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AMOUNT OF UNDERGROUND PLANT MATERIALS IN DIFFERENT GRASSLAND CLIMATES

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Fig. 1 (upper).—True prairie in midsummer at Anita, near Atlantic, in southwestern Iowa. The vegetation is chiefly composed of little bluestem, prairie dropseed, and needle grass but an abundance of non-grasses, or forbs, also occurs.

Fig. 2 (lower).—Mixed prairie in eastern Colorado. The bunch grass is little bluestem; the understory consists of various short grasses and sedges. This prairie is only moderately grazed and the vegetation is in good condition.

Amount of Underground Plant Materials in Different Grassland Climates

NORTH AMERICAN PRAIRIE

FROM the highlands of central Mexico entirely across the United States and northward into Canada extends the great midcontinental area of grassland. From this central mass, prairie extends westward across Wyoming into eastern Utah, and southwestward through northern New Mexico into northern Arizona. Other grasslands in the northwest cover most of southern Idaho, a part of northern Utah, large areas in eastern Oregon and Washington, and recur in British Columbia. The Pacific prairie occupies the Great Valley of California, and the Desert Plains grassland much of southern Arizona and New Mexico and southwestern Texas.[1] Together they constitute the Grassland or Prairie Formation, which is the most extensive and most varied of all the natural units of vegetation of the North American continent. In fact, grassland formerly covered 38 per cent of the land surface of the United States (Shantz & Zon 1924).

KINDS OF PRAIRIE

Throughout the entire prairie or grassland formation the climate is more favorable to grasses than to trees or shrubs or indeed any other type of vegetation. But within the vast range of grassland climate there are marked differences in degrees of favorableness or unfavorableness to growth even for species of grassland, as is illustrated especially by differences of precipitation and relative rates of evaporation. Temperature and length of growing season are of less importance, since all of the grasslands seem to lie well within summer temperature limits favorable to growth of the grass life form. Since rainfall decreases and evaporation increases from east to west in the great midcontinental area, there have resulted several different types or associations of prairie, each limited in extent by a distinctly different minor grassland climate. These associations have been determined and their approximate boundaries delimited after long study by Dr. Frederic E. Clements, ecologist

[1] The distribution of grassland, forest, desert, etc., is shown on the colored map in Weaver and Clements, Plant Ecology, 1938.

for the Carnegie Institution of Washington. They are known as Tall-grass Prairie, True Prairie, and Mixed Prairie, respectively, figs. 1 and 2.

In correlation with the amount of precipitation, grasses fall rather naturally into three groups: *tall grasses,* such as big bluestem and slough grass; *mid grasses,* as June grass and prairie dropseed; and *short grasses,* illustrated by buffalo grass and blue grama. Prairie everywhere owes its character to the most important or dominant grasses. These are called dominants since they largely control the abundance, vigor of growth, and often the very existence of other species. This control is exerted through their effects upon the water supply, light, and other factors of the surroundings or environment. Most of these dominants are bunch-formers although some propagate by rhizomes, and rarely by stolons, to form a dense sod.

The true prairie covers a great area extending from Manitoba to Texas. To it belong southern Manitoba, western and southern Minnesota, southern Wisconsin, northwestern Indiana, most of Illinois, Iowa, northern and western Missouri, and the eastern half of Oklahoma. The western boundary extends from Oklahoma through central Kansas and Nebraska northeasterly through the Dakotas. The most important grasses are needle grass (*Stipa spartea*), prairie dropseed (*Sporobolus heterolepis*), little bluestem (*Andropogon scoparius*), side-oats grama (*Bouteloua curtipendula*), tall dropseed (*Sporobolus asper*), June grass (*Koeleria cristata*), and western wheat grass (*Agropyron smithii*). All are grasses of moderate height (approximately 2 to 3.5 feet), *i.e.,* mid grasses. Wheat grass is a sod-former, side-oats grama and little bluestem are intermediate in habit in this prairie, while all of the other dominants are bunch grasses.

The tall-grass prairie consists of grasses often 6 to 8 feet high, fig. 3. The major tall grasses are big bluestem (*Andropogon furcatus*), Indian grass (*Sorghastrum nutans*), and a tall form of little bluestem. In more moist places nodding wild rye (*Elymus canadensis*) and tall panic grass (*Panicum virgatum*) also occur. Southward there are numerous other important species. A part of the tall-grass prairie occurred as openings in the deciduous forest or formed a narrow interrupted belt along its margin. But just as forest trees extend far into the grassland along streams, the tall grasses are also found throughout the western prairies in places of unusually

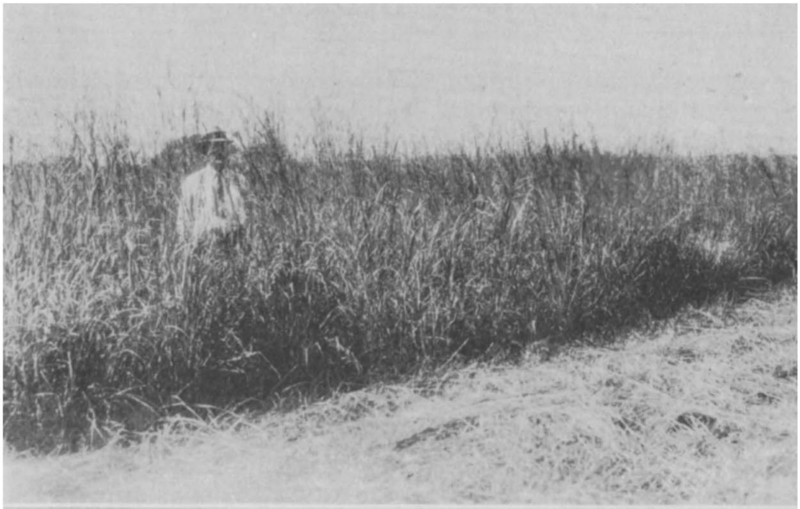

Fig. 3 (upper).—Tall-grass prairie on low ground near the Missouri river at Union, Nebraska. Big bluestem is the chief dominant. This prairie produces three tons of hay per acre during years of normal precipitation.

Fig. 4 (lower).—Short grass near Burlington, Colorado, resulting from many years of close grazing which caused the death of the mid grasses that formed the upper layer. Nearly pure stand of buffalo grass.

favorable moisture content. They border the forests along river bottoms, occupy moist ravines and lower slopes where trees do not occur, and are found abundantly in sandy plains, sand hills, etc., the most notable example being the sand-hills complex of Nebraska. Here there is little or no loss of water by runoff as on "hard" land, evaporation from the soil surface is inhibited by the dry sand mulch, and root systems penetrate deeply. Sand reed (*Calamovilfa longifolia*), sand-hills bluestem (*Andropogon hallii*), and other tall grasses of sandy soil indicate a good water supply in soil and subsoil.

Mixed prairie lies west of the true prairie from southern Canada to northwestern Texas. The name is derived from the intimate mixture of mid and short grasses. The former constitute the upper story and short grasses the lower one. The mid grasses are in part those of the true prairie, as June grass and wheat grass, or they are closely related species, such as needle grass (*Stipa comata*) and sand dropseed (*Sporobolus cryptandrus*). Wire grass (*Aristida*) and other dominants also occur. Blue grama grass (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*) are the chief short grasses, but *Carex stenophylla* and *C. filifolia* (the latter known as thread-leaf sedge and niggerwool) are also important dominants.

Over a large portion of the mixed prairie, especially the part with lower rainfall and higher evaporation, the mid grasses are usually inconspicuous or even absent, leaving the short grasses in control, fig. 4. This dominance of short grasses has resulted from long-continued overgrazing which handicaps the taller grasses and correspondingly favors those of the lower layer. There is much evidence to support the fact that the short-grass plains are really mixed prairie, a conclusion that has been reached after many years of field research and study of their history. This portion of the Great Plains is therefore designated as a disturbance climax or, for brevity, the mixed prairie disclimax (Weaver & Clements 1938).

It is notably much easier to find areas of virgin true prairie, which when protected yield a fine crop of hay annually, than similar ones of mixed prairie, except in the eastern border of this association. The rest has been grazed and often much overgrazed.

NATURE OF PRAIRIE

Prairie is not merely land covered with grass. It is a complex and definite organic entity with interrelated parts developed and adjusted throughout very long periods of time.

Prairie is the handiwork of climate and of soil. Vegetation is not only closely adjusted to these agencies but is an expression of them. It is quite as proper to speak of prairie soil and prairie climate as of prairie vegetation. Prairie may be considered from many points of view; a most important one is that of the species of which it is composed. Although a prairie is distinguished by its dominant species, subdominant and secondary species are also important.

Several years of study over an area of 60,000 square miles in the true prairie of the Missouri Valley have shown that there are about 10 dominant or controlling species which make up the general background of vegetation. In addition, a group of 25 minor grasses and sedges of uplands was determined. Among these the most important were Kentucky bluegrass (*Poa pratensis*), Scribner's panic grass (*Panicum scribnerianum*), Wilcox's panic grass (*P. wilcoxianum*), and Pennsylvania sedge (*Carex pennsylvanica*). All these are of lower stature than the dominants, adapted to grow in the shade produced by them, and occupy the interspaces between the larger individual bunches. Kentucky bluegrass is not a native but an introduced species which has spread widely since the cessation of prairie fires and under the practice of annual mowing. Another lot of about 25 species of minor grasses and sedges was found to occur more or less regularly on more moist prairie land. Thus the matrix or background of prairie consists of grasses and grasslike plants.

Grasses are well adapted to withstand the grazing that has been imposed upon them through thousands of years by herds of bison, elk, and other native animals, followed by the settlers' cattle. Near the base of the leaf there is a transverse intercalary zone of growth. Hence if the major portion of the leaf is cut or bitten off the part can readily be replaced, that is, the leaf can grow until it reaches or surpasses its former size. Stems of most grasses as well as the leaves are bitten off in grazing. Growth then takes place from buds produced in the axils of sheathing bases of the leaves at the lower ends of the stems. These buds are usually not destroyed except by very close grazing, when the grasses are said to be "eaten out." Frequent grazing of many species of meadow grasses, such as big bluestem, results in a greater degree of leafiness. Where buds occur just within or below the soil (as on grasses with underground stems) they are even more effectively protected from both overgrazing and fire. Moreover, grasses expose their long, narrow leaves in such manner as to receive a maximum of light and their fibrous roots are so minutely

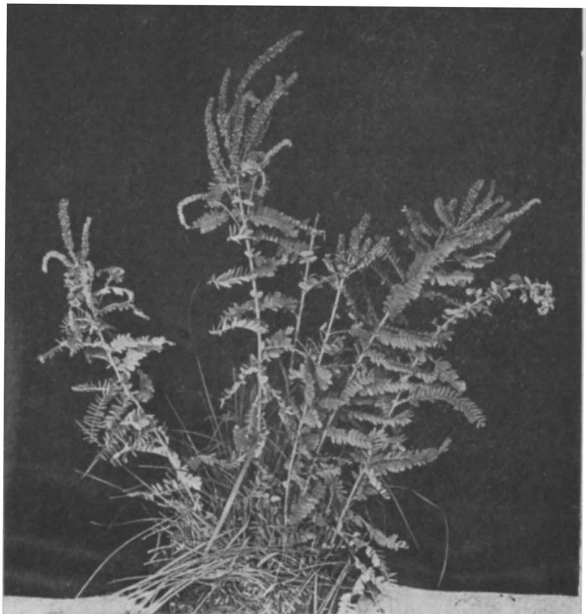

Fig. 5 (upper).—Lead plant or prairie shoestring, *Amorpha canescens,* in blossom on June 30 at a height of about 15 inches. Aside from the grasses, this legume is the most important species of uplands.

Fig. 6 (lower).—A mat-forming plant, prairie cat's-foot, *Antennaria campestris,* very common in prairie and blossoming early in spring. It forms an excellent protection to the soil.

branched as to occupy thoroughly the soil. But grasslands contain other kinds of plants—herbs that do not have the grass life form. These are designated as forbs.

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. In the extensive studies 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 prairie shoestring or lead plant (*Amorpha canescens*), a half-shrub behaving as an herb under annual mowing, was the most important, fig. 5. This species occurred in practically all of the upland prairies. It also was frequently found on lowlands. The stiff sunflower, many-flowered aster, prairie cat's-foot, daisy fleabane, smooth goldenrod, and silvery psoralea were next in order of greatest importance, fig. 6. A different group of species of similar great abundance and importance was found on low ground (Weaver & Fitzpatrick 1934).

About 225 species of grasses and forbs of considerable importance were found in the prairies of the Missouri Valley region. Dr. Shimek (1931), a well known student of the prairies of the early days, states that 265 species make up the bulk of the prairie flora of Iowa, while Steiger (1930) found 237 species of prairie plants on a single section (640 acres) of land near Lincoln, Nebraska.

That the forbs are largely under the control of the grasses is shown in several ways. There are more species of forbs and their development is greatest in true prairie. Here the mid-grass dominants do not so greatly shade them as in the areas of tall grass under greater precipitation eastward, while rainfall still furnishes enough water for both grasses and forbs. In mixed prairie westward the water content of soil becomes a limiting factor and forbs decrease gradually both in numbers, size of individuals, and in the extent of their groupings or societies.[2]

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

[2] An excellent description of mixed prairie in west central Kansas is given by F. W. Albertson (1937).

Fig. 7 (upper).—False indigo, *Baptisia leucophaea*, a prairie legume, in full bloom on June 1, a time at which it overtops the grasses.

Fig. 8 (lower).—New Jersey tea or red-root, *Ceanothus pubescens*, in June. This shrub is only 2 feet high since it was cut the previous fall in mowing the hay.

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.

The earliest prevernal bloomers appear in the warmer situations late in March or early in April.[3] Among the most important are Pennsylvania sedge, prairie cat's-foot, pasque flower, dog's-tooth violet, windflower, and fennel-leaved parsley. Needle grass, June grass, 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.

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 fall 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 wood-sorrel, and prairie violet rapidly develop both foliage and flowers before the light is too much obscured by the growth of the grasses. The new shoots of 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 (cf. Weaver & Fitzpatrick 1934). Among these are found blue-eyed grass, yellow star grass, puccoons, old-man-of-the-Platte, wild onions, vetches, false indigo, spiderworts, and many others, all enhancing the beauty of prairie in spring. The yellow of the golden parsnip, the bright pink or purple of the prairie phlox, the white masses of flowers of New Jersey tea, and the ground plum with its abundance of violet-purple flowers were all familiar sights to the pioneers of the midwest, figs. 7 and 8.

"The estival or summer aspect begins during the last week of May. By this time bluegrass has blossomed, the spikes of

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

Fig. 9 (upper).—Tooth-leaved primrose, *Meriolix serrulata,* blossoms during summer. The large, 4-petaled yellow flowers are both abundant and conspicuous.

Fig. 10 (lower).—Society of black-eyed Susan, *Rudbeckia hirta,* in big bluestem sod near Lincoln, Nebraska. The large orange-yellow blossoms are conspicuous from late June until well into August.

