ROOT DEVELOPMENT IN THE GRASSLAND FORMATION

A CORRELATION OF THE ROOT SYSTEMS OF NATIVE VEGETATION AND CROP PLANTS

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INTRODUCTION.

This book is intended to be a companion volume to "Ecological Relations of Roots."* The latter may be considered a pioneer work of rather an intensive nature, giving the results of investigations in local areas in many widely separated plant communities. Since its appearance investigations have been greatly extended and examinations of the root systems of plants have been made at more than 25 stations in the grassland associations of Kansas, Colorado, South Dakota, and Nebraska. Practically all of the grassland dominants have now been studied, many of them in two or more associations and under widely different conditions of environment. The descriptions of 38 new root systems of important species of plants of prairie, sandhills, and plains are included. A preliminary correlation of the root development of certain crop plants, especially the cereals, with the different types of the natural vegetation, has been determined. More than 80 examinations of the root systems of crop plants have been made in widely varying soil types and conditions of growth. Investigations were carried on at many stations in the prairie, mixed prairie, and short-grass plains extending from the Missouri River to the Rocky Mountains. A study was made also of the development of the root systems of certain crop plants on sites at Lincoln, Nebraska, formerly covered with and now adjoining typical high and low prairie. Aside from a study of the root development of these crop plants in the two habitats, some illuminating correlations with the root development of native dominants have been found. For the proper setting of these studies "Ecological Relations of Roots" forms the background.

A knowledge of root development and distribution and of root competition under different natural and cultural conditions is not only of much practical value, but it also readily finds numerous scientific applications. The phenomena of plant succession, whether ecesis, competition, or reaction, are controlled so largely by edaphic conditions and particularly by water-content that they can be properly interpreted and their true significance understood only from a thorough knowledge of root relations. It is obvious that a knowledge of root habit is essential to the proper use of plants and plant communities as indicators. The plant community has integrated all of the environmental factors of its habitat; it is the fundamental response to controlling conditions. The individual root habit and the community root habit especially, together with the more familiar above-ground parts,

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serve to interpret these environmental conditions. Both of these criteria are needed to reveal the judgment of plants as to the fitness of the habitat in which they grow or in which crop plants are to be grown. In classifying lands for afforestation, for grazing, or for agriculture, a knowledge of root habit and extent is of prime importance. Indeed, such a study not only forms a basis for judging the natural vegetation as an indicator of the value of lands for crop production, but also for determining the kind of crop to be most profitably grown (Shantz, 1911). It readily leads to the intelligent solution of problems of range improvement (Sampson, 1914, 1917, 1919), the selection of sites for afforestation (Korstian, 1917), and of numerous other problems where natural vegetation or crop plants are concerned (Clements, 1920). The applications of a knowledge of the root development of crop plants in the preparation of the seed-bed, rate of seeding, methods of tillage, use of fertilizers, irrigation, and crop rotation are too patent to need further discussion here.

The method used in excavating root systems, whether of native species or of crop plants, was the same as that formerly employed (Ecological Relations of Roots, 1919). By the side of the plant to be examined, a trench was dug to a depth of about 5 feet and of convenient width. This afforded an open face into which one might dig with a hand-pick furnished also with a cutting-edge, and thus make an examination of the root system. This apparently simple process, however, requires much practice, not a little patience, and wide experience with soil texture. In these investigations more than 1,500 root systems have been examined, and for practically all of the species encountered it has been possible to excavate the root systems almost in their entirety. In cases where considerable reconstruction was necessary, this has been rendered more accurate and less difficult by methods of record in the field. The extensive examination of species at different periods and in different soil types has permitted the choice of specimens for complete excavation from soils when optimum water-content and working conditions prevailed. With certain crop plants, and not infrequently with native vegetation, the original trenches were deepened as work progressed and the working level often reached a depth of 8 to 10 feet, sometimes much deeper. To assure certainty as to the maximum depth of the root termini, the soil underlying the deepest roots was usually undercut for about a foot below the root-ends and was carefully examined as it was removed.

The root descriptions, except as otherwise indicated, are of mature perennial plants. The former practice of examining several roots of a given species and then writing a working description was followed. This was kept at hand and as new roots of the same species were studied any variation from the original description was noted. While many of the root systems, especially those of the grasses, were removed in their entirety and photographed against an appropriate background, many others were drawn in place. In the drawings the root systems are arranged as nearly as possible in the natural position in a vertical plane. The sketching was first done with pencil on a large drawing-sheet ruled to scale. Drawings were made simultaneously with the excavating of the roots and always to exact measurement. When entirely completed they were retraced with India ink. Such drawings, carefully executed, often represent the extent, position, and minute branching of the root system even more accurately than a photograph, for under the most favorable conditions, especially with extensive root systems, the photograph is always made at the expense of detail, many of the finer branches and root-ends being obscured.

The writer wishes to acknowledge the faithful assistance of Miss Annie Mogensen in the execution of many of the drawings. He is also indebted to Professor J. C. Russel, of the Nebraska Experiment Station, for soil analyses, and to Dr. J. O. Belz, of the United States Bureau of Plant Industry, for the determination of wilting coefficients. It is a pleasure to acknowledge the helpful suggestions given by Dr. F. E. Clements and Dr. R. J. Pool throughout the period of the work. To both Doctor Clements and Professor T. J. Fitzpatrick the writer is indebted for careful reading of the manuscript and proof.

I. THE PRAIRIE-PLAINS GRASSLAND FORMATION.

Extending from the Missouri River to the foothills of the Rocky Mountains is a vast grassland formation. Pronounced climatic variations, especially in rainfall and evaporation, have clearly differentiated the vegetation of the eastern portion, the prairies, from that of the western, the plains. The former are dominated by a luxuriant growth of many species of tall-grasses and numerous societies of tall-growing herbs. The latter bear a sparser growth of shorter grasses and fewer herbaceous societies. Thus the two extremes are clearly defined. But where short-grasses meet tall-grasses on more or less equal terms over a considerable area, a third or mixed type of vegetation is clearly evident (plates 1 to 3). Having repeatedly traversed this grassland and having made careful vegetational studies at many stations throughout the past five years, the writer is in hearty agreement with the classification of Clements (1920), in recognizing in this area three plant associations. For the area concerned these are: (1) the true prairie; (2) the short-grass plains; and (3) the mixed prairie.

THE TRUE PRAIRIE.

The true prairie (*Stipa-Kœleria* association), as determined by Clements, is as follows:

> "It occupies a distinct belt between the subclimax prairie on the east and the mixed prairie on the west, reaching from Manitoba to Oklahoma. The eastern edge runs southward from Manitoba along the western boundary of Minnesota and then swings southeastward with the Minnesota Valley, reaching its limits between 92° and 93° W. It stretches across northern and central Iowa in the vicinity of the ninety-third meridian, and then trends southwestward across northwestern Missouri and eastern Kansas, where it turns south to the Oklahoma line. The western boundary begins in Manitoba between the one hundredth and one hundred and first meridian and continues more or less due south to near the Nebraska line, where it turns southeastward around the sandhill region, beyond the ninety-ninth meridian. It then follows this in a general way into northern and central Kansas and finally approaches the Oklahoma line in the vicinity of the ninety-eighth meridian. It reaches its greatest breadth of 7° of longitude along the forty-third parallel, and tapers more or less irregularly in both directions to the width of 1 to 2 degrees in Manitoba and Kansas."

While the true prairie is a climatic association and, undisturbed, would probably not be invaded by shrubs or trees, or at most only to a slight degree, the subclimax prairies, with their greater rainfall, denser sod, and more mesophytic and taller dominants, will be replaced by scrub or woodland wherever fire, cultivation, or grazing does not prevent (Weaver, 1919; Clements, 1920).

The vegetation of the true prairie is characterized in the first place by an abundance of tall, sod-forming grasses. Chief among these are *Andropogon scoparius*, *Stipa spartea*, *Agropyrum glaucum*, *Stipa comata*, *Andropogon furcatus*, and *Kœleria cristata*. Others, like *Andropogon nutans*, *Elymus canadensis*, *Panicum virgatum*, and *Poa pratensis*, while of less importance, agree with most of the preceding in having basal leaves 1 to 2 feet high, and shoots normally 2 to 4 feet tall. The group is one of typical tall-grasses. Since the water-content of the soil is abundant for grassland, large numbers of other herbs find congenial growth conditions and form more or less extensive societies. Different groups of these subdominants help characterize the seasonal aspects, many reaching their maximum development at intervals between the flowering of the dominant grasses. Typical of the more important ones are *Amorpha canescens*, *Psoralea tenuiflora* (plate 5, B, C), *P. argophylla*, *Erigeron ramosus*, *Astragalus crassicarpus*, *Aragallus lambertii*, *Petalostemon candidus*, *P. purpureus*, *Glycyrrhiza lepidota*, and species of *Aster* and *Solidago*. Briefly, true prairies occur in regions of sufficiently favorable soil and air moisture conditions to permit the growth of large numbers of dominant tall-grasses with which are intermixed a great number of other herbs, the whole forming a luxuriant vegetation. For a general ecological discussion of prairie vegetation the reader is referred to Pound and Clements (1900), Thornber (1901), Harvey (1908), Shimek (1911), Weaver and Thiel (1917), Pool, Weaver, and Jean (1918), Weaver (1919), and Clements (1920).

THE SHORT-GRASS PLAINS.

The short-grass plains (*Bulbilis-Bouteloua* association) are characterized by a few short, sod-forming grasses, especially *Bulbilis dactyloides* and *Bouteloua gracilis* (plates 2 and 9, A). Clements states:

> "The short-grass association ranges from southwestern Nebraska and the western half of Kansas through eastern Colorado into northwestern Texas, northern New Mexico and Arizona. It is also developed to some extent in southeastern Utah and southwestern Colorado." (Clements, 1920:140.)

The short-grasses grow in a region of light rainfall and are well adapted to a brief growing-season, maturing seed in July. They form such a dense sod and render the soil so compact that run-off is high and water-content consequently normally low. This, together with the intense competition of these short-grasses, practically excludes the taller grasses and other herbaceous vegetation. Moreover, most prairie species find the short-grass plains an uncongenial habitat because of the high evaporating power of the air, and especially the scarcity of water during late summer, just at a time, often, when their demands upon the habitat are greatest. This absence of taller vegetation makes the typical short-grass cover very uniform and monotonous.

The leaves of the grasses are seldom over 2 to 8 inches in height, while the flowering stalks do not usually exceed 0.5 to 2 feet. While *Bouteloua gracilis* or *Bulbilis dactyloides*, or the two intermixed, constitute the mass of the cover, *Muhlenbergia gracillima* and *Bouteloua hirsuta* (with *Hilaria jamesii* southward, Clements, 1920: 141) frequently form consociations. Compared with the prairies, herbaceous societies are not only much fewer in number, but of much less importance in the vegetational structure, nor are the individuals so well developed. Typical of these are *Artemisia frigida, Liatris punctata, Senecio aureus, Gutierrezia sarothræ, Psoralea tenuiflora, Opuntia polyacantha, Helianthus pumilus, Grindelia squarrosa,* and *Aragallus lambertii.* (*Cf.* Pound and Clements, 1900; Shantz, 1911; Pool, 1914; Weaver, 1919; and Clements, 1920.)

THE MIXED PRAIRIE.

The mixed prairie (*Stipa-Bouteloua* association) occupies a region of greater precipitation or more favorable edaphic conditions than the short-grass plains. As pointed out by Clements (1920: 137), the most significant difference from true prairie is the practically universal presence of one or more of the short-grasses or sedges as a lower layer under the taller prairie species, while the distinctive feature of the association is the intimate mixing of the tall-grasses with the shorter ones. Such dominants as *Bouteloua gracilis, Bulbilis dactyloides, Carex stenophylla,* and *C. filifolia* form a layer beneath *Stipa comata, Agropyrum glaucum, Kœleria cristata,* and other true prairie species (plates 3, 7, and 8). Competition between the two types of vegetation seems nicely adjusted. While the short-grasses have a disadvantageous light-relation because of their height, this is counterbalanced by their more favorable position as regards evaporating power of the air and especially their greater ability to successfully withstand grazing. Eastward, under more favorable growth conditions, the short-grass layer disappears and the mixed prairie merges into true prairie; while in drier areas, especially southward and westward, the gradual disappearance of the taller grasses reveals the changed climatic or edaphic conditions and gives the plant cover the impress of the plains short-grass association. Thus Clements (1920: 135) states as follows regarding the mixed-prairie association:

"It is composed of the dominants of both prairie and plains, but it is essentially prairie in its tall-grasses, numerous societies, and successional relations. Mixed prairies occur from central North and South Dakota, central Nebraska, and northwestern Kansas, throughout Montana and Wyoming to the Rocky Mountains, and southward in Colorado along the foothills of the Front Range. They extend well north into Saskatchewan and Alberta, and are assumed to have covered much of northern New Mexico before the period of intensive overgrazing. On the east, the association is found in more or less typical form at Medicine Hat in Saskatchewan, Minot and Mandan in North Dakota, Winner in South Dakota, and Long Pine and McCook in Nebraska. Along the west it occurs from near Calgary, Alberta, southward to Lewiston and Billings, Montana, Douglas and Laramie, Wyoming, and Colorado Springs and Trinidad, Colorado. Beyond the eastern limit, *Bouteloua* and *Bulbilis* merely persist as alternes in xerophytic situations in the midst of the prairie." (*Cf.* Pound and Clements, 1900; Shantz, 1906, 1911, 1917; Pool, 1914; Weaver, 1919; and Clements, 1920.)

In concluding this summary statement of the grassland associations, it may be well to point out that while the major factor is water-content, precipitation and evaporation are so greatly modified by edaphic conditions that two types of vegetation are often found in juxtaposition. Thus at Limon, Colorado, native and crop plants in adjacent fields have been excavated, one lot from typical short-grass land, the other in sandy soil in typical mixed prairie. Even in the midst of the prairie region, at Lincoln, Nebraska, an epitome of decreasing rainfall and consequent mixed prairie and short-grass plains vegetation may be found on a single hillside (Weaver, 1919). The base is clothed with tall prairie grasses and herbs, while the gravelly crest, which is of glacial origin, is covered with a nearly pure growth of *Bouteloua gracilis* and *B. hirsuta*. On the upper slopes the short-grass layer is overtopped by *Kœleria cristata*, *Stipa spartea*, and *Andropogon scoparius*. Here, as everywhere throughout the formation, root relations are important and root competition plays a decisive rôle.

In "Ecological Relations of Roots" it has been pointed out that every plant association has a rather definite community root habit. The peculiar set of edaphic conditions of an association, especially its water-content, leaves its impress upon root distribution. Roots of true prairie show distinct differences in habit from those of the plains, and these in turn are unlike those of sandhills. In fact, the same species when grown in the different associations usually takes on the root habit best adapted to meet its needs in that particular environment. Following the description of the root habit of the individuals of each association there is a summary statement of the root habit of the plants as a group. Finally, the correlations between root habit and factors of the environment are pointed out.

II. ROOT SYSTEMS OF TRUE-PRAIRIE SPECIES.

During 1919, studies of the root systems of dominant and subdominant true prairie species were made at the base station on both high and low prairie areas near Lincoln, Nebraska. In addition to further studies of certain species, the root systems of which have already been described (Weaver, 1919), the following plants were excavated:

Aster multiflorus.—This autumnal subdominant, while occurring throughout much of the grassland formation, reaches its greatest abundance and best development in the true prairie. Here it is conspicuous from the time its many white or purplish flowers begin to blossom in August until late in October. Clumps of this rather bushy plant are connected by tough, woody rhizomes 4 or 5 mm. in diameter and from an inch to over 8 inches in length. Frequently they are short and the plants densely matted together. The plant is supplied with numerous fibrous roots usually 2 mm. or less in diameter. While some descend rather vertically downward, more often they run obliquely and at a depth of a foot may be 1.5 feet from the base of the plant. This criss-crossing of the roots underneath a clump is often quite marked, the soil being filled not only with the larger roots which penetrate deeply, but also with numerous finer and shorter ones which absorb mostly or entirely in the surface foot of soil. They are light tan in color, very tough and wiry, and the larger ones give off few branches near the soil surface. Throughout their course to a working depth of 5 feet they give off branches from time to time (fig. 1). These are sometimes 10 or more inches in length, but more frequently they are 0.5 to only 2 or 3 inches long. In general they are poorly rebranched. The production of laterals, however, is quite variable. Some roots are furnished at intervals of 0.2 to 0.5 inch with rebranched laterals over an inch in length, while others, especially near the tip, run for distances of several inches without branching. However, these unbranched portions are often densely covered with root-hairs. Several roots ended in the seventh and eighth foot of soil. The tips are poorly branched. The root system as a whole is deep-seated and very little provision is made for surface absorption.

Solidago missouriensis.—This goldenrod is of considerable importance in the structure of grassland vegetation and is widely distributed. It forms autumnal societies in true prairie and mixed prairie from Washington to Manitoba, extending southward to Texas. It propagates by woody rhizomes from 3 to 8 mm. in diameter and from 2 to more than 12 inches in length. From the base of the clump and along the rhizomes arise clusters of roots which are 0.5 to 3 mm. in diameter (fig. 2). Many of these are relatively short, branch repeatedly, and end in the first foot or two of soil. The larger, white, cord-like roots descend laxly and obliquely, seldom at angles of less than 20 or 30 degrees with the horizontal. Some run obliquely a few inches from the rhizome and then penetrate vertically downward. In fact, the root spread is only 12 to 20 inches from the base of the plant. Below the first foot the roots frequently run for several inches without giving off a single lateral or at best only rarely an unbranched rootlet not over a 0.5 inch long. Others give rise, at rather regular intervals of 0.2 to 1 inch, to horizontal laterals a centimeter or less in length and unbranched, but rarely to branched rootlets with a length of 2 to 3 inches. In the harder loess soil, below 4 feet, many of the roots are more or less crinkled. Even at 5 feet many of the larger ones

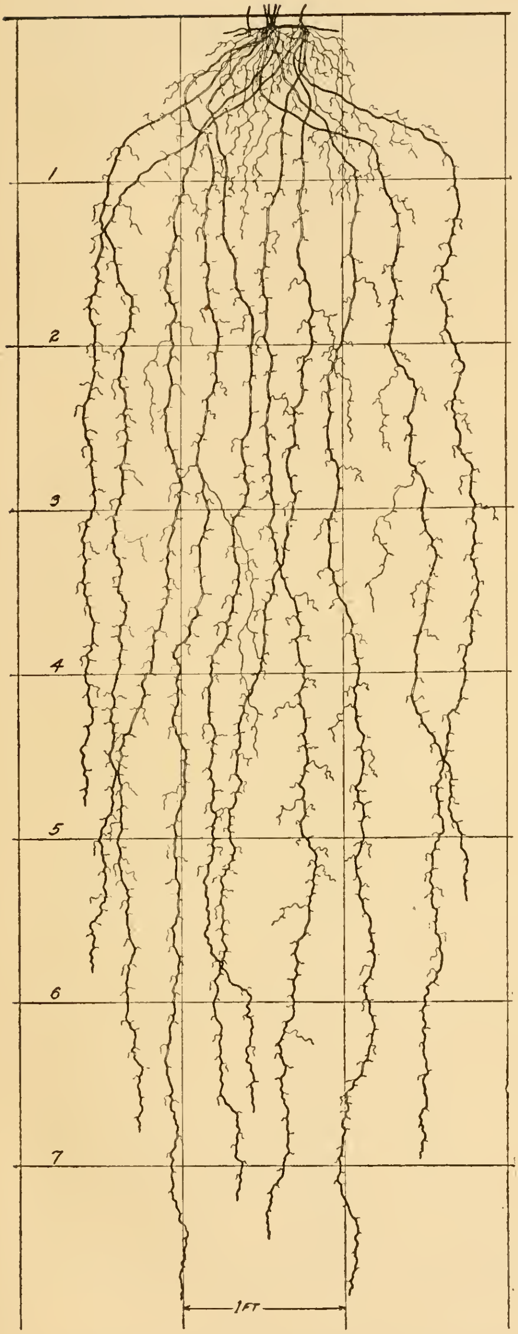


FIG. 1.—Root system of *Aster multiflorus*.

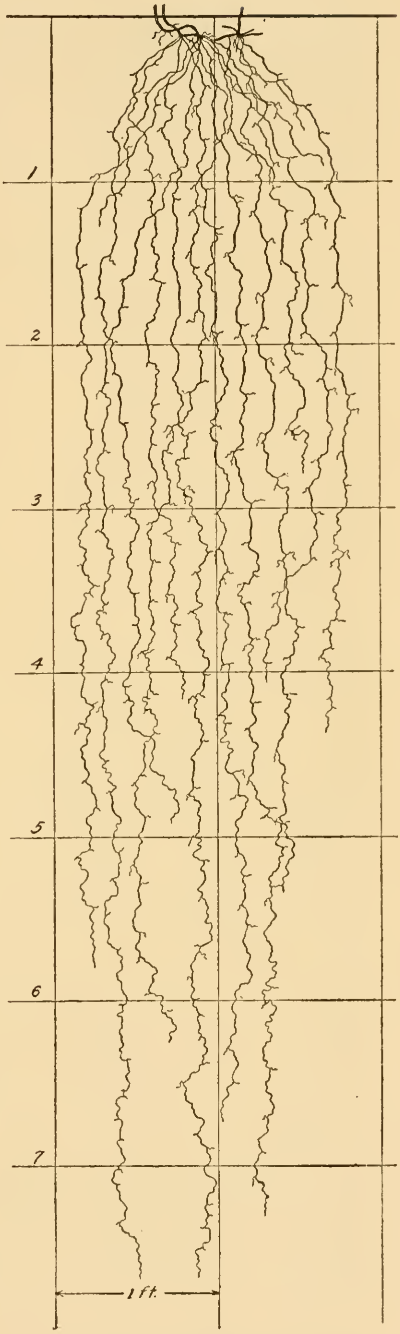


FIG. 2.—Root system of *Solidago missouriensis*.

maintained their original diameter, while others tapered to an end at about this level. In general, the branching is somewhat more pronounced below the fifth foot, thread-like laterals 1 to 3 inches in length coming off in small clusters. Of the four plants examined, the working level was determined at about 5.5 feet, although many roots penetrated beyond. Some extended well into the seventh foot of soil. The maximum depth recorded was 8.2 feet. This species is similar to the preceding in penetrating deeply and relying but little upon the surface soil layers for water and solutes.

Agropyrum glaucum.—Wheat-grass is a dominant of both true and mixed prairie vegetation. Because of its height and dense growth, due to its excellent system of rhizomes, it frequently dominates local areas, sometimes almost excluding other plants (plate 12, B). It forms extensive consociations in both types of prairie vegetation, these usually being more extensive in mixed prairie (plate 3, A, B). If at all abundant it is an indicator of favorable deep soil-moisture conditions, but in thin stands and as dwarfed individuals it occurs in rather dry soil. Height-growth seems closely related to soil-moisture.

The plants here described were growing in the high prairie not far from the base station. They were in complete control of the local area. The individuals are connected by tough rhizomes from 1 to 2 mm. in diameter and from 0.3 to over 1.5 feet in length. The rhizomes, which lie 0.5 to 3 inches below the surface, are frequently branched, abundantly covered with scale leaves, and tipped with long, sharp-pointed buds. From the nodes of the rhizomes at intervals of 1 to 1.5 inches, arise tough white roots. There are usually 2 to 4 at each node. Like those arising from the base of the clumps, they are about 0.5 to 1.5 mm. in diameter, quite coarse in texture, and do not spread much laterally from their place of origin. In the main their course is rather vertically downward (fig. 3). They all branch profusely and somewhat regularly. The branches are usually less than an inch in length and often pursue a course more or less at right angles with the larger roots from which they arise. Some, however, are occasionally 2 to 3 inches long and run off obliquely downward. The laterals throughout are very abundant to within 1 to 1.5 feet of the tip, below which point they are less pronounced. In fact, some of the root-ends may extend for distances of 0.7 to 1.2 feet with scarcely any branching, while on others, where laterals are present, they are usually short. Many of the roots penetrate the moist soil to the working depth of 8 feet, while the maximum root depth was about 9 feet. Specimens examined in low prairie adjoining the base station (p. 37) showed, in this moister, richer, alluvial soil, a working depth of 7 feet and a maximum penetration of 8 feet.

This root habit is in rather close agreement with that described for the same species growing in the mixed prairie near Colorado Springs. The chief difference is the surface absorbing system, which is much more poorly developed. In the mixed prairie numerous short horizontal roots arose from the base of the clumps and from the rhizomes. These were profusely branched and rebranched to the third and fourth order, the ultimate branches being almost microscopic in size and furnishing a splendid surface absorbing system (*cf.* Weaver, 1919:52). This difference is a characteristic one for many species of mixed prairie and short-grass plains as contrasted with those of the true prairie. It is undoubtedly a response to the water-content. Moreover, the root system was not so deeply placed in the more arid region, for few roots were found below 7 feet, while the working depth was about 6 feet.

