drought relics and ruderals occurred. Extensive sampling in 1952 revealed that 60 per cent of the vegetation was little bluestem, and that big bluestem furnished 30 per cent. Bluegrass and side-oats grama had each been reduced to 3 per cent. Sand dropseed and blue grama had almost or entirely disappeared, but 1 to 2 per cent of the small panic grasses and penn sedge remained. In fact the bluestem type thus developed had fewer dominant grasses than the adjacent prairie.

Vegetation of the mid portion of the pasture, which was traversed by a ravine, was now composed of 83 per cent big bluestem. Little bluestem and bluegrass furnished 11 and 6 per cent of the cover, respectively. This may be considered, so far as the grasses are concerned, rather typical lowland prairie.

Extensive quadrating on the level lowland showed that there was almost no mixing of blue grass and big bluestem. Instead, alternating areas were dominated either by one species or the other. Dense, nearly pure stands of big bluestem covered 58 per cent of the area; there was only 2 per cent little bluestem, but nearly 40 per cent bluegrass.

A comparison of the little bluestem type with climax prairie revealed that in the prairie samples there were nearly always two or three dominant grasses intermixed, and frequently four. But prairie dropseed, needlegrass, and tall dropseed were still scarcely represented in the subsere. On lower land the moderate to dense sod of big bluestem was found in almost pure stands. In adjacent climax prairie its stands were always more open or even scattered. Here, intermixed with the bluestems, were prairie dropseed, needlegrass, tall dropseed, and often an abundance of Indian grass and switchgrass. In addition an understory of sedges, low-growing grasses, and forbs was present. These were represented very sparsely if at all in the vegetation of the pasture.

This restored prairie with its overwhelming abundance of relatively few species of grasses and scanty population of forbs was very different from the adjoining thousand-year-old native prairie. But the cover of grasses in the subsere now furnished adequate protection from sun and drying winds. They had produced an organic mulch which enriched and mellowed the surface soil and thus prepared a suitable habitat for the development of seedlings.

Each year one observed the return of species new to the recovering grassland. But many common prairie forbs had not reappeared. Among these were prairie violet (*Viola pedatifida*), Pitcher's sage (*Salvia pitcheri*), long-fruited anemone (*Anemone cylindrica*), bastard toadflax (*Comandra richardsiana*), downy gentian (*Gentiana puberula*), and tall goldenrod (*Soldiago altissima*). The following have reappeared only within the last three or four years: Prairie turnip (*Psoralea esculenta*), Illinois tick trefoil (*Desmodium illinoiense*), ground plum (*Astragalus crassicarpus*), prairie larkspur (*Delphinium virescens*), blue-eyed grass (*Sisyrinchium campestre*), and tooth-leaved primrose (*Oenothera serrulata*). Each was still represented only by scattered individuals. Even the lead plant (*Amorpha canescens*) was almost rare. In an area two rods wide but extending throughout the length of the pasture, less than 50 stems of this plant were found, but in a similar parallel strip in prairie there were more than 1,000. Not a single isolated stiff sunflower (*Helianthus laetiflorus*) was observed until 1952. Plants were abundant in prairie, and several dense patches of this species had spread by rhizomes from the edge of the prairie 5 to 25 feet into the old pasture, considerably thinning the grasses. Also societies of white prairie clover (*Petalostemum candidum*) and silver-leaf psoralea (*Psoralea argophylla*) had recently been developed. The following species will probably not return for a long time: prairie phlox (*Phlox pilosa*), scarlet strawberry (*Fragaria virginiana*), entire-leaved rosinweed (*Silphium integrifolium*) and cup plant (*S. perfoliatum*), purple vetch (*Vicia americana*), showy tick trefoil (*Desmodium canadense*), large-flowered beardtongue (*Penstemon grandiflorus*), and prairie fringed orchid (*Habenaria leucophaea*).

One could follow with pleasure and profit for many years the incoming of new forbs and the increase in numbers of those already present, as well as other adjustments within the community.