June grass are beginning to open, and needle grass is often in full bloom. The bluestems and other dominant grasses now cover the uplands with a deep foliage of green and on the lowlands a height of 12 to 18 inches has been attained. Many spring flowers are gone. Although certain vernal species continue to bloom, there is a distinct transition from spring to summer. The landscape is rapidly becoming redecorated with extensive societies of daisies, legumes, and the rose. Wild alfalfas (*Psoralea*), where at all abundant, give a distinctive tone to the landscape. Milfoil, daisy fleabane, pentstemons, larkspurs, wild flax, primroses, and niggerheads 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 prairie shoestring. 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 several weeks. The white and purple prairie clover, black-eyed Susan, tick trefoil, wild licorice, wild bergamot, and rosinweeds adorn the rolling hills and lowlands, figs. 9 and 10. "The patterns are endlessly variable in detail. Each week new elements appear and old ones gradually decline as the season advances. The blooming of the sunflower and the yellowing of the inflorescences 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 (Weaver & Fitzpatrick 1934).[4]

"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 the tall panic grass 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 autum-

[4] Quotations in the description of seasonal aspects and layering, often with omissions and slightly modified, are from The Prairie, by Weaver and Fitzpatrick, 1934.

FALL-BLOOMING PRAIRIE FORBS THAT EXTEND HIGH ABOVE THE SURROUNDING GRASSES.

Fig. 11 (left).—The rosin weed, *Silphium integrifolium,* is 5 feet tall and shows a wealth of orange-yellow flowers.

Fig. 12 (center).—A blazing star, *Liatris scariosa,* with rose-purple flowers, is 3.5 feet tall and in early bloom on September 1.

Fig. 13 (right).—The tall goldenrod, *Solidago altissima,* extends about 3 feet above the general level of the big bluestem.

nal aspect, at least for a time. Now the yellow and gold of the sunflower and rough oxeye intermingle with the purple of the 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 prairie boneset, the gray color of the prairie sage, and the black fruiting heads of lespedeza. Ironweeds, gentians, evening primroses, and many others are found. Numerous asters blossom from August until late fall, their colors varying from white or lavender to blue or purple, figs. 11, 12, and 13.

"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 dropseed are held aloft above the level of the foliage. About the first week in September 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.

"As a result of natural deterioration, augumented by the work of the wind and assisted by the weight of ice 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. But the prairie is still a living thing—though underground and dormant—awaiting only another summer to build anew the parts above the soil."

Layering above Ground.—"Many forbs of early spring always remain near the surface of the soil. They make a rapid growth, flower, and produce seed early and thus complete the important work of the season before they are overshadowed by the grasses. Such are the violets, the ground plum, the wood-sorrel, and prairie cat's-foot. Throughout the summer such low-growing species carry on their vegetative activity in the subdued light of the understory or later wither

Fig. 14 (upper).—The wild strawberry, *Fragaria virginiana*, in full bloom in low prairie on May 6, before the bluestem grasses have developed much foliage.

Fig. 15 (lower).—A prairie legume, *Psoralea floribunda*, about 3.5 feet high and far overtopping the little bluestem. The plant grows rapidly to a height of 12 to 15 inches before the branches are expanded or the leaves much developed. Photographed June 20.

away. Certain species are probably too moisture-loving to continue growth under the direct heat of the midsummer sun, and are actually benefited by the shade, the protection afforded from drying winds, and the community benefit of having the transpired moisture held about them."

Approximately 70 per cent of the late spring species are likewise of low stature. These include star grass, blue-eyed grass, wood-sorrels, bedstraw, etc., fig. 14. The dominant grasses in the main have not yet so completely overshadowed them as to form a material handicap in the relation to light. Of the remaining 30 per cent only a few, such as phlox, New Jersey tea, and golden meadow parsnip, are at or above the height of the grasses. Most are submerged by midsummer to the general grass level.

Plants which blossom during midsummer or fall have likewise started an early vigorous development. They grow rapidly. Week by week during early summer the struggle for light becomes more and more severe. Species of the summer aspect reach a moderate height in relation to the grasses. Among the host of summer bloomers, about 40 per cent reach the general level of the grasses, only 10 per cent are found in the understory, and 50 per cent have attained a height greater than that of their grass competitors, fig. 15.

Autumnal blooming plants continue to develop until they are mostly far above the dominant grasses. Not one is found in the understory. Except for the gentian, all are conspicuous at or above the general grass-level and many reach a height of 4 to 6 feet or more.

Layering in the prairie is the result of a process of adaptation and selection that has taken place throughout past centuries. "So numerous are the individuals that those of greater stature shade the shorter ones, often to the extent that seedlings and lower leaves die for lack of sufficient light to manufacture food. Through thousands of years there has resulted an adjustment of the species to environment." The more numerous the plants of the upper layers and the more completely they occupy the available space, the greater must be the tolerance of the lower layer to reduced light intensity. At a height of 12 inches, light is frequently reduced to 25 to 35 per cent of full sunshine, and near the surface of the soil to only 1 to 3 per cent.

The several seasonal aspects are thus marked by species of varying stature. The prevernal and vernal are characterized by those of low or moderately low growth; the summer or estival aspect by plants of greater height, most of which have an equal advantage with the grasses in the struggle for light. Autumnal species are nearly all of sufficient height to reach the grass-level or indeed to extend several feet above it.

Layering below Ground.—"Within the prairie cover one finds the conditions of life severe. Though the soil is rich and deep, water is frequently scarce and the plants sharing it are legion. Deficiency of water usually occurs when the air too is driest, the temperature high, and the prairie swept by desiccating winds.

"The problem of an adequate water supply has been met by the development of deeply penetrating, usually widely branching, and thoroughly efficient root systems. The perennial life habit is exhibited by all of the dominant species as well as by practically all of the others." Perhaps only 2 to 5 per cent of prairie species are annuals. Reproduction is largely vegetative. Only rarely in this crowded community do seedlings, although sometimes abundant, develop into mature plants. Hence, a good absorbing system once established may be used throughout a long span of years. Of course, there is deterioration; some branches may die or be cut off by rodents, but new ones take their place and the general root system may increase in size with the enlargement of the tops. Moreover, the roots and other underground parts are storehouses of food during the long period of winter dormancy and account for the rapid growth of the plants following their early awakening in spring.

"The roots do not all draw upon the same soil level for their supplies of water and nutrients. In fact the root habit is so fixed in this respect that the various species may be grouped according to the layer or layers of soil occupied by them. Thus, the species on a single square yard of soil surface frequently obtain their water and nutrients from a volume of three or more cubic yards of soil. For example, on upland prairie June grass absorbs to a general level of only about 1.5 feet; little bluestem extends its roots through the first 4 or 5 feet of soil. Many-flowered aster and prairie shoestring (the latter enriching the soil with nitrogen throughout) penetrate to about 7 and 12 to 16 feet, respectively." Among 43 species selected as typically representative of the true-prairie flora, only 14 per cent absorb almost entirely in the surface 2 feet of soil; 21 per cent have roots extending well below 2 feet but seldom beyond 5 feet; but 65 per cent have roots that reach depths

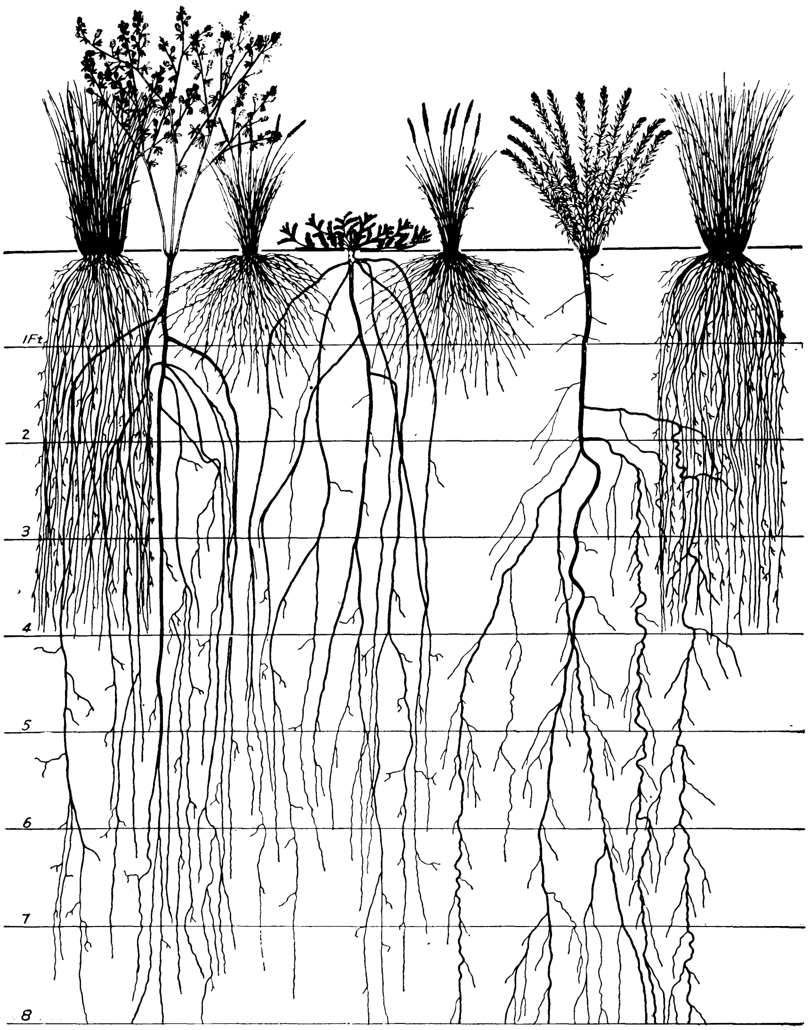

Fig. 16.—Layers above and below ground. Left to right, little bluestem, psoralea, June grass, ground plum, and false prairie boneset with the strong taproot. Note the three layers below ground; that the grasses absorb at different levels; and that the forbs, which absorb but little in the first foot, extend much deeper, some to 17 feet.

below 5 feet, a penetration of 8 to 12 feet being common and a maximum depth of over 20 feet sometimes being attained (Weaver 1920). Indeed, the bulk of the prairie is below and not above the surface of the ground, fig. 16.

Fig. 17 (upper).—Upland prairie in eastern Nebraska with an abundance of a legume, silvery psoralea, *Psoralea argophylla*. Photographed June 10.

Fig. 18 (lower).—Typical true prairie in September, after mowing and stacking the hay. The dense sod excludes introduced weeds. Even after the crop is removed the soil is well protected from erosion.

"This segregation of the root systems into several more or less distinct levels for absorption is one of the chief adaptations of plants of the prairie to their environment. Because of the extensive development of the absorbing organs, the soil is thoroughly occupied by the various root systems, especially the fine fibrous roots of the grasses, even to within one-half inch of its surface. The entire water supply is under tribute. The balance between species is so well adjusted that a considerable increase of one at the expense of another rarely occurs except as a result of such a major catastrophe as the recent great drought.

"Just as roots occur at different levels, so too are found the underground parts primarily for food accumulation and propagation. Corms, bulbs, tubers, and root offshoots abound but much more frequently the rhizomes of grasses and forbs. These occur in dense masses, mostly within a very few inches of the soil surface or just below it. Roots and rhizomes form a dense network below the bunches and mats of sods. Between the plants or plant masses the water-absorbing system extends in so complete a network that invaders in the apparently bare areas cannot successfully compete. The effect of this community habit and of the excellent condition of tilth resulting from it is such that the soil rarely cracks with consequent exposure of large surfaces to evaporation as frequently occurs during drought after the vegetation has been removed or seriously weakened as in overgrazing.

"Thus the plan of life in the prairie is very diverse. So many species can exist together only by sharing the soil at different levels, by obtaining light at different heights, by making maximum demands for the factors at different seasons of the year, by fitting into the niches unoccupied by other species, and by actually profiting by the incidental benefits afforded by the community of which they are a part. Legumes add nitrogen to the soil; the taller plants protect the lower ones from the heating and drying effects of full sunshine; the mat-formers and others prostrate on the soil further reduce water loss by covering its surface, fig. 17. They live in an atmosphere much better supplied with moisture than the windswept plants above. Light is absorbed at many levels, the more or less vertical leaves of the dominant grasses permitting some light to filter between them as the sun swings across the heavens."

Stability.—The great stability of the prairie denotes a high degree of equilibrium between the vegetation and its habitat under the control of the existing climate. Large tracts of prairie remain after 90 or more years of settlement 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. With rare exceptions, they remain free from weeds although surrounded for years by weedy fields and pastures, fig. 18. For example, a recent list of the immigrant flora of Iowa alone contains 263 species (Cratty 1929), a number large enough to equal that of the bulk of the native species (Shimek 1931).

Stability is increased by the long life span of many prairie species. The dominant grasses such as little bluestem and prairie dropseed, once established, retain their vitality for many years. The bunches enlarge slowly year by year. Often the central portion may decay and the periphery may be separated into fragments which may become rejuvenated because of less competition now that competing parts are dead. They may live on for many years. Very old plants of false prairie boneset, blazing star, etc., with root-crowns several inches in diameter are common. Their life span may extend over several decades. Rhizomatous species as big bluestem and slough grass extend beyond the parent several inches in a single year, branching and continually giving rise to new shoots and new roots and finally, by decay of the rhizome, becoming separated from the original plant. Thus, in this prairie thicket of intermingled grasses the life span is long and the resulting stability is great. 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. In fact it is more than this, for the vegetation has had no small part in determining the physical, chemical, and biological properties of the soil. Prairie soil and prairie climate are in a sense an expression of one and the same thing.

REACTIONS OF GRASSLAND VEGETATION

The effects that plants exert upon the place in which they live are designated, in ecological terminology, as reactions. Vegetation modifies conditions both below and above ground.

Reactions on Soil Formation.—A remarkable dependence of long standing has existed between soils and their natural vegetation. Indeed, the development of the soil and a parallel development of the plant cover have gone hand in hand from the beginning of rock weathering to the production of mature soil covered with climax vegetation. "Geologic materials including mantle-rock and bedrock are necessary, but are passive rather than active elements in soil formation. From them, the soils develop through constructional processes that involve the growth of vegetation, the accumulation and decomposition of organic substances, the formation of new chemical compounds, the progressive breaking down of the parent materials, the translocation of materials in the soil, and the formation of a more or less layered profile.[5]

"The constructional processes of soil development are due largely to the incorporation of plant parts among the mineral particles. This may occur following the accumulation of the parent materials or along with it. Vegetation introduces both directly and indirectly the biological factor into soil formation. 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 supply food for visible and microscopic soil organisms; these soil organisms decompose the plant remains, which ultimately become incorporated into the soil as humus."

It should be clearly understood that the residues of grassland vegetation, when not removed from the land, have returned more to the soil than the green plants have absorbed from it. Throughout their lives they have synthesized many organic substances, especially sugars, starches, celluloses, fats, and proteins. "Most of these materials return to the soil when the plant dies. The 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. The soil soon becomes the abode of bacteria, fungi, and many other organisms. Throughout the whole process of soil development, plant and accompanying animal residues are converted, largely by the activities of microorganisms, into the dark-colored organic matter of the soil. Thus, the two functions of living matter in soil development are synthesis and decomposition."

The amount of living organic materials in prairie soils is very great, often 3 to 4 tons per acre in the surface 4 inches alone,

[5] This and the three following quotations from Weaver and Clements' Plant Ecology are used by permission of the publishers, McGraw-Hill Book Co., Inc., New York.