Poa pratensis.—Kentucky bluegrass was probably formerly indigenous only in the North and West. Since the settlement of the prairie region it has

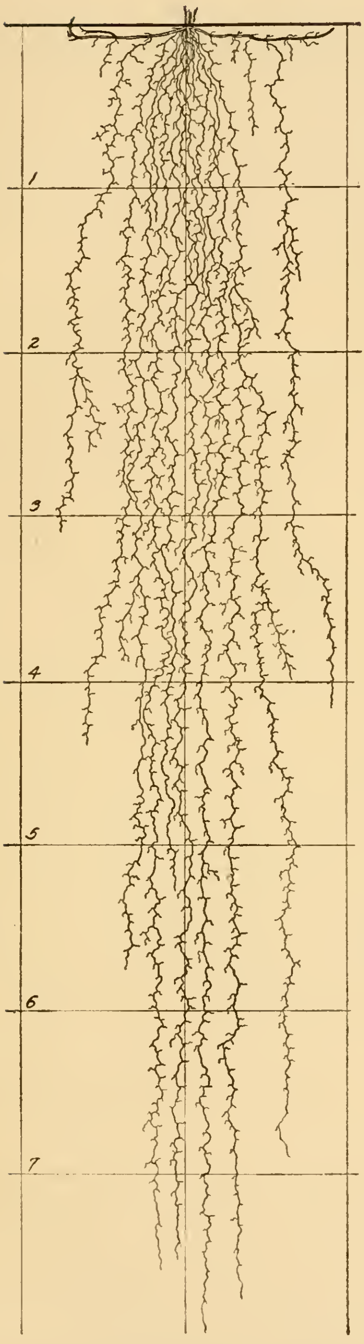


FIG. 3.—Roots and rhizome of *Agropyrum glaucum.*

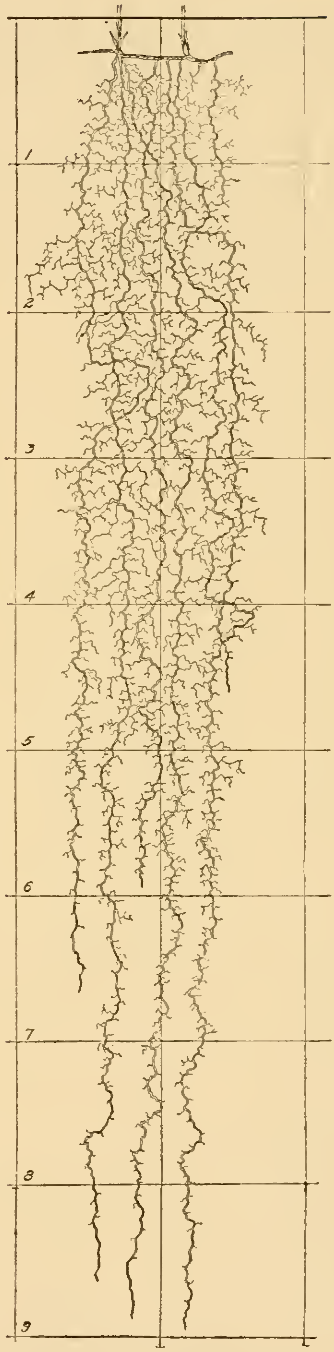


FIG. 4.—Roots and rhizome of *Spartina cynosuroides.*

escaped from cultivation and, because of its prolific seeding and rapid propagation, it has become an important species in natural grassland. It is especially abundant in low prairie and competes successfully with natural vegetation even on the upland. It is confined to the less arid parts of the grassland formation.

The roots of this species have been examined under three sets of edaphic conditions at Central City and Lincoln, Nebraska. At the former station the plants were growing in a soil of mixed sand and clay overlaid with about 2 feet of wind-blown sand. Below the stratum of clay, which had a thickness of 6 feet, almost pure white sand occurred. As at Lincoln, the plants had evidently been in possession of the area for several years.

The grass spreads by rhizomes, which were somewhat variable as to depth (0.5 to 4 inches), the normal level undoubtedly being more or less disturbed by the movement of the sand. The rootstocks are 1 to 2 mm. in diameter and well branched. The dark-colored, fine, fibrous roots occur in such abundance that with the creeping rootstocks they form a dense, tough sod. Some of the roots have a wide lateral spread, often running nearly parallel with the soil surface at depths of only 0.2 to 0.3 foot for distances of 1 to 1.5 feet from their origin. Usually they run more obliquely or even vertically downward. They completely fill the soil to a depth of about 2.5 feet, below which they are abundant for 2.5 feet more, while a few reach depths of 7 feet. These fine roots are abundantly supplied with hairlike laterals, usually less than an inch in length, but branched and rebranched to the third order. Even the root-tips are well branched with rootlets 1 to 3 inches long.

The second examination was made in an area of high prairie near Lincoln in a very stiff clay-loam. The upper 1.2 feet of soil was dark in color and rich in humus. Below this was a subsoil of stiff yellow to slate-colored clay about 2 feet thick. This was somewhat intermixed with streaks of decomposed Dakota sandstone which modified its tenacity. Below 3.2 feet the clay became very hard and much jointed, roots being largely confined to these joints. It was intermixed with pockets and streaks of chalk, the latter sometimes being an inch in thickness. The soil, especially the deeper portion, was so hard that it was removed with considerable difficulty. Its glacial origin was shown by pebbles often 2 or 3 inches in diameter which occurred throughout, but these were nowhere very abundant. The bluegrass sod was in control of local areas. The greatest root development was in the surface 2 feet of soil, although roots were fairly abundant to a depth of 3.3 feet, while a few penetrated to a maximum depth of 5.8 feet. The wide lateral spread of surface rootlets so highly developed in the sand occurred to a much less extent in the clay-loam.

A third lot of plants was excavated at the low-prairie station, where they were growing in a silt-loam alluvial soil. The working depth was determined at 2.8 feet, although many penetrated deeper, some even reaching a maximum depth of 5 feet (plate B).

All of these investigations give a greater root depth for *Poa* than is indicated by the results of King (1893) in Wisconsin (about 2 feet) or Ten Eyck (1904) in Kansas. At the latter station a few roots reached a depth of nearly 4 feet, but at 2 feet the number was small and comparatively few roots extended below a depth of 1.5 feet. It is quite apparent that edaphic conditions greatly modify the root habit, as seen in the plants examined on high prairie, which had a greater depth of penetration than those on the more moist lower areas. The successful competition of bluegrass with native species is probably largely due to its methods of propagation, its massive root system, and dense sod-forming habit. While it requires a fairly moist climate to thrive and it becomes especially dominant during seasons with an excess of rainfall, it is not easily destroyed by drought. During a dry time it ceases growth, and as a result of protracted dry periods may even become brown and apparently dead, but upon the advent of rain it quickly revives. Its ability to withstand trampling and its early growth in the spring, as well as late in the fall, make it an excellent pasture grass over wide areas in the true and subclimax prairies. However, its cessation of growth during dry midsummers is very disadvantageous to the stock raiser. A study of its root habit affords a much better understanding of its growth and its success as an invader in stabilized vegetation. It is a species exceptionally well adapted for absorption in the surface soil, but in times of drought it must rely to a large extent upon absorption by the deeply penetrating roots.

Spartina cynosuroides.—This tall, coarse grass of low lands is a dominant in the subclimax prairie (Clements, 1920), and also occurs in moist areas in true prairie. Its rank growth and dense sod-forming habit frequently exclude other plants entirely. It is an indicator of land with a high water-content. This species was excavated in alluvial soil near the station on the low prairie at Lincoln, where it formed a pure growth over a limited area. The first 6 inches of soil is filled with a mat of coarse, woody, very much-branched rhizomes from 5 to 10 mm. in diameter. They vary greatly in length, some extending only 2 or 3 inches and others over 12 inches before giving rise to erect shoots. They are covered with long, dry, overlapping leaf-scales; the younger ones, especially, are tipped with long, sharp-pointed buds. From the base of the clumps the roots arise in groups of 2 to 5 or more. They also originate, usually singly, at distant intervals along the rhizomes. They are very coarse and tough, some measuring 3 or 4 mm. in diameter. They taper so gradually that at a depth of 7 to 8 feet they are still 1 to 1.5 mm. thick. Some were traced to a maximum depth of 9 feet and may have penetrated a foot or two deeper, but at this level the water seeped so rapidly into the trench as to prevent further excavation. In general, their course is vertically downward, although they zigzag frequently through distances of 0.5 to 6 inches (fig. 4). The branches may run off rather horizontally for 5 or 6 inches and then continue downward. The soil beneath the plant is quite filled with roots, especially the first 5 feet, and many extend to the water-level at 9 feet. The laterals are threadlike and very abundant, usually an inch or less in length, crooked and poorly rebranched. However, some of the branches reach lengths exceeding 3 inches. The ultimate branches are usually only a few millimeters long. This grass has the coarsest roots of any examined. Its great depth of penetration is surprising when the water relations of its habitat are considered (*cf.* table 3).

Salvia pitcheri.—This sage occurs throughout the grassland communities from Minnesota to Texas. It is conspicuous from July to September, when the tall plants, which often form societies, overtop the grasses. The large blue flowers lend pleasing variety to the purple and yellow of blazing-stars, goldenrods, and sunflowers. Several specimens 4 feet tall and in full bloom were examined near the high-prairie station at Lincoln. This autumnal bloomer has a short woody rhizome usually not over 10 mm. in diameter and often only 1 to 3 inches in length. From the base of the plant and from the rhizome there arise many tough, rather woody roots. As many as 18 of these were counted on a single inch of the rhizome. These vary from 4 mm. to less than a millimeter in diameter, many being about 2 mm. thick. The older ones are nearly black in color, with a bark which peels off rather easily; the

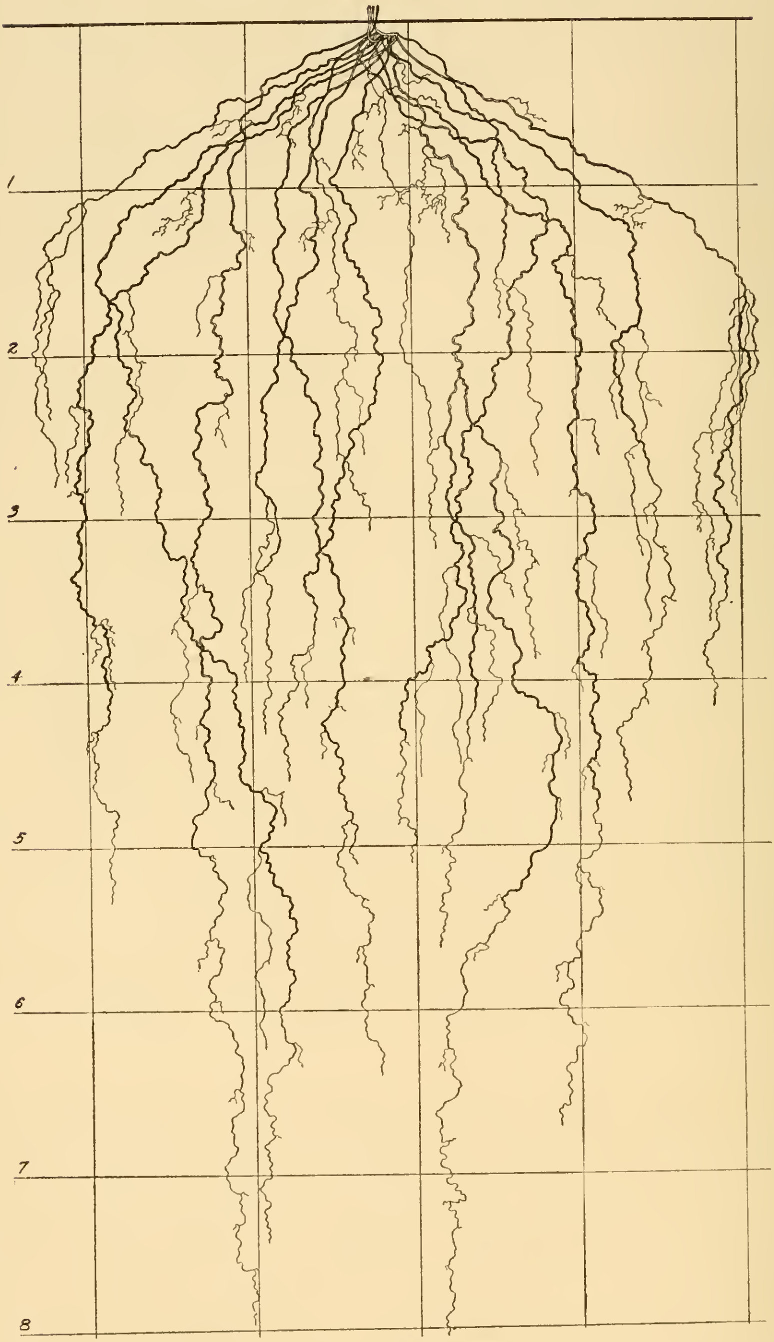


Fig. 5.—*Salvia pitcheri.*

younger ones are a dark tan. Some of the roots run obliquely to horizontal distances of 2 feet from the base of the plant before turning downward, while others run almost straight down to distances of 5 to 9 feet (fig. 5). The root system throughout is rather poorly branched, the larger roots especially often running distances of 6 to 8 inches without giving off branches. On the other hand, the smaller roots may branch in a forked manner, and these rebranch into long, slender rootlets furnished rather abundantly with hairlike laterals. These rootlets, although several inches in length, are, like the root-tips, only moderately rebranched. In the surface soil, however, the rootlets may be well branched to the third and fourth order, while in soil crevices, and in earthworm burrows especially, a great network of hairlike branches often occurs. Thus *Salvia* exemplifies the deeply penetrating, widely spreading, but rather coarse root system characteristic of so many prairie plants.

Melilotus alba.—White sweet clover is a biennial ruderal throughout much of the grassland formation where it has escaped from cultivation. It is an excellent forage crop for semiarid regions, withstanding drought better than alfalfa and often thriving where the latter crop fails. This species was examined on rather low-lying level land adjoining a sandy ridge near Central City. The old bluegrass sod had been covered to a depth of 1.2 feet by wind-blown sand from the adjacent hills. The sweet clover was planted to prevent further local soil-shifting (p. 64). The roots were examined early in July, 1919, when the plants were just 12 months old. At this time they were 3 feet high, but formed rather a poor stand. The plant described had 15 stems arising from the crown of the fleshy tap-root. Below the drifted sand was a layer of 1 foot of black sandy loam, underlaid by 2.8 feet of fairly pure sand, while at 5 feet in depth a very hard, black clay-loam was encountered, above which the water oozed into the trench. The largest plant examined (plate 18, B) had a tap-root 1.5 inches in diameter. It tapered off gradually and at a depth of 1.7 feet was only a centimeter thick. Although no major branches were given off in the surface layer of sand, 5 large laterals, 5 to 8 mm. in diameter, came off at a depth of 1.3 to 2 feet. The tap-root pursued a nearly vertically downward course until it reached the hard layer of soil, when it turned abruptly, ran horizontally for about 7 inches, and then penetrated the hard black clay for only 2 or 3 inches. The first 1.5 feet of the tap-root gave off numerous small laterals only a millimeter or two in diameter. These ran off horizontally to distances of 0.5 to 1.5 feet or even more, filling the surface sand with a delicate network of absorbing roots. Few of the main laterals spread to a greater distance than 2 feet from the downward course of the tap-root, but most of them reached depths of about 5 feet. All were abundantly supplied with extremely well-branched sublaterals, so that the soil was well filled with roots to a depth of 5 feet. Other plants examined, though somewhat smaller, agreed in branching habit with the one described, though many gave off major branches in the surface stratum of sand (*cf.* p. 131). Thus sweet clover is not only quite deeply rooted, but is also fitted to absorb at all levels in the soil.

Helianthus rigidus.—This sunflower is a prairie species of wide distribution and forms extensive autumnal societies which are conspicuous both because of the height and abundance of the plants. Like so many other prairie species, it propagates by means of rhizomes. From the base of the plant there often arise a number of these, with diameters of 2 to 4 mm., which run off in soil usually not more than 6 or 8 inches deep and often at a depth of only 3 or 4 inches. In length they vary from 0.3 to 1.5 feet. In the main they are rather destitute of roots. The rhizomes are often enlarged throughout the last 6 inches nearest the tip. The roots vary from those that are fibrous, herbaceous, and only 0.5 mm. thick to those that are tough, woody, and 6 or 7 mm. in diameter (fig. 6). While some descend vertically, the larger roots more

Fig. 6.—Roots and rhizome of *Helianthus rigidus*.

commonly run off obliquely for at least 1 or 2 inches before turning downward, while still others continue their oblique course until they have extended laterally 1 to 1.5 feet from the base of the plant. However, these roots, unlike those of many plains species, do not run off in the surface soil. There is ample provision for surface absorption by means of the finer, shorter roots, as well as by numerous branches from the larger ones. These run off in all directions, especially in the first foot of soil, and are branched and rebranched to the third and fourth order. Branching is well developed in the first and second foot, but below this depth laterals are less numerous and more poorly rebranched. In fact, in the third to sixth foot of soil the roots, which are now only a millimeter or two in diameter, are poorly provided with threadlike laterals, sparsely rebranched, and only 0.5 to 2 inches in length. Three or four roots of each of the plants examined were traced to a depth of about 7 feet; 7.8 feet was the maximum depth recorded for this species. The deeper roots often wander back and forth through small distances, the tips frequently being 1 or 2 feet distant horizontally from the base of the plant. The tips are not well branched. The roots are rather tough, except the younger portions, which are quite brittle. They are tan to white in color, except in the shallow soil, where they are often tinged with red like the base of the stems. Summarizing briefly, we find that the roots are not only deep-seated, but that this species is also fairly well adapted to absorb efficiently in the surface foot of soil, especially below a depth of 4 inches.

PRAIRIE ROOT SYSTEMS AND PRAIRIE ENVIRONMENT.

An examination of these data reveals the fact that none of the roots of the prairie species here described are superficial. All extend into the fifth foot of soil, and indeed most of them go a great deal deeper. They afford further evidence for the conclusion already reached, namely, that true-prairie species are provided with well-developed, deep-seated, and extensive root systems. In order to present these facts concisely, all of the prairie species thus far studied (43 in number) are arranged in table 1 into three groups, according to the depth of root penetration. In the first group may be found plants with such shallow roots that they seldom extend below the first 2 feet of soil. These consist entirely of grasses. This group is the smallest and makes up only 14 per cent of the total. The second group is composed of species with roots extending well below the second foot, but seldom deeper than 5 feet. These may be termed intermediate in root depth. Here are to be found 21 per cent of the prairie species. The last and largest list, made up of plants whose roots extend beyond a depth of 5 feet (some to 12 or even 20 feet), includes 65 per cent of the species selected as typical of the prairie flora.

SUMMARY OF PRAIRIE SPECIES.

For these species the working depth is also given in table 1. By working depth it is meant to designate the average depth reached by a large number of roots or branches of the root system and to which depth considerable absorption must take place. It has no absolute value like maximum depth of penetration, but can usually be determined for most root systems with a considerable degree of accuracy. While many roots may not reach the working depth of the plant, others usually penetrate beyond. For cereal crop plants (p. 122) the working

TABLE 1.—*Root depth and surface lateral spread of true prairie species.*

Species.	Maximum depth, in feet.	Working depth, in feet.	Lateral spread in surface soil.[1]
Aristida oligantha	3.3	1.2	Moderate; not over 0.5 foot in surface 0.3 foot of soil.
Distichlis spicata	2.2	1.5	Few roots in surface 0.3 foot.
Elymus canadensis	1.8	1.3	About 1.7 feet; roots penetrate diagonally downward.
Kœleria cristata	1.8	1.3	About 0.7 foot.
Sporobolus longifolius	3.3	1.5	1 to 1.7 feet.
Stipa spartea	2.2	1.5	A few roots spread laterally and diagonally downward to 0.8 to 1 foot.
Andropogon nutans	4.9	3.3	Small; about 0.3 foot.
Andropogon scoparius	5.4	3.2	About 1.2 feet; relatively few spread so widely.
Bouteloua gracilis	3.8	1.7	Small; seldom over 0.3 foot.
Bulbilis dactyloides	6.1	3.5	Do.
Grindelia squarrosa	6.1	3.3	Many fine rootlets 0.3 to 0.8 foot long, occupy surface soil.
Helianthus subrhomboideus	4.2	3.8	0.5 to 0.7 foot in surface 0.5 foot of soil.
Petalostemon candidus	5.7	3.3	Small; laterals run obliquely downward.
Solidago rigida	5.2	3.3	1 to 1.5 feet; roots run obliquely downward.
Verbena stricta	4.3	3.7	1 to 1.2 feet in first 0.5 foot of soil.
Agropyrum repens	8.0	6.0	Roots penetrate vertically downward.
Agropyrum glaucum	9.0	7.0	Roots penetrate quite vertically downward.
Amorpha canescens	16.5	7.0	Practically no absorption above 3 feet.
Andropogon furcatus	9.3	5.0	About 1 foot; relatively few spread so widely in surface 0.3 foot.
Aster multiflorus	8.0	5.0	Not great above 0.5 foot.
Astragalus crassicarpus	6.5	6.0	Little surface absorption.
Baptisia bracteata	6.7	6.0	Practically no absorbing laterals in first 2 or 3 feet.
Bouteloua curtipendula	5.5	4.5	Moderate; about 0.7 foot.
Brauneria pallida	8.0	5.0	No absorption in surface soil.
Ceanothus ovatus	14.5+	11.0	1 to 5 feet by some surface laterals.
Glycyrrhiza lepidota	12.0+	9.0	Little absorption in surface soil.
Helianthus rigidus	7.8	6.0	Considerable absorption in first foot below 0.3 foot.
Kuhnia glutinosa	17.3	13.0	Very little surface absorption.
Lespedeza capitata	7.8	5.5	1 to 2.5 feet.
Liatris punctata	15.8	6.0 to 10.0	Usually no surface absorbing laterals.
Lygodesmia juncea	20.6+	15.0	Little surface absorption.
Melilotus alba	5.0+	5.0	Usually small in surface 0.3 foot.
Panicum virgatum	9.2	7.0	Very little; 0.3 foot or less.
Poa pratensis	7.0	3.3	0.3 to 0.5 foot or more; much surface absorption.
Psoralea argophylla	6.0	6.0	Little surface absorption.
Psoralea tenuiflora	9.0	6.0	Little absorption in first 2 feet of soil.
Rosa arkansana	21.2	16.0	Little surface absorption.
Salvia pitcheri	9.0	6.0	Very small in surface 0.5 foot.
Silphium laciniatum	13.7	8.0	Little surface absorption.
Solidago canadensis	11.0	8.0	Moderate; surface absorption relatively small.
Solidago missouriensis	8.2	5.5	Usually not over 0.3 foot.
Spartina cynosuroides	9.0+	8.0	Roots descend nearly vertically.
Vernonia baldwinii	11.5	9.0	Very little surface absorption.

[1] In the table, as well as throughout the descriptions, the lateral spread indicates the radial distance to which roots penetrate from the base of the plant.

level is easily determined. Where unbranched or poorly branched tap-roots are concerned, the working depth is often synonymous with maximum depth. In almost every case the working depth has been determined and averaged for several individuals of a species.

Another important character of the root habit is also shown in the table. This is the lateral spread of the roots in the surface soil. In general this is not pronounced and is usually only 1 to 4 inches. It is greatest among the shallow-rooted species composing the first group, but even here some have few roots in the surface layer, while in most cases the shallower roots run obliquely in such a manner as to reach their maximum spread in deeper soil. Examination of the deeper-rooted species shows that relatively few (only about one-fifth) rely to any marked degree upon the shallow soil for their water and solutes, while many carry on relatively little absorption in the first, second, or third foot. This root habit is in marked contrast to that of the majority of plants of the more arid mixed prairies and short-grass plains, where surface rootlets are often extremely well developed. This root habit is also very marked in sandhills vegetation, as has been pointed out heretofore (Weaver, 1919). Further studies have added more evidence to warrant this conclusion. Of all the grassland habitats where water-content readings have been made, the prairies show rather uniformly greater moisture in the deeper soils. This, it is believed, accounts for the deeply penetrating root habit of most prairie species. Plains species need to rely much more upon water supplied to the surface soils by summer showers, and the response has been, in many species, the development of widely-spreading shallow roots. Even *Bouteloua gracilis* and *Bulbilis dactyloides*, grasses with notably wide-spreading surface roots, under true-prairie environment at Lincoln show only a small lateral spreading of their roots (*cf.* tables 1 and 9).

COMPARISON OF TRUE- AND MIXED-PRAIRIE ENVIRONMENT.

A comparison of the environmental conditions at a typical true-prairie and plains station respectively (plate 4), together with an exact picture of the vegetational covering as revealed by chart quadrats and quadrat-bisects, goes far toward illustrating and explaining these variations in root habits.