Plant succession, or nature's putting back what was there in the first place, has been a slow although constantly accelerated process. The re-established prairie is poor in kinds of grasses, deficient in numbers of forbs, and almost lacking in plant societies. It is not yet the type of climax with a rich and varied flora in dynamic equilibrium with the climate, despite the 13 years with favorable conditions for growth that have passed since its four-year struggle for recovery during drought.

Role of Bluegrass in Regeneration of Pastures

The persistence with which bluegrass retains its hold in pastures is remarkable. For example, a study of succession in a heavily grazed prairie in northwestern Iowa has been made by Anderson (1946). This bluegrass pasture had not been grazed since 1930. Kentucky bluegrass still accounted for one-half to three-fourths of the cover in 1946. The record from the quadrats is evidence of the extreme stability of the plant cover and the slowness with which changes take place. After a period of 15 years bluegrass was in all the plots and showed little or no diminution in abundance over former years (Rudman and Pohl, 1951).

In mowed pasture in eastern Nebraska, bluegrass maintains its place with great tenacity. Its dense sod-forming habit and vigorous growth in early spring and late fall make its replacement by other grasses difficult. But with the cessation of mowing or grazing, the deep mulch formed by the tall grasses soon overwhelms the bluegrass. Its disappearance where widely scattered tufts of big bluestem persisted was studied in the lowland pasture described in the preceding chapter. Here the native prairie had degenerated into an almost pure stand of bluegrass. This occurred as a result of overstocking from early spring until late fall during a period of 4 years.

Two permanent exclosures, each 48 feet long and 18 feet wide, were established in early spring of 1948. They were fenced with both woven and barbed wire in such a manner that livestock could not disturb any part of the vegetation. The development of the relic vegetation in the exclosures was compared with similar relics outside under year-long grazing. Both list and clip quadrats were used extensively. At the end of each season all vegetation remaining in the exclosures was clipped at a height of 2 to 3 inches and removed.

During 1948 and 1949, both good years for growth, the studies were carried on by Mentzer (1951). "Stems of big bluestem in the exclosures had increased in 1949 more than fourfold, compared with a 16 per cent decrease in the pasture. Its regained vigor was shown by the production the second year of 742 flower stalks of normal stature compared with only 28 weak ones the first year. Similar increase in stems of little bluestem were more than eightfold. Needlegrass also recovered rapidly.

"The first year, pasture grasses [mostly bluegrass] in the exclosure furnished 48 per cent of the total yield; the second year only 28 per cent. Prairie grasses composed only 46 per cent of the total yield the first year but 69 the second. Due to the recovery of prairie grasses, total plant production in 1949 far exceeded any increase due to difference in seasonal environment.

"Under protection, a strong successional trend had begun which would eliminate nearly all bluegrass and weeds and rapidly restore a near-climax or climax vegetation."

This study was continued by the writer during 1950 and 1951. Environmental conditions were favorable to growth, although there was much more precipitation during the second year. Big bluestem continued to thicken its stand until over five-sixths of the exclosure it became almost continuous (Fig. 87). Some flourishing plants of Indian grass and switchgrass were intermixed. A few bunches of little bluestem were clearly at a disadvantage in respect to light; some clumps were half filled with the invading stems of big bluestem. Bluegrass was entirely shaded out in many places under this dominant, and elsewhere the much weakened plants formed an open, sparse growth. This was not due to the mulch, which was only one-fourth inch thick, but to the very low light intensity. Near the soil surface, the light on clear days in midsummer ranged from one-tenth per cent to less than 3 per cent of full sunshine.

Needlegrass grew in a nearly pure, vigorous stand in a third of one exclosure. Here bluegrass was not so greatly suppressed. Other grasses were almost rare. Forbs were scarce except for persistent clumps of the tall-growing Baldwin's ironweed. Even these were somewhat dwarfed. It seemed that this lowland prairie was nearing a climax condition.