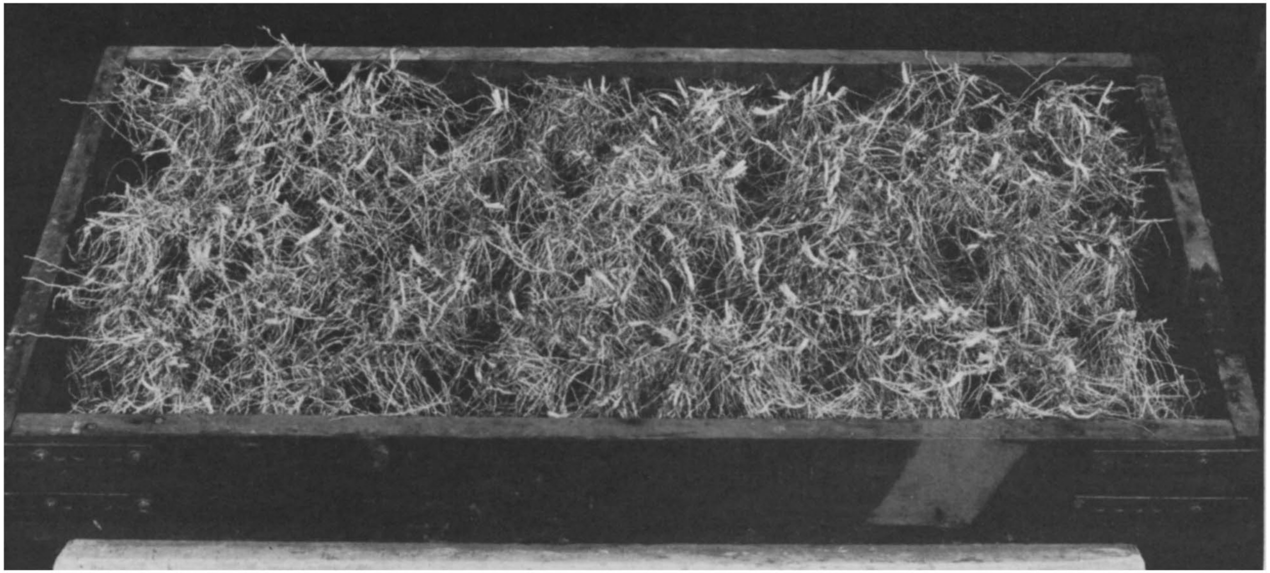

Fig. 19.—One-half square meter sample of the underground parts of big bluestem from Union, Nebraska, after all of the soil has been carefully washed away to a depth of 4 inches.

fig. 19. Researches by Weaver, Hougen & Weldon (1935) have shown that in Lancaster loam 60 per cent of the underground parts of little bluestem occur in the surface 6 inches. The remainder of the root system was distributed to a depth of 4 feet. In Wabash clay loam, 68 per cent of the underground parts of big bluestem were found in the surface 6 inches; the remainder of the root system extended to a depth of 7 feet. They found further that roots and rhizomes constitute only about one-tenth of the total organic matter in the surface 6 inches of soil, and but 3 to 4 per cent in the second 6 inches. Thus 30 to 40 tons of organic matter per acre are found in the surface soil of native prairie.

Much of this organic matter, of course, has its origin from aboveground plant parts, and small amounts from the remains of microscopic soil organisms, especially bacteria. As plants grow, die, and are replaced by others, new sources of humus are constantly available. But just as organic matter is constantly being formed, it is also continually being broken down by an enormous microscopic population in the soil, which may total one or more tons per acre (Russell 1932). These organisms depend upon this material for their food and energy. Under virgin conditions the plant growth ultimately reaches an equilibrium which is a result of the interaction of the climatic conditions, conditions in the soil, and plant growth itself.

Another reaction of grassland upon soils results from the high capacity of grasses for the absorption of lime. "The calcification process of soil development is most typically maintained under grasses or grasslike vegetation and climates with restricted precipitation. There may be considerable leaching, but not enough to remove the calcium and magnesium carbonates. Consequently these accumulate in the lower part of the solum. The plants absorb and transport bases from the lower soil horizons to the surface in relatively large amounts. The soil does not become acid, or if so only slightly acid, and the colloids, both organic and inorganic, in the presence of abundant calcium are not eluviated. The micropopulation is predominantly bacterial; the decomposed organic materials are relatively insoluble and remain in the upper part of the soil. There is little or no movement of clay or other colloidal material from the A to the B horizon. The kinds of grasses and their abundance determine largely the depth of color, content of organic matter, and thickness of the soil itself."

The distribution of organic matter in the prairie soil is due in part to the action of earthworms, insects, and other organisms which find in these rich, mild soils an ideal habitat. Other mixing of humus and parent rock materials is due to the extensive burrowing of rodents. But most of the humus of deeper soil is derived from the roots of plants which decay where they grew, deep in the soil, making it rich and porous. In these

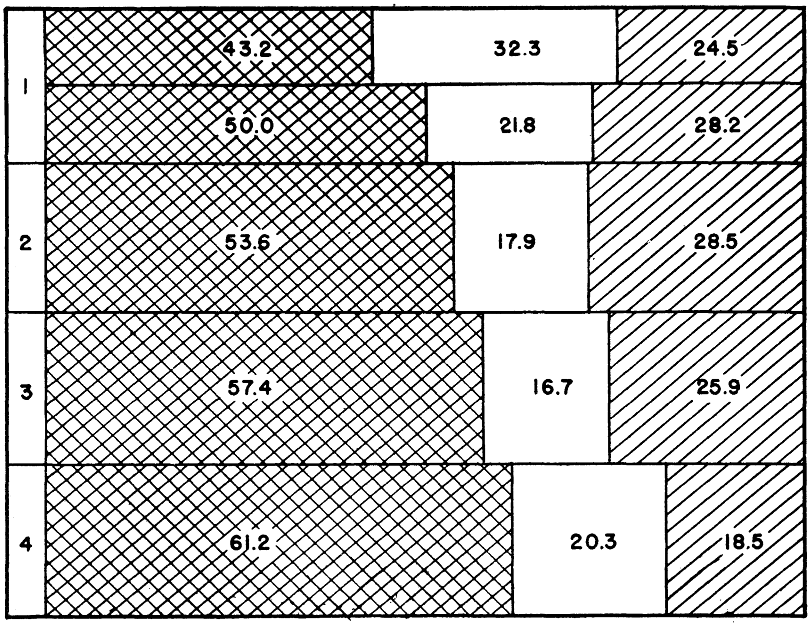

Fig. 20.—Diagram showing the percentage of solid matter (cross-hatch) and total pore space in the first 4 feet of Lancaster loam soil covered with little bluestem. Portion of pore space occupied by water (single-hatch) is based upon average water content during 1932; white portion is air space.

ways the activities of grasses have exerted a powerful reaction as a soil-building influence.

Reactions on Water Relations.—Owing to the excellent crumb structure, largely brought about by the activities of plants, and the network of channels where roots have decayed, grassland soil is very porous and consequently receptive to water. A pore space of 40 to 60 per cent has been determined in true prairie soil, even to a depth of 7 feet (Weaver, Hougen & Weldon 1935). This space, of course, is occupied by both air and water, fig. 20.

The cover of prairie vegetation also exerts a pronounced effect upon soil water through transpiration. Experiments have been made with native sod in large weighed containers placed at the soil level in the prairie where they were surrounded by undisturbed natural vegetation. Average daily water losses during the growing season at Lincoln over a period of five years ranged from 19 to 32 tons per acre. Thus the soil reservoir is depleted and made ready to absorb the precipitation

Fig. 21.—A fine stand of big bluestem near Glenwood, Iowa, about 40 inches tall and beginning to produce flower stalks (July 28). More than half the rainfall is usually intercepted by such a cover and never reaches the soil.

from subsequent showers. There is no evidence, however, that this transpired water has any influence upon increasing rainfall. Recent studies of the conditions in the upper air show rather conclusively that water given off by any type of vegetation or evaporated from pond, river, or wet land surfaces has very little effect upon our rainfall. "The principal amount of moisture returned to the atmosphere by continental evaporation is absorbed by continental, or dry, air masses that are generally incapable of immediately releasing their moisture and that pass off continental areas with large gains in moisture. The supply of moisture for precipitation over the United

States is derived principally from maritime air masses that obtain their moisture mainly from evaporation from oceanic provinces, only a very small part being attributable to continental evaporation" (Holzman 1937).

The amount of precipitation as measured by a rain gauge is a poor index of the amount of water that reaches the prairie soil. Much of the water is intercepted by the great expanse of foliage spread out to receive light at all levels to the topmost leaf. Careful measurements of the leaf area of grasses and other plants show conclusively that an acre of prairie presents 5 to 10 acres of leaf surface which intercepts and holds much water until it is evaporated. Clark (1939), in his recent extensive studies, has shown that native lowland prairie of big bluestem intercepted 75 to 80 per cent of lighter showers and 60 to 70 per cent where the rainfall varied from 1 to nearly 2 inches, fig. 21. He had previously stated (1937), "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." In relatively dry climates these losses of water to the soil are of great significance and this plant reaction alone is sufficiently important to warrant extended study.

A reaction of the prairie cover of major importance occurs in breaking the force of beating rains. Even torrential downpours, so characteristic of prairie climate, reach the soil with the velocity of the raindrops much decreased. In virgin prairie, the soil is further protected by a mulch of fallen leaves, fragments of stems, flowers and fruits, etc., which forms a somewhat continuous cover of varying thickness. Not only is the force of the impact reduced, but the surface soil is not churned into a muddy suspension, the fine particles of which would clog the pores as the water entered the soil (Lowdermilk 1930). That the pores remain open is a chief reason for the great absorptive power of prairie soil. Runoff in prairies is usually slight unless rains are heavy. Abundant humus creates a spongelike condition in the topsoil which increases its capacity to absorb and hold water. The water that does run off is usually clear since the soil is protected by litter and leaf mold and held firmly in place by the bases of the plants and their widely and deeply spreading root systems. Nor does erosion by wind occur where there is a natural cover of grass.

Grassland soils have been thoroughly protected by the unbroken mantle of prairie vegetation through untold centuries.

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.

BREAKING THE PRAIRIE

Undisturbed through millenia, finally comes the prairie's conqueror. The breaking of prairie in Iowa is vividly portrayed by Quick (1922).

"The plow itself was long, low, and yachtlike in form; a curved blade of polished steel. The plowman walked behind it in a clean new path, sheared as smooth as a concrete pavement, with not a lump of crumbled earth under his feet—a cool, moist, black path of richness. The furrow-slice was a long, almost unbroken ribbon of turf, each one laid smoothly against the former strand, and under it lay crumpled and crushed the layer of grass and flowers. The plow-point was long and tapering, like the prow of a clipper, and ran far out under the beam, and above it was the rolling colter, a circular blade of steel, which cut the edge of the furrow as cleanly as cheese. The lay of the plow, filed sharp at every round, lay flat, and clove the slice neatly from the bosom of earth where it had lain from the beginning of time. As the team steadily pulled the machine along, I heard a curious thrilling sound as the knife went through the roots, a sort of murmuring as of protest at this violation—and once in a while, the whole engine, and the arms of the plowman also, felt a jar, like that of a ship striking a hidden rock, as the share cut through a red-root—a stout root of wood, like red cedar or mahogany, sometimes as large as one's arm, topped with a clump of tough twigs and with clusters of pretty white blossoms. [Fig. 8.]

"As I looked back at the results of my day's work, my spirits rose; for in the east a man might have worked all summer long to clear as much land as I had prepared for a crop on that first day. This morning it had been wilderness; now it was a field—a field in which . . . [one could plant] . . . corn, by the simple process of cutting through the sods with an ax, and dropping in each opening thus made three kernels of corn."

Only recently has detailed study been made of the binding network of roots and rhizomes that held the furrow-slice together (Pavlychenko 1939). After thoroughly soaking the soil, and most carefully washing away under water the soil particles and leaf mold, it has been determined that a single strip of prairie sod, 8 inches wide, 100 inches long, and with a depth of 4 inches, is filled with a tangled network of roots having a total length of more than 20 miles, fig. 19.

RESUMÉ—PURPOSE OF EXPERIMENTAL WORK

The enormous importance of vegetation in soil formation has been recognized only relatively 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 (Kellogg 1936). Likewise, investigators of soil conservation, after fully evaluating the factors of slope and soil type, have determined that cover is of first importance in protecting the soil, which it has such an important part in producing, from erosion by wind and water (Bennett 1934). Thus, in addition to the scientific facts acquired by determining the amounts of plant materials in soils, the practical significance is of very great importance.

Although the different types and productivity of grassland above ground are well known, knowledge of the quantities of living plant materials in the soil is meager. In fact, a clear understanding of root depth and distribution in prairie soils has been gained only during the last 20 years (Weaver 1919, 1920, 1926; Sperry 1935; Albertson 1937). Very recently investigations revealing the great lengths attained by the root systems of individual plants have been made (Pavlychenko 1937; Dittmer 1937). 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.

Weaver & Harmon (1935) studied quantitatively the amount of plant materials in prairies and pastures of eastern Nebraska. Using large numbers of one-half square meter samples, they determined that the surface 4 inches of soil alone contained 3.3 tons of living plant materials per acre in the *Andropogon scoparius* type. Yield of the *Stipa spartea* type of prairie was only 1.87 tons, but that of *Andropogon furcatus* was 4.1 tons per acre. Where long-continued grazing had caused the replacement of the native mid grasses by other types, underground yield also decreased. That from pure bluegrass pasture

(*Poa pratensis*) was 39 per cent less, and samples from short-grass pasture (*Buchloe dactyloides* and *Bouteloua gracilis*) yielded 42 and 27 per cent less, respectively, than the original upland prairie vegetation which they replaced.

Further work by Kramer & Weaver (1936) extended the studies to include various types of tame pastures and field crops. In general, the underground parts decreased to only 16 to 48 per cent of that of unbroken prairie. Despite the comprehensive nature of these investigations, the study was purposely confined to a single small area.

The present investigation is a reconnaissance of a wide prairie region, from moist true prairie, through mixed prairie, well into the disclimax of the Great Plains. It thus includes several grassland subclimates. The purpose was to determine the correlation, if any, between amounts of underground plant materials and an increase in aridity. All samples, unless otherwise indicated, were collected during 1935 and 1936.

LOCATION AND DESCRIPTION OF THE AREAS

These investigations were pursued in both true and mixed prairie. The portion of the true prairie studied extends from Guthrie Center and Creston, Iowa, situated approximately 75 miles east of the Missouri river, to Nelson, Nebraska, and Montrose, Kansas, about 200 miles southwestward, fig. 22. Mean annual precipitation varies from 33 inches at the eastern stations to only 26 at those on the western border of the true prairie. Moreover, wind movement and rate of evaporation are increasingly greater from east to west, while other conditions favorable to growth, such as water content of soil, gradually decrease (Clements & Weaver 1924). The less favorable grassland climate has made sufficient impress upon the structure and development of the vegetation to warrant its division for the purpose of this study into three groups which are designated as areas.