At Lincoln, Nebraska, in the true prairie, the mean annual precipitation is 28.6 inches. At Colorado Springs, Colorado, in the mixed prairie, it is only 14.6 inches. At both stations most of the precipitation falls during the growing-season, a distribution of moisture very favorable for the growth of grasses. Although the summer rains in both areas are not infrequently torrential, the run-off at the mixed-prairie station (as is true in general over most of the non-sandy plains) is much greater because of the compactness of the soil. In short-grass plains it may total 30 to 43 per cent (Shantz, 1911:35). This run-off greatly decreases the amount of water which would enter the soil and become available for plant growth.

The fertile, dark-colored soil at the prairie station is of the type commonly called loess, but is more or less confounded with glacial drift. The soil at the upland prairie station consists of Marshall silt-loam; at the low-prairie station the soil is of alluvial origin and is designated as Wabash silt-loam. At both stations the soil is very deep. The water-holding capacity of the surface foot at the two stations is 60 and 70 per cent. The wilting coefficients are 13.5 and 16.8 per cent, respectively. At the mixed-prairie station the soil consists of a light-colored loam intermixed with some sand. It is so very compact that it is spaded with extreme difficulty and in digging trenches for root examinations a large pick was kept in constant use. At a depth of 6 to 10 feet it is underlaid with sand. The water-holding capacity of the surface foot is 45 per cent, while the wilting coefficient is 8.2 per cent.

Water-content data have been obtained at the mixed-prairie station for two successive growing-seasons (1918 and 1919), while at Lincoln they extend, although somewhat interruptedly, over a longer period of years. They show that both true-prairie and mixed-prairie plants grow under semiarid climatic conditions in which the supply of water is the chief limiting factor of plant growth. During certain portions of the growing-season extremely xerophytic conditions prevail. It has been shown that the water-content of the soil is reduced to the wilting coefficient of Briggs and Shantz (1912) to a depth of 4 to 5 feet in both habitats, at least during certain years. This occurred during 1918, when the daily evaporating power of the air was very high, 38 c. c. and 49.5 c. c. in true prairie and mixed prairie respectively. The fact that the plants, including many species whose roots do not extend beyond a depth of 4 to 5 feet, did not wilt[1] has led the writer to conclude that grassland vegetation can extract water from the soil beyond the point indicated by the wilting coefficient. Brown (1912), working in Arizona, found that plants wilted with a greater amount of water in the soil when the rate of evaporation was high than when it was low. Caldwell (1913), and Shive and Livingston (1914) have shown that the permanent wilting of plants occurred with varying amounts of moisture in the soil, depending upon the evaporating power of the air. The work of Alway, McDole, and Trumbull (1919) offers convincing evidence that plants exhaust water to a greater degree than is indicated by the wilting coefficient of Briggs and Shantz. They have shown from soil-moisture data obtained in the mixed prairies near McCook and

[1] An exception to this statement occurred during the summer of 1919 at the mixed-prairie station at Colorado Springs. Here, during certain periods when hot winds were blowing and the evaporating power of the air exceeded 45 or 50 c. c. per day, certain broad-leaved herbs partially wilted during the day, but always recovered at night.

Wauneta in southwestern Nebraska, after periods of prolonged drought, that "the concordance of the moisture-content with the hygroscopic coefficient (wilting coefficient ×0.68, *i. e.*, the amount of water a dry soil will absorb when placed in a saturated atmosphere with a constant temperature) was very striking, as though the plant roots, while not recognizing the wilting coefficient, practically ceased to withdraw water as soon as the hygroscopic coefficient had been reached. There was little difference in moistness between the surface foot and the succeeding 2 or 3 feet, and even the deeper subsoil was but little if at all moister. At no level and in none of the fields was there any growth water, the moisture-content being below the computed wilting coefficient." They also computed the hygroscopic coefficients from the data of Shantz (1911) in the short-grass plains at Akron, Colorado, and of Burr (1914) at North Platte, Nebraska. At Akron the soil-water, even during a season of excessive rainfall, was reduced below the wilting coefficient and approached or reached the hygroscopic coefficient at depths of 0.5 to 1.0 and 1.0 to 1.5 feet and at the fifth and sixth foot at certain periods during the growing season. At North Platte the water-content at all levels to 6 feet fell by the end of June (1912) to a point practically equal to the hygroscopic coefficient, there being no evidence of further drying of the subsoil. These data throw much light upon the degree of dryness to which the subsoil may be reduced by natural vegetation, and lead to the conclusion that under field conditions water is still available for growth after it has been reduced to the wilting coefficient (*cf.* Alway 1913 and 1917 on movement of capillary water in dry soils).

Eastward from the short-grass plains and through the mixed prairie the gradual amelioration of the severe climatic conditions for growth is indicated by a corresponding transition to a better developed type of vegetation. At the Lincoln station not only the natural vegetation and agricultural practice, but also the soil composition and the moisture conditions of the subsoil, show that the region is much more humid (Alway, 1916). Concerning investigations at Lincoln, Alway (1919) states:

"On only three occasions in the six-year period (1906-1912) did we find in the surface two or three feet the dry condition which indicates the approaching exhaustion of available moisture . . . . Thus as near the surface as the sixth foot, when conditions were such as to develop the driest subsoil, the ratio (of actual water-content to hygroscopic coefficient) was not much below that found in the deep subsoil under normal conditions. This failure of the natural vegetation of the prairies of eastern Nebraska to exhaust the free water of the deeper sub-soil is in sharp contrast with the conditions found on the short-grass prairies of the southwestern part of the State."

An examination of soil-moisture data from various prairie sites taken during the growing-seasons of 1916 to 1918 reveals the fact that at no time was the water-content reduced to the hygroscopic coefficient to a depth of 5 feet (Weaver, 1919).

In table 2, water-content determinations at the Colorado Springs station for 1918 and 1919 and at Lincoln for 1919 are recorded. The former station is located on a nearly level tract of land and the latter is on a level hilltop which represents upland-prairie conditions (plate 4). In the table, only water in excess of the hygroscopic coefficient is given. In the few instances where evaporation has depleted the water-content of the surface soil to a point below the hygroscopic coefficient this condition is indicated by the minus sign.

TABLE 2.—*Water-content of soils in excess of hygroscopic coefficient in true prairie at Lincoln and mixed prairie at Colorado Springs.*

Date.	0.0 to 0.5 foot.			0.5 to 1 foot.			1 to 2 feet.		
	Colorado Springs.		Lincoln.	Colorado Springs.		Lincoln.	Colorado Springs.		Lincoln.
	1918	1919	1919	1918	1919	1919	1918	1919	1919
June, second week	3.1	......	......	2.2	......	......	3.4	......	......
June, third week	1.5	......	16.6	2.2	......	16.6	5.1	......	......
June, fourth week	2.0	−0.3	......	1.7	−0.4	......	4.8	[1]3.9	......
July, first week	−1.0	6.7	11.5	−0.6	0.3	10.0	2.8	[1]3.5	9.5
July, second week	−0.3	4.2	2.3	0.3	0.0	5.3	1.0	[1]1.7	9.2
July, third week	7.5	0.2	0.0	3.5	1.4	3.5	2.7	[1]1.1	5.2
July, fourth week	0.5	2.0	−0.6	2.7	0.3	1.2	3.4	[1]2.6	1.6
August, first week	−2.2	8.8	......	−0.5	7.0	......	2.0	[1]4.7	......
August, second week	−1.5	4.5	4.4	−1.3	2.9	2.0	1.2	[1]1.5	2.0
August, third week	−0.9	−1.1	......	−0.3	3.0	......	......	[1]1.3	......
August, fourth week	......	−0.5	10.4	......	6.5	3.2	......	[1]1.5	2.2
September, first week	......	−1.9	1.2	......	−2.4	3.3	......	[1]1.0	3.4
Hygroscopic coefficient	5.4	5.4	9.5	5.7	5.7	8.7	3.3	3.3	8.6
Wilting coefficient	7.9	7.9	14.0	8.4	8.4	12.9	4.9	4.9	12.6

Date.	2 to 3 feet.			3 to 4 feet.		
	Colorado Springs.		Lincoln.	Colorado Springs.		Lincoln.
	1918	1919	1919	1918	1919	1919
June, second week	1.9	......	......	1.3	......	......
June, third week	5.5	......	......	4.1	......	......
June, fourth week	......	......	......	......	......	......
July, first week	......	......	9.9	......	......	10.0
July, second week	......	......	10.7	......	......	9.2
July, third week	4.1	2.0	......	3.2	1.6	......
July, fourth week	......	......	7.1	......	......	11.1
August, first week	......	......	......	......	......	......
August, second week	0.6	2.0	3.3	1.3	1.0	7.0
August, third week	......	......	......	......	......	......
August, fourth week	......	......	5.4	......	......	5.4
September, first week	......	......	5.6	......	......	8.3
Hygroscopic coefficient	3.5	3.5	7.1	4.4	4.4	6.3
Wilting coefficient	5.1	5.1	10.5	6.5	6.5	9.1

[1] Samples taken at a depth of 1.0 to 1.5 feet.

An examination of table 2 shows that water in excess of the hygroscopic coefficient was present, with occasional exceptions in the surface soil, at all depths at both stations. With the exception of a single determination, this excess of water was much greater at the true-prairie station at all depths below 1 foot, while in the surface soil it was often much greater than at the mixed-prairie station. In this comparison it should be kept in mind that the water-content data were obtained from an upland station and are much lower throughout than in lowland-prairie sites (*cf.* table 3). It is interesting to note that at the mixed-prairie station the soil moisture at all depths fell below the wilting coefficient, while even at Lincoln this condition obtained to a depth of 3 feet.

A study of water relations of plants must take into consideration not only the available supply but the rapidity with which this is expended. The evaporating power of the air is the environmental factor chiefly controlling the latter. During the growing-season of 1919, synchronous readings of the evaporation from Livingston's non-absorbing, white, cylindrical, porous-cup atmometers were made at the true-prairie and mixed-prairie stations. These were operated in the usual manner in duplicate, the evaporating surface extending from 2 to 5 inches above the soil surface. The readings are reduced to those of the standard cup. These data are shown in figure 7, where the read-

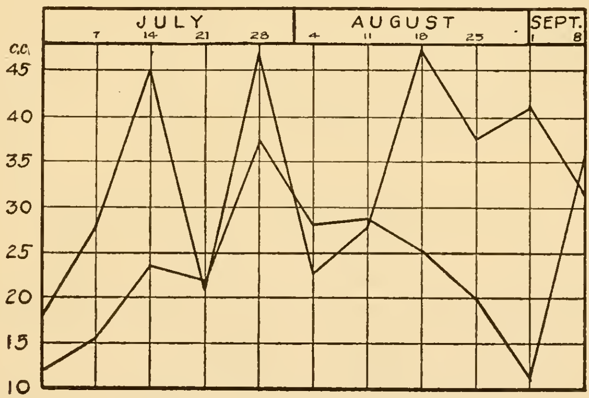


FIG. 7.—Graphs showing the average daily evaporation rates in the mixed prairie (upper line) and true prairie (lower line) during 1919.

ings from the atmometers on low and high prairie are averaged so as to represent a mean between the two prairie types. The much higher evaporation rate at the mixed-prairie station, where in fact it is often more than twice that in the true prairie, is clearly evident, and is an exceedingly important environmental difference in the two grassland habitats. That higher evaporating power of the air in the mixed prairie is the rule rather than the exception is further indicated in figure 8, where the data from the true-prairie stations at Lincoln, Nebraska for 1916 and 1917 are plotted with those obtained from the mixed prairie at Colorado Springs, Colorado, during 1918. At both stations the day losses are by far the greater. A consideration of the lower temperature of the mixed prairie at night in contrast with the conditions in true prairie, emphasizes the probability that the evaporating power of the air during the day in mixed prairie may exceed that of the true-prairie community even to a greater degree than the graphs indicate. The effect of excessively dry air, coupled with low water-

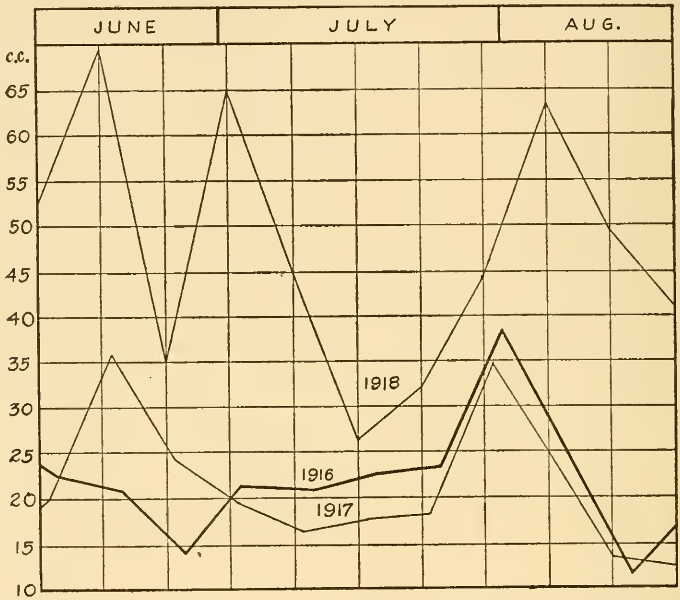


FIG. 8.—Graphs showing the average daily evaporation rates in the mixed prairie (1918) and true prairie (1916 and 1917).

content, accounts for the absence here of many true-prairie mesoxerophytes and the relative dwarfness of many true-prairie species when growing in the mixed-prairie habitat.

The average weekly day and night temperatures at the two stations during 1919 have also been determined. These data were obtained from the weekly record-sheets of thermographs placed in appropriate shelters among the vegetation at a height of about 4 or 5 inches. The averages for day temperatures were found by adding the temperatures beginning at 8 a. m. and every 2 hours thereafter until 6 p. m. for each day and dividing the sum by the total number of 2-hour intervals. Those for night temperature were calculated in a similar manner, beginning at 8 p. m. and including the readings until 6 a. m. An examination of the temperature graphs in figure 9 shows that, with few exceptions, the true prairies have a more favorable temperature for growth both by night and by day. The wide daily fluctuations in temperature at the mixed-prairie station, especially the relatively low temperatures at night, are certainly less favorable to plant growth than are the conditions prevailing in the true prairie. At the Colorado Springs station the daily fluctuation of air temperature among the plants was usually about 35° to 40° F., the air reaching a maximum of 90° or 95° F. in the shade in the afternoon and falling to 50° or 60° F. in the morning.

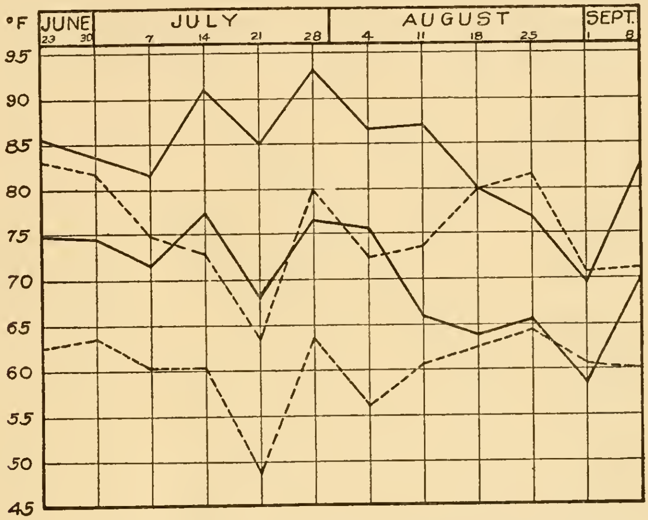


Fig. 9.—Graphs showing the average weekly day and night temperatures in the mixed prairie (broken lines) and true prairie (solid lines) during 1919.

According to Weather Bureau records, the season without killing frost usually extends from April 19 to October 10 at Lincoln, and from May 3 to October 3 at Colorado Springs. The Lincoln station is at an elevation of only 1,200 feet, that at Colorado Springs at 6,000. However, it seems quite certain that water-content of soil and air, and not temperature, are by far the principal factors in plant development. Further study will probably show that growth is often temporarily suspended for some mixed-prairie species, and perhaps permanently for others, by more or less extended periods of drought.

While soil temperatures were not obtained synchronously at the two stations, a comparison of the records taken at a depth of 4 and 8 inches at Colorado Springs during 1918 with those at Lincoln during 1916, 1917, and 1919 shows some marked differences. Those in the mixed prairie show an extreme variation in temperature during the 24-hour period. This ranged from 60° or 70° F. to 90° or 95° F. or even more at the shallower depth. During the latter part of the summer, even at a depth of 8 inches, the daily fluctuation was usually about 10° F. within the range of 70° to 85° F. The temperature of the surface soil shows an extreme variation. Not infrequently it ranges from 55° or 60° F. in early morning to 120° or 125° F. in the afternoon. Relatively greater insolation resulting from a sparser cover of vegetation to absorb radiant energy and an average lower specific heat of the drier, dark-colored soil, both combine to increase the day soil temperatures, especially of the more superficial layers, over those of true prairie. Such variations must have considerable influence upon the germination and ecesis of such species as *Kœleria cristata,* which may start growth in June upon the ripening of seed. At Lincoln, the soil at a depth of

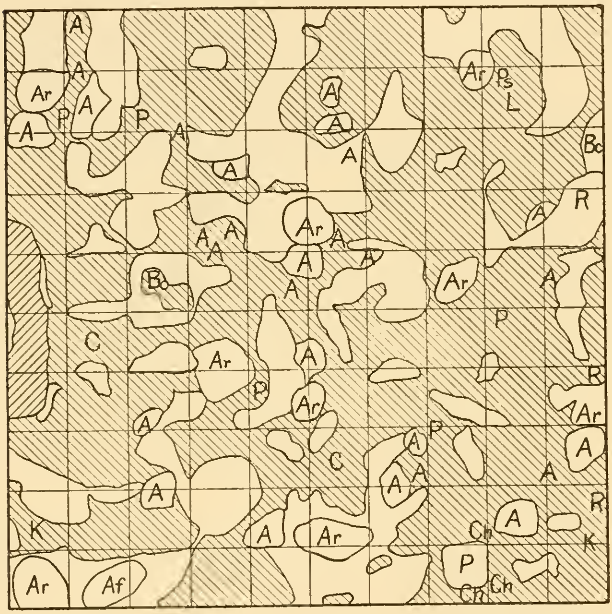


Fig. 10.

A meter quadrat in the mixed prairie community at Colorado Springs, Colorado. A, *Andropogon scoparius;* Af, *Artemisia frigida;* Ar, *Aristida purpurea;* \\\\, *Bouteloua gracilis;* Bc, *Bouteloua curtipendula;* Bo, *Bœbera papposa;* C, *Carex pennsylvanica;* Ch, *Chrysopsis villosa;* K, *Kœleria cristata;* L, *Lithospermum linearifolium;* ////, *Muhlenbergia gracillima;* P, *Psoralea tenuiflora;* Ps, *Pentstemon angustifolius;* R, *Ratibida columnaris.*

6 inches showed an average daily temperature range of 5° to 7° F. at the low and high prairie stations respectively; the soil temperatures varied from an average minimum of about 65° F. at the low-prairie station in early summer to a maximum of about 85° F. at the high-prairie station in August.

Comparatively few investigations have been made on the evaluation of soil temperature as an ecological factor in root growth. The work of Cannon (1918) on certain desert species is indicative of the importance of this factor not only in the development of the root system, but also in the general distribution of vegetation. Thus it has been shown that the general distribution of the cacti as a family is closely related to the response of the roots to the temperature of the soil. Even in the latitude of southern Arizona the conditions of soil temperature for most favorable water absorption do not prevail in winter, and the effect is a limitation in the development of both root and shoot of winter annuals (Cannon, 1911:88). With such superficially rooted species as *Opuntia polyacantha* and *O. camanchica*, abundant both in the short-grass plains and mixed prairie, as indeed with all persistent portions of perennial roots in the surface soil, the seasonal changes in soil temperature must be extreme. Soil temperature, like soil aeration, affects the development of root systems not only directly, but also plays a part in the life activities of soil microorganisms. These, as conditioned by soil temperature, may affect the plants directly (Jones, 1917) or alter the chemical composition of the soil and thus influence the root environment, which in turn may modify its development. Thus, soil temperature as an ecological factor is clearly of much importance and warrants careful study.

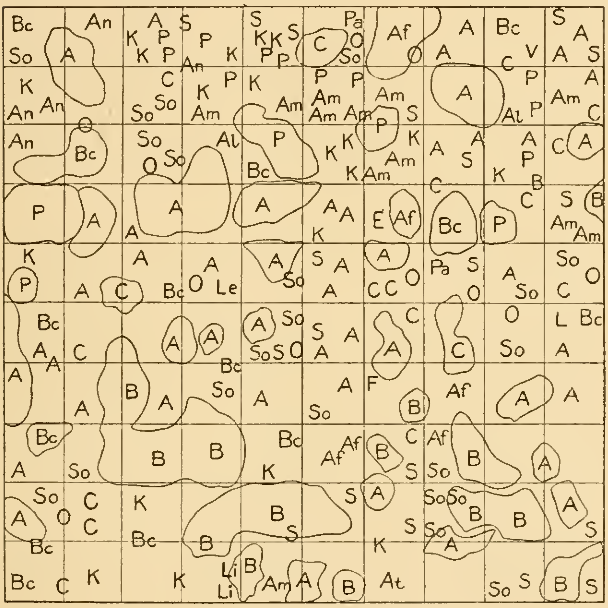


Fig. 11.
A meter quadrat in the true-prairie community at the upland station at Lincoln, Nebraska. A, *Andropogon scoparius;* Af, *Andropogon furcatus;* Al, *Allium mutabile;* Am, *Amorpha canescens;* An, *Andropogon nutans;* At, *Aster multiflorus;* B, *Bouteloua gracilis;* Bc, *Bouteloua curtipendula;* C, *Carex pennsylvanica;* E, *Euphorbia serpens;* F, *Festuca octoflora;* K, *Kœleria cristata;* L, *Linum sulcatum;* Le, *Lepidium virignicum;* Li, *Liatris punctata;* O, *Oxalis stricta;* P, *Poa pratensis;* Pa, *Panicum scribnerianum;* S, *Stipa spartea;* So, *Solidago missouriensis;* V, *Viola pedatifida.*

Summarizing, these combined differences of lower rainfall, drier soil, greater evaporating power of the air, and less favorable temperatures for growth at the mixed-prairie station are reflected both in the vegetational cover and in the root habit. Figure 10 shows a meter quadrat of the vegetation at the station in the mixed prairie (plate 4, A). In figure 11 is shown a similar area from the upland-prairie station at Lincoln (plate 4, B). Although these are limited areas when considering the vegetation as a whole, still the fact remains that a few carefully selected quadrats well made and thoroughly studied reveal much more concerning the structure of vegetation than long lists of species. In fact, the more exact quadrat method necessitates considerable familiarity with the vegetation.

In the mixed-prairie quadrat the dominance of the short-grasses, *Bouteloua gracilis* especially, but also some *Muhlenbergia gracillima*, and the grass-like *Carex pennsylvanica*, is at once apparent. This is due to the close grazing over the area previous to the establishment of the station. This likewise accounts for the abundance of *Aristida purpurea* (a plant eaten by stock only when other vegetation is scanty) the growth of which has been favored by the close grazing of its competitors. However, the real mixed-prairie nature of the vegetation is revealed by the frequent occurrence of *Andropogon scoparius* and the presence of *Kœleria cristata* and *Bouteloua curtipendula*, representing the tall-grasses. Although careful mapping reveals a considerable bare area, a condition which indicates a low water-content, and one usually underestimated in a casual survey, still the presence of *Artemisia frigida*, *Chrysopsis villosa*, *Lithospermum linearifolium*, *Psoralea tenuiflora*, and other subdominant herbs indicates a sufficient supply for both herbs and grasses. The absence of *Plantago purshii*, *Schedonnardus paniculatus*, and other ruderal or semi-ruderal species indicates that the vegetation is stable and has suffered no serious disturbance. Since inclosed in 1918, the tall-grasses and herbs are rapidly gaining in importance in the short-grass turf.

The quadrat on the hilltop in the true prairie (fig. 11 and plate 5, A) is typical for upland conditions. *Andropogon scoparius*, *Kœleria cristata*, *Bouteloua curtipendula*, and *Stipa spartea* with *Carex pennsylvanica* occur rather abundantly throughout. *Andropogon furcatus* and *A. nutans*, both more typical of low prairies, occur only sparingly and are associated with *Poa pratensis*. The grouping of these three less xerophytic plants in one portion of the quadrat and the presence of *Bouteloua gracilis* in another indicates differences of an edaphic nature. When field studies become more intensive, such differences may be readily understood. Constant differences in available water have not infrequently been found at stations only a few feet apart. Local areas of the shorter grasses are frequent on prairie ridges, but they are seldom of great importance. The large number of individual plants or clumps of plants in the area (over 215), the intimate mixture of so many other herbs, and the closed nature of the vegetational cover are all indicative of the more favorable growth conditions. This is further indicated by the presence of certain species (*Oxalis stricta*, *Poa pratensis*, etc.) which do not occur in the drier areas westward, but especially by the greater height growth and leaf development of plants like *Kœleria cristata* and *Bouteloua curtipendula*, which are found throughout both grassland communities. A further statement of the development of mixed-prairie vegetation, and especially of root systems, may be found in Chapter IV (*cf.* Chapter IV, and particularly plate A in "Ecological Relations of Roots").