The fine stands of grass were harvested, as before, in mid-August from 16 plots each 9 square feet in area. The yield was always from plots that had not been clipped before, except in clearing the exclosures in October. In 1951 the foliage height varied between 2.5 and nearly 3 feet. Relatively few flower stalks had completed growth, but in September they were 5 to 6.5 feet tall. Flower stalks of needlegrass had fallen, but the general foliage level was about 18 inches. The increase in yield of prairie grass was remarkable. If the 1948 yield is considered as unity or 1, then yields during the 3 following years were 3, 12.7, and 23.8 times as great, re-pectively. Prairie grasses, which in 1948 furnished 46 per cent of the total yield, had increased this increment in 1951 to 97 per cent. The

FIG. 87. Return of big bluestem: views of pasture exclosure after 2 and 4 years' protection, respectively.

weight of bluegrass was very small. Initially it furnished 48 per cent of the yield, but finally only 2 per cent. The yield of forbs had also greatly decreased, from 6 per cent of the total to about one-third of 1 per cent.

This study illustrates how nature is always trying to put back on prairie land the kind of vegetation that was there in the first place. Perhaps a better understanding of vegetation has been gained by studying plant succession than in any other way.

IN RETROSPECT

The disappearance of a major natural unit of vegetation from the face of the earth is an event worthy of causing pause and consideration by any nation. Yet so gradually has the prairie been conquered by the breaking plow, the tractor, and the overcrowded herds of man, and so intent has he been upon securing from the soil its last measure of innate fertility, that scant attention has been given to the significance of this endless grassland or the course of its destruction. Civilized man is destroying a masterpiece of nature without recording for posterity that which he has destroyed.

The prairie provides us with a background against which we may measure the success or failure of our own land use and management (Hanson and Vorhies, 1938; Hanson, 1939). Before the western prairies disappear as gradually and completely as have those of the east, let us follow the judicious plan of the conservationists in the great prairie state of Iowa and preserve some representative tracts forever for ourselves and for posterity (Hayden, 1946).

Nature is an open book for those who care to read. Each grass-covered hillside is a page on which is written the history of the past, conditions of the present, and predictions of the future. Some see without understanding; but let us look closely and understandingly, and act wisely, and in time bring our methods of land use and conservation activities into close harmony with the dictates of nature.

As formerly expressed by the author (1944), the prairie itself is an intricately constructed community. The climax vegetation is the outcome of thousands of years of sorting of species and adaptations to soil and climate. "Grassland soils through untold centuries have been thoroughly protected by the unbroken mantle of prairie vegetation. The vegetation and soil are closely related, intimately mixed, and highly interdependent upon each other and upon the climate. Hence prairie is much more than land covered with grass. It is a slowly evolved, highly complex organic entity, centuries old. It approaches the eternal. Once destroyed, it can never be replaced by man."