The central group of stations—the Lincoln area—with precipitation of 28 to 30.8 inches and other factors of growth, except during severe drought, those of a moderately mesophytic grassland, centers in eastern Nebraska on the extreme western edge of the Prairie soils, but includes the two most western stations in Iowa (Glenwood and Oakland) with similar precipitation, fig. 22. These stations lie entirely within the zonal soil group designated as Prairie soil (Kellogg 1936), although near its western border, which is clearly delimited by the

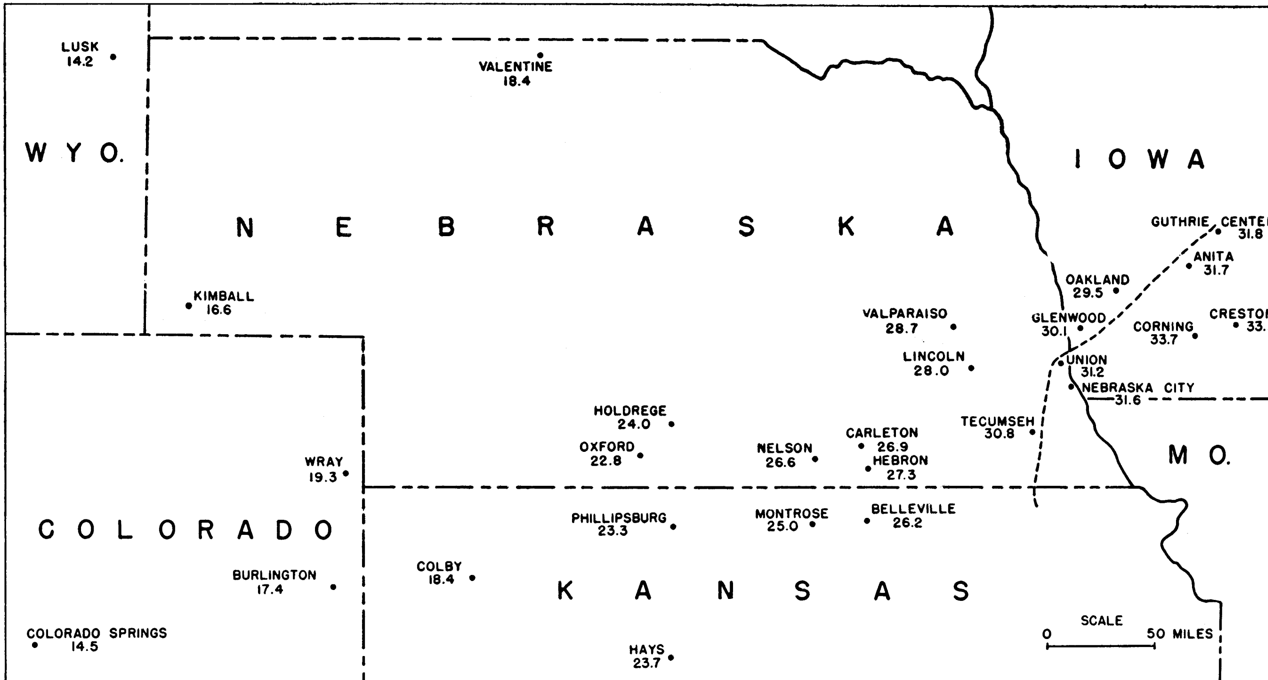

Fig. 22.—Map of portions of five states showing the stations where samples of underground plant parts were taken. The figures indicate mean annual precipitation. Stations east of the broken line of 31 inches precipitation belong to the Anita group.

"lime line." This line separates the Prairie soils from the Chernozems. These soils are very dark in color, rich in humus, very deep and of high fertility. The soil series at each station where samples were taken was ascertained and is recorded with the sample.

An eastern group of stations—the Anita area—with precipitation of 31.2 to 33.7 inches, centers in western Iowa in well-developed Prairie soil, but includes two stations of similar high rainfall (Nebraska City and Union) in the same zonal type in southeastern Nebraska.

The southwestern group of stations in Kansas and southern Nebraska—the Nelson area—with mean annual precipitation of only 25 to 27.3 inches, is located entirely in 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 Prairie soils, but productivity is less because of the decreased precipitation. This area is distinctly more xerophytic than either of the preceding.

This classification of different degrees of true prairie climate agrees rather closely with that of Weaver & Albertson (1936) in their consideration of the effects of the great drought, and is substantiated by productivity of native vegetation.

In the mixed prairie, underground plant production was determined at two groups of stations. The first—the Phillipsburg area—was located in west-central Kansas at Hays and Phillipsburg and northward to Oxford, Nebraska. Here the precipitation is approximately 23 inches, a decrease of nearly 10 inches from that at the most mesophytic stations, and other climatic conditions for plant development are decidedly less favorable. The area is located in the extreme western portion of the Chernozem soils.

The westernmost group of stations—the Burlington area—included stations scattered over a wide semiarid territory from Colby, Kansas, through Burlington and Wray, Colorado, to Colorado Springs. Mean annual precipitation in this area decreases from 19.3 inches at Wray, on the east, to 14.5 inches at Colorado Springs, and averages 17.4 inches for the four stations. This is 6 inches less than the precipitation at the eastern mixed-prairie stations and is a decrease of 15 inches from that at the most mesophytic group of stations in the true prairie. These stations are located in the Dark Brown and Brown zonal soil groups. Here the solum is shallower than in the Chernozem; the lime layer, at approximately 12 to 24 inches below the soil surface, indicates the usual depth of water penetration. Wind movement is frequent and high, humidity relatively low, evaporation great, and periods of summer drought frequent. Plant growth is controlled by available soil water.

These five areas of study extend through three of the climatic provinces delimited by Thornthwaite (1931). All of the soils are porous and offer no unusual obstruction to root penetration. Root depth of the grasses is 4 to 7 feet eastward but decreases with lighter precipitation westward where it is limited by dry subsoil, in some places to a depth of 2 to 3 feet.

PROCEDURE AND METHODS

The prairies selected for study were, with very few exceptions (westward), undisturbed except for annual mowing. Their previous history is well known. The topography and soil of each prairie were typical of the surrounding region. The samples taken were one meter long (39⅜ inches), one-half meter wide, and a decimeter (4 inches) deep. They were secured from typical portions of each individual prairie. Composition of vegetation, basal area, and foliage cover were the chief criteria employed in selecting the general local area for sampling. All samples, with a single exception, were taken from soils mapped as silt loam and from typical slopes of the particular area. Where more than one sample was secured from the same prairie, they were obtained at intervals of several rods in order to get an equitable representation of the vegetation.

Series of samples were secured from nearly pure stands of little bluestem (*Andropogon scoparius*), big bluestem (*A. furcatus*), mixed bluestem, blue grama grass (*Bouteloua gracilis*), buffalo grass (*Buchloe dactyloides*), and western wheat grass (*Agropyron smithii*), as well as from numerous mixtures of two or more of these species or other prairie dominants. In addition, a few samples were secured of prairie dropseed (*Sporobolus heterolepis*), slough grass (*Spartina pectinata*), and gama grass (*Tripsacum dactyloides*).

Approximately 200 samples of prairie sod were collected from 24 stations distributed over a region extending 600 miles from east to west. More than 10 tons of soil were removed from prairies of Iowa, Nebraska, Kansas, and Colorado and transported to Lincoln.

The soil was removed in blocks of convenient size (about 8 to 10 inches in width), after all vegetation had been clipped to the surface of the soil, and the bottoms cut away so that they were exactly 4 inches deep. To avoid transporting large quantities of soil great distances, some of the samples from the more distant stations were placed on a tarpaulin and the soil crumbled into fine particles. Most of the underground plant materials were then readily separated from the soil. The remaining soil was thoroughly mixed and half of it discarded. It was again mixed and one-half of the remainder, which contained one-fourth of the remaining fine roots, was transported, with the other underground parts, to Lincoln.

Methods of washing varied somewhat depending upon the amount of clay. A screen 5 feet long and 3 feet wide, with 11 meshes per inch was laid upon a second screen of coarse mesh which was fastened to a wooden frame supported in a horizontal position. About 100 pounds of soil were placed on the screen at one time and sprayed with a gentle stream of water from a hose. By tilting the screen repeatedly the soil was rolled upon it in such a manner that the clay was washed from the soil mass without having to penetrate through it. By continued washing and later by kneading the soil with the hands there was finally left on the screen only the plant parts and a small amount of coarse soil particles. Care was always exercised not to direct the stream of water through a thin layer of soil against the screen, and no roots were lost. During the washing process the larger roots were removed from the soil as they became visible and placed in water in large buckets. To these were added the residue of soil and roots when washing was complete. The water in the buckets was stirred vigorously whereupon the roots floated on the surface and were recovered by pouring the water through a screen of 28 meshes per inch. This process was repeated several times in order to recover all of the roots. It was estimated that less than 1 per cent of the roots was lost, a negligible amount considering the variation in root distribution in the prairie. After the roots and other plant materials were partly dry but not yet brittle, each lot was carefully examined in detail, and any foreign matter, such as lime or iron concretions, fragments of leaves, etc., removed.

The plant materials thus obtained were not entirely 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 the soil was, in the main, similar to that of living materials.

Some doubt was at first experienced as to the treatment of the roots and other underground parts of forbs, which occurred at least in small amount in practically all of the samples. A single woody root of the lead plant (*Amorpha canescens*), for example, bulked large both in volume and dry weight as compared with that of the roots of the grasses. Since the underground parts of the forbs were so irregularly distributed and were so variable in quantity, the error introduced by them in determinations of volume and dry weights was avoided by discarding them from every sample.

After washing, the plant materials were squeezed by hand in order to remove most of the water. They were then spread in a thin layer on a thick absorbent cloth to which they did not cling. This was rolled tightly, the dry cloth absorbing all visible water external to the roots. Volume was then determined. A glass jar, 18 inches high and 4.75 inches in diameter, had attached to it a U-tube of 5 mm. diameter, which served as a siphon. The jar was filled with water and the water then allowed to siphon out to the level of the short end of the tube outside the jar, about 3.5 inches from the top, the long arm extending to the bottom. When rhizomes and attached roots were then submerged, the overflow water was caught in a 500 cc. graduate and the volume of the plant parts was read directly as cubic centimeters of water displaced.

Dry weight was determined after the materials were first air dried, and then oven dried at 100° C until the weight remained constant. When three-fourths of the finer roots were discarded with the soil left in the field, the volume and weight of the remaining lot were each multiplied by four.

RESULTS

Little Bluestem Series.—Previous to the great drought of 1934, *Andropogon scoparius* was one of the principal dominants in both true and mixed upland prairies over the eastern two-thirds of the region described. This species forms a more or less tufted sod of small bunches in the more mesophytic portions of the region, but the bunch habit is pronounced in drier ones. This bunch habit, however, is not so apparent below the surface of the soil as it is above, since the parts underground branch widely and fill most of the space between the plants with a dense network of fine, fibrous roots. Samples were taken where little bluestem alone formed 88 to 98 per cent of the vegetation.

Twenty-two samples were secured in this series: seven from the Anita area, nine from the one about Lincoln, and six from that centering about Nelson, table 1. All samples were

Table 1.—Volume and dry weight of underground parts of little bluestem from 12 stations in true and mixed prairie.

STATION	ANNUAL PRECIPITATION	VOLUME	DRY WEIGHT	SOIL SERIES (SILT LOAM TEXTURE)
	inches	*cc.*	*gm.*	
Corning	33.7	1099	350	Shelby
		1077	295	Shelby
Guthrie Center	31.8	1010	326	Shelby
Anita	31.7	1250	425	Marshall
		1227	410	Marshall
		807	288	Marshall
Nebraska City	31.6	1427	377	Carrington
Average	*32.2*	*1128*	*353*	
Oakland	29.5	852	272	Marshall
Glenwood	30.1	1113	302	Marshall
		918	264	Marshall
Tecumseh	30.8	767	262	Carrington
Lincoln	28.0	1098	332	Lancaster*
		1075	303	Lancaster
		1067	308	Lancaster
		1094	317	Lancaster
Valparaiso	28.7	895	259	Shelby
Average	*29.4*	*988*	*291*	
Carleton	26.9	852	259	Crete
		807	235	Crete
Nelson	26.6	877	260	Crete
		818	250	Crete
Belleville	26.2	918	283	Crete
		910	288	Crete
Average	*26.6*	*864*	*262*	

* Lancaster loam.

taken from soils of uplands. The soil series from which each sample was secured is given in table 1. So far as could be determined from extensive field observations, the soil types encountered had much less influence upon quantity of plant materials than did water content of soil as controlled by precipitation and, to a less degree, by slope exposure. For example, of the three samples from Anita, the one of smallest volume and weight was obtained on a higher slope than those of greater yield. The average yield from these stations of highest precipitation was 1128 cc. of underground materials

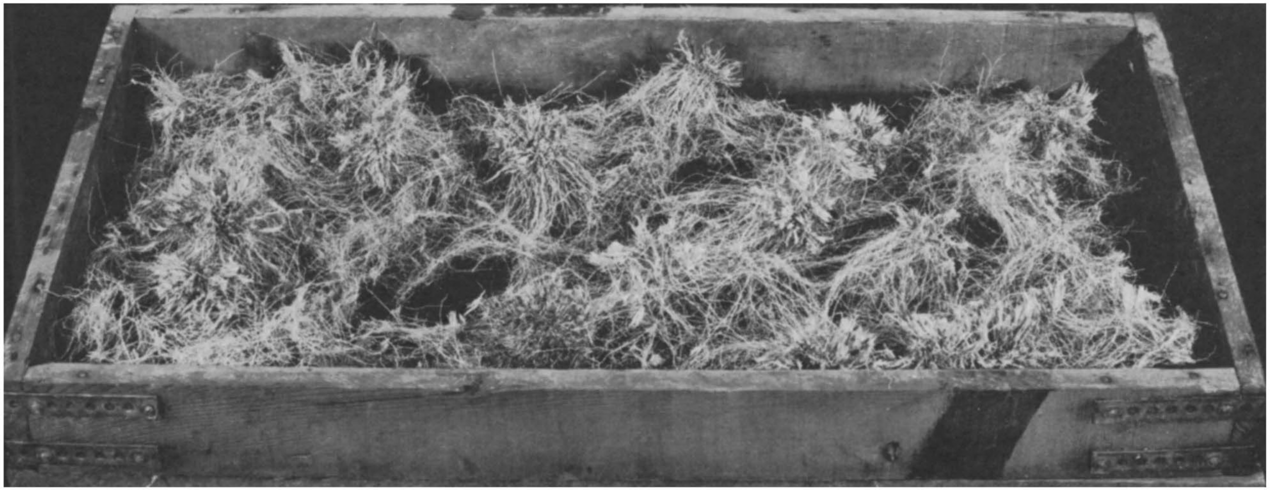

Fig. 23.—One-half square meter of underground parts of little bluestem to a depth of 4 inches. Nelson, Nebraska.

with a dry weight of 353 grams. The large size of the samples contributed towards uniformity in yield (Weaver & Harmon 1935). All of the samples yielded from approximately 300 to more than 400 grams.

Samples from the Lincoln area, with a decrease in precipitation of 2.8 inches, yielded less, without exception, whether measured by volume or dry weight, than the average of all the samples from the more mesophytic area 80 miles eastward. Samples from each of the five stations consistently yielded less material, based on dry weight. The average volume was 988 cc., the weight 291 grams. Thus, with a decrease in mean annual precipitation of 2.8 inches, yields decreased 12.4 per cent in volume and 17.6 per cent in weight.

This decline in quantity of underground plant materials continued westward. No samples from the Nelson area equalled the average of those from about Lincoln in either volume or weight. The samples were well distributed through this semiarid area, fig. 23, and were remarkably uniform in quantity of root materials. The average volume was only 864 cc.; the weight 262 grams. Decrease in precipitation from that of the Lincoln area was 2.8 inches. This was accompanied by a decrease of 12.6 per cent in volume of plant materials and 10 per cent in weight. Compared with precipitation and production in the Anita area, the decreases in the Nelson area were 5.6 inches in precipitation and 23.4 and 25.8 per cent, respectively, in volume and weight.