COMPARISON OF HIGH AND LOW TRUE-PRAIRIE AREAS.

The station maintained in the low-prairie area during 1919 was located in Salt Creek Valley at the foot of the hill, a quarter of a mile distant and 60 feet lower than the one on the hilltop in the high prairie (plate 6). The alluvial soil is Wabash silt-loam. The high water-holding capacity and wilting coefficient (70 and 16.8 per cent for the first foot) indicate the presence of much clay and silt. Indeed, it is very similar to that of the cropped lowland plats at the same level and less than a quarter of a mile distant. A mechanical and chemical examination of the soil from the latter station may be found on page 140. The water-table is reached at a depth of about 9 feet. Using the vegetational cover as the indicator, this area was selected as representing typical low-prairie conditions. A comparison of the water-content at the two prairie stations is given in table 3.

At the upland station the water-content of the soil was lowered beyond the wilting coefficient to a depth of 3 feet. At the station in the lowland this condition was reached only once (at 2 feet) below the first foot of soil. However, the greater margin of water-content above the hygroscopic coefficient in the lowland is clearly shown by an examination of the table. The differences are especially marked in the deeper soils. This surplus available moisture has a profound effect upon the structure and development of the vegetation. Undoubtedly during years of drought it is the determining factor in selecting the plant population. The season of 1919 was one of excessive rainfall, especially during the spring and early in summer.

The evaporating power of the air at the two stations (measured as already described, from May 6 to September 14, 1919) is shown in figure 12. The parallelism of the graphs is a striking feature, but no

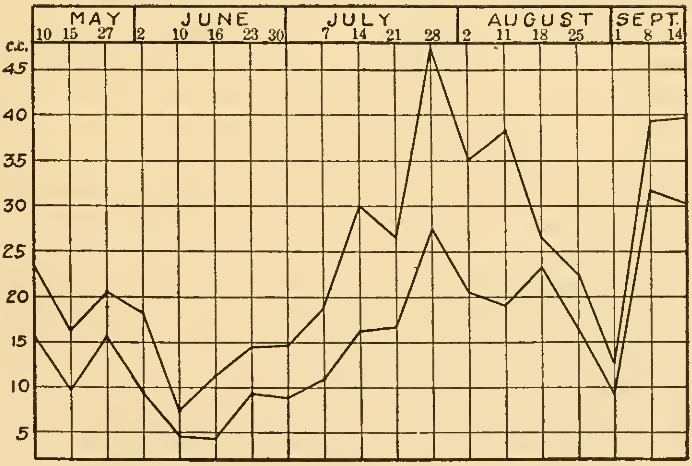


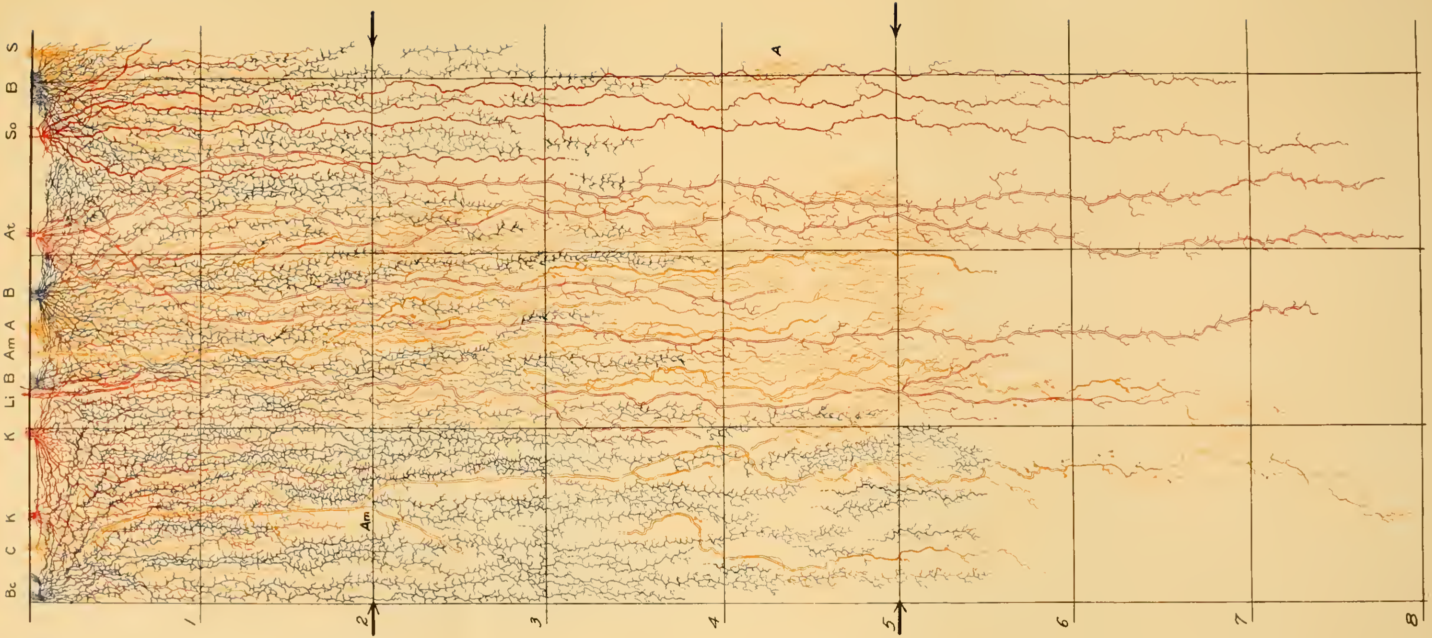
Fig. 12.—Graphs showing the average daily evaporation rates in the high prairie (upper line) and low prairie (lower line) at Lincoln, Nebraska, during 1919.

more so than the constantly higher evaporating power of the air at the upland station. Greater wind movement at the upper station is an important factor in causing the difference in evaporation, although humidity also requires consideration. The greater evaporating power of the air at the upland station, especially during periods of stress, is alone sufficient to cause considerable difference in the plant populations and, when coupled with water-content, satisfactorily accounts for the variations in the grassland vegetation. From July 7 to August 18, the average daily evaporation was 64 per cent greater at the upland station. During this period the average daily evaporation rates at the two stations were 20.8 and 34.1 c. c. respectively.

Thermograph records of soil temperatures at the two stations at a depth of 6 inches show no marked differences. The daily range at the lowland station was usually 4° to 7° F.; in the drier soil of the upland station 4° to 12° F. The minimum soil temperatures were 2° or 3° F. lower at the former station and the maximum 3° to 9° F. higher on the upland. Soil temperatures varied from a minimum of 53° F. (average 60° to 65° F.) late in May, when the instruments were installed, to a maximum of 85° F. (average 70° to 78° F.) in August. Except in early spring, when low temperatures on the lower, wetter soil may retard growth, while higher temperatures of the soil at all depths on the upland may facilitate absorption, it is not probable that the effects of temperature in the development of vegetation at the two stations is very different. However, as previously pointed out, our knowledge of soil temperature as an ecological factor is far from comprehensive.

A comparison of the two sets of thermograph records shows that differences of air temperature greater than 5° F. are rare at the two stations. It seems certain that such small differences in temperature variations in the range of the growth conditions (minimum 65° F. late in May, maximum 105° F. in July and August) would be almost negligible in the development of natural grassland. Selecting the week ending July 14 as illustrative, the maximum temperatures of 93° to 105° were reached at about 4 p. m., the minimum temperatures of 68° to 72° F. at $6^{h}30^{m}$ a. m. Not only are the amplitudes of the graphs on the record sheets at the two stations similar, but their courses are almost identical. Greater wind-movement on the upland frequently causes greater minor fluctuations. The night temperatures at the lower station are sometimes a few degrees lower (probably due to cold-air drainage on still nights), but quite as frequently they are slightly higher. The average day and night temperatures throughout the growing season at the high-prairie station may be found in figure 9.

These differences in habitat factors, and especially in air and soil moisture, reflect themselves variously in the structure and root development of the vegetation. The structure of the vegetation at the upland station has already been discussed. The low-prairie area is dominated



Quadrat-bisect showing root distribution of certain dominant and subdominant species of upland true prairie. Bc, *Bouteloua curtipendula;* C, *Carex pennsylvanica;* K, *Koeleria cristata;* Li, *Liatris punctata;* B, *Bouteloua gracilis;* Am, *Amorpha canescens;* A, *Andropogon scoparius;* At, *Aster multiflorus;* So, *Solidago missouriensis;* S, *Stipa spartea.*

by a few less xerophytic species; many of the species of the high prairie are absent, but are replaced in part by others of a more mesophytic kind. The dominant grasses, each often covering small areas with a pure or nearly pure growth, are *Andropogon furcatus*, which sometimes reaches a height of over 6 feet, *Panicum virgatum*, and *Poa pratensis* (plate 6). Species of considerable importance are *Spartina cynosuroides*, *Bouteloua gracilis* (especially where the soil is lighter in composition), *Solidago canadensis*, *Glycyrrhiza lepidota*, *Aster multiflorus*, *Poa compressa*, and *Solidago missouriensis*. Other common species are *Agropyrum glaucum*, *Physalis heterophylla*, *Polygonum muhlenbergii*, *Artemisia gnaphalodes*, *Zizia cordata*, *Callirhoë alcœoides*, *Eragrostis pectinacea*, *Achillea millefolium*, and *Veronica serpyllifolia*.

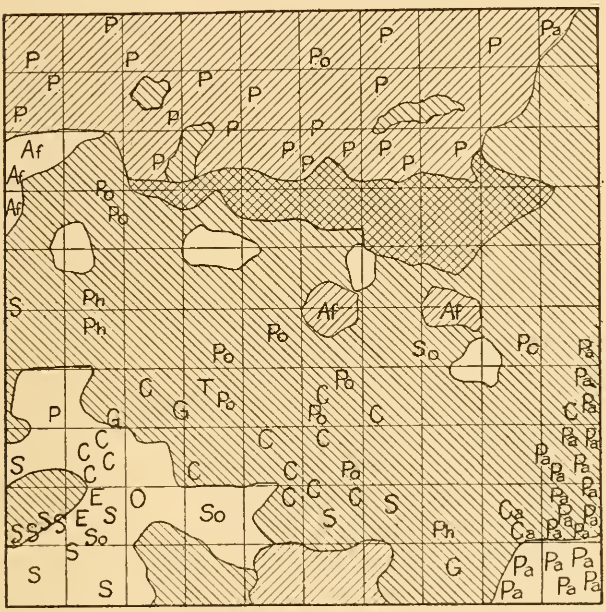


Fig. 13.

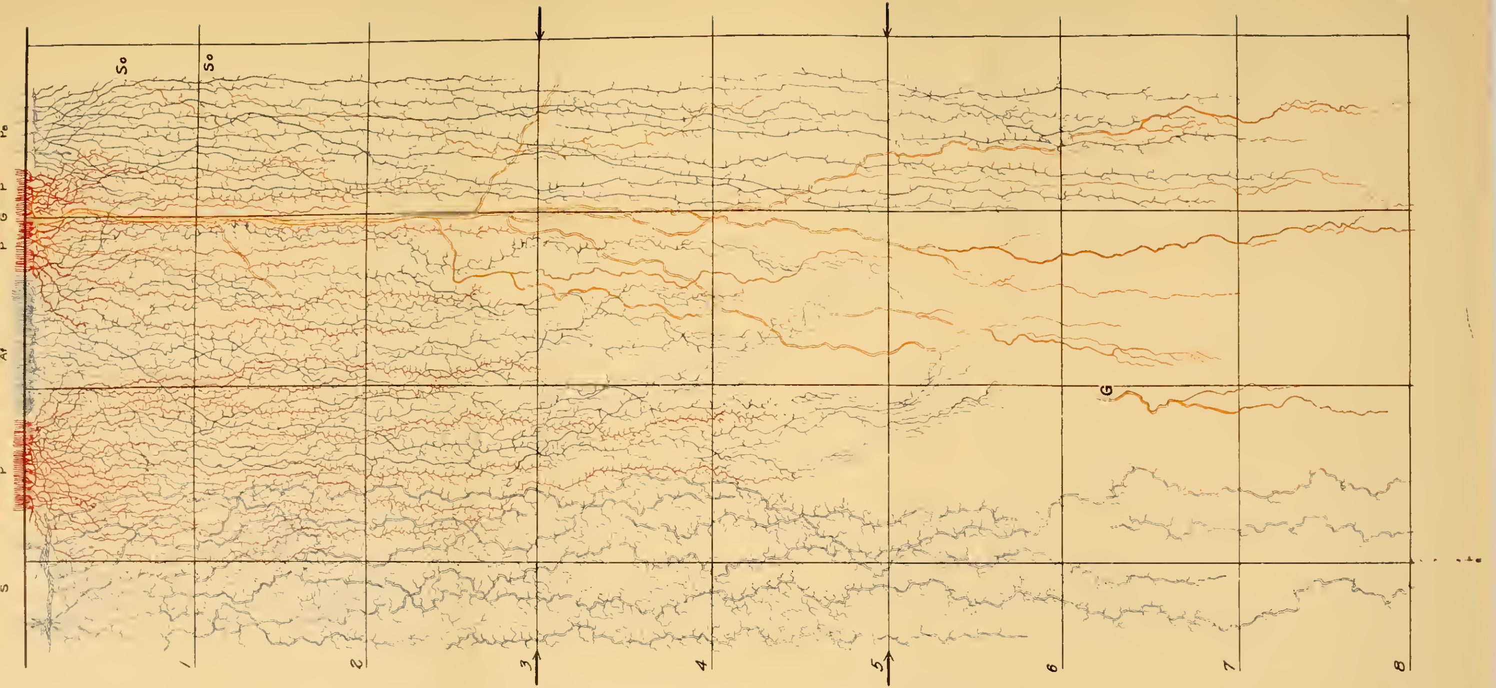
A meter quadrat in the true-prairie community at the lowland station at Lincoln, Nebraska. Af or ////, *Andropogon furcatus;* C, *Chætochloa viridis;* Ca, *Carex* sp; E, *Euphorbia maculata;* G, *Glycyrrhiza lepidota;* O, *Oxalis stricta;* P or \\\\, *Poa pratensis;* Pa, *Panicum virgatum;* Ph, *Physalis heterophylla;* Po, *Polygonum muhlenbergii;* S, *Spartina cynosuroides;* So, *Solidago altissima;* T, *Trifolium pratense.*

A carefully selected quadrat, typical of this low-prairie area, is shown in figure 13. The control of the three dominants mentioned above may be seen at a glance. This contrasts rather strikingly with the vegetation shown in figure 11 (*cf.* also plates 4, B, and 6, A).

Bisects along the sides of these two quadrats reveal some interesting root relations. In plate A, a bisect along the lower portion of the quadrat (fig. 11) on the high prairie may be seen. The above-ground parts in this quadrat are shown in plate 5, A. These bisects are made in the following manner: After charting and photographing the vegetation, a trench is dug at the side of the quadrat, care being taken to have the wall corresponding with the side of the quadrat cut smooth and perpendicular. Then, by the use of a hand-pick, the soil is carefully removed from the roots in the trench-wall along the edge of the quadrat to a horizontal distance of 3 inches. While this is under way the roots are measured and drawn in position to scale. This gives a picture of the exact root distribution in a block of soil a meter long, 3 inches wide, and to the depth of root penetration. Dotted lines indicate the entry or exit of roots into or from this soil area, respectively. In this way it is possible to show both the lateral and downward extent of the roots, the area occupied by each, and to get a picture of their interrelations. In the case of prairie grasses, however, it is not possible to picture all of the roots, as they are so numerous that this would confuse the situation and thus defeat the very purpose of the bisect.

A glance at plate A reveals the great masses of roots which fill the surface 3 or 4 feet of soil and the intense competition for water and solutes which must result. If the first impression is one of a confusion of details, this will only emphasize the difficulties met in the excavation of roots. It requires a very great amount of the most careful, painstaking effort, and repeated study under many conditions, until methods have been developed and a sufficient technique has been acquired so that one may become quite as familiar with the root systems as the aerial parts. However, a study of this plate shows that the root systems of the different species form layers in the soil. In fact, three of these layers are quite evident. The first extends to a level of about 2 feet, where the roots of *Stipa spartea*, *Kœleria cristata*, and *Carex pennsylvanica* mostly terminate. A second layer, extending to a depth of about 5 feet, is dominated by *Andropogon furcatus*, *Bouteloua gracilis*, and *B. curtipendula*. Extending far below this level, and extracting much water from the deeper soil, are *Liatris punctata*, *Aster multiflorus*, *Solidago missouriensis*, and *Amorpha canescens*. In this group of species none is well fitted for much absorption in the surface soil. In fact, there is little or no direct competition between these plants and those enumerated in the first group. Such a root distribution, together with maximum activities above ground at different times of the year (resulting in seasonal aspects), makes it very clear how so many plants can not only live but show normal development in such limited surface areas, *e. g.*, 215 individuals or individual groups in a single square meter.

The bisect along the edge of the quadrat (fig. 13) at the low-prairie station is shown in plate B. Here many of the plants are coarser rooted, especially *Spartina cynosuroides*, *Panicum virgatum*, and *Andropogon furcatus*. Three root layers are more or less apparent, the upper one being demarked by *Poa pratensis*, the second by *Andropogon furcatus*, while all of the other species extend well below the 5.5-foot level, beyond which depth the roots of *Andropogon* do not reach. In fact, the root systems of several species excavated on both high and



Quadrat-bisect showing root distribution of certain dominant and subdominant species of lowland true prairie. S, *Spartina cynosuroides;* P, *Poa pratensis;* Af, *Andropogon furcatus;* G, *Glycyrrhiza lepidota;* Pa, *Panicum virgatum;* So, *Solidago altissima.*

TABLE 3.—*Water-content of soils in excess of the hygroscopic coefficient at the upland and lowland stations in the true prairie at Lincoln during 1919.*

Date.	Depth 0 to 0.5.		Depth 0.5 to 1.		Depth 1 to 2.		Depth 2 to 3.		Depth 3 to 4.	
	High.	Low.	High.	Low.	High.	Low.	High.	Low.	High.	Low.
Apr. 28	18.5	24.4	22.2	26.5	19.1	......	13.8	......	11.4	16.1
May 5	19.8	26.1	18.2	17.3	15.6	16.1	9.8	17.5	14.2	19.5
May 27 [1]	8.2	8.8	13.7	17.8	11.2	16.4	......	......	......	......
June 16	16.6	24.5	16.6	18.6	......	......	......	......	......	......
July 1 [2]	11.5	11.7	10.0	11.1	9.5	17.1	9.9	17.1	10.0	18.5
July 8	2.3	5.4	5.3	5.7	9.2	16.8	10.7	17.1	9.2	20.6
July 14	0.0	4.4	3.5	5.6	5.2	9.6	......	......	......	......
July 28	−0.6	0.1	1.2	1.9	1.6	5.1	7.1	13.3	11.1	18.5
Aug. 11	4.4	6.8	2.0	3.6	2.0	5.9	3.3	8.1	7.0	18.1
Aug. 26	10.4	17.2	3.2	6.1	2.2	7.3	5.4	8.9	5.4	17.9
Sept. 6	1.2	−0.2	3.3	4.4	3.4	2.6	5.6	9.3	8.3	18.9
Sept. 26	14.5	17.2	15.0	15.2	5.2	5.8	2.6	10.0	5.7	16.2
Wilting coefficients	14.0	17.3	12.9	16.3	12.6	15.1	10.5	15.0	9.1	17.5
Hygroscopic coefficients	9.5	11.8	8.7	11.1	8.6	10.3	7.1	10.2	6.2	11.9

[1] The soil had been no drier at any time since May 5.
[2] Samples taken a few days after heavy rains.

low prairie areas yield data which indicate that the root development is not so extensive in the more moist lowland soil. This is of considerable interest in itself and is especially significant, since many crop plants are found to respond to these different environments in a similar manner. Thus the root development of the natural vegetation may be used as an indicator of the development of those of crop plants. The data on root habits of prairie species are summarized in table 4, while those of cultivated crops are discussed in Chapter VII.

TABLE 4.—*Root development of grasses on low and high prairies.*

Species.	Station.	Maximum depth, in feet.	Working depth, in feet.
Agropyrum glaucum	Lowland	8.0	7.0
Do	Upland	9.0	8.0
Andropogon furcatus	Lowland	5.5	4.7
Do	Upland	6.8	5.2
Poa pratensis	Lowland	5.0	2.8
Do	Upland	5.8	3.3

III. ROOT SYSTEMS OF SHORT-GRASS-PLAINS SPECIES.

Although root excavations of both native and crop plants of short-grass plains have been made at six stations and the dominants thoroughly studied, only two new species in addition to those already reported (Weaver, 1919) are here described. Indeed, the short-grasses usually have such profound control of the area that other grasses and herbs are relatively rare. In the chapter on ecads, the root systems of these dominants will be fully discussed. They have been repeatedly excavated and studied in many localities, not only in the short-grass plains but also in mixed and true prairie.

Opuntia polyacantha and *Schedonnardus paniculatus* were examined on the short-grass plains about 5 miles northwest of Sterling, Colorado (fig. 14). The precipitation at Sterling is only about 17 inches. The run-off must be high, for, although much of the ground is bare between the alternating mats of *Bulbilis dactyloides* and *Bouteloua gracilis*, the roots extend throughout the surface soil and bind the hard silt-loam into a very compact substratum (plate 2, A). A so-called "hardpan"

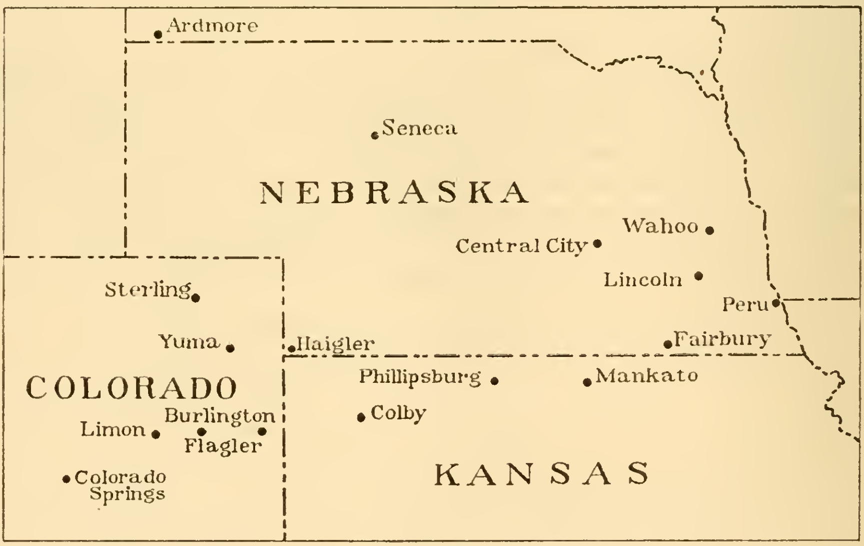


FIG. 14.—Map showing stations in the grassland associations where studies of root systems have been made.

occurs here at a depth of about 2 feet. Aside from the dominant grasses, *Opuntia polyacantha* and *O. camanchica* were the most conspicuous species. But as in all typical short-grass plains areas (*cf.* p. 109) more or less of *Aristida purpurea*, *Psoralea tenuiflora*, *Festuca octoflora*, *Plantago purshii*, *Artemisia frigida*, *Schedonnardus paniculatus*, etc., are to be found. The relative abundance and luxuriance of these species is a reliable criterion of favorable or unfavorable conditions for crop development. This is further discussed in Chapter VI (*cf.* also Shantz, 1911, and Clements, 1920).

Opuntia polyacantha.—This cactus enjoys a wide range from the subclimax prairie along the Missouri, through the true and mixed prairies to the short-grass plains of Colorado and New Mexico. In fact, it reaches its best development and greatest abundance under the more arid conditions. It is greatly favored in its competition with the grasses by close grazing of the latter, and consequently it becomes an indicator of overgrazed areas. In such places it is frequently the most conspicuous feature of the landscape (plate 11, A),

Three specimens growing on the short-grass plains were examined. As in the case of *Opuntia camanchica* and *O. fragilis* (Weaver, 1919: 61), and other cacti (Preston, 1900), the root system consists of two distinct parts—a few vertically descending anchorage and deep absorptive roots and a much more extensive absorbing system in the surface soil. The deeper roots of the specimens examined were only 3 to 5 in number, about 2 to 3 mm. in diameter, and glistening white in color. They were fairly well branched, with rebranched laterals mostly 0.2 to 0.3 foot in length, and reached depths of 1.5 to 2 feet. Unlike the brownish surface roots, they were quite fragile. The surface root-system consists of 14 to more than 24 roots, varying in diameter from 5 to 6 mm. to mere threads. They originate from the base of the plant and often from the partially buried branches. These roots seldom penetrate beyond 3 or 4 inches and are often found nearer the surface. They pursue rather tortuous courses parallel with the surface of the soil and reach a distance of 5.5 feet from the base of the plant. For example, one root, 3 mm. in diameter and 5 feet in length, was traced at a depth of 3 inches to a distance of 4 feet from the place of its origin. The roots taper very slowly in spite of much branching. They branch repeatedly from their origin at the base of the plant to their extremity, with both large and small branches, which ramify in all directions and thus furnish an enormous absorbing surface. The ultimate root-ends, whether of the shorter or larger branches, consist of much-divided and very delicate brush-like termini, to which the soil clings with great tenacity. Only the larger roots run for distances of several inches without a profuse supply of laterals. As a whole the root system is strikingly like that of *Opuntia camanchica* and is distinctly superficial in its position in the soil. Such plants can compete successfully with the grasses for the moisture in the surface soil afforded by summer showers.