Common Names Used Without Accompanying Scientific Names

GRASSES

Big bluestem	*Andropogon gerardi*
Blue grama	*Bouteloua gracilis*
Bluegrass	*Poa pratensis*
Bluejoint	*Calamagrostis canadensis*
Buffalo grass	*Buchloe dactyloides*
Canada bluegrass	*Poa compressa*
Canada wild-rye	*Elymus canadensis*
Crested wheatgrass	*Agropyron cristatum*
Downy brome	*Bromus tectorum*
Eastern gamagrass	*Tripsacum dactyloides*
Feather bunch grass	*Stipa viridula*
Foxtail barley	*Hordeum jubatum*
Hairy chess	*Bromus commutatus*
Hairy grama	*Bouteloua hirsuta*
Indian grass	*Sorghastrum nutans*
Junegrass	*Koeleria cristata*
Kentucky bluegrass	*Poa pratensis*
Little barley	*Hordeum pusillum*
Little bluestem	*Andropogon scoparius*
Needle-and-thread	*Stipa comata*
Needlegrass	*Stipa spartea*
Nodding wild-rye	*Elymus canadensis*
Northern reedgrass	*Calamagrostis inexpansa*
Penn sedge	*Carex pennsylvanica*
Plains muhly	*Muhlenbergia cuspidata*
Prairie cordgrass	*Spartina pectinata*
Prairie dropseed	*Sporobolus heterolepis*
Prairie three-awn	*Aristida oligantha*
Purple lovegrass	*Eragrostis spectabilis*
Redtop	*Agrostis alba*
Reed canary grass	*Phalaris arundinacea*
Rice cutgrass	*Leersia oryzoides*
Saltgrass	*Distichlis stricta*
Sand dropseed	*Sporobolus cryptandrus*
Scribner's panic grass	*Panicum scribnerianum*
Side-oats grama	*Bouteloua curtipendula*
Six-weeks fescue	*Festuca octoflora*
Sloughgrass	*Spartina pectinata*
Smooth brome	*Bromus inermis*
Straw-colored paspalum	*Paspalum stramineum*
Switchgrass	*Panicum virgatum*
Tall dropseed	*Sporobolus asper*
Western wheatgrass	*Agropyron smithii*

American germander	*Teucrium canadense*
Annual sunflower	*Helianthus annuus*
Arrow-leaved aster	*Aster sagittifolius*
Baldwin's ironweed	*Vernonia baldwini*
Beardtongue	*Penstemon*
Black-eyed Susan	*Rudbeckia hirta*
Blazing star	*Liatris*
Blue-eyed grass	*Sisyrinchium campestre*
Blue flag	*Iris versicolor*
Buffalo bur	*Solanum rostratum*
Bur oak	*Quercus macrocarpa*
Bush clover	*Lespedeza capitata*
Butterfly weed	*Asclepias tuberosa*
Canada anemone	*Anemone canadensis*
Canada goldenrod	*Solidago canadensis*
Canadian milk vetch	*Astragalus canadensis*
Carolina anemone	*Anemone caroliniana*
Cattail	*Typha*
Compassplant	*Silphium laciniatum*
Coneflower	*Ratibida pinnata*
Coralberry	*Symphoricarpos orbiculatus*
Culver's root	*Veronicastrum virginicum*
Cup plant	*Silphium perfoliatum*
Daisy fleabane	*Erigeron strigosus*
Dogtooth violet	*Erythronium albidum*
Dogwood	*Cornus*
Dotted button snakeroot	*Liatris punctata*
Downy gentian	*Gentiana puberula*
Entire-leaved rosinweed	*Silphium integrifolium*
False boneset	*Kuhnia eupatorioides*
False indigo	*Baptisia*
False sunflower	*Helenium autumnale*
Fleabane	*Erigeron*
Flowering spurge	*Euphorbia corollata*
Fringed loosestrife	*Steironema ciliatum*
Golden meadow parsnip	*Zizia aurea*
Golden ragwort	*Senecio aureus*
Ground cherry	*Physalis*
Ground plum	*Astragalus crassicarpus*
Gum plant	*Grindelia squarrosa*