The data in table 1 have been treated statistically and the correlation between volume and weight found to be very significant. The coefficient of correlation is .870. The difference between the mean of the dry weight of samples from the Anita area and that of samples from either the Lincoln or Nelson area is very significant. The difference between the Lincoln and Nelson areas might occur 15 times out of 100 and hence is not distinguishable in random sampling. This may be due to the relatively small number of samples taken in the Nelson area. Correlation between the average dry weight and the mean annual precipitation at each station was also determined statistically and found to be very significant. The coefficient of correlation was .642.

Big Bluestem Series.—*Andropogon furcatus* is the most important dominant of well-drained lowlands and lower moist slopes. This postclimax tall grass often forms nearly pure stands, and almost always composes at least 85 per cent of the vegetation in its type. It is a sod-forming species with coarse rhizomes, one-eighth inch or more in diameter, and an abundance of coarse, deep roots. Because of its great root depth, 5 to 7 feet, this grass suffered less during the early years of drought than did *A. scoparius,* which usually extends its roots to depths of only about 4 feet.

Table 2.—Volume and dry weight of underground parts of big bluestem from 18 stations in true and mixed prairie.

Station	Annual Precipitation	Volume	Dry Weight	Soil Series (Silt Loam Texture)
	inches	*cc.*	*gm.*	
Creston	33.1	1487	422	Muscatine
Corning	33.7	1334	459	Shelby
Guthrie Center	31.8	1654	553	Shelby
Anita	31.7	1785	607	Carrington
Nebraska City	31.6	1575	486	Carrington
Union	31.2	1408	524	Wabash
		1382	513	Wabash
Average	*32.2*	*1518*	*509*	
Oakland	29.5	1155	401	Marshall
Glenwood	30.1	1588	438	Marshall
		1222	308	Marshall
Lincoln	28.0	1305	440	Wabash
		1085	398	Wabash
		1248	414	Wabash
		1060	422	Wabash
Valparaiso	28.7	1201	355	Shelby
Average	*29.1*	*1233*	*397*	
Carleton	26.9	1102	359	Crete
		1059	356	Crete
Hebron	27.3	1077	323	Nuckolls
Belleville	26.2	1343	406	Crete
Montrose	25.0	1352	392	Hastings
Average	*26.3*	*1187*	*367*	
Phillipsburg	23.3	1047	365	Holdrege
		1190	387	Holdrege
		1049	339	Holdrege
Hays	23.7	1205	361	Hays
Oxford	22.8	1050	345	Holdrege
Average	*23.3*	*1108*	*359*	
Colorado Springs	14.5	1111	343	Unclassified
		1029	317	
Average	*14.5*	*1070*	*330*	

Twenty-seven samples were secured from 18 prairies, including two new stations, Creston and Union, in the Anita area, and two, Montrose and Hebron, in the Nelson group. Samples were obtained from three stations in the Phillipsburg area and, in addition, two samples were taken from one prairie (Colorado Springs) in the Burlington group, table 2.

Seven samples from the six stations in the Anita area ranged in dry weight from 422 to 607 grams. The greatest yield was from the lower slope of the Anita prairie and not from the level lowland at Union. Moreover, the sample of least weight was taken from Creston, a station with greater mean annual precipitation. The average yield from this area was high, 1518 cc. by volume and by weight 509 grams.

Average yields from each station in the Lincoln group (except from Glenwood, which has the highest precipitation) were smaller both in volume and weight than those from any prairie in the preceding group of greater precipitation. Average yield of the eight samples from the four stations was 1233 cc. and 397 grams. Thus, a decrease of 18.8 per cent in volume and 22 per cent in weight seems directly correlated with a decrease in precipitation of 3.1 inches, from 32.2 to 29.1 inches.

Decrease in quantity of underground parts in the Nelson area was much less marked. The five samples from the widely separated stations, however, were remarkably uniform, dry weight varying from 323 to 406 grams. The 2.8 inches decrease in precipitation—from 29.1 to 26.3 inches—resulted in a decreased volume of only 3.7 per cent and loss in weight of 7.6 per cent.

Samples from the more arid Phillipsburg area were likewise uniform in amount. Among five lots of material from the three stations the dry weight ranged from 345 to 387 grams. The average volume of 1108 cc. gave a decrease of 6.7 per cent from the preceding area and the average weight (359 grams) was 2.2 per cent less. This decline was somewhat less than was anticipated since the precipitation decreased 3.0 inches, *i.e.*, from 26.3 to 23.3. This may be due to the fact that the more torrential nature of the rainfall westward resulted in greater runoff. This would, of course, increase water content on the lower slopes where big bluestem thrives. This condition has been clearly shown by extensive soil sampling by Albertson (1937) at Hays, Kansas. It is also borne out by the fact that samples from Colorado Springs, where rainfall is only 14.5 inches annually and big bluestem areas are rare, yielded only 3.4 per cent less by volume and 8.1 per cent less by weight than those in the Phillipsburg area.

Statistical treatment shows that the correlation between volume and weight is again very significant, the coefficient of correlation being .874. The mean of the dry weights of samples

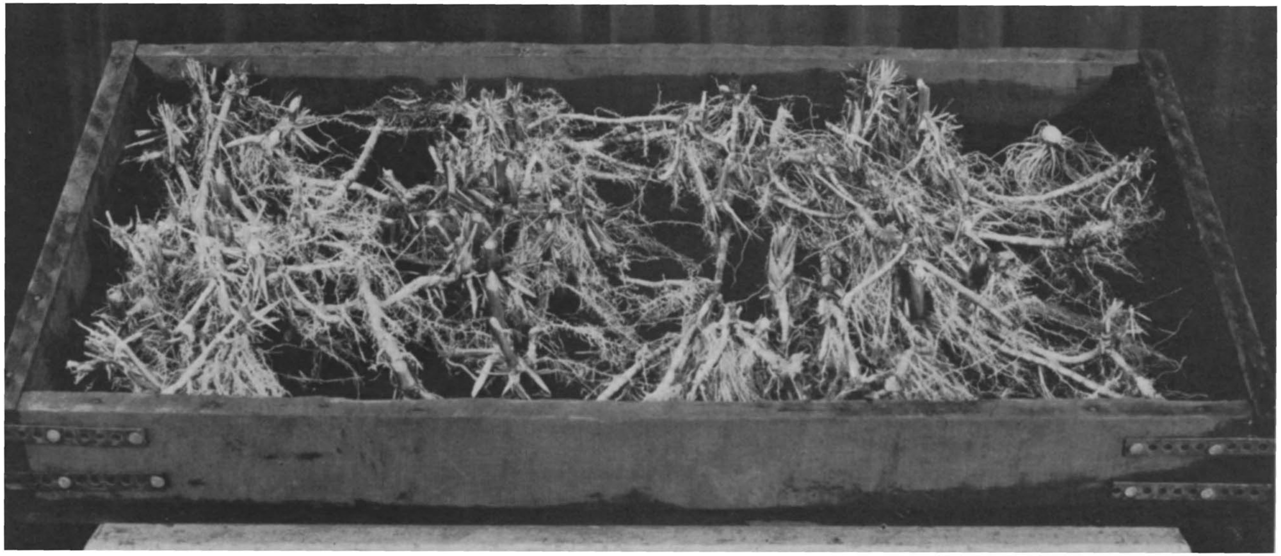

Fig. 24.—Roots and rhizomes of slough grass in one-half square meter sample of soil from Union, Nebraska.

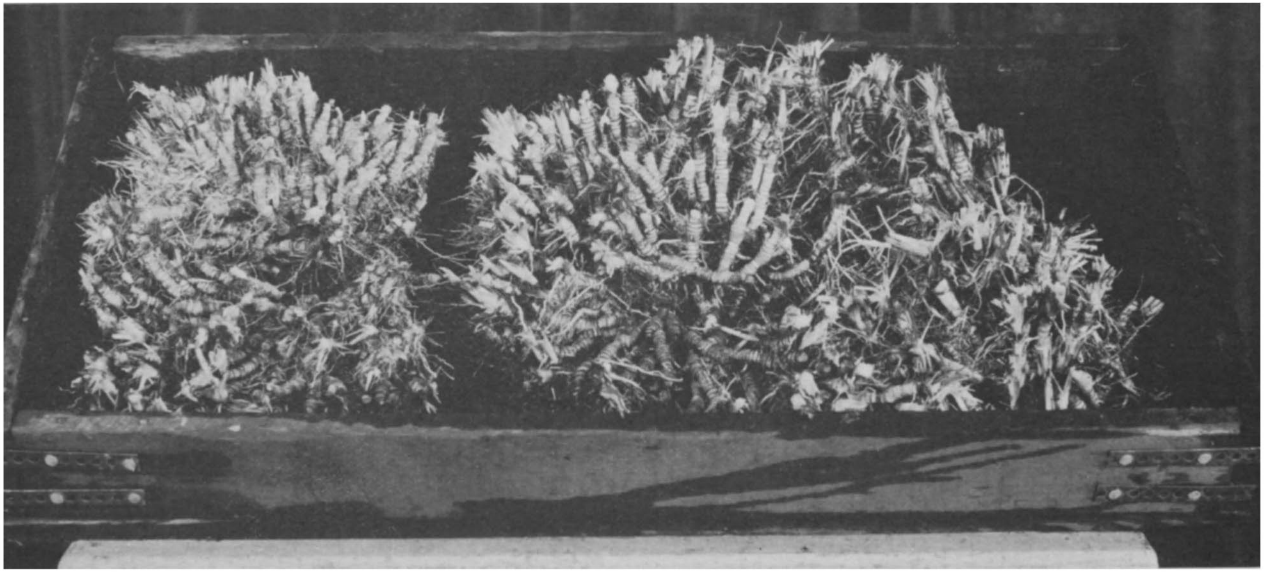

Fig. 25.—Dense masses of underground parts of eastern gama grass in one-half square meter sample of soil from Union, Nebraska.

from the Anita group is significantly different from that of samples from each of the other groups, and the mean of the Lincoln group is significantly different from the mean of the combination of the three more xerophytic groups—Nelson, Phillipsburg, and Colorado Springs. The correlation between the average dry weight and the mean annual precipitation at each station was found to be very significant. The coefficient of correlation was .673.

Slough Grass and Gama Grass.—Slough grass (*Spartina pectinata*) occurs in pure stands only in soils that are too wet and consequently too poorly aerated for big bluestem. The coarse stems of this sod-forming grass usually attain a height of 6 to 10 feet. The rhizomes are 5 to 10 mm. in diameter and 6 to more than 12 inches long. These and the coarse stem bases and thick roots form an open network and bulk large in both volume and weight. Four samples from poorly drained lowlands at Creston, Nebraska City, and Union averaged 2048 cc. in volume and 680 grams in dry weight. The weights varied from 607 to 782 grams, fig. 24. Yield of four samples at Lincoln, from soils of varying water content, ranged from 437 to 864 grams. The average yield was considerably less than eastward, 1921 cc. and 620 grams. All of these samples were from Wabash silt loam.

Eastern gama grass (*Tripsacum dactyloides*) was found in pure stands only at Union, where it grew in a habitat similar to that of slough grass. It is of similar growth habit but even coarser, the plants tending to grow in large clumps. Underground parts averaged 4167 cc. in volume and 1610 grams in weight. The yield was twice that of slough grass and three times as great as big bluestem taken from the same prairie, fig. 25.

Although these samplings furnish no regional data on underground plant materials, they are of scientific interest and a knowledge of them is of much practical importance in connection with resodding wet ravines, spillways, etc. The natural habitat of these plants is areas that are frequently subjected to flooding and sometimes to submergence under rushing bodies of water.

Mixed Bluestem Series.—Since the distribution of little bluestem is predominantly on uplands and that of big bluestem mostly on lowlands, there is consequently a transition zone which is shared by the two species in a fairly uniform mixture. Samples of such mixtures were collected from three areas, eight from Anita, five from Lincoln, and three from Nelson.

Underground materials of samples from the eastern area varied in volume from 915 to 1467 cc. and in weight from 320 to 494 grams, the prairie at Anita furnishing both the largest and the smallest samples. The average volume of materials of all samples from the Anita area was 1230 cc. and the average weight 383 grams, table 3.

Table 3.—Volume and dry weight of underground parts of mixed bluestems from 12 stations in true and mixed prairie.

STATION	ANNUAL PRECIPITATION	VOLUME	DRY WEIGHT	SOIL SERIES (SILT LOAM TEXTURE)
	inches	*cc.*	*gm.*	
Creston	33.1	1290	385	Muscatine
Corning	33.7	1467	396	Shelby
		1399	403	Shelby
Guthrie Center	31.8	1096	367	Shelby
Anita	31.7	1249	494	Marshall
		1128	335	Marshall
		915	320	Marshall
Nebraska City	31.6	1300	361	Carrington
Average	*32.4*	*1230*	*383*	
Oakland	29.5	950	301	Marshall
Tecumseh	30.8	1055	323	Carrington
Lincoln	28.0	1064	353	Carrington
		1013	337	Carrington
Valparaiso	28.7	952	270	Shelby
Average	*29.2*	*1007*	*317*	
Carleton	26.9	927	295	Crete
Hebron	27.3	873	275	Nuckolls
Belleville	26.2	935	284	Crete
Average	*26.8*	*912*	*285*	

Of the five samples from the Lincoln area, two yielded less in weight than the smallest from the preceding one, and all were less than the average from the Anita area in both volume and weight. Average volume for the Lincoln area was 1007 cc. and average weight 317 grams. This was a decrease of 18.1 per cent in volume and 17.2 per cent in dry weight from that of the more mesophytic prairies; the corresponding decrease in precipitation was 3.2 inches.

Yields from stations in the Nelson area were all lower by volume than the least from the Lincoln territory. This is true also in regard to weight if the very light sample from Valparaiso is excluded. The average volume was 912 cc. and the average weight 285 grams. The average volume for this area is 9.4 per cent less, and the average weight decreased 10.1 per cent with a corresponding decrease of 2.4 inches in mean annual precipitation. These yields of the mixed bluestems were intermediate between those of pure stands of big and little bluestem.

Table 4.—Volume and dry weight of underground parts of blue grama grass and buffalo grass from 10 stations in true and mixed prairie.

STATION	ANNUAL PRECIPI-TATION	BLUE GRAMA Vol.	BLUE GRAMA Wt.	BUFFALO GRASS Vol.	BUFFALO GRASS Wt.	SOIL SERIES (SILT LOAM TEXTURE)
	inches	*cc.*	*gm.*	*cc.*	*gm.*	
Lincoln	28.0	645*	186	975*	280†	Lancaster
		1049	255	850*	246†	Lancaster
		1158	278	1020*	278†	Lancaster
		1243	296			Lancaster
		1175	264			Lancaster
Average	*28.0*	*1054*	*256*	*948*	*268*	
Nelson	26.6	1350	368			Crete
Belleville	26.2			898*	280	Crete
				839*	216	Crete
Montrose	25.0	898	231	865	239	Hastings
		998	243			Hastings
Average	*25.9*	*1082*	*280*	*867*	*245*	
Phillipsburg	23.3	1379	361	1196	281	Holdrege
		808	211	1013	259	Holdrege
		683	205	598	167	Holdrege
Oxford	22.8	665	192	674	186	Holdrege
Average	*23.0*	*884*	*242*	*870*	*223*	
Colby	18.4	1128	316	1015	333	Keith
				1053	373	Keith
Burlington	17.4	1229	319	872	230	Keith
		1180	297	802	222	Keith
		980	248	517*	159	Keith
		711*	206			Keith
Wray	19.3	948	282	880	255	Rosebud
Colorado Springs	14.5	671*	156			Unclassified
		471*	121			
Average	*17.4*	*915*	*243*	*856*	*262*	

* Samples from grazed pastures.
† These three samples are from Wabash silt loam.