Schedonnardus paniculatus.—This annual or sometimes short-lived perennial grass is nearly always present in small numbers in short-grass sod. On denuded areas it becomes more abundant and usually replaces the earlier weed stages and is in turn replaced by more stable vegetation. It is an excellent indicator of overgrazing or other disturbance of the natural plant cover. It was examined on the short-grass plains near Sterling, where some bunches were growing in the open sod of buffalo grass and grama. The shallower roots are very much like those of *Aristida purpurea*. They spread out laterally, at 0.1 to 0.2 foot below the surface, in such a manner that at a depth of 0.4 to 0.5 foot they may be from 1 to 1.5 feet horizontally away from the plant, although some penetrate more or less vertically downward. These roots were traced to a depth of 2 feet, where they broke off so easily and were so nearly like those of *Bouteloua gracilis* that, although several clumps were examined, none could be recovered in their entirety from the hard soil to a greater depth. It is probable that they extend a little deeper, although the root system as a whole is relatively shallow.

IV. ROOT SYSTEMS OF MIXED-PRAIRIE SPECIES.

A study of the root systems of mixed-prairie species has been made both in hard, black-loam soils and in the sandhills. Since root development is usually quite different under varying edaphic conditions, even where the same species is concerned (Weaver, 1919:110), it will be more convenient to consider the root systems in the two kinds of soil separately.

SPECIES EXCAVATED IN SANDY SOIL.

Extensive investigations were made in the sandhills near Haigler, Seneca, and Central City, Nebraska, and Yuma, Colorado (plates 7, 8, 9, and 10). Because of the wide territory investigated during the field season, no regular stations for the securing of habitat factors were maintained in the sandhills. Complete records of environmental factors, however, were taken in the mixed prairie at Colorado Springs. These have already been contrasted with those of true prairie (p. 27). Since run-off is slight and evaporation of soil moisture low in sandy soil, some notion of water-content may be gained from the precipitation records. The average annual precipitation at Haigler is 16.5 inches; at Yuma, 17.5; at Seneca, approximately 20; and at Central City, 26. This last station is in the extra-regional sandhills which lie at the extreme eastern border of the mixed prairie, if indeed not in the true-prairie region.

The vegetation at Haigler, in extreme southwestern Nebraska, is characterized by numerous species of bunch-grasses, a fairly well-developed layer of short-grasses and sedges, and by the large, bushy sandhill sage. Where overgrazing has occurred and the grasses have been reduced both in size and number, *Artemisia filifolia,* greatly increased in abundance, stands out alone as dominant (plate 7, A). The taller dominant grasses are represented by *Andropogon scoparius, Stipa comata, Andropogon hallii* and *Calamovilfa longifolia. Kœleria cristata* and *Aristida purpurea* are of lesser importance. The short-grasses are well represented by *Bouteloua hirsuta* and *B. gracilis.* These, with the less abundant *Carex pennsylvanica, Festuca octoflora,* and *Carex stenophylla,* which are common throughout, form mats over extensive areas, especially in the more compact soil. In the loose sands of blowouts, *Redfieldia flexuosa* and *Sporobolus cryptandrus,* with the shorter *Muhlenbergia pungens,* are abundant. Subdominant species are numerous; the following are the most important:

Acerates spp.
Allionia linearis.
Artemisia filifolia.
Asclepias arenaria.
Carduus plattensis.
Chrysopsis villosa.
Cyperus schweinitzii.
Erigeron bellidiastrum.
Eriogonum annuum.
Frœlichia floridana.
Haplopappus spinulosus.
Helianthus subrhomboideus.
Ipomœa leptophylla.
Liatris punctata.
Liatris squarrosa.
Lygodesmia juncea.
Meriolix serrulata.
Paspalum setaceum.
Pentstemon angustifolius.
Petalostemon villosus.
Thelesperma gracile.
Yucca glauca.

The vegetation at this station, in the main, belongs to "the bunch-grass association" of Pool (1914), except in the local blowouts and in the valley of the Republican River, where sod-forming vegetation is in control. The following species were examined here:

Paspalum setaceum.—This grass is frequently rather abundant in dry sandy soils. Several bunches, from 1.5 to 8 inches in diameter, were examined. The plants are connected by very thick rhizomes. From the base of the plant

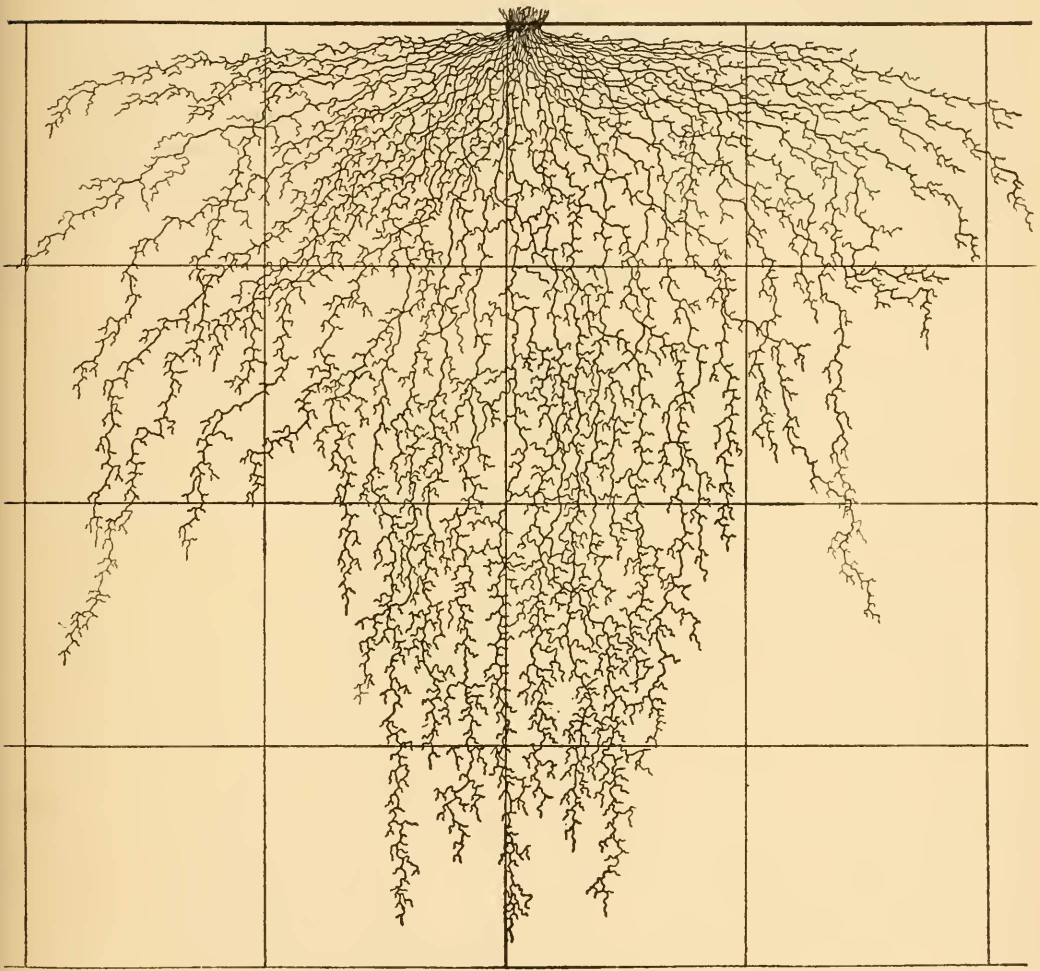


Fig. 15.—Root system of *Paspalum setaceum.*

and from the rhizomes originate great numbers of tough, wiry roots; 40 of these were counted on a single clump only 1.5 inches in diameter. The roots are only about 0.5 mm. in thickness, but because of their characteristic dark-brown color they can be traced with great certainty among the roots of the other species. They fill the soil not only beneath the plant, but on all sides. Some of the roots penetrate vertically downward to maximum depths of 3.8 feet; others pass obliquely downward at all angles, while some run off at a depth of only 0.1 to 0.2 foot or slightly deeper and nearly parallel to the soil surface. The latter may end in the first 0.5 to 1 foot of soil at distances of 1 to 2 feet from the plant (fig. 15). Beginning in the second inch of soil, the roots are exceedingly well branched. These branches are very fine; the older ones are black and the younger ones lighter in color. They vary from a millimeter to 8 centimeters in length. While some are only slightly branched, others are branched to the second or third order. The working depth is 3.2 feet. Thus this grass is well fitted for absorption in the surface 2 or 3 feet of soil for a distance of 1 to 1.7 feet on all sides of the clump.

Erigeron bellidiastrum.—This subdominant, much-branched annual frequently forms extensive societies in the sandhills. At this station the plants were very abundant, 1 to 1.2 feet high, and in full bloom. All of the eight specimens examined had tap-roots from 2 to 5 mm. in diameter, which tapered so rapidly that at a depth of a foot they were never over 1 or 2 mm. thick. Beginning about an inch below the surface, branches come off in great profusion. The largest of these, which are usually 3 to 7 in number, varying with

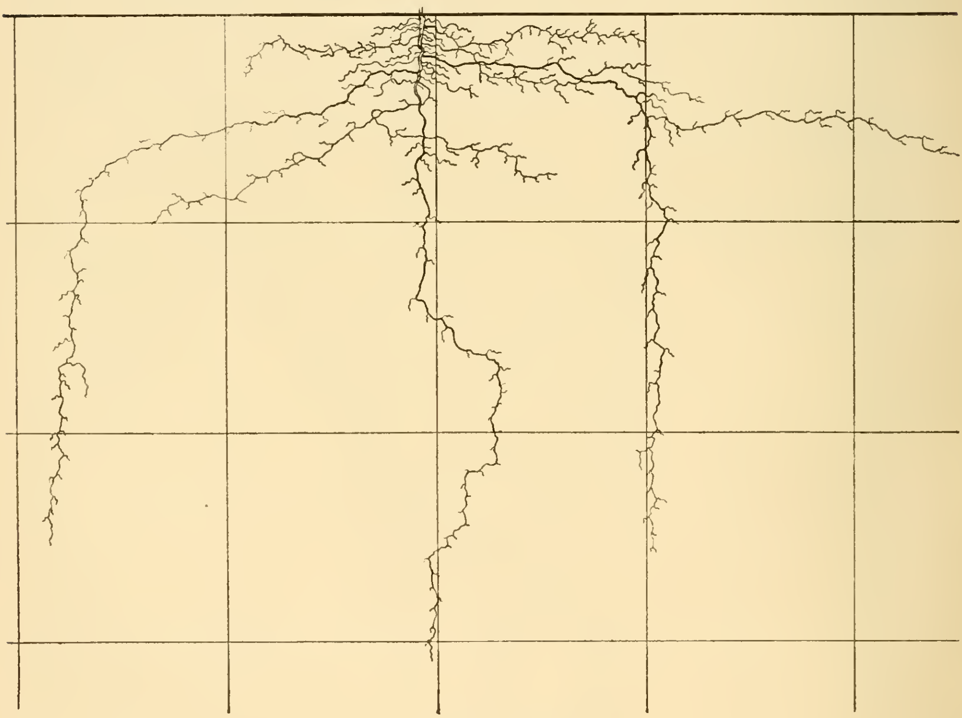


Fig. 16.—*Erigeron bellidiastrum.*

the size of the plant, are only 1 to 2 mm. in diameter, while the others are much smaller, some being hairlike. Most of the larger ones run off in a direction more or less parallel with the soil surface for distances of 0.7 to 1.7 feet before turning downward. While some of these end without descending below the first foot, other branches were traced to depths of 2.5 feet (fig. 16). The tap pursues a more or less devious downward course, but seldom meanders more than a foot horizontally from the base of the crown. Both the tap and larger laterals are abundantly supplied with threadlike, mostly unbranched, secondary rootlets. These are very fine and range in length from a few millimeters to more than 3 centimeters. Practically all of the larger branches originate within the first 6 to 8 inches of soil. No roots were found at a depth greater than 3.2 feet. The whole root system is light tan in color. This species, then, has a widely spreading but not deeply seated root system.

Liatris squarrosa.—The blazing-stars are herbs which form extensive autumnal societies throughout the grassland formation. This species blossoms somewhat earlier than the others and from July to September its bright purple flowers are a conspicuous feature of the landscape. A number of plants were examined on a sandy hillside. They were 1 to 1.2 feet in height and in full bloom. This species, unlike *Liatris punctata* with its strong, deep tap-root (Weaver, 1919:9), is provided with a large number of rather fibrous roots originating from a corm, thus resembling *Liatris scariosa.* The corm varies in depth from 3 to 8 inches. It ranges in diameter from 0.7 to 1 inch

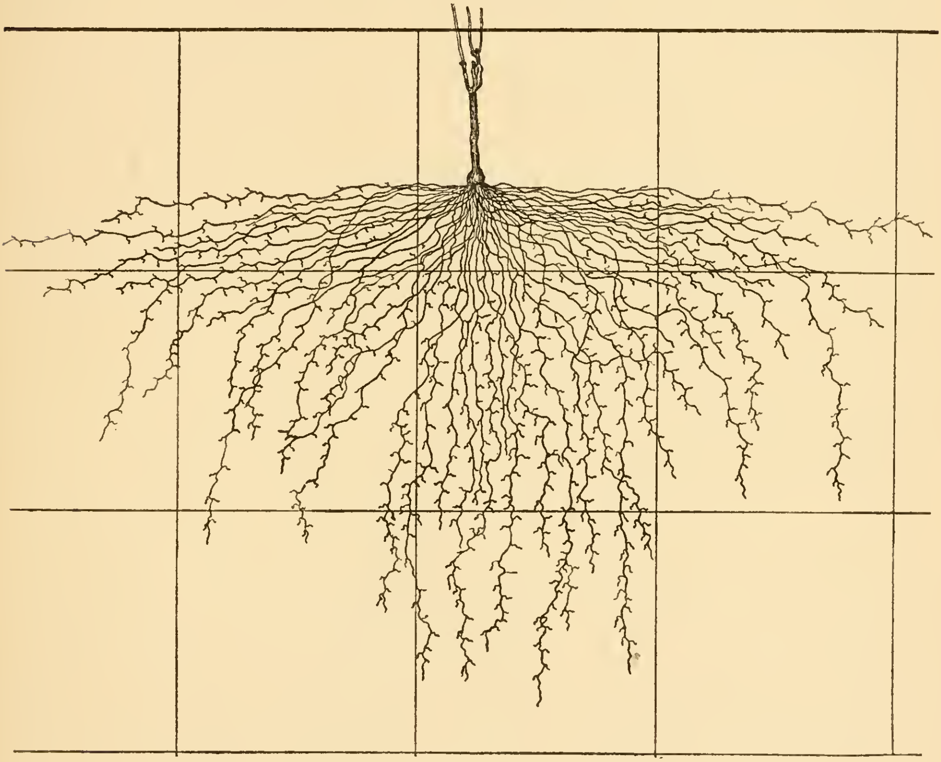


Fig. 17.—Corm and root system of *Liatris squarrosa.*

and is from 1 to 1.3 inches long. From the base of the corm arise great clusters of whitish roots, 36 to 80 of which were counted on different plants. The largest are about a millimeter in diameter. All of the roots are extremely fragile and hence traced with great difficulty. They spread out in the sandy soil in such a manner as to form roughly a half sphere (fig. 17). Some of them run parallel with the soil surface for a distance of 2 feet. Others penetrate vertically downward to a depth of 2.8 feet. Within a radius of 4 to 6 inches from the corm there are practically no branches. Otherwise the roots are fairly well supplied with unbranched laterals seldom over an inch in length. In fact most of them have an extent of less than 0.5 inch. Here, again, is a widely spreading but relatively shallow root system.

Asclepias arenaria.—This milkweed, while seldom occurring in great abundance, is a widely distributed component of mixed-prairie vegetation of the sandhills. Three specimens were examined on a fairly well covered hillside. The plants were about 2 feet high and in blossom. One tap-root gave rise to two stems, the others each to one, at depths of 6 and 8 inches respectively.

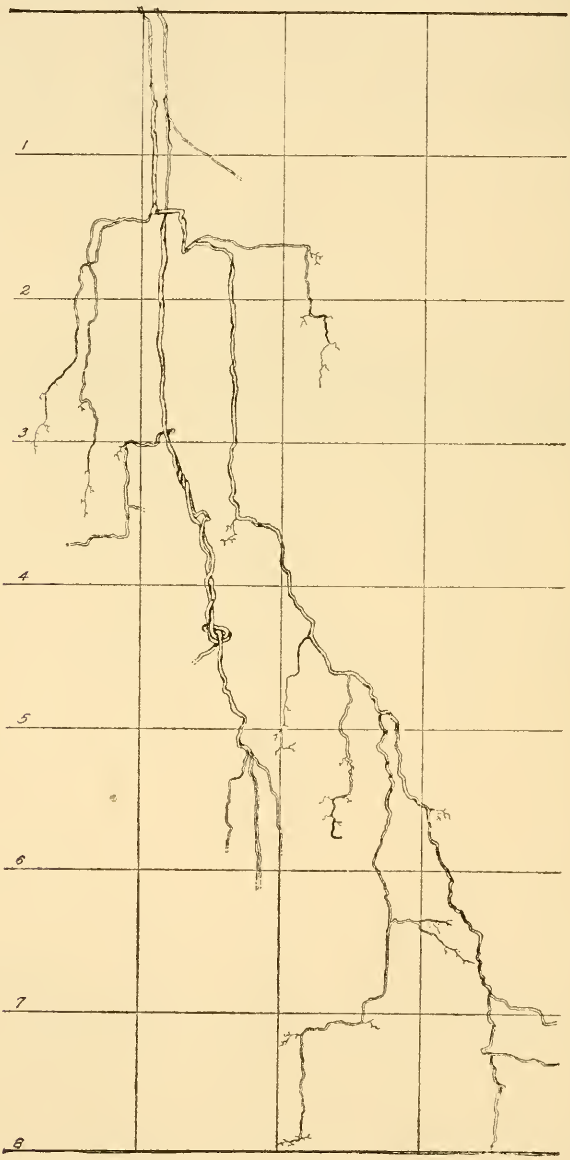


Fig. 18.—Root system of *Asclepias arenaria*.

The large fleshy tap varies from 12 to 25 mm. in diameter, often being thicker in the deeper soil than at its point of origin. These light-tan-colored roots are very brittle; they are definitely characterized by a very tortuous course, turning at sharp angles, and frequently by much twisting and looping (fig. 18). The branches, both large and small, often arise where the roots turn abruptly. Some of the major laterals are as large as the tap-root; and indeed the tap-root may split up, usually at considerable depths, into branches of almost equal size. Several of the main roots were traced beyond a depth of 8 feet, the caving sand not permitting further excavation. It is probable that they penetrated 2 or 3 feet deeper. This is perhaps the most poorly branched root system examined in the sandhills. Even the limited number of small branches that do occur end abruptly and have only a few small unbranched laterals.

Haplopappus spinulosus.—This composite has a wide distribution throughout the drier portions of the grassland formation from Canada to northern Mexico. It is a subdominant, frequently occurring in extensive societies. This species was examined on a fairly well covered slope in mixed prairie. It had a strong woody tap-root, 8 mm. in diameter and dark brown in color, which ran almost vertically downard and tapered rather rapidly, so that at a depth of a foot it was only 2.5 mm. thick; below this point it narrowed slowly to its end at a depth of 5 feet. Most of the branches were thrown off in the first foot of soil. The largest were not over 2 mm. in diameter, while many were threadlike (fig. 19). The larger laterals ran obliquely outward and downward, so that at a depth of a foot they had reached their maximum distance of 1 to 1.3 feet horizontally from the base of the plant. Below this depth they ran rather vertically downward to distances of 3.5 to 4.5 feet. Like the tap-root, these laterals are clothed with a great number of rather poorly branched whitish rootlets. These stand out in striking color contrast to the larger brown roots. These finer rootlets are 1 to 5 inches (usually 2 or 3 inches) in length and end with very little branching. Below 1 foot the tap was poorly branched to a depth of 2.5 feet, where some long laterals originated, as shown in the drawing. In the moist sand the root-endings were fairly well branched, but with rather coarse laterals. This species is illustrative of a moderately branched, rather wide-spreading, and fairly deep-seated root system.

Meriolix serrulata.—This primrose is an estival bloomer of wide distribution. It occurs not only in mixed prairie, but frequently also in the short-grass plains. It reaches its best development and forms the most marked societies, however, in the true prairie. In drier areas it is usually much dwarfed and the bright-yellow flowers are much smaller. Several plants were examined. They were growing on a partly covered, sandy hillside. They have woody tap-roots, 8 to 15 mm. in diameter and of a reddish-brown color. The propagation of the plant by its widely spreading underground parts is shown in figure 20. In places the sand had blown away and left portions of these unearthed. All of the larger roots are characterized by their lax and meandering courses. While reaching a depth or distance from the base of the plant of only 2 or 3 feet, they may actually be 4 or 5 feet long. Both the tap-root and its major branches taper very slowly. While well supplied with larger branches, which often originate in a dichotomous manner, smaller branches are not very abundant. Usually the root termini are well branched and occasionally fairly well-branched sublaterals occur. The maximum depth of root penetration was found to be 4.5 feet. The characteristic meandering course, wide spread, and depth of penetration is well illustrated in figure 20.