Hawkweed	*Hieracium longipilum*
Hazel	*Corylus americana*
Hedge nettle	*Stachys palustris*
Hoary vervain	*Verbena stricta*
Honey locust	*Gleditsia triacanthos*
Horseweed	*Conyza canadensis*
Illinois tick trefoil	*Desmodium illinoense*
Indian hemp	*Apocynum sibiricum*
Indian plantain	*Cacalia tuberosa*
Ironweed	*Vernonia baldwini*
Jerusalem artichoke	*Helianthus tuberosus*
Large-bracted wild indigo	*Baptisia leucophaea*
Large button snakeroot	*Liatris scariosa*
Large-flowered beard tongue	*Penstemon grandiflorus*
Large white wild indigo	*Baptisia leucantha*
Larkspur	*Delphinium virescens*
Lead plant	*Amorpha canescens*
Licorice	*Glycyrrhiza lepidota*
Long-fruited anemone	*Anemone cylindrica*
Loosestrife	*Lythrum alatum*
Many-flowered aster	*Aster ericoides*
Maximilian's sunflower	*Helianthus maximiliani*
Meadow violet	*Viola papilionacea*
Milfoil	*Achillea millefolium*
Mint	*Mentha*
Missouri goldenrod	*Solidago missouriensis*
Mountain mint	*Pycnanthemum*
Mugwort	*Artemisia ludoviciana*
Oxeye	*Heliopsis helianthoides*
Pale purple coneflower	*Echinacea pallida*
Pasque flower	*Anemone patens*
Peppergrass	*Lepidium densiflorum*
Pigweed	*Amaranthus retroflexus*
Pitcher's sage	*Salvia pitcheri*
Poppy mallow	*Callirhoe alcaeoides*
Prairie button snakeroot	*Liatris pycnostachya*
Prairie cat's-foot	*Antennaria neglecta*
Prairie coneflower	*Ratibida columnifera*
Prairie false dandelion	*Microseris cuspidata*
Prairie ground cherry	*Physalis*
Prairie larkspur	*Delphinium virescens*

Prairie phlox	*Phlox pilosa*
Prairie ragwort	*Senecio plattensis*
Prairie rose	*Rosa suffulta*
Prairie turnip	*Psoralea esculenta*
Prairie violet	*Viola pedatifida*
Psoralea	*Psoralea tenuiflora*
Puccoon	*Lithospermum*
Purple prairie clover	*Petalostemum purpureum*
Purple vetch	*Vicia americana*
Pursh's plantain	*Plantago purshii*
Ragweed	*Ambrosia*
Ragwort	*Senecio*
Rattlesnake master	*Eryngium yuccifolium*
Redroot	*Ceanothus ovatus*
Rosinweeds	*Silphium*
Rough pennyroyal	*Hedeoma hispida*
Rush-like lygodesmia	*Lygodesmia juncea*
Russian thistle	*Salsola kali*
Sage	*Artemisia ludoviciana*
Saw-tooth sunflower	*Helianthus grosseserratus*
Scaly blazing star	*Liatris squarrosa*
Scarlet strawberry	*Fragaria virginiana*
Showy goldenrod	*Solidago speciosa*
Showy tick trefoil	*Desmodium canadense*
Silver-leaf psoralea	*Psoralea argophylla*
Sleepy catchfly	*Silene antirrhina*
Smooth goldenrod	*Solidago missouriensis*
Spiderwort	*Tradescantia bracteata*
Star grass	*Hypoxis hirsuta*
Stiff goldenrod	*Solidago rigida*
Stiff marsh bedstraw	*Galium tinctorium*
Stiff sunflower	*Helianthus laetiflorus*
Sullivant's milkweed	*Asclepias sullivantii*
Swamp milkweed	*Asclepias incarnata*
Tall goldenrod	*Solidago altissima*
Tall meadow rue	*Thalictrum dasycarpum*
Thistle	*Cirsium*
Tickseed	*Coreopsis palmata*
Tooth-leaved primrose	*Oenothera serrulata*
Velvety goldenrod	*Solidago mollis*
Venus' looking-glass	*Specularia perfoliata*
Violet sheep sorrel	*Oxalis violaceae*

Water hemlock	*Cicuta maculata*
Water hoarhound	*Lycopus americanus*
Water smartweed	*Polygonum coccineum*
Western ironweed	*Vernonia fasciculata*
Western red lily	*Lilium philadelphicum*
White-flowered parsley	*Lomatium orientale*
White prairie clover	*Petalostemum candidum*
Wild bergamot	*Monarda fistulosa*
Wild indigo	*Baptisia*
Wild lettuce	*Lactuca ludoviciana*
Wild onion	*Allium canadense*
Windflower	*Anemone*
Yarrow	*Achillea millefolium*
Yellow flax	*Linum sulcatum*
Yellow sheep sorrel	*Oxalis stricta*

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