The correlation between volume and weight in table 3 is again very significant, the coefficient of correlation being .699. The mean of the dry weights of samples from the Anita group is significantly different from that of samples from either the Lincoln or Nelson group. Moreover, correlation between the average dry weight and the mean annual precipitation at each station was found to be very significant, the coefficient of correlation being .827.

Blue Grama Grass and Buffalo Grass Series.—The short grasses (*Bouteloua gracilis* and *Buchloe dactyloides*) are more or less continuously distributed in the mixed prairie, *i.e.*, in the Phillipsburg area and westward, as a lower story to the mid grasses. At most of the stations in the Burlington area, however, the mid-grass layer has been removed by the long-time impact of grazing, and usually only short grasses remain in this disclimax. In the Anita area short grasses do not occur. Westward in true prairie they form small preclimaxes on the driest hilltops and ridges and have often taken complete possession of pastures. Blue grama and buffalo grass are nearly ecological equivalents, the former being somewhat more xerophytic. Usually they are intimately intermixed in an extensive grouping or faciation in the Kansas-Colorado portion of the mixed prairie, but also considerable areas of pure or nearly pure stands occur.

Although these dense, sod-forming grasses are of relatively limited growth above ground—usually 3 to 6 inches—yet their root systems are very dense. They have played a leading role throughout the long processes of soil formation in giving the Dark Brown and Brown soils their remarkably dark color, considering the aridity of the climate.

Whenever possible samples were secured from apparently undisturbed prairies or from ranges that had been protected from grazing over a period of years. When such areas were not available, samples from moderately grazed ranges were selected. It was found that grazing which did not impair the density of the vegetative cover had little or no injurious effect on the root system. Samples from pastures known to have been recently grazed are designated in table 4 by an asterisk after the volume.

The samples of blue grama grass taken from the Lincoln station gave an average volume of 1054 cc. and dry weight of 256 grams. The yields in the Nelson area (1082 cc. and 280 grams) were slightly higher because of the sample of unusually high yield from one station. They decreased to 884 cc. and 242 grams, respectively, in the Phillipsburg area, despite the wealth of roots in one sample from Phillipsburg, fig. 26. Average yields (915 cc. and 243 grams) were slightly greater in the Burlington area but, like the preceding, were somewhat less than from the stations eastward. Four of the largest samples were obtained from three separate stations in the most westerly areas, and four samples with the smallest yields were taken from prairies which had been grazed.

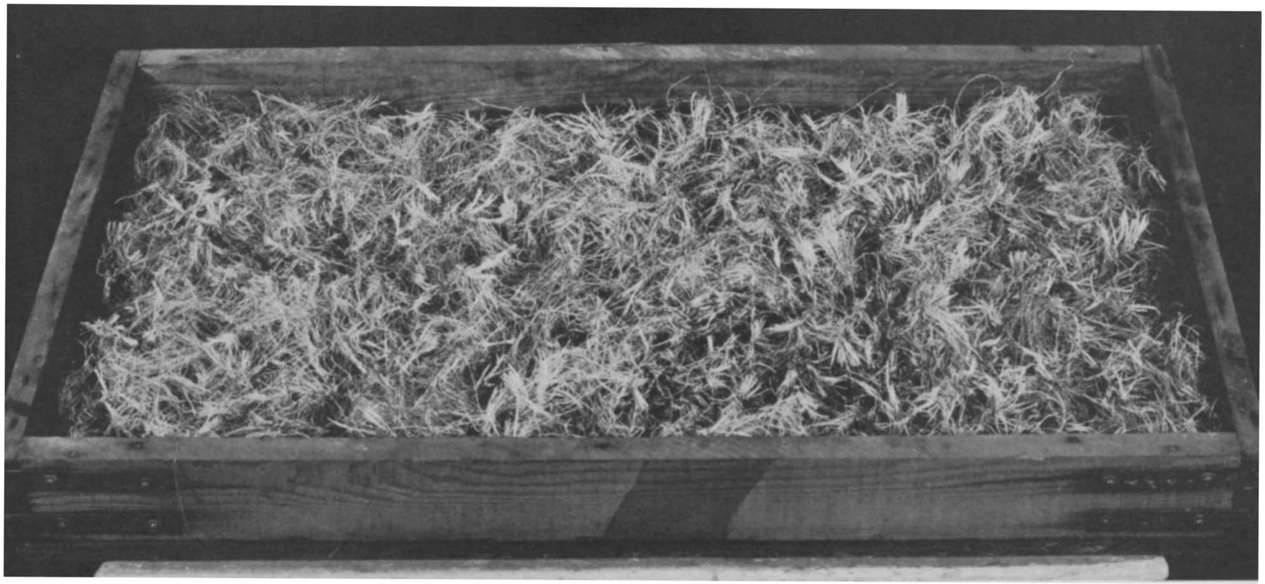

Fig. 26.—Underground parts of a pure stand of grama grass in a sample from Phillipsburg, Kansas.

Yields of buffalo grass were somewhat more uniform. Average volumes for the several areas were 948, 867, 870, and 856 cc.; the dry weights were 268, 245, 223, and 262 grams. The third sample from Phillipsburg (167 grams) was from a young stand, while a similar sample of light weight from Burlington resulted from overgrazing.

No consistent differences in dry weights of underground parts of the two grasses in the several areas were found. Volumes of the buffalo grass were uniformly somewhat lower than those of grama grass.

Correlation between volume and weight of both *Bouteloua gracilis* and *Buchloe dactyloides* separately treated statistically is very significant. The coefficients of correlation are .954 and .846, respectively. No significant difference, however, was found in the means of weight or volume for either species.

Prairie Dropseed and Mixed Grasses.—A series of 14 samples, mostly of various upland grass mixtures, was secured from the five areas. Two of nearly pure prairie dropseed (*Sporobolus heterolepis*) were taken at Creston and Corning and four from Lincoln. The former averaged 1510 cc. in volume and in weight 417 grams. Both volume and dry weight of the Lincoln samples were much less, 1050 cc. and 343 grams, respectively.

Two samples of an approximately equal mixture of *Agropyron smithii* and *Bouteloua gracilis* from Carleton averaged 326 grams in weight and 1224 cc. in volume. Two samples of mixed *Andropogon furcatus, Bouteloua gracilis,* and *Buchloe dactyloides* were taken at Phillipsburg (average volume 761 cc. and weight 215 grams) and three of *Andropogon scoparius* and *Buchloe dactyloides* from Hays (1018 cc. and 280 grams). Finally, a single sample of *Andropogon scoparius* and *Bouteloua gracilis* from Colorado Springs yielded 722 cc. and 212 grams.

Summarizing, the average dry weights of the materials from these miscellaneous upland samples, from the most mesophytic to the driest area, were 417, 343, 326, 254, and 212 grams, respectively.

Summary of Upland Grasses.—Upland grasses depend entirely for their water supply upon precipitation, although the water content of soil in habitats populated by slough grass, eastern gama grass, and even big bluestem (especially westward) is augmented either by a high water table or by collected runoff. Hence, a comparison of the yields of all samples from upland in the several areas in connection with precipitation is of especial interest. This includes 82 samples of little bluestem, mixed little and big bluestem, short grasses (except buffalo grass from low ground at Lincoln), prairie dropseed, and mixed grasses, table 5.

Table 5.—Average volume and dry weight of underground parts of all upland grasses from the five areas.

AREA	AVERAGE PRECIPITATION	NO. SAMPLES	VOLUME		DRY WEIGHT	
	inches		*cc.*	%	*gm.*	%
Anita	32.2	17	1221	100	375	100
Lincoln	29.1	23	1027	84	301	80
Nelson	26.2	14	963	79	272	73
Phillipsburg	23.3	13	892	73	241	64
Burlington	17.4	15	879	72	249	66

Table 5 reveals some significant facts. There was a decrease of 16 per cent in volume and 20 per cent in dry weight from the Anita to the Lincoln area. A further but smaller decrease of 5 per cent in volume and 7 per cent in weight occurred in the Nelson area. This was followed by still further decreases (6 to 7 and 7 to 9 per cent, respectively) in the more arid western areas. Practically no differences, either in volume or weight, occurred, however, between the groups of samples from the two mixed-prairie areas.

A statistical analysis of the data presented in table 5 shows that all correlations between volume and weight for the several areas are very significant, the coefficients of correlation in sequence of the station groups being .812, .695, .847, .958, and .907, respectively. The mean of the dry weights from the Anita group is very significantly different from that of each of the other groups. The mean of the Lincoln and Nelson groups combined and that of the Phillipsburg and Burlington groups combined are also very significantly different.

In considering causes for these differences, it should be noted that change in type of vegetation had some effect upon the weight of underground parts. Yield of little bluestem, although 12 per cent greater in weight than that of the short grasses in the Lincoln area, was the same as that of blue grama and buffalo grass in the Nelson territory. No samples of this grass alone were taken westward. Hence, the decrease in underground plant material in the Phillipsburg and Burlington areas is accompanied by the disappearance of little bluestem. Once the short grasses gain control of the mixed prairie disclimax, no further consistent decreases with reduced rainfall were found. This is probably due to selecting better prairies than average in the area of lower precipitation.

Fig. 27 (upper).—Portion of a bluestem prairie at Carleton, Nebraska, where the former grasses have been almost completely replaced since the great drought by western wheat grass.

Fig. 28 (lower).—Area in which big bluestem has died of drought being invaded by western wheat grass. The lines of leafy stems indicate the position of the new rhizomes in the soil.

The general decrease westward from Nelson with increasing aridity in climate is further supported by a series of 13 additional samples taken at Valentine, in north-central Nebraska, almost due north of Colby, Kansas, and at Lusk, Wyoming. The precipitation at Valentine, 18.4 inches, is in close agreement with that of the most eastern station of the Burlington area, while at Lusk it is 14.2 inches, or approximately that of the most westerly one, Colorado Springs. The soils, however, were somewhat more sandy. These mixed-prairie samples were of little bluestem and short grasses, or of mixed needle grass (*Stipa comata*), wheat grass, and short grasses. The average volume was 653 cc. and dry weight 188 grams compared with similar average values of 963 cc. and 272 grams from the Nelson station on the western edge of true prairie.

Western Wheat Grass.—A series of samples of western wheat grass (*Agropyron smithii*) was secured from all but the most eastern area, where none occurred. This grass is an important dominant over a wide territory in both true and mixed prairie, especially northward and westward, where it forms dense stands, often appearing in midsummer like fields of thinly sown grain. Before the great drought, it was poorly represented in any of the prairies from which other samples were secured. The fact that it became very abundant in the Lincoln and Nelson areas after the great drought, beginning in 1934, is worthy of consideration, fig. 27.

The great losses sustained by the bluestems, Kentucky bluegrass, and various other prairie species and the bare areas thus produced made possible the remarkable spread of wheat grass. In fact, the increase in abundance of this grass was one of the most striking phenomena of the drought. Extensive earlier studies in the prairies of eastern Nebraska, Kansas, and South Dakota by Weaver & Fitzpatrick (1934) have shown that wheat grass constituted scarcely any part of this grassland. It occurred along roadways, occupied the compacted soils along trails or paths through the prairie, and was found in abundance locally where very wet soils in spring made conditions unfavorable to growth for the usual prairie grasses. Occasionally a few stems were found about such disturbances as gopher mounds, and plants very thinly scattered throughout bore seed occasionally during dry years. In native pastures, centers of infestation often occurred on knolls or about gateways where cattle or horses congregated and trampled the soil while stamping to free themselves from flies.

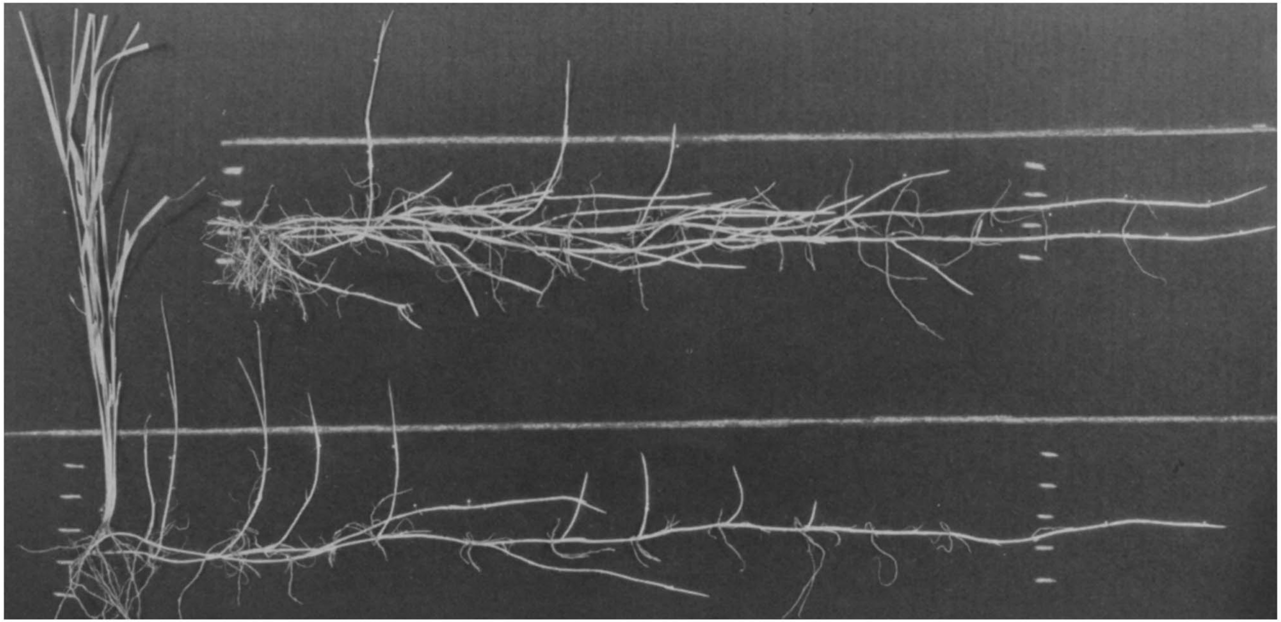

Fig. 29.—Rhizomes of western wheat grass, showing development of new stems and roots. Horizontal lines indicate surface of the soil; the depth is shown in inches.

Immediately after 1934, wheat grass became increasingly abundant in both pastures and prairies. It has continued its spread over all types of terrain until today it is often the most important species in many Nebraska prairies and pastures to within 40 miles of the Missouri river. In addition to being a good seed-producer, large, more or less circular areas where other species are practically absent indicate the excellent and rapid method of migrating by long, much branched rhizomes, figs. 28 and 29. Since the shallow rootstocks are from .5 to more than 3 feet long, much branched, and grow very rapidly, the result is great increase in territory. Moreover, the vitality of the rhizomes and their resistance to drought seem remarkably great. During unfavorable years they may give rise to few stems which grow poorly and fail to flower and hence are apt to be passed unnoticed. But once liberated from competing species (as by drought) great fields of stems—often more than 1000 per square meter—spring up, reach a height of 2.5 to 3.5 feet, and flower so abundantly that the whole appearance of the prairie is changed.