Mentzelia nuda.—This tall, coarse, somewhat woody herb is a species of rather wide distribution throughout the drier portions of the grassland formation. It is often locally abundant and forms marked societies when the large yellowish-white flowers are in bloom during July and August. Three large plants were examined on the well-covered rim of a blowout. The largest had a tap-root an inch in diameter, from which arose 4 erect stems over 2 feet high. The crowns of all three plants were more or less decayed and somewhat spongy

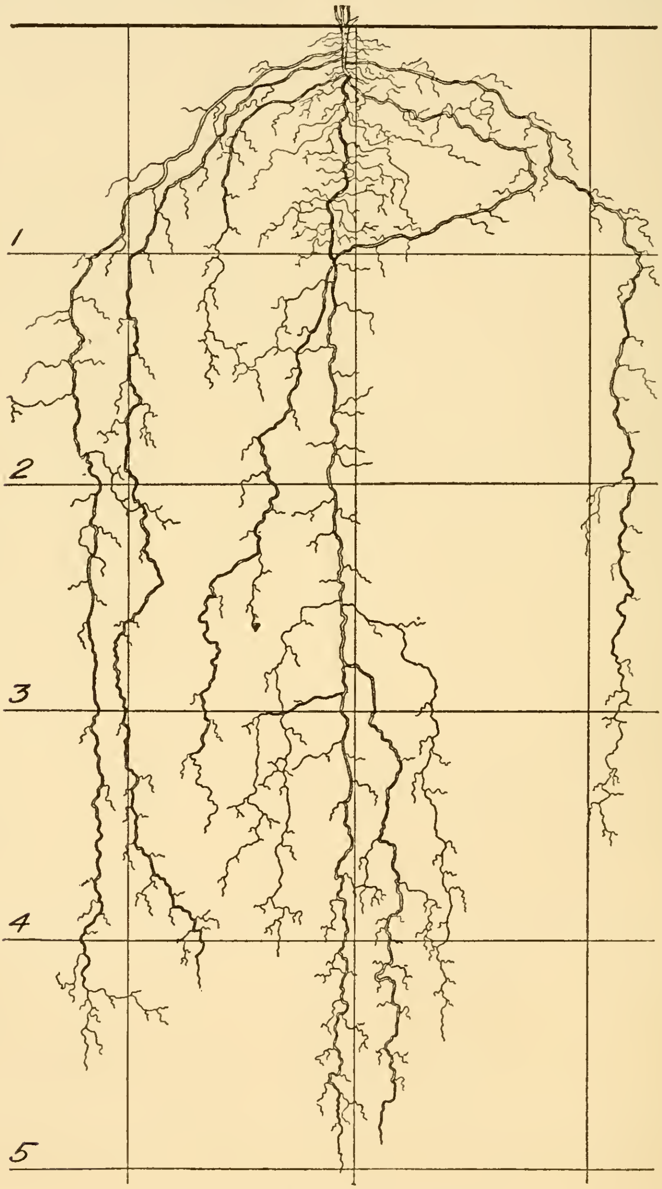


Fig. 19.—*Haplopappus spinulosus.*

in texture. The tap-roots keep their dominance throughout and at a depth of 5 feet one was still 2 mm. in diameter. They reached a maximum depth of 5.3 feet. No branches were given off in the first 6 to 8 inches of soil, but below this-point branches from 2 to 6 mm. in diameter arose. These seldom ran out

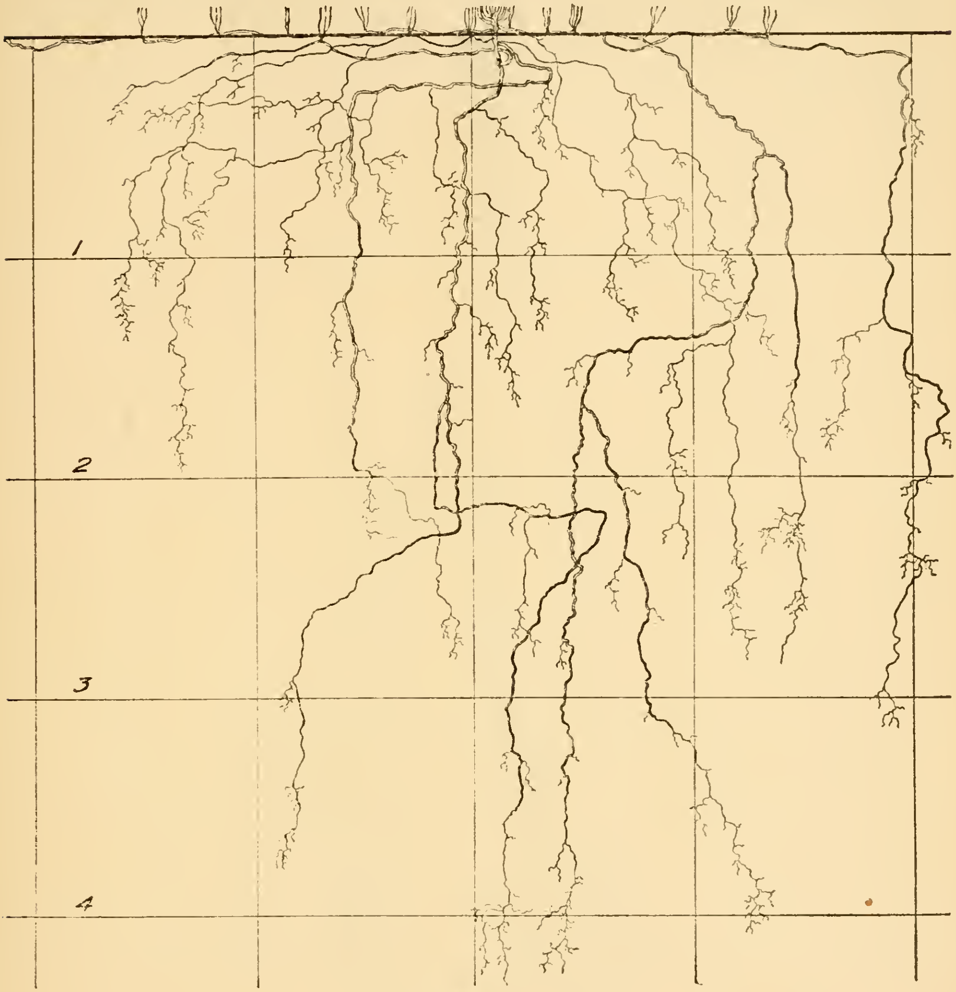


Fig. 20.—*Meriolix serrulata.*

laterally for greater distances than a foot from the tap. They branched only poorly. The fleshy, dark-tan-colored root is kinked and curved and the smaller branches especially are very brittle. Even the root-tips end abruptly with only a few branches. Figure 21 illustrates the dominance of the tap-root, paucity of small laterals, and the depth of penetration.

Eriogonum annuum.—This tall, erect annual is a very common component of sandhills vegetation, frequently occurring in considerable abundance. The plants examined near Haigler, Nebraska, were 2 feet tall and just ready to blossom. It has a tap-root 3 to 5 mm. in diameter, yellowish in color, and somewhat woody, which tapers very rapidly, so that at a depth of 8 inches it is seldom over 2 mm. in diameter. Just below the ground-line it gives off large numbers of rootlets usually running in a direction parallel with the soil surface, and varying from threadlike to those with a diameter of 3 mm. Some were traced at a depth of 0.2 to 0.3 foot to 3 feet from the base of the plant. As shown in

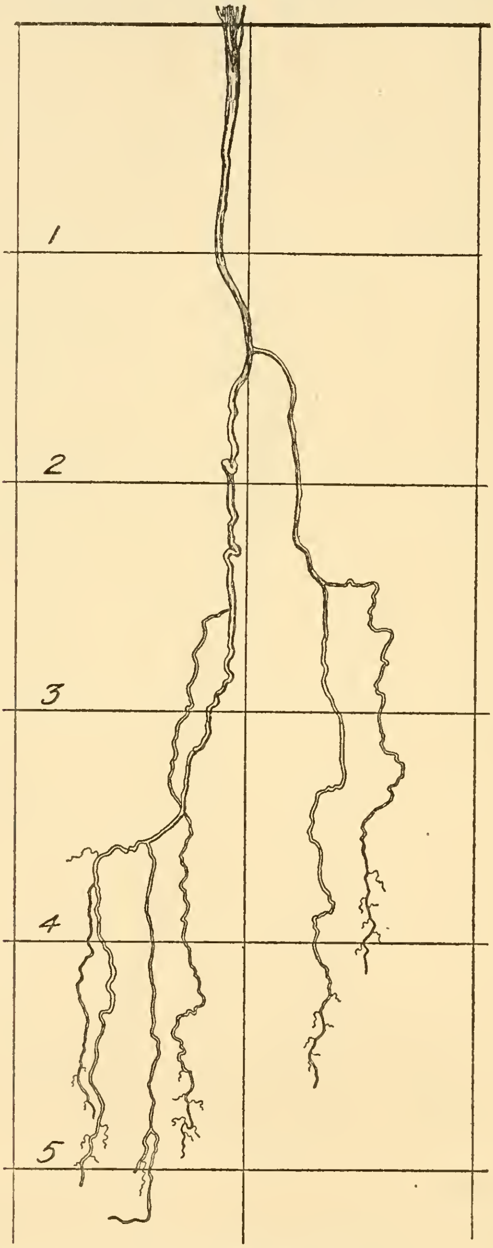


Fig. 21.—*Mentzelia nuda.*

figure 22, they are well branched throughout and end in the surface soil. The deeper branches are also wide spreading. Usually the tap dominates throughout. A maximum depth of 5.3 feet was recorded for one of the plants. Another had a tap-root 5 feet long. While this may appear to be a remarkable growth for an annual, it is no greater than that of many crop plants of similar

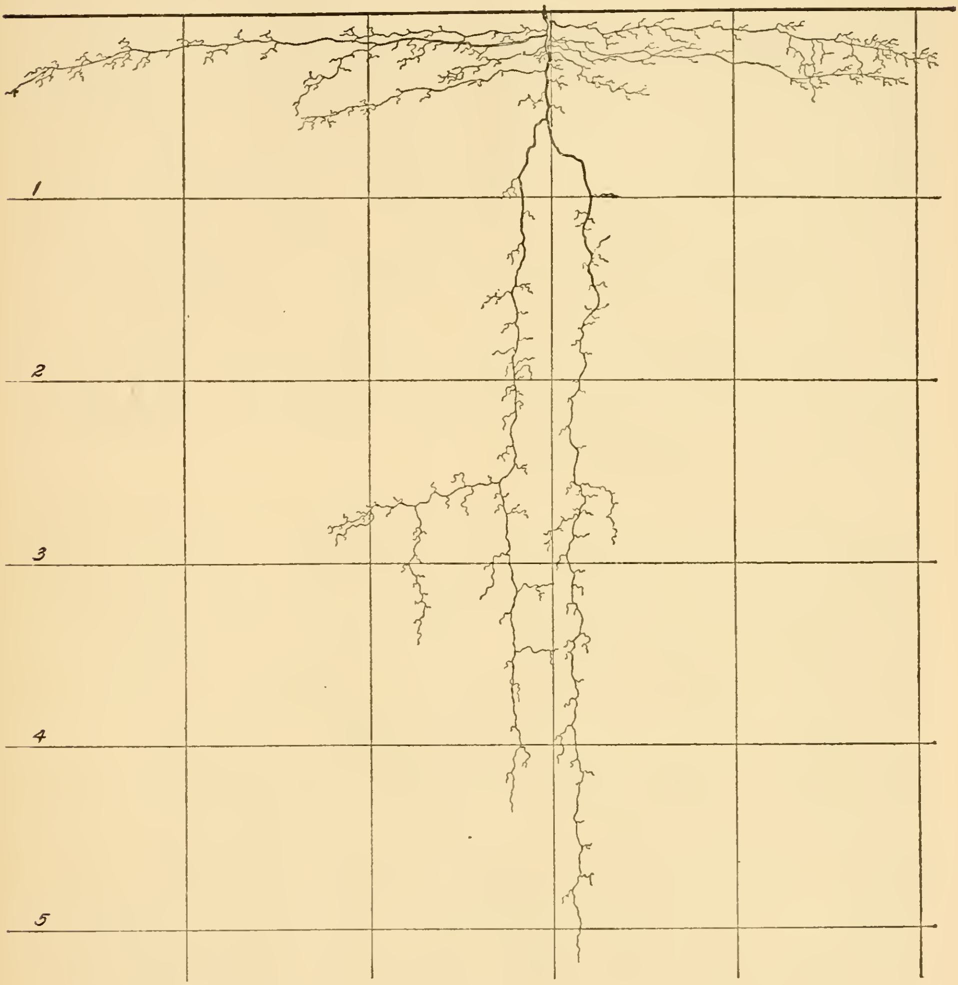


FIG. 22.—Widely spreading and deeply penetrating root system of *Eriogonum annuum*.

life duration (*cf.* Chapters VI and VII). Few or no long branches originate below 3 feet. The tips of the deeper roots are poorly branched. The ultimate branches are threadlike. The rootlets of the surface laterals are much finer than those of the deeper ones, in fact, the root as a whole has its surface branches much better developed than the deeper ones, although the tap-root is often more prominent than shown in figure 22. This species with its widely spreading surface laterals and moderate depths of penetration is typical of many sandhills plants.

Seneca, Nebraska, where further studies were made, lies in the heart of the main body of the Nebraska sandhills. Here the hills rise abruptly from the narrow flood plain of the Middle Loup River to a height of about 200 feet. In the main they are well covered with grass and freely dotted with shrubs and coarse herbs (plate 8). Blowouts in all stages of development may be found. Here are to be seen *Redfieldia flexuosa* with *Psoralea lanceolata, Cyperus schweinitzii, Pentstemon haydenii,* and others colonizing areas of bare sand; mats of the prickly-leaved *Muhlenbergia pungens,* or local areas dominated by the coarse sand-reed, *Calamovilfa longifolia.* However, most of the hillsides are well covered with many species of bunch-grasses, shrubs, interstitial herbs, short-grasses, and sedges. Many of the latter exhibit varying degrees of the bunch-grass tendency. Unlike conditions in the true prairies and even in the better developed mixed prairies on harder lands, the plant cover is open. Only in the most favored situations on protected north slopes is the light-colored substratum hidden from view, while normally bare intervals of sand are the rule. This prevailed, although the area examined was ungrazed and, judging from the amount of accumulated débris in the "pockets," had not been burned over for a number of years.

Andropogon scoparius, A. hallii, and *Calamovilfa longifolia,* with *Stipa comata, Kœleria cristata,* and *Panicum virgatum* (in less exposed places), are the dominants among the tall-grasses. *Bouteloua hirsuta* and *B. curtipendula* with *Carex pennsylvanica* and *C. stenophylla* make up the major portion of the lower layer of grasses and grass-like species. *Yucca glauca* is fairly abundant. *Ceanothus ovatus* (including the pubescent variety), *Prunus besseyi,* and well-developed clumps of *Rosa arkansana* constitute the shrubby or half-shrubby species. The sand-cherry is most abundant in the more open portions of the vegetative cover. Isolated bushes of *Ceanothus* occur throughout, even dotting the crests of the hills, while *Rosa arkansana* makes its best development in sheltered places. The open nature of the bunch-grasses makes possible the presence of a great many subdominant species. In the main they are similar to those described at Haigler, a station 145 miles south and west (fig. 14). The most marked difference aside from the better development of the grasses at this station is the abundance of *Artemisia filifolia* in the former area and its almost complete absence in the less compact soils of the rougher topographic region about Seneca. At this station the following species were examined:

Onagra biennis.—The common evening-primrose is a species of frequent occurrence in both true and mixed prairies, where it forms societies. It is most common in rather dry situations and where the vegetation is somewhat open. It usually indicates disturbed conditions.

A number of specimens of this primrose were excavated on a grassy hillside. The plants were in full bloom. In one root system the tap-root was

17 mm. in diameter, but tapered so rapidly that at a depth of 12 inches it was only 2 mm. thick and scarcely as large as some of its laterals. It descended vertically downward, branching into two equal parts at a depth of 2.8 feet. These ran practically parallel to a maximum depth of 6.8 feet. The tap gave off 17 laterals from 1 to 4 mm. in diameter (most of them from 1 to 1.5 mm.) and 20 smaller ones in the surface foot of soil. Most of these ran off parallel with the soil surface and at a depth of only 2 to 10 inches. These roots reach distances of 1.7 to 3 feet or more from the base of the plant, but their course is so tortuous that they are actually often much longer. They may end in the first foot of soil, but usually penetrate deeper. For example, one root with a diameter of 3 mm. ran off laterally at a depth of 0.7 to 1.3 feet for a distance of 7 feet before turning downward. It tapered so slowly that at the bend, 7 feet from its origin, it was still a millimeter in diameter. Like many others, it reached a depth of 4 feet. The branching is rather poorly developed. The laterals are threadlike, from a millimeter to over 2 inches in length, and scarcely rebranched. They arise only at long intervals, although in places 4 to 6 may come off from a single inch of the root. The general tendency of these laterals is to run nearly parallel with the soil surface, although they may descend obliquely and frequently ascend vertically to near the ground-line. Not more than half a dozen roots exceeding 3 inches in length arose below the first foot. The last foot of the tap was fairly well branched, with rather numerous but short unbranched rootlets. Other root systems were very similar, although some had more large and fewer small branches. It is evident that this plant has a root habit well adapted to get most of its water and solutes from the first 3 or 4 feet of soil.

Commelina virginica.—The day-flower is a rather common component of sandhills vegetation, where it frequently forms societies. Several fine specimens, 6 to 8 inches tall, and in full bloom, were examined in a partially revegetated blowout. The fleshy roots, which are brown to black in color and 2 to 3 mm. in diameter, usually originate at a depth of 4 to 8 inches below the surface of the sand. Mostly 3 to 5 come off from the base of a single plant. They rarely grow vertically downward, but spread out obliquely in such a manner that at depths of 2 to 3.2 feet they are 0.3 to 1 foot horizontally away from their point of origin. For example: one large root reached a depth of 3.2 feet, its characteristic whitish blunt tip ending a foot to one side of the plant, while another younger root, only 0.8 foot long, ended at a depth of 0.5 foot. The roots taper slowly and are very brittle near their tips. None was found at depths greater than about 3 feet. Except near the growing ends, they are densely coated with hairs. The branching is only poorly developed. Some roots had no laterals, others had as many as 6, confined mostly to the surface 8 inches of soil. Some of these delicate tan-colored rootlets run off in the surface soil, perhaps at a depth of only 0.2 foot, to a distance of 1 to 2.3 feet from their origin. They are seldom over a millimeter in diameter, but, like the main roots, taper only slowly. They give off throughout their course great numbers of delicate rebranched laterals from 0.5 to 8 inches in length. These are distributed in the surface soil. As a whole the root system of this species is shallow and especially well adapted for surface absorption.

Pentstemon angustifolius.—This beard-tongue, like several other members of the genus, is a subdominant of rather wide occurrence in the more stabilized areas of sandhill vegetation. Three plants in fruit were excavated on a grassy hillside. Each had 3 or 4 stalks which reached a height of about a foot. The roots arise from a woody rhizome, usually 2 to 5 inches in length and 4 to 8 mm. in diameter. As many as a dozen may originate from a single inch of the rhizome. They are usually less than 2 mm. thick. Many of them spread widely in the surface soil. Even in the first inch or two of soil, roots were traced laterally for distances of 0.8 to 2.3 feet. These were well supplied with laterals only an inch in length and about 0.5 inch apart all along their course. These roots often end in the surface soil with a fairly good brush of mostly unbranched rootlets. Frequently the larger roots also give off, in addition to these shorter rootlets, branches 6 to 10 inches in length and fairly well rebranched. They run in all directions, but only a few directly downward. The threadlike bushy rootlets form a good absorbing system in the surface soil. Some of the larger roots, after running out laterally and often more obliquely than those described, turn downward and reach a maximum depth of 4.8 feet. Thus, while many roots end in the surface soil, perhaps half of them run obliquely outward from 1 to 2 feet or more; then turning, they penetrate to depths of 5 or 6 feet. They are branched very poorly, except in the last 1 to 1.5 feet. Although the branching in the first 6 inches from the rhizome is very poor, small roots in this region are densely clothed with root-hairs. Such a root system is especially efficient in absorbing water and solutes in the surface soil as well as at much greater depths.

Cyperus schweinitzii.—This perennial sedge thrives in sandy soil. While perhaps more often a component of stabilized vegetative areas, it is frequently found among the pioneers or forming families in the shifting sands of blowouts. It is characterized by short tufts made up of a few grasslike, spreading stems and produces a very open type of the bunch-grass form.

Several clumps, about 2 feet high and in fruit, were examined in an old blowout. These plants originated from short, hard, woody, much-branched rhizomes 2 to 4 mm. in diameter, which were found at depths of 3 to 6 inches. Hard, sharp-pointed buds arise from the thickened corm-like bases of the erect stems. From the base of the stems and from the rhizomes arise great numbers of fibrous roots, scarcely more than 0.5 mm. in diameter. These almost immediately begin to give rise to great clusters of exceedingly fine and minutely branched laterals which permeate the soil in all directions. The laterals are very well branched to the second and third order with hair-like branches from 2 mm. to 2 or 3 inches or even more in length. They are especially well developed in mat-like areas in the surface soil. In fact, most of the root system occurs in the surface foot of soil, while practically all of the root system lies above the 1.7-foot level, although a few branches penetrated to 2.3 feet. The lateral spread is very great. Roots were traced parallel with the soil surface at depths of only 0.2 to 0.3 foot for distances of over 3.5 feet. This shallow-rooting habit is shown in plate 13, A. The dark-brown, rather tough roots were readily excavated. It is quite probable that this shallow, widely spreading root system in more stabilized areas becomes, because of competition, much deeper seated.

Thelesperma gracile.—This perennial species is a subdominant over a wide range of territory in the more arid portions of the grassland formation. It frequently forms extensive societies both on the hard land and in sandy soil. A number of plants were examined in an area only poorly clothed with vegetation. A single typical specimen will be described. It had a tap-root 4 mm. in diameter, which gave rise to 4 flowering stalks about 1.8 feet high. The dark tan-colored tap-root ran vertically downward, tapering very slowly and reaching a maximum depth of 3 feet. At a depth of 0.3 foot a branch 1.5 mm. in diameter came off and ran almost horizontally into the hillside, where, at a distance of 1.7 feet and a depth of 1.3 feet, it gave rise to a new plant. This underground part was unbranched and had only a few threadlike rootlets, about a centimeter or less in length, arising at infrequent intervals along its course. The tap-root was fairly well branched throughout. At a depth of 0.3 foot, three threadlike branches occurred; at 0.5 foot two laterals, each 0.5 mm. in diameter, arose; while three branches, 1 mm. in diameter, came off at 1.6 to 1.7 feet, and still another 0.2 foot deeper; besides these, numerous fine branches ran off for distances of only 0.2 to 0.4 foot. The larger laterals spread widely. Some ran rather horizontally away from the tap for distances of 2.5 to 3.3 feet before turning downward. Even in the surface 0.2 to 0.5 foot of soil, laterals were traced to a distance of 2.5 feet from the base of the plant. Many of these larger laterals reached depths of 2.5 to 3 feet, while one ended at a maximum depth of 3.8 feet. The laterals are only poorly rebranched. However, the root-ends, including the last foot, are fairly well supplied with rootlets, most of which are unbranched. Thus it may be seen that this species has the characteristic widely spreading root habit, and that although rather meagerly supplied with small laterals, the root system is adapted for absorption in relatively shallow soil layers.

Ceanothus ovatus.—This low shrub is quite common, not only in the subclimax and true prairies, but in the mixed prairie of the sandhills as well. The pubescent variety is more common than the glabrous form in the latter area. Here the individual plants become much branched and very bushy, reaching heights of 1.5 to 3 feet and forming clumps 3 to 25 feet in diameter. They frequently dominate even the highest hills and sometimes occur in such abundance as to shade out most other species.

Two large specimens, both about 10 years old, were excavated. They had strong woody tap-roots an inch in diameter. On one the crown was buried a foot in the sand. From its three major parts 12 stems arose to a height of 1.3 or 1.5 feet, the whole forming a bush over 3 feet in width. The top of the other plant was somewhat smaller. In the first 2 feet of soil, but especially in the surface 1.5 feet, large numbers of fine roots, a millimeter or less in diameter, arose not only from the tap-root but also from the buried stems. These ran off somewhat parallel with the surface soil for distances varying from 0.2 foot to over 3 feet. These roots afford a considerable absorbing area in the surface soil for this shrub and permit it to compete directly with sandhill grasses for the water afforded by light showers. Between a depth of 2 and 3 feet, 7 large laterals from 3 to 6 mm. in diameter were given off by one plant. They spread widely (3 to 5 feet from the descending tap-root) and pursued very tortuous courses, but ultimately turned downward, reaching depths of 9 to 11 feet. The other plant gave off 4 similar laterals at a depth of about 3.3 feet. At a depth of 5 feet the tap-roots were 10 and 14 mm. in diameter respectively. A foot deeper, the one broke up into two nearly equal branches, both of which pursued crooked downward courses. At 9 feet, one of these branches had wandered a distance of 3.6 feet horizontally from the base of the crown; the other now turned abruptly quite across the 4-foot trench before again running downward. Roots of both plants were traced to a depth of 12 feet, further excavation not being made because of the caving sand. Even at this depth the tap-roots were a millimeter in diameter. Besides the branches described, numerous others (both short and long) were given off at intervals at all depths, the whole root branching and rebranching freely. While some of the roots branched coarsely and ended abruptly, others formed a most delicate mass of absorbing rootlets. Even below 10 feet some of the deeper roots threw off laterals abundantly in the moist sand, although others ran for a foot or more without branching. Most of the roots were bright red in color, except the older parts, which were reddish brown. All but the oldest parts are more or less streaked with white. Much of the root is woody and extremely hard. This deep-seated, widely spreading root habit is very similar to that described for the same species when growing in the subclimax prairie (Weaver, 1919:17).

Croton texensis.—This widely distributed annual is frequently very abundant in sandy soil. A number of plants were excavated near the foot of a sandhill, where they formed an extensive socies. They were about 1.7 feet tall, but had not yet blossomed. They have tap-roots 3 or 4 mm. in diameter, which taper slowly and descend nearly vertically downward, often to depths of 7 or 8 feet. In the first 1.5 feet of soil, and especially in the surface 0.7 foot, the tap-root is usually supplied with 6 to 14 large laterals 0.5 to 2 mm. in diameter, as well as with smaller ones. These usually run off mostly parallel with the surface to distances of 0.5 to 1.5 feet, branching freely and ending in great clusters of poorly branched laterals. Below the 1.5-foot level the tap is seldom more than a millimeter in diameter, but it maintains this thickness almost to its maximum depth. Large branches are few, but there is an abundance of threadlike ones from 0.5 to 3 inches long. These are furnished with secondary branches about 0.5 inch in length. This branching occurs throughout, even to the tip. The abundant superficial laterals and their wide spread in the surface soil is a characteristic sandhills root habit, but the great depth of penetration of the tap-root is quite marked for an annual.

The sandhills near Yuma, Colorado, are a continuation of those in southwestern Nebraska; they are relatively low and, while blowouts are frequent where overgrazing has occurred, large stretches of nearly level sand are to be found. As one leaves the hard lands clothed with their characteristic cover of buffalo and grama grasses and approaches the sandy areas, the first indications of changing soil conditions are given by a greater abundance and better development of *Artemisia frigida*, *Psoralea tenuiflora*, *Chrysopsis villosa*, and *Aristida purpurea*, and by the appearance of an occasional plant of *Ipomœa leptophylla*, *Stipa comata*, *Thelesperma gracile*, *Artemisia canadensis*, etc. As the sand increases the short-grass cover gradually gives way to a mixed type of vegetation with *Aristida purpurea* often dominating, while the still later appearance of *Andropogon scoparius* and *Artemisia filifolia* indicates a very sandy, permeable soil (plate 9). In typical ungrazed areas the dominants are *Stipa comata*, *Aristida purpurea*, *Calamovilfa longifolia*, *Bouteloua hirsuta*, and *B. gracilis*. *Kœleria cristata*, *Andropogon hallii*, and *Carex pennsylvanica* are fairly abundant and important. *Andropogon scoparius*, which is dominant in an adjoining lowland (plate 7, B), *A. furcatus*, *A. nutans*, and *Bouteloua curtipendula* are characteristic true-prairie elements. *Petalostemon purpureus*, *Liatris punctata*, *Artemisia gnaphalodes*, and *Meriolix serrulata* intermixed freely with such characteristic plains species as *Opuntia camanchica*, *O. polyacantha*, *O. fragilis*, *Chrysopsis villosa*, *Plantago purshii*, and others. Both *Yucca glauca* and *Artemisia filifolia* were very abundant on adjoining grazed areas, but other shrubs were conspicuously absent. The soil was of a firmer type than that at Seneca and quite comparable with that at Haigler. The following species were excavated:

Artemisia canadensis.—This sage is a widely distributed subdominant and frequently forms socies in the sandhills vegetation. Of the several plants examined, the strong, brown, woody tap-roots varied from 6 to 11 mm. in diameter. They tapered so rapidly that at a depth of a foot they did not exceed 1.5 mm. in thickness. Beginning just below the surface, and in the

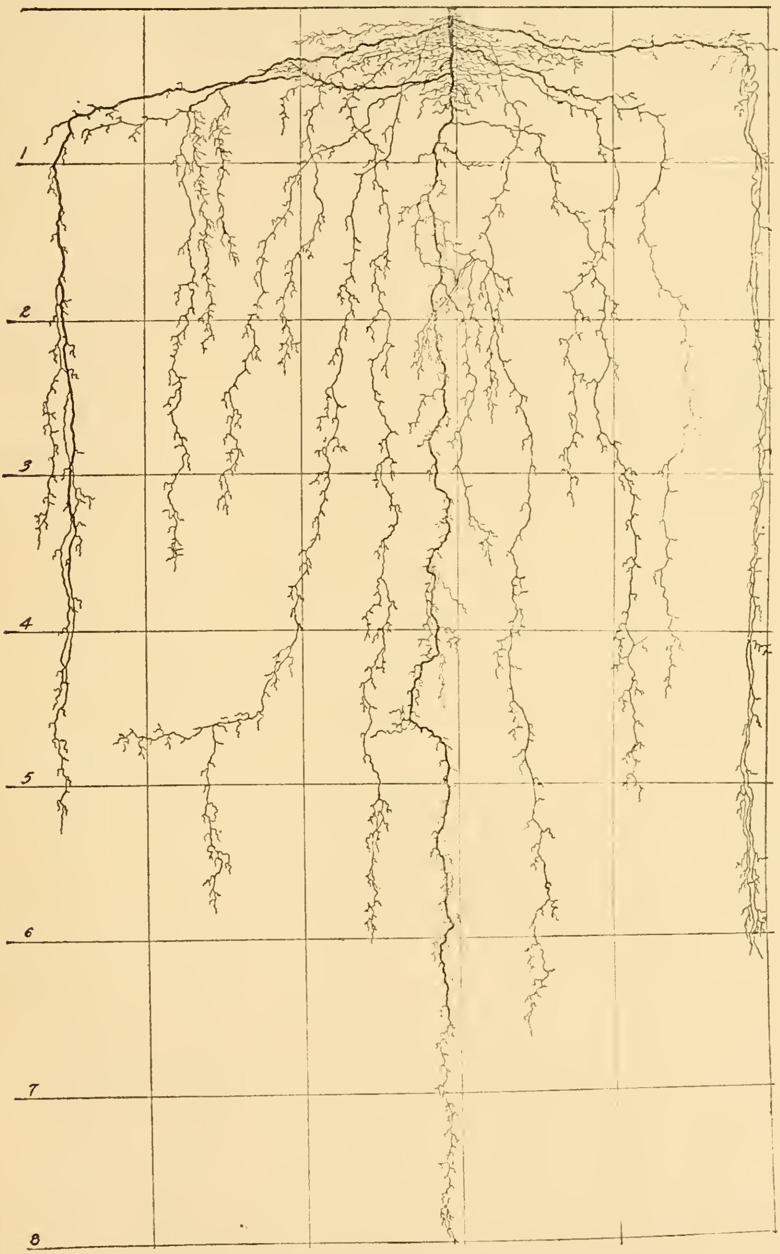


Fig. 23.—Well-developed root system of *Artemisia canadensis*.

first 1.5 feet of soil especially, great numbers of lateral roots arise. These vary in size from mere threads to those over 2 mm. in diameter. In this soil stratum a single tap-root often has 8 to 10 of the larger laterals, besides great numbers of smaller ones (fig. 23). All are profusely branched with

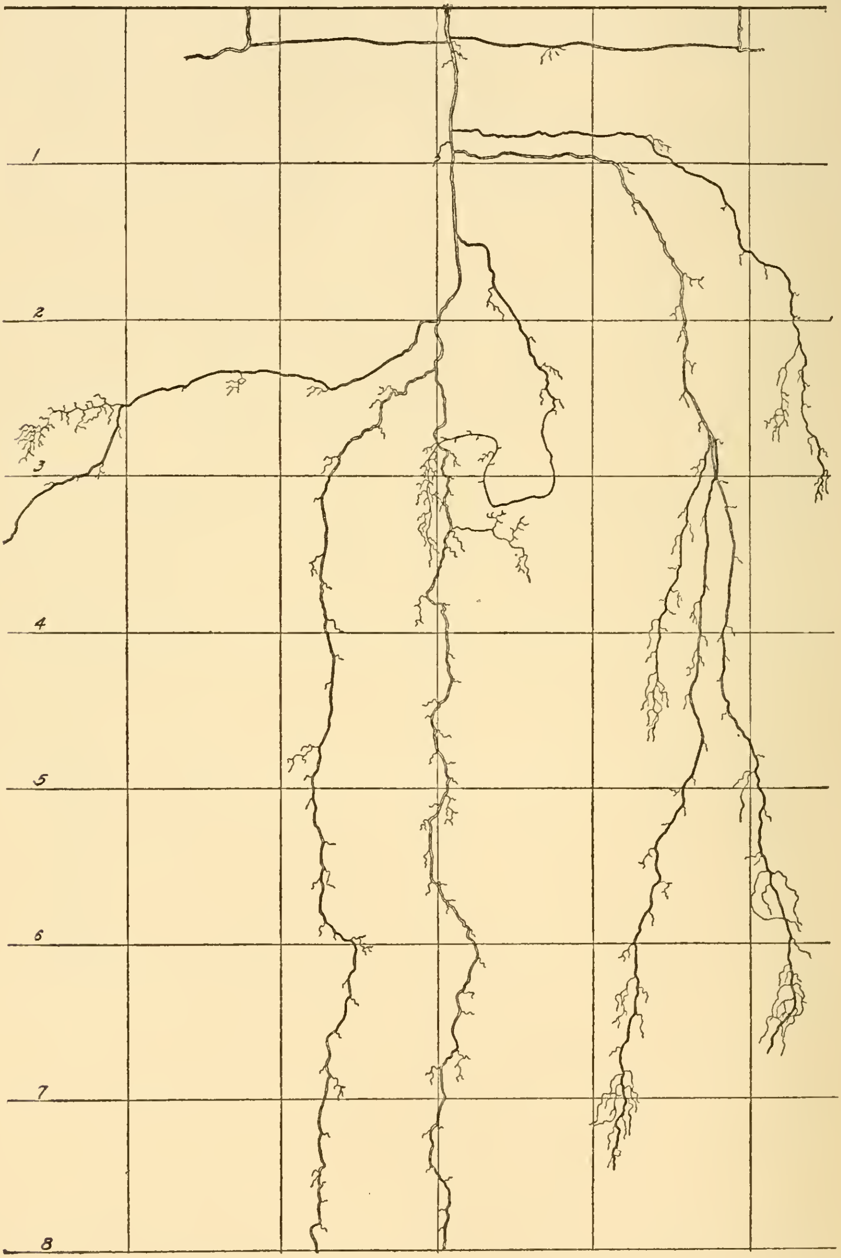


Fig. 24.—Underground portion of *Anogra cinerea*.

threadlike sublaterals 1 to 3 inches in length, and sometimes so numerous as to form brushlike mats. Many of the laterals extend out almost parallel with the surface or only slightly obliquely, the larger ones to distances of 1 to 2.5 feet before turning rather abruptly downward. They may descend vertically, but frequently pursue a more or less tortuous course, some to a depth of over 6 feet. Below the first foot of soil the branches of the tap-root are usually much shorter. However, the tap-root is often well-branched throughout. These tap-roots, which keep their identity to the end, were traced to a depth of 8 feet. The specimens examined were all from 1 to 1.5 feet in height and each had from 5 to 10 large branches. The great extent of this large root system may be made more apparent by a study of figure 23.

Anogra cinerea.—This evening-primrose is widely distributed throughout the drier parts of the grassland formation. It is often an important subdominant in the mixed-prairie vegetation of sandhills. A family of several plants was examined on a poorly stabilized sandhill. Many of the plants were connected by means of rhizomes which ran at a depth of only 4 to 6 inches below the surface. Some of these rhizomes, although 2 mm. in diameter and over 2 feet in length, were without shoots and had practically no roots. The tap-roots on some of the larger specimens were 14 to 16 mm. in diameter. They were traced to a depth of over 9 feet, at which point some were still 2 mm. thick. Further excavation was not made because of the caving sandy trench-walls. A glance at figure 24 shows that this plant has a deeply placed root system, and probably does little absorbing in the surface soil. The strong laterals, some of which, at their point of origin, are of almost equal diameter with the tap-root, spread very widely and penetrate to depths of from 7 to 9 feet. Compared with many species, they are rather poorly branched, but near the root-ends of the larger laterals, as well as sometimes on smaller ones, large clusters of much-branched rootlets occur. These rootlets are from 0.5 to several inches in length and fairly well rebranched. The roots are yellowish in color, rather fleshy, and provided with a tough stele. Like the preceding species, this coarse, rather meagerly branched root system is very deep-seated, but unlike the sage it is poorly equipped for absorption in the surface soil.

Chrysopsis hispida.—This rather low, spreading composite, like *C. villosa*, has a wide range throughout the grassland formation. In the sandhills and other more arid regions it is a society-forming subdominant. Several plants were excavated on a sand dune near Yuma. The soil was quite moist to a depth of over 9 feet. The root habit of this species is similar to that of *Chrysopsis villosa*, especially when grown under similar edaphic conditions (Weaver, 1919: 117). The grouping of the plants is accounted for by the root offshoots, as shown in figure 25. The tap-root of the largest plant examined was 16 mm. in diameter and it was traced to a depth of 9 feet, when the danger of caving of the trench became so great that work on it was abandoned. For the first 2 or 3 feet of its length the tap is woody; it descends rather vertically downward and usually keeps its identity throughout. The branching in the first 2 feet of soil is especially well developed. Several large laterals and almost countless smaller ones run off at right angles from the tap to distances of 1 to 2.5 feet, where the smaller ones may end. The larger ones, which are 2 or 3 mm. in diameter, may have an even greater lateral spread before they turn downward. The branching throughout is irregular and even in the deeper soils the roots may meander still farther away from the base of the plant. While the smaller laterals are exceedingly abundant, they are only poorly rebranched. A glance at figure 25 shows that while some absorption takes place in the deeper soil, most of it is confined to the first 2 or 3 feet. In fact, the tap-root below 4 feet is usually poorly supplied with laterals.

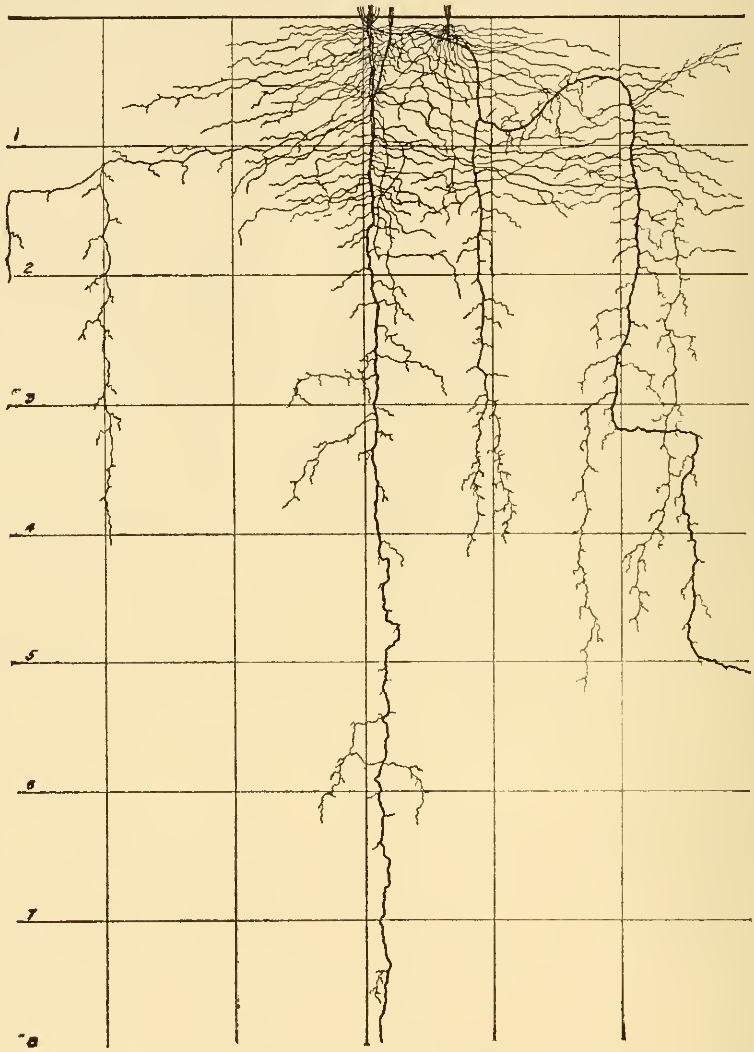


Fig. 25.—Underground portion of *Chrysopsis hispida*.

Pentstemon ambiguus.—This diffusely branched perennial is widely distributed over the plains from Colorado to Texas and westward to Utah and Arizona. Its flowering habit from May to September, together with its great abundance, often causes it to form conspicuous societies. The specimens examined were bushy plants, 1 to 1.5 feet in diameter and about 1.3 feet high; they were in fruit. The individual plants are connected by strong, woody rhizomes, 4 to 8 mm. in diameter, and from 3 to more than 12 inches in length. These are densely matted and twisted. From the rhizomes, especially under the clumps, arise clusters of roots. Some have a diameter of 8 mm., but most of them are only 2 to 4 mm. thick. Like the rhizomes, they are reddish-brown in color. The roots usually run off obliquely to distances varying from 0.5 to 1.5 feet horizontally from the base of the clump before turning abruptly downward (fig. 26). From here their course is in general vertically downward,

FIG. 26.—Root system of *Pentstemon ambiguus*.

although they meander back and forth through distances of 4 to 8 inches. They were examined to a depth of 10 feet, a very few penetrating beyond this depth. In the first foot of soil they are practically unbranched; indeed, the branching is poor throughout. Sometimes the roots extended 1 to 3 feet, giving off scarcely a single branch. Near the ends of the roots the branching is fairly well developed, while rather infrequently along their course groups of well-branched rootlets arise. This plant, like *Artemisia canadensis*, which was excavated from the same trench (p. 59), has an extensive, deep-seated root system.

Several other species were studied in this sandhills area. Since they have been described heretofore (Weaver, 1919) they will be mentioned in the chapter on ecads.

The sandhills near Central City, in east-central Nebraska, are of especial ecological interest. Between the Platte River on the south and the Loup River on the north there lies, well back from their respective flood-plains, an area of long, low ridges of hills, approximately 8 miles wide and consisting of very sandy soil. These are extra-regional sandhills and probably represent their furthest eastward extension in Nebraska. They are surrounded by rather typical true prairies, but, under the edaphic conditions afforded by the sand and often as a result of overgrazing, the tall-grasses show an undergrowth of short-grasses resulting in mixed prairie.

In the area studied the hills had been greatly overgrazed. Much destruction had been wrought in the grassland both by wind erosion and deposit. In several places large active blowouts were in evidence, while perhaps a mile away drifting sand had covered the more stable valley vegetation to depths of a few inches to more than a foot (*cf.* p. 23). This condition had prevailed for several years, when all stock was removed and an attempt was made to reclaim the land by planting rye, sorghum, millet, and sweet clover (plates 10 and 20, A). Most of the typical sand-binding pioneers are to be found in the blowouts, and whole hillsides are being reclaimed by a rank growth of *Calamovilfa longifolia*, *Andropogon hallii*, *Redfieldia flexuosa*, and *Sporobolus cryptandrus*. On the other hand, the valleys are sodded over with *Poa pratensis*, *Andropogon nutans*, *Panicum virgatum*, and mats of *Bouteloua hirsuta* and *Carex stenophylla*, while all intermediate conditions between these extremes prevail. Much of the area is passing through a ruderal stage, with *Salsola tragus*, *Cycloloma atriplicifolium*, and *Cenchrus tribuloides* dominating. The successional record shows all stages in the reclamation of blowouts, distinct lines of demarcation existing between stable and disturbed populations. The thoroughness of the destruction even in the valleys, is evidenced by the occurrence of *Juncus balticus*, partially unearthed, its rhizomes and roots dangling from hummocks of sand 2 feet above the eroded valley floor. Naturally, in these sandhill outposts, the soil is often mixed with clay. The presence of these clay spots, although the surface soil may be quite sandy, is indicated by such stable mesophytes as *Poa pratensis*; hence the excavation of sandhills plants was carried on elsewhere. The following species were studied:

Panicum scribnerianum.—This species usually plays the rôle of an interstitial among the taller prairie grasses, occurring in both moist and dry soil. In the sandhills, however, it sometimes becomes dominant over local areas. It was examined at the base of a hill where it was growing very abundantly. The individuals are connected by short rhizomes. The fibrous roots are very abundant. They are only about 0.3 mm. in diameter, except near the growing tips, which are often a millimeter thick. They are very tough and quite easily excavated. They have a lateral spread of approximately 2 feet from the base of the plant. This maximum lateral spread is reached at a depth of about 1 to 1.7 feet. Few roots were found running parallel with the soil surface. Beyond this depth the roots usually penetrate more or less vertically downward. While some are only a foot long, many, including most of those that pursue a vertically downward course from their origin, reach depths of 3 feet; still others grow as deep as 3.9 feet. All of the roots are very abundantly supplied with multitudes of well-branched laterals 0.5 to over 2 inches in length (plate 14, A).

Tradescantia occidentalis.—The western spiderwort forms societies, especially in sandy soil, in both the true and mixed prairies of the grassland formation. The large blue or reddish flowers make the plants quite conspicuous from early spring to midsummer. A half dozen individuals of this species, all full-grown and in blossom, were excavated on the crest of a sandy hill. They have fleshy roots, 2 or 3 mm. in diameter, of which 15 or 20 occur on a single plant. Some of these take a course almost parallel with the soil surface and extend off for distances of 1 to 1.5 feet, where the roots end at depths of only 0.3 or 0.4 feet. Others run obliquely, but seldom vertically downward, Some reach depths of 3 feet, but most of the roots lie in the first 1.5 feet of soil. Few roots were found just beneath the base of the plant; they are fleshy, tan-colored, and very brittle, especially the younger parts. Nor is the diameter uniform, some portions enlarging to almost twice the size of other parts. The roots throughout are very poorly branched. Indeed, they branch scarcely at all, except at infrequent intervals along their course, and these laterals are usually less than an inch in length and entirely unbranched. In general, this shallow, widely spreading root system is similar to that of *Tradescantia virginiana* (Weaver, 1919:74), except that it is more extensive but much less branched.

Bouteloua hirsuta.—Hairy grama, like *Bouteloua gracilis*, is a species of wide distribution and diverse ecological habit, forming a sod in its northern range and growing in isolated clumps in the southern part. This habit also varies with the water-content conditions. Both species furnish excellent forage for all classes of stock and, like buffalo grass, are exceedingly valuable for winter forage, since they "cure" on the ground. *Bouteloua hirsuta* is more drought resistant than *B. gracilis* and so fills an important place in the drier regions, especially on sandy plains; in fact, it reaches its best development on stable sandy or sandy-loam soils.

This grass was excavated on the lower slope of a sandy hill, where, as in the adjacent valley, it was dominant, forming a rather dense sod. The soil was very sandy to a depth of at least 6 feet, except the surface foot, which consisted of a dark-colored sandy loam. The clumps are connected by strong rhizomes 2 or 3 mm. in diameter and of a variable length, but they usually give rise to new clumps at intervals of 3 to 5 inches. Numerous roots arise from the base of the clumps as well as from the rhizomes. These roots are 1 to 1.5 mm. in diameter. They vary in number from 3 to more than 16 from an individual clump, depending upon its size. Many of these run off in a direction almost parallel with the soil surface or only slightly obliquely, to a distance of 1 to 1.5 feet, or sometimes even further from the base of the clump before turning downward (plate 15, B). They are abundantly supplied with laterals, which are usually only 1 to 1.5 inches in length, but exceedingly well-branched with delicate sublaterals. This dense network of roots completely occupies the soil to the working depth of 1.7 feet. Not a few of the roots grow deeper, the well-branched tips of some reaching a maximum depth of 2.6 feet. A large number of individuals were examined.

Further studies of this species were made on a well-covered sandhill near Seneca, Nebraska. The plants were in blossom and had flowering stalks 6 to 8 inches high. They showed the same root habit as regards widely spreading surface roots and profound branching. However, the working depth was found to be somewhat greater. It averaged 2.8 feet, while a few roots reached a maximum depth of 3.3 feet. The wide lateral spread was found to be constant.

Several other characteristic sandhills species were excavated and studied in this area, but, since they have also been investigated in other habitats, these data will be given in the chapter on ecads.

SPECIES EXCAVATED IN HARD LANDS.

In the preceding pages have been described the species excavated in sandy soil of mixed prairie only. In addition are the root systems of several species which were examined in typical hard lands. These plants were excavated at Colorado Springs and Limon, Colorado, and at the United States dry-land experiment station at Ardmore, South Dakota (fig. 14). A sufficiently complete account of the vegetation and soil at Colorado Springs has already been given on page 27. At Limon, 70 miles eastward, and under approximately the same precipitation, some typical areas of mixed prairie occur. The distribution of vegetation, like the root development of certain crop plants in this area (p. 116), is largely determined by edaphic conditions. Where the soil consists of compact silt-loam, there is a marked expression of the short-grass vegetation, but where it is of a sandier consistency typical mixed prairie occurs. Although considerably overgrazed, the area where roots were excavated was dominated by *Stipa comata*, *Aristida purpurea*, and *Agropyrum glaucum* with *Bulbilis dactyloides* and *Bouteloua gracilis*. Numerous other grasses, especially *Kœleria cristata*, *Festuca octoflora*, *Sitanion hystrix*, and *Schedonnardus paniculatus*, and the sedge *Carex stenophylla* were present, together with societies of *Psoralea tenuiflora*, *Astragalus microlobus*, *Chrysopsis villosa*, *Gutierrezia sarothræ*, *Artemisia frigida*, *Grindelia squarrosa*, and *Aragallus lambertii*.

Other common species are *Opuntia fragilis*, *Senecio aureus oblanceolatus*, *Erigeron cæspitosus*, and *Coreopsis tinctoria*.

Throughout northwestern Nebraska and western South Dakota some fine mixed prairies occur. On the uplands at Ardmore, *Agropyrum glaucum* reaches a height of over 2 feet, while the flowering stalks of *Bouteloua gracilis* have a length of 12 inches, both indicating very favorable growth conditions. The rainfall is somewhat greater (17.8 inches) than at either of the preceding stations. Evaporation is probably much lower and may be an important factor. Although the run-off must be high, the Pierre clay soil is very retentive of water.