Long narrow belts of wheat grass around the brows of hills indicate where early drought was most severe. Often a whole hillside or perhaps almost the entire prairie is covered with a pure stand of this grass, and many lowlands, once occupied by big bluestem, are a continuous sea of undulating wheat grass. Examination within the soil confirms the replacement of one kind of grass by another, for here are found the dead remains of big bluestem threaded with the long, shining, white rootstocks of the invader, fig. 30. Wheat grass is also an early invader, frequently the first, into soils that have drifted over other vegetation causing its death. It has always been abundant, usually with short grasses as an understory, in the most westerly areas of this study.

Samples of local pure stands were available only in disturbed places in 1935-36, mostly along roadsides. The considerable study given this species since the drought shows clearly that density of underground parts is affected both by the length of time of occupancy of an area, and the nature of the bared soil into which it spreads, especially its permeability to water. Where the subsoil is moist, the tough, white roots, arising from both the stem bases and rhizomes, penetrate to depths of 7 to 9 feet (Weaver 1920). Where deep penetration is prevented by dry soil, roots in the surface layers are much more numerous and more branched. The rhizomes are placed shal-

Fig. 30.—Invasion of western wheat grass into big bluestem sod. The soil was washed away from this one-half square meter area, revealing the dead underground parts of the former dominant (black) and the shining white rhizomes of wheat grass. Belleville, Kansas.

lowly, and were all included in the samples. Where the plants grow thickly, as in a well developed sod, roots and rhizomes form a continuous tangled network.

Because of the variable factors due to soil disturbance, degree and time of occupation, etc., no such correlation between precipitation and yield of underground parts of this species was found as with most of the preceding grasses and grass mixtures, table 6.

Table 6.—Volume and dry weight of underground parts of western wheat grass from 9 stations in true and mixed prairie.

STATION	ANNUAL PRECIPITATION	VOLUME	DRY WEIGHT	SOIL SERIES (SILT LOAM TEXTURE)
	inches	*cc.*	*gm.*	
Tecumseh	30.8	800	234	Carrington
Lincoln	28.0	1188	214	Carrington
		585	135	Carrington
		428	109	Carrington
		1038	288	Carrington
Average	*29.4*	*880*	*196*	
Belleville	26.2	1265	273	Crete
Carleton	26.9	1131	265	Crete
Average	*26.5*	*1198*	*269*	
Phillipsburg	23.3	248	75	Holdrege
Oxford	22.8	430	127	Holdrege
Average	*23.0*	*339*	*101*	
Colby	18.4	372	88	Keith
Burlington	17.4	729	190	Keith
		1154	332	Keith
		784	257	Keith
Wray	19.3	1042	291	Rosebud
Average	*17.4*	*816*	*232*	

The small yields of the samples from Phillipsburg and Colby are definitely known to be due to recent invasion, while the two heavy samples from Lincoln and the largest one from Burlington were secured from long-established stands. That the heavy sample from Belleville was of recent origin, but on favorable soil, was clearly shown by the great masses of dead but undecayed roots and rhizomes of big bluestem intermixed with it.

Non-grasses or Forbs.—There has been a marked decrease during the drought in nearly all legumes, composites, and other non-grassy species or forbs of the prairie. A few have increased enormously. Chief among these are many-flowered aster (*Aster multiflorus*), daisy fleabane (*Erigeron ramosus*), and smooth goldenrod (*Solidago glaberrima*). With the death of the prairie vegetation in thousands of local areas, they invaded the bared ground, either by seeding thickly (notably daisy fleabane) or by invasion by rhizomes. These almost worthless weeds became so extremely abundant as to make valueless many of the prairies or large portions of them for the production of hay. In fact, during 1935-36 it appeared that these forbs, especially the aster, would ruin the prairie. As a result, considerable native sod was broken because of the seriousness of this pest.

Consequently, it seemed pertinent to this study to determine the relative amounts of underground materials of these widely spread invaders and to compare them with those produced by the native grasses. Samples of each species were taken at Lincoln during 1938.

The aster was found in 75 to 85 per cent of the prairies of eastern Nebraska and Kansas before the great drought, and although quite abundant it usually occurred as isolated individuals 12 to 20 inches tall or in groups of only a few stems. The root system is fibrous and although it penetrates deeply (7 to 8 feet) numerous finer and shorter roots absorb mostly or entirely in the surface foot, although the bulk of the supply of water and nutrients is probably obtained from the deeper soil.

A dense, pure growth of aster, consisting of 156 separate stems about 24 inches high, completely covered the half square meter examined, fig. 31. Well-branched rhizomes were abundant and roots were exceedingly numerous but only 1 to 2 mm. in diameter. They formed a network in the soil but one far less complete than that of the grasses. Volume (178 cc.) and dry weight (47 grams), however, were only a small part of that of the underground parts of the grasses which they had replaced.

The enormous increase of daisy fleabane (*Erigeron ramosus*) in most of the true prairie areas was one of the outstanding features of the drought period. It is an annual or short-lived biennial, the rosettes of the first summer producing flower stalks the following growing season. It is a species which had a very wide and remarkably uniform distribution before the drought, its abundance varying greatly from year to year. The plants were scattered more or less individually, although often thickly, among the grasses but seemed to have little harmful effect upon them.

Fig. 31 (upper).—Drought-bared area in true prairie at Lincoln, Nebraska, covered with many-flowered aster, *Aster multiflorus.*

Fig. 32 (lower).—Increase of daisy fleabane, *Erigeron ramosus,* in lowland prairie following the great drought.

When bare ground appeared, it was soon covered by this weed. By midsummer daisy fleabane offered a profusion of blossoms which at a distance appeared as newly fallen snow. The dried stems greatly depreciate the value of prairie hay, fig. 32. A sample was taken in a mature, dense stand which was about 32 inches tall. There were no rhizomes and the poorly branched taproots were only 3 to 5 mm. in greatest diameter. Root volume was but 38 cc. and dry weight 8 grams.

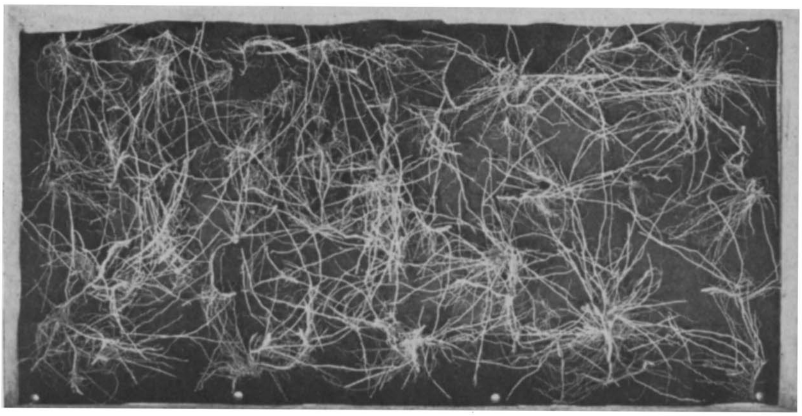

Fig. 33.—Roots and rhizomes of many-flowered aster in the surface 4 inches of soil. The sample is one-half square meter in area.

The smooth goldenrod has increased greatly in many prairies as well as in pastures. Although partially obscured by unmown prairie grasses, its abundance is revealed especially in July with the appearance of the yellow flowers. Under ordinary predrought conditions the plants were generally scattered, arising only at rather wide intervals from the rhizomes. But in drought-bared prairies they became densely aggregated.

The sample contained 125 stems which averaged 2 feet high. The rhizomes were 2 to 14 inches long and 2 to 6 mm. in diameter and formed a continuous network similar to that of aster. These coarser underground parts bulked larger (240 cc.) and weighed more (60 grams) than those of the aster but much less than little bluestem or other grasses.

With the death by drought of the little bluestem and its replacement by aster, daisy fleabane, and goldenrod, the soil lost approximately 90 per cent of living underground plant materials upon the basis of either volume or dry weight, fig. 33.

DISCUSSION

A three-year study (1920-22) of the native plant production and the controlling edaphic and aerial factors has been made at stations in each of three of the areas under consideration, *viz.*: Lincoln, Phillipsburg, and Burlington (Weaver 1924). The experimental areas were on silt loam soils of high fertility and of similar high water-holding capacity.

At Lincoln, a sufficient amount of water to promote good growth was available at all depths and at all times; with few exceptions there was at least 5 to 10 per cent available moisture above the hygroscopic coefficient. Soil moisture deficiencies at Phillipsburg occurred in July of two years and in August of each year; during two seasons no available water was present to a depth of 4 feet in late summer. Although the surface soils at Burlington were usually moist in spring and early summer, available water in the third and fourth foot was practically always exhausted by midsummer and often there was none even in spring. Deficiencies or complete exhaustion of the available supply in the first and second foot occurred regularly in June and only occasionally was the supply temporarily replenished during summer.

The value of water content to vegetation is not determined entirely by its quantity, but largely also by its rate of loss through the plants and by surface evaporation. These, in turn, are greatly affected by the aerial factors of humidity and evaporation. The average day humidity was, with few exceptions, 10 to 15 per cent, and often 25 to 30 per cent, higher at Lincoln than at Burlington; that at Phillipsburg was usually intermediate. Evaporation rates at the three stations, as measured by porous cup atmometers, show clearly the increasing stress as regards water relations under which the vegetation develops westward. At Lincoln, the average daily evaporation by weeks during the three summer months varied from 8 to 33 cc., at Phillipsburg from 8 to 43, and at Burlington from 15 to 63 cc. These stations were similar in temperature efficiency. It was early determined in the investigation cited "that water relations of soil and air were controlling, other factors being merely contributory" (Weaver 1924; Clements & Weaver 1924).

Yields of mid grasses, mixed mid and short grasses, and of short grasses were determined by means of scores of meter quadrats during the three-year period. In every case the yield of a certain grass or grass mixture was found to decrease from true prairie through mixed prairie to the short-grass plains disclimax directly in proportion to available water content of soil and inversely proportional to the evaporating power of the air. Moreover, the averages for each year at the several stations showed a graduated series, plant production decreasing with decrease in efficient rainfall. The average yields for the three years in grams per square meter are given in table 7.

Table 7.—Yields in grams (dry weight) of grasses from clipped quadrats in several grassland climates.

YEAR	LINCOLN	PHILLIPSBURG	BURLINGTON	RATIO
1920	458	378	183	1:.83:.40
1921	603	402	353	1:.67:.59
1922	442	311	224	1:.70:.50
Average	*501*	*364*	*253*	*1:.73:.50*

That the vegetation in the Anita area is taller and the yields somewhat greater than those from Lincoln has been repeatedly observed and also confirmed by numerous measurements. Likewise, height of vegetation and yields from the Nelson area averaged less than those from Lincoln. Yields of hay from uplands varied from 1 to 1.5 tons per acre in Iowa to .5 to 1 ton in the Nelson area. Conditions more favorable to growth eastward in the true prairie are also expressed in numerous other ways. Tall grasses, especially big bluestem and tall panic grass, extend their dominance farther up the slopes and there is a marked tendency towards the greater partial replacement of little bluestem. The more favorable growth is also shown in the greater density of stems within the sod or bunch. Clumps of little bluestem in the drier prairies westward are frequently only one-third to one-half occupied by green stems; in the best situations eastward, 75 to 90 per cent of the area of the clump is completely filled with stems. Still another indicator of relative drought is shown by the much greater tendency toward production of flower stalks eastward where they are well developed and abundant on even the driest uplands. This is in striking contrast to their small number and dwarfed appearance in the western true prairie except in the wettest years. Certain forbs characteristic of areas of greater rainfall are found only eastward, and certain other species occurring on the uplands of western Iowa are confined to lower ground in Nebraska and Kansas (Weaver & Fitzpatrick 1934).

Expressed in tons per acre, decreases in underground plant materials with decrease in precipitation are very great. Little bluestem yielded 3.15, 2.60, and 2.34 tons in the Anita, Lincoln, and Phillipsburg areas, respectively. The underground yield of big bluestem decreased from 4.54 tons per acre at Anita to 3.54 at Lincoln, and to 3.17 in the areas westward. Yields of mixed bluestems from Anita through Lincoln to the Nelson area were 3.42, 2.83, and 2.54 tons per acre, respectively. Yields of short grasses were less but showed no consistent variation with precipitation. Yields at Lincoln were 2.32 tons, at Nelson 2.35, and at Phillipsburg 2.08 tons. Underground yields of upland grasses, involving 82 samples, are probably the best index of the relationship between precipitation and underground plant production. From east to west they were 3.35, 2.69, 2.43, and 2.19 tons per acre, respectively, the last figure being the average for the two western areas.

Weaver & Harmon (1935) have devised a method of securing one-half square meter samples of prairie sod intact to a depth of 4 inches, placing them under uniform conditions of slope, force and amount of water used, etc., and thus evaluating the effect of the underground plant parts in resisting soil erosion. They have shown that there is no direct relation between the weight of underground parts of different types of vegetation and their ability to hold the soil from washing away. Bluegrass sod, for example, with a volume of 940 cc. and a weight of 282 grams, was just as resistant to water erosion as that of big bluestem with a volume of 1535 cc. and a dry weight of 544 grams. They have also shown quite as clearly that reduced amounts of underground parts of the same species, resulting from close grazing, greatly increased the ease of soil erosion.

In the present study, 28 samples were taken as solid blocks by this method. Nineteen of these were from upland, 14 being bluestems. When time of erosion of all these samples was averaged by areas, it was found that the five from Anita required 92 minutes, the seven from Lincoln 80, and the seven from the Nelson area only 62 minutes. Although the number of samples is too limited for reliable conclusions, in general the trend seems to indicate that the time of erosion decreases from east to west as does also the amount of living plant materials in the soil or above its surface.

ORGANIC MATTER AND NITROGEN

Plant materials growing in and on the soil produce the organic matter. Humus consists not only of substances undergoing decay and of constituents resistant to further decomposition but also of complex compounds resulting from decomposition and of various substances built up by plant and animal microorganisms in the soil. The virgin grassland soils are rich in nitrogen and organic matter. Unlike forest soils, where most of the organic matter is found in the upper portion, in grassland soils this enriching material is distributed from the

Table 8.—Percentage of organic matter and nitrogen in grassland soils to a depth of four inches at the several stations in each area.

STATION	ANNUAL PRECIPITATION	MEAN ANNUAL TEMP.	ORGANIC MATTER	NITROGEN	SOIL SERIES (SILT LOAM TEXTURE)
	inches	*° F*	*per cent*	*per cent*	
Anita	31.7	48.4	7.98	.329	Carrington
Guthrie Center	31.8	48.1	7.36	.324	Shelby
Corning	33.7	49.3	6.64	.288	Shelby
Creston	33.1	48.7	6.56	.292	Muscatine
Average	*32.6*	*48.6*	*7.14*	*.308*	
Lincoln	28.0	50.8	6.25	.260	Carrington
Tecumseh	30.8	51.9	6.07	.278	Carrington
Oakland	29.5	49.0	6.06	.261	Marshall
Glenwood	30.1	50.2	5.92	.285	Marshall
Average	*29.6*	*50.5*	*6.08*	*.271*	
Belleville	26.2	53.0	5.68	.264	Crete
Montrose	25.0	52.6	5.43	.252	Hastings
Hebron	27.3	51.6	5.34	.230	Nuckolls
Nelson	26.6	52.8	5.18	.244	Crete
Average	*26.3*	*52.5*	*5.41*	*.248*	
Phillipsburg	23.3	53.7	4.56	.206	Holdrege
Hays	23.7	53.9	4.52	.217	Hays
Oxford	22.8	52.2	4.18	.178	Holdrege
Holdrege	24.0	51.7	4.43	.190	Holdrege
Average	*23.4*	*52.9*	*4.42*	*.198*	
Colby	18.4	52.1	3.06	.129	Keith
Wray	19.3	50.7	2.43	.110	Rosebud
Burlington	17.4	50.4	2.28	.125	Keith
Kimball	16.6	47.6	2.91	.154	Rosebud
Average	*17.9*	*50.2*	*2.67*	*.130*	

surface to a considerable depth. The virgin dark-colored Prairie and Chernozem soils are the most fertile soils known.

Soil samples for the determination of organic matter and nitrogen were secured to a depth of 4 inches after clipping the vegetation at the surface of the soil and removing all litter. Each sample consisted of a mixture of 10 individual cylindrical soil cores 4.7 cm. (1⅞ in.) in diameter, thoroughly intermixed and, as is usual, including whatever underground plant parts occurred in the sample. The cores were taken at random in a circular area with a radius of 3 feet. From these the sample for analysis was obtained. Organic matter was determined by a modification of the hydrogen peroxide method (Robinson 1927), and nitrogen by the usual Gunning method (Association of Official Agricultural Chemists 1930). Percentages are expressed by weight on the oven-dry basis.[6] Samples were taken from the several stations in each area as shown in table 8.

The fact that the more arid soils contain less organic matter is due partly to the smaller amount of vegetation from which it is formed and partly because it is rapidly oxidized. Both phenomena are a result of the more arid climate westward. Comparison with table 5 shows a striking correlation between the decrease in dry weight of underground plant parts and organic matter at all but the two most westerly areas. Here the decrease in organic matter is great while underground plant parts showed none. Although the bulk of materials for organic matter, as previously stated, originates from vegetation above ground, yet there is usually a more or less close correlation between weights of roots and tops. It is believed, as before indicated, that the difference has resulted from selecting prairies of better than average conditions for underground parts in the Burlington area, and that the decrease in organic matter content, which changes very gradually, indicates more nearly the true relationship between soils, vegetation, and climate.

In the prairies of eastern Washington, for example, under 20 inches of precipitation there is more than four times as much organic matter formed as in similarly fine-textured soils westward where the precipitation is only 8 inches (Sievers & Holtz 1922).

By statistical treatment of the data in table 8, it was determined that the mean from the Lincoln area was significantly different from that of the Nelson area and that the means from each of the other areas showed a very significant difference from the mean of any other group of stations. An exception was that no significant difference was found between Lincoln and Nelson in nitrogen content.

Climate and soil have a profound effect upon the production of organic matter and total nitrogen in soils both in determining the amount of vegetation, and the extent, nature, and rate and completeness of the decay of the materials produced. They likewise greatly affect the amount of loss of these materials

[6] These analyses were made for the writers by the soils section of the Department of Agronomy, University of Nebraska.

by erosion and leaching. Decomposition of organic matter in the soil is primarily a microbiological process. Hence, both temperature and water content resulting from precipitation profoundly affect its formation. With increasing temperature soil organic matter decreases because of the greater activity of soil microbes; with decreasing temperature it steadily increases. "In well-aerated soils of the humid, warm tropics, with average temperatures of 25° C and higher, humus cannot maintain itself nor can it accumulate" (Jenny 1930). On the other hand, it was found by Jenny "that in high altitudes, where the annual temperature is around or below 0° C, the soils contain on the average as much as 20 to 40 per cent organic matter, in spite of the meager grass vegetation." Extensive researches (Jenny 1930) have shown that within regions of similar moisture conditions the nitrogen and organic matter of upland, terrace, and first bottomland prairie soils decrease from southern Texas to North Dakota. For each decrease of 18° F in annual temperature the average nitrogen and organic-matter content of soils increases approximately two to three times. In the present study, the temperature factor needs little consideration since all of the samples were taken from areas with nearly similar mean annual temperatures. Extreme variation among stations is from 48.6° to 52.9° F.

The present results are in accord with those of Alway & McDole (1916) who determined the organic matter to a depth of 6 feet in the prairie-covered loess soil of Nebraska at six stations from near the Missouri river to Wauneta in southwestern Nebraska. Organic matter in the first foot decreased from 4.98 per cent at the easternmost station, where the annual precipitation was 30 inches, to 2.77 per cent at the most westerly one with a precipitation of only 18.5 inches.

Russel & McRuer (1927), in their intensive work on organic matter and nitrogen content of prairie soils, state that in a series of homogeneous soil types, nitrogen content and organic matter vary with the rainfall and with topography. Level types contained more nitrogen and organic matter than rolling ones under the same precipitation, probably because of a difference in the effectiveness of the rainfall.

Jenny (1930) concludes that within regions of similar temperature, the organic matter content and nitrogen content of grassland soils increase logarithmically with increasing factors of humidity.

SUMMARY

Grassland formerly covered about 38 per cent of the land surface of the United States, the largest continuous area occurring in the midcontinent east of the Rocky mountains.

Three types of prairie are found in this central massive area, *viz.*: tall-grass prairie in the portions with the most favorable water relations, true prairie over much of the eastern part, and mixed prairie westward.

Each type has its characteristic dominant grasses — tall grasses in the most mesophytic part, mid grasses in true prairie, and both mid and short grasses in mixed prairie. Where decades of heavy grazing have destroyed the mid grasses, the remaining short ones constitute the short-grass plains disclimax.

Prairie is an organic entity with interrelated parts developed and adjusted throughout very long periods of time.

Grasses, which are well adapted by structure and habit of growth to withstand grazing, form the bulk of prairie vegetation. Often only 8 to 12 species are dominant or controlling, 40 to 50 more are of secondary importance, but many others occur.

Forbs are also always present and often abundant, composites and legumes ranking highest in importance.

Prairie presents four distinct aspects during the growing season: prevernal, vernal, estival, and autumnal. These result from the seasonal activities of different groups of forbs. From early spring until late fall different species are blossoming and ripening seed.

Nearly all low-growing species blossom and ripen fruit in spring before they are much shaded by the grasses. Summer-blooming plants are taller. Those of autumn reach the height of the grasses or extend far above them. Thus, the vegetation consists of three levels or layers above ground as a response to the struggle for light.

Layering below ground permits prairie plants to absorb at different soil levels. About 14 per cent of the species of true prairie absorb almost entirely in the surface 2 feet of soil; 21 per cent have roots extending well below 2 feet but seldom beyond 5; but 65 per cent have roots that reach depths below 5 feet, a penetration of 8 to 12 being common and a depth of more than 20 feet sometimes being attained.

The great stability of prairie, resulting in part from the long

life span of many species, denotes a high degree of equilibrium between vegetation, soil, and climate.

Grassland vegetation has exerted a powerful reaction as a soil-building influence. It introduces both directly and indirectly the biological factor into soil formation.

Vegetation exerts numerous reactions on the water relations. Chief among these are interception of rainfall, prevention of runoff, and removal of water by absorption and transpiration.

The surface soil of prairie is anchored by 2 to 4 tons per acre of a fibrous network of roots and rhizomes. A single strip of virgin sod 100 inches long and 8 inches wide is threaded with many miles of root length.

A study was made of the amount of underground plant materials at five groups of stations centering, respectively, at Anita in southwestern Iowa, at Lincoln in southeastern Nebraska, at Nelson 90 miles southwestward, at Phillipsburg in north-central Kansas, and at Burlington in eastern Colorado.

Mean annual precipitation decreased from east to west in the several areas as follows: 33 to 29 to 26 inches in true prairie, and to 23 and 17 inches in mixed prairie. Mean annual temperature remained fairly constant—about 49° to 53° F.

Zonal soil groups varied from Prairie to Chernozem and then to Dark Brown and Brown soils. All samples, which were one-half square meter in area and 10 cm. deep, were taken in silt loam soil.

Underground plant materials were secured by washing away the soil. Volume was determined by displacement of water, and the oven-dried material was weighed.

A series of 22 samples of little bluestem from the Anita, Lincoln, and Nelson areas yielded 3.15, 2.60, and 2.34 tons per acre, respectively, of underground plant parts.

Underground yield of a series of 27 samples of big bluestem decreased from 4.54 tons per acre at Anita to 3.54 at Lincoln and to 3.17 tons in the areas westward.

Yields of a series of 16 samples of mixed bluestems from the Anita, Lincoln, and Nelson areas were 3.42, 2.83, and 2.54 tons per acre, respectively.

Statistical treatment of the data from each series shows that the correlation between volume and weight is very significant. The coefficients of correlation are .870, .874, and .699, respectively.

The difference between the mean of the dry weight of little bluestem from the Anita area and that from either the Lincoln or the Nelson area is very significant. The mean of the dry weights of big bluestem from the Anita group is significantly different from that of each of the other groups, and the mean of the Lincoln group is significantly different from the mean of the combination of the three drier western groups. The mean of the dry weight of mixed bluestems from the Anita group is significantly different from that of either the Lincoln or Nelson group.

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 is .642, of the big bluestem series .673, and of mixed bluestems .827.

Yields of slough grass and gama grass far exceeded those of big bluestem.

Blue grama grass and buffalo grass showed no consistent variations in yields from the Lincoln area where they occurred sparingly to the short-grass plains disclimax where they are dominant. Yields varied between 2 and 2.35 tons per acre.

Weights of 82 samples of upland grasses showed a consistent decrease with decreasing precipitation westward. They were 3.35, 2.69, 2.43, and 2.19 tons per acre, respectively, the last figure being the average from the two driest areas. Coefficients of correlation between volume and weight in the sequence of station groups are .812, .695, .847, .958, and .907, respectively. The mean of the Anita group is very significantly different from that of each of the other groups. The mean of the Lincoln and Nelson groups combined and that of the Phillipsburg and Burlington groups combined were also very significantly different.

Western wheat grass showed no correlation between precipitation and yield of underground parts, because of the variable factors due to soil disturbance and degree and time of occupation of the soil following the great drought. Highest yields were about 2.75 tons per acre.

Underground parts of certain prairie forbs (aster, daisy fleabane, and goldenrod) that have greatly increased since the drought were examined. Despite their dense growth, they furnished only approximately 10 per cent of underground plant materials normally supplied by the grasses.

Organic matter and nitrogen in the surface 4 inches of soil were determined at four stations in each of the five areas. Average percentage of organic matter decreased from east to west from 7.14, 6.08, 5.41, and 4.42 to 2.67. Statistical treatment of the data on organic matter shows that the mean from each area is significantly different from the mean of any other area.

Per cent of nitrogen decreased from .308, .271, .248, and .198 to .130. Although no significant difference was found between Lincoln and Nelson, otherwise the mean from each area is very significantly different from that of any other area.

BIBLIOGRAPHY

ALBERTSON, F. W. 1937. Ecology of mixed prairie in west central Kansas. Ecol. Mono. **7**:481-547.

ALWAY, F. J., and G. R. MCDOLE. 1916. The loess soils of the Nebraska portion of the transition region: I. Hygroscopicity, nitrogen and organic carbon. Soil Sci. **1**:197-238.

ASSOCIATION OF OFFICIAL AGRICULTURAL CHEMISTS. 1930. Official and tentative methods of analysis. 3rd ed., p. 5.

BENNETT, H. H. 1934. Dynamic action of rains in relation to erosion in the humid region. Trans. Am. Geophys. Union **15**(2):474-88.

CLARK, O. R. 1937. Interception of rainfall by herbaceous vegetation. Science **86**(2243):591-2.

CLARK, O. R. 1939. Doctorate thesis. Unpublished.

CLEMENTS, F. E., and J. E. WEAVER. 1924. Experimental vegetation. Carnegie Inst. of Wash. Pub. **355**.

CRATTY, R. I. 1929. The immigrant flora of Iowa. Ia. State Col. Jour. Sci. **3**:247-69.

DITTMER, H. J. 1937. A quantitative study of the roots and root hairs of a winter rye plant (*Secale cereale*). Amer. Jour. Bot. **24**:417-20.

HOLZMAN, B. 1937. Sources of moisture for precipitation in the United States. U.S.D.A. Tech. Bul. **589**.

JENNY, H. 1930. A study on the influence of climate upon the nitrogen and organic matter content of the soil. Univ. Mo. Ag. Exp. Sta. Bul. **152**.

KELLOGG, C. E. 1936. Development and significance of the great soil groups of the United States. U.S.D.A. Misc. Pub. **229**.

KRAMER, J., and J. E. WEAVER. 1936. Relative efficiency of roots and tops of plants in protecting the soil from erosion. Univ. Neb. Cons. and Surv. Div. Bul. **12**.

LOWDERMILK, W. C. 1930. Influence of forest litter on run-off, percolation, and erosion. Jour. For. **28**:474-91.

PAVLYCHENKO, T. K. 1937. Quantitative study of the entire root systems of weed and crop plants under field conditions. Ecol. **18**:62-79.

PAVLYCHENKO, T. K. 1939. Doctorate thesis. Unpublished.

QUICK, H. 1922. Vandemark's Folly. Pp. 228-9. A. L. Burt Co., New York.

ROBINSON, W. O. 1927. The determination of organic matter in soils by means of hydrogen peroxide. Jour. Ag. Res. **34**:339-56.

RUSSEL, J. C., and W. G. MCRUER. 1927. The relation of organic matter and nitrogen content to series and type in virgin grassland soils. Soil Sci. **24**:421-52.

RUSSELL, E. J. 1932. Soil conditions and plant growth. P. 406. Longmans, Green and Co., New York.

SHANTZ, H. L., and R. ZON. 1924. Natural vegetation. U.S.D.A. Atlas of American Agriculture, part 1, sec. E.

SHIMEK, B. 1931. The relation between the migrant and native flora of the prairie region. Univ. Iowa Stud. Nat. Hist. **14**(2):10-16.

SIEVERS, F. J., and H. F. HOLTZ. 1922. The silt loam soils of eastern Washington and their management. Wash. Ag. Exp. Sta. Bul. **166**.

SPERRY, T. M. 1935. Root systems in Illinois prairie. Ecol. **16**:178-202.

STEIGER, T. L. 1930. Structure of prairie vegetation. Ecol. **11**:170-217.

THORNTHWAITE, C. W. 1931. The climates of North America according to a new classification. Geograph. Rev. **21**:633-55.

WEAVER, J. E. 1919. The ecological relations of roots. Carnegie Inst. Wash. Pub. **286**.

WEAVER, J. E. 1920. Root development in the grassland formation. Carnegie Inst. Wash. Pub. **292**.

WEAVER, J. E. 1924. Plant production as a measure of environment. Jour. Ecol. **12**:205-37.

WEAVER, J. E. 1926. Root Development of Field Crops. McGraw-Hill Book Co., Inc., New York.

WEAVER, J. E., and F. W. ALBERTSON. 1936. Effects of the great drought on the prairies of Iowa, Nebraska, and Kansas. Ecol. **17**:567-639.

WEAVER, J. E., and F. E. CLEMENTS. 1938. Plant Ecology. McGraw-Hill Book Co., Inc., New York.

WEAVER, J. E., and T. J. FITZPATRICK. 1934. The prairie. Ecol. Mono. **4**:109-295.

WEAVER, J. E., and G. W. HARMON. 1935. Quantity of living plant materials in prairie soils in relation to run-off and soil erosion. Univ. Neb. Cons. and Surv. Div. Bul. **8**.

WEAVER, J. E., V. H. HOUGEN, and M. D. WELDON. 1935. Relation of root distribution to organic matter in prairie soil. Bot. Gaz. **96**:389-420.