Besides the wheat-grass, *Stipa comata*, *Aristida purpurea*, *Poa sheldoni*, *Bouteloua curtipendula*, and *Andropogon scoparius* are tall-grass dominants. The layer of *Bulbilis dactyloides*, *Bouteloua gracilis*, *Carex stenophylla*, *C. filifolia*, and *Festuca octoflora* is well developed (plate 3, A, B). Besides the grasses, of which the dominant species alone are here recorded, the presence of numerous societies is indicative of the rather favorable climatic conditions. Some of the more important of these are *Psoralea tenuiflora*, *P. argophylla*, *Artemisia frigida*, *Opuntia polyacantha*, *Astragalus drummondii*, *Aragallus lambertii*, *Malvastrum coccineum*, *Plantago purshii*, and *Grindelia squarrosa*. In these mixed prairies the following plants were examined:

Bouteloua curtipendula.—This species of grama has a wide range and considerable forage value. Although it seldom occurs in pure growth in the areas under consideration, it is nearly always present in true prairie vegetation and is often of considerable abundance in mixed prairies also. It normally grows in tufts or bunches, but under certain conditions forms a good sod. A number of fine specimens were examined in the mixed prairie near the base station at Colorado Springs. Like most prairie grasses, it propagates by rhizomes. These are 1 to 2 mm. in diameter and usually not over 2 to 6 inches n length. From the base of the clumps, as well as from these rhizomes, there iarise great numbers of roots, the largest of which are seldom over a millimeter in diameter (plate 13, B). Many of these run off more or less parallel with the soil surface and at a depth of only 2 to 4 inches. In this manner they reach out to a distance of 1 to 1.5 feet from the base of the plant before turning downward. This root habit is very characteristic of most grasses of mixed prairies and short-grass plains. Many other roots pursue a course more obliquely downward, reaching the working depth of 4 feet at a horizontal distance of only 8 to 10 inches from the base of the clump. Still others extend more or less vertically downward, some reaching a maximum depth of 5.5 feet. Below this depth none was found, although the walls of the trench were undercut to a depth of 7 feet. All of the roots are abundantly supplied with delicate rebranched laterals not unlike those of *Bouteloua gracilis*. They are especially well-developed in the surface 2 feet of soil, which is in fact literally filled with them. The main branches are 1 to 3 inches in length and their laterals, while only about an inch long, are exceedingly well furnished with almost microscopic rootlets only a few millimeters in extent. Below 2.5 feet the roots are much less abundant and the branches are much shorter. However, the roots are quite abundant to 4 feet, the working depth, while only a few extend to the maximum depth of 5.5 feet.

In plate 14, B, may be found a specimen of *Bouteloua curtipendula* excavated and photographed on August 25, 1919, and only 124 days after the seed was planted in the greenhouse on April 23, the seedlings having been transplanted in the field on May 10. Several fine specimens were thus raised on tilled soil adjoining the high-prairie station at Lincoln, Nebraska (*cf.* pp. 28 and 126). The plants were 2 feet tall and the clumps from 1 to 1.5 inches in diameter at the base. The maximum root depth was 3 feet, while the maximum lateral spread of 1.5 feet from the base of the clump was reached at a depth of about 2 feet. This conforms with the general root habit of prairie grasses, which as a group do not show so great a tendency to spread widely in the surface soil as do most species in the drier mixed prairies and short-grass plains.

Further examination of this species was made in the typical mixed prairies at the United States dry-land experiment station near Ardmore. The plants were growing in Pierre clay, a soil of very hard texture, underlaid at a depth of 2.3 feet with a sandy and somewhat gravelly subsoil. The roots had the wide lateral surface spread already described for those at Colorado Springs. The working depth was found to be 3.7 feet, while some reached a maximum depth of 4.3 feet. Near the root-ends the lateral branches were 2.5 inches long and the ultimate rootlets were exceedingly fine and well developed. Thus *Bouteloua curtipendula* is characterized by a widely spreading, moderately deep, but exceedingly well-branched root system.

Stipa viridula.—This species of porcupine grass is distinctly less xerophilous than *Stipa comata.* It is usually best developed in soils which permit of considerable water penetration and occurs in greatest abundance in the plains region where the stable vegetation has been disturbed, and in broad swales.

A number of specimens were examined in an old road near the base station at Colorado Springs. It formed an almost pure luxuriant growth, being over 2 feet high (plate 22, C). The larger roots are coarse, tough, and wiry, especially in the first 5 to 7 feet of soil. They are about a millimeter in diameter. Just below the soil surface some of the roots run off in a course almost parallel with it and at a depth of only 2 to 4 inches to distances of from 1 to 1.5 feet or sometimes even further before turning downward. Others run off obliquely with a maximum spread of only 8 inches on either side of the plant. The rest run rather vertically downward, some to a depth of over 11 feet. In the first 5 feet of soil the roots are much less brittle than in the deeper strata. For this reason only a portion of the very extensive root system is shown in plate 16, A. The root branching is very much like that of *Stipa comata*, the entire area under the plant and for a distance of more than a foot on either side being filled with the profuse and delicate branches of this very deep root system. At a depth of 5 feet some of the roots are still a millimeter in diameter. The lateral branches may exceed 3 inches in length and are well supplied with delicate rootlets. Below 9 feet the roots are much finer. Some penetrated to a maximum depth of 11.7 feet. Indeed, they are fairly abundant to 11 feet. They end in well-branched tips, the branches being usually less than 1 inch in length but poorly rebranched. The lateral spread of the roots of this species is quite characteristic for grasses of the more xerophytic portions of the grassland formation, but the great depth of penetration is remarkable, even exceeding that of *Bulbilis dactyloides*.

The marked differences in the water-content of the soil in the abandoned road among the roots of *Stipa* and in the undisturbed mixed prairie at the base station about 15 rods away is shown in table 5.

Even at depths of 5 to 12 feet the soil was quite moist (9.5 to 11 per cent water-content) when the roots were excavated on June 23. On August 9 the water-content at depths of 5 and 6 feet was 9 and 10 per cent respectively. Shantz (1917), in his study of plant succession on abandoned roads in eastern Colorado, points out the effect which the destruction of the original plant-cover produces on the water-content of the soil, the selection of the plant populations in the various stages of succession, their reactions upon the habitat, and the final replacement of such species as *Stipa* and *Gutierrezia* by a short-grass turf. By absorbing the water in the surface soil, *Bulbilis dactyloides* and *Bouteloua gracilis* effectively cut off the moisture-supply to the deeper soils and consequently deep root systems are no longer effective in supplying water to the plant. The general stages of succession are similar at this station, but the climax is mixed prairie. However, it must be kept in mind that *Bouteloua*, and especially *Bulbilis*, while more superficially rooted than *Stipa viridula*, have just as deeply seated absorbing organs as *Gutierrezia sarothræ* and many other short-grass-plains and mixed-prairie species. It seems probable that the cause of succession as regards a reduced water-content is due not entirely to the position of the roots in the soil, but also to their efficiency in absorption.

Table 5.—*Water-content of soil in Stipa viridula consocies and in adjacent stabilized mixed prairie.*

Station.	Date.	Depth of samples in feet.			
		1 to 1.5.	1.5 to 2.	2 to 3.	3 to 4.
Stipa consocies.....	June 23, 1919	....	10.3	8.0	10.4
Mixed prairie......	June 23, 1919	....	5.4	5.5	6.0
Stipa consocies.....	Aug. 9, 1919	5.7	7.3	10.0	8.3
Mixed prairie......	Aug. 7, 1919	4.7	5.3	5.5	5.4

Astragalus microlobus.—This legume forms estival societies which are especially well-developed in mixed prairie. Several plants were examined in the sandy-loam soil near Limon. They are sometimes connected by rhizomes, often only 4 to 8 inches in length and only 1 to 3 mm. in diameter. The tap-root is well developed. One plant had a strong tap-root 10 mm. thick, which descended rather vertically downward, tapering gradually, to a depth of 5.2 feet. A branch was given off at 8 inches in depth, while at 5 and 10 inches 2 laterals, each about 2 mm. in diameter, originated. These ran off rather horizontally for a distance of 1 to 1.5 feet and then turned downward, reaching depths of 3 and 5 feet respectively. As a whole, the root was poorly branched. About a foot from its end the tap-root divided into several parts, each of which branched repeatedly and in such a manner as to form a network of rootlets several inches in extent. The ends of the large laterals terminated in a manner similar to that of the tap-root. Aside from these, the branching was rather poorly developed. The roots were considerably kinked and curved through small distances. They are dark-brown in color. This rather coarse, moderately branched root system, especially with its lack of surface absorbing rootlets, is not greatly unlike that of *Astragalus crassicarpus*.

Eriocoma cuspidata.—This grass, although somewhat variable in habitat, generally grows in sandy soil. It frequently plays an important part in re-colonizing blowouts and is abundant also in more stabilized vegetation.

A number of large bunches, growing at the head of a "break" near Ardmore, South Dakota, were examined. Here the sandy and gravelly subsoil came within a foot of the surface, where it was overlaid by Pierre clay. The plants were about 2.1 feet high, fully mature, and in seed. The clumps each had 25 flowering stalks. From the base of the clumps 80 to 150 fibrous roots originated. These roots were about a millimeter or less in diameter. The lateral spread on either side of the clump was only 0.7 to 1 foot. Most of the roots descended rather vertically or at such angles that at no depth were they more than 1 to 1.2 feet horizontally away from the base of the plant. The working depth was found to be 2.3 feet and no roots were found at a depth greater than 3.2 feet. They are well supplied with laterals, seldom over 2 inches in length, but fairly well rebranched with short sublaterals, so that the absorbing system as a whole, although limited to the first 2 or 3 feet of soil, is a very good one.

Carex filifolia.—This species, with *Carex stenophylla*, sometimes plays a rôle of almost equal importance with the grasses in plains and mixed-prairie vegetation. They are important range species, since they afford considerable forage early in the spring before many of the grasses have resumed growth. The tough, black, wiry roots of these species bind the surface soil so firmly that new roads through the grassland are very rough for several years until the root clumps are worn through.

Several plants of *Carex filifolia* were examined in the mixed prairies near Ardmore. The plants often grow in clumps 4 to 6 inches in diameter. Not infrequently they die out in the center and grow only around the periphery of the clumps. They are furnished with an enormous number of tough, wiry roots, a millimeter or less in diameter. These seldom descend vertically, but run obliquely away from as well as under the plant, forming a great tangled mat to a depth of 1.2 to 1.5 feet. Laterals were traced horizontally away from the plant to a distance of 2.7 feet and at a depth of only 0.3 to 0.5 foot. While the larger and older roots are not so well branched for the first few inches from their origin, a very large number of smaller, profusely branched roots care for surface absorption close to the clump. All of the roots are supplied very abundantly with laterals ranging in length from 0.5 inch to over 3 inches. These terminate in brush-like masses of laterals, the ultimate branches being very fine and delicate. Not only is the surface soil filled with roots, but many go obliquely downward, criss-crossing at various angles, and reaching a working depth of about 4 feet. Not a few were found below this level, while some reached a maximum depth of 5 feet 2 inches. The roots end in brush-like branches. The younger roots, like those of *Carex pennsylvanica*, vary from light-brown to nearly black in color, while the older exposed and dead ones are black. This, with their wiry, matted appearance, accounts for the vernacular name "nigger wool" which is applied to this plant. The abundant, deep, widely spreading roots of these plants were excavated in the same soil type as that described for the preceding species.

Astragalus drummondii.—This legume was also examined in the mixed prairies at Ardmore, where it forms extensive societies, as in many places throughout the more arid portions of the grassland formation. In digging the trench, the first 4 feet of soil was found to be hard Pierre clay. This was underlaid by a 1.5-foot stratum of sand and coarse gravel, so closely compacted that it was necessary to remove it with a pick. Below 5.5 feet this gave way to a stiff sandy loam. Two large specimens were examined. Each had a strong, woody tap-root 17 mm. in diameter. The crown of each plant was about 1.5 inches below the soil surface. The tap-roots descended rather vertically downward and tapered rather rapidly. In the one plant at a depth of 1.7 feet it was only 3 mm. in diameter, while in the other it was about a millimeter in diameter at a depth of 2.7 feet. The first plant examined reached a maximum depth of 4 feet. In the first foot of soil, beginning at a depth of 0.3 foot, it gave off 8 major branches, 4 to 5 mm. in diameter; there were also 5 smaller ones. Below the first foot the branching was very sparse to the end of the tap-root. One of the largest laterals, which originated at a depth of 0.8 foot, spread horizontally from the base of the crown to a distance of nearly 3 feet, where at a depth of only 2 feet it gave off 5 major branches, each about 2 mm. thick. These spread widely and ran for distances of 1 to 2 feet before turning downward. Besides these branches, the root was furnished with numerous unbranched laterals less than an inch in length. The root-tips were only poorly branched in the very hard soil. Nodules about a millimeter in thickness and 2 mm. long occurred at intervals throughout its entire length. The other specimen reached a maximum depth of 4.3 feet, although it seems certain that in less compact soil the root depth would have been much greater. In the first 1.2 feet of soil it gave off 20 branches, 2 mm. or more in diameter, 3 of the larger ones being 4 mm. in width. There were also great numbers of smaller ones, so that the soil was quite filled with roots to a depth of about 3 feet. Below 1.5 feet on the tap-root branching was much less profuse and the laterals were smaller in size. The lateral spread was again very pronounced and some of the larger, widely spreading roots reached depths of nearly 4 feet. None of the root-tips were well-branched. Clusters of tubercles were found at various depths, forming X, Y, and H patterns 5 to 6 mm. in diameter. Summarizing, we find this legume has a tap-root which penetrates rather deeply and is abundantly supplied with numerous, rather coarse, moderately branched but widely spreading laterals, most of which originate in the surface 0.3 to 1.5 feet of soil.

This completes the list of plants whose root systems have been examined for the first time in mixed prairie. It will be best, however, instead of summarizing root habits here, to postpone this to the end of the chapter on ecads, as we may thus include a large number of species which have been examined in other habitats, but for the first time under growth conditions of the mixed prairie. To this list we may also add certain dominant and subdominant species which heretofore have been described only in mixed prairie (Weaver, 1919), but which have now been examined in a wide range of habitats.

V. ECADS.

The preceding pages have dealt with species the roots of which were undescribed and were excavated in only one or two places. The present chapter treats of plants, most of which are dominants, that have been examined in many places and under widely varying habitats from the Missouri River to the Rocky Mountains. These include species characteristic of sandhills, mixed prairies, and short-grass plains.

Bulbilis dactyloides.—This dominant of short-grass plains has a very wide distribution. It makes up much of the lower layer in mixed-prairie vegetation and occurs as alternes far eastward in the true prairies. Perhaps no other grass of the western plains, except grama, is better known for its valuable characteristics as a pasture grass, while for winter forage it has no equal.

In 1918 the roots of a dozen plants of this species were examined in a low-prairie area on alluvial soil near Lincoln. These fine roots scarcely spread at all laterally, but formed a dense mat to a depth of 1 to 1.5 feet. Below this depth they become less numerous, so that the deeper soils are sparsely occupied However, many roots occurred at 4.5 feet, and numerous others continued vertically downward to a maximum depth of 5 to over 6 feet, and in one of the trenches in gumbo soil to the ground-water level. This root behavior was so different from that reported by Ten Eyck (1904), in eastern Kansas, where "the roots are numerous but do not penetrate deeply into the soil," and by Shantz (1911) in Colorado, that careful examinations of the root habits of this dominant were made at eight different stations. Shantz's finding that "almost the entire root system of the short-grasses (*Bulbilis dactyloides* and *Bouteloua gracilis*) is limited to the first 18 inches of soil" was not confirmed in any instance. In fact, it will be shown that both of these xerophytic species, in addition to having a splendid absorbing system near the surface, are also deeply rooted.

Bulbilis roots were excavated in the short-grass plains near Yuma, Colorado. Here the soil consists of a chocolate-brown silt-loam, which is very hard and breaks out in lumps, showing more or less of a columnar structure. At a depth of 2.8 feet (in the trenches where the roots were excavated) it became lighter in color, but little harder in texture. This whitish-colored layer was 8 to 10 inches thick. Below it and extending to the maximum depth excavated (8 feet), the soil was much looser and consisted of yellowish clay, silt, and very fine sand, which at a depth of 7 feet became almost ashy in consistency. Soil samples taken in duplicate at the two ends of the long trench and to a depth of 8 feet on July 17, 1919 (table 6), show that the water-content throughout was exceedingly low.

Table 6.

Depth of sample.	Water-content.
feet.	*per cent.*
0 to 1	5.5
1 to 2	8.5
2 to 3	9.8
3 to 4	8.7
4 to 5	6.5
5 to 6	5.4
6 to 7	5.1
7 to 8	5.8

The vegetation is of the closed mat type (plate 9, A) and quite unlike that at Sterling, but very similar to that described at Burlington, Colorado (p. 74 and plate 2). Buffalo grass was far more abundant than grama.

The short, frequently branched rhizomes lie mostly within the first inch of soil. They are only 1.5 to 2.5 mm. in diameter, brittle and woody, and usually not over 0.5 to 2.5 inches in length. The stolons are usually very much longer. From the base of the plant clumps the roots

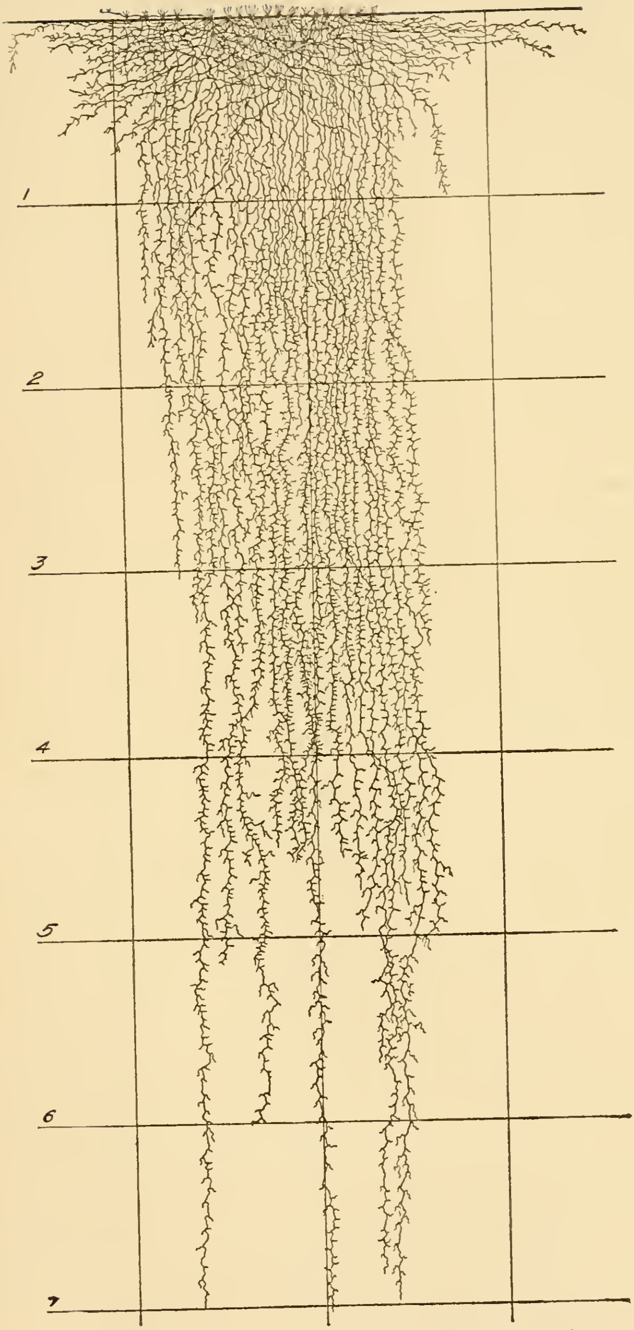


Fig. 27.—Buffalo grass in short-grass-plains association.

arise mostly in clusters of 3 to 10. They also originate from other points along the rhizomes and from the nodes of the stolons, but usually in smaller numbers. The roots are less than a millimeter in diameter, but very tough and wiry. Many of the surface roots spread laterally to distances of 0.8 to 1.7 feet from their origin. The tiny laterals are usually not over 0.5 inch in length and rebranch rather poorly. The working depth was determined at about 5 feet, but some roots were traced to a depth of 7 feet (fig. 27).

At Burlington, Colorado, are also found typical short-grass areas. In the area examined the sod of buffalo grass was well developed and bare areas were not much in evidence (plate 2, B). Other species were relatively few and of much less importance. They consisted of *Bouteloua gracilis*, *Festuca octoflora*, small patches of dwarfed, unbranched *Grindelia squarrosa*, *Opuntia polyacantha*, and *O. fragilis*. *Psoralea tenuiflora* and *Ratibida columnaris* occurred rarely, and *Aristida purpurea* only occasionally and then in small amounts, while *Plantago purshii* was scattered sparingly throughout.

A trench was dug in the pure buffalo-grass sod. The soil consisted of a silt-loam. At a depth of about 2.3 feet, lighter colored but only slightly firmer textured "hardpan" was encountered. It was 0.5 to 0.8 foot thick. The soil was fairly moist to a depth of 3.5 feet, below which it was powdery. The roots literally filled the soil to a depth of 2.5 feet. They were fairly abundant to 4.3 feet. The maximum penetration was not determined, but buffalo-grass roots were found to penetrate deeply in adjoining fields which made up a part of this level area and where roots of crop plants were traced to a depth of 5 to 6 feet (p. 112). In all cases they reached depths as great as the crop plants and in some of the trenches penetrated even farther.

At Sterling, Colorado, in a rather open mat type of vegetation of buffalo and grama grass (*cf.* p. 42), where the silt-loam was underlaid at about 2 feet with "hardpan," further examinations were made. The soil was dry throughout. At a depth of 4.7 feet occurred a layer of gravel and small pebbles mixed with some sand. This was very dry, as was also the sandy loam below. Many roots reached a depth of 5.5 feet, and probably penetrated somewhat farther, while the working depth was determined to be 3.6 feet.

At Limon, Colorado, the roots of buffalo grass were again examined, both on short-grass land and in mixed prairie. The variation of the type of vegetation is due to edaphic conditions, the compacted silt-loam being covered with short-grasses, while the sandier soil is rather clearly marked by mixed-prairie species. The vegetation of the latter community at this station has already been briefly described on page 66. While buffalo grass and grama formed a more or less interrupted layer throughout, in the area where it was excavated it was more nearly pure, wire-grass, mountain sage, etc., being rather rare. Such patches, although on high ground, and not to be confused with areas to be described where run-off water collects and stands, indicate a firmer soil texture. The surface foot of soil in this area of buffalo grass consisted of a dark-colored loam of hard texture in striking contrast to the easily spaded sandy loam found only a few meters distant, where *Astragalus microlobus* and other species were excavated. The subsoil was also less sandy and more compact in the buffalo-grass trench. Moreover, while in the other trench the soil was moist to a depth of 4 feet, in the latter it was powdery at a depth of 2.5 feet. Undoubtedly the difference is largely due to run-off, coupled with greater evaporation from the less sandy soil surface. The roots literally filled the soil to a depth of 2.2 feet, while they were still quite abundant to 3.7 feet, a few reaching a depth of 4.5 feet.

Low areas in swales where water collects and stands are clothed with a dense sod of nearly pure buffalo grass. A long trench was dug near the edge of one of these "sinks" in such a manner that while one end was in the buffalo-grass area, the other permitted the excavation of the bordering wheat-grass, *Psoralea*, and mountain sage. The wheat-grass roots thus growing in competition with the buffalo grass are described elsewhere (p. 78), but it may be noted here that the roots of the two species grew at the same depth. Both grasses were abundant to a level of 4.3 feet, where the very hard, black soil was underlaid with sand and both had a maximum depth of 5.2 feet. The wheat-grass was only 1 to 1.2 feet high (plate 11, B).

Further examination of this species was made late in June in the mixed prairie at Phillipsburg, Kansas, over 230 miles eastward. The better conditions for prairie express themselves not only in the greater development of species, but also by the presence of many true-prairie forms. *Andropogon furcatus* was second only to *A. scoparius* in importance; *Agropyrum glaucum* reached a height of 3 feet, and often controlled over extensive areas, while *Elymus canadensis* was abundant. Societies of *Psoralea tenuiflora, Erigeron ramosus, Coreopsis tinctoria,* and *Ratibida columnaris* were very conspicuous at this time. In many places the layer of *Bulbilis dactyloides* and other short-grasses and sedges was present, while in pastured areas the buffalo grass formed a dense sod in which isolated clumps of *Psoralea* reached a height of about 2 feet.

The soil is a dark-brown silt-loam, with some sand intermixed to a depth of about 1.7 feet, where it becomes more clayey, although when moist it takes on a dark-brown color to a depth of 4.5 feet. Below this it becomes lighter in color and more clayey in texture. In all of the four trenches, some of which were made on tilled land (p. 119), it was moist enough to hold firmly when molded by the hand at all depths to over 7 feet. The buffalo-grass roots were examined in the same trench with the tall-grass competitor, *Andropogon scoparius*. Both had a maximum root depth of about 6 feet. The short-grass roots were very abundant to a depth of 2.5 feet and fairly abundant at the 5-foot level, while not a few reached the maximum depth of 6 feet and some penetrated even deeper.

A final examination of this species was made in the mixed prairies near Ardmore, South Dakota. A trench was dug to a depth of over 8 feet in an area where the tall wheat-grass (2 to 2.3 feet high) was competing with the buffalo and grama grasses (plate 3, B). All showed an excellent growth, *Bouteloua gracilis* being 10 to 12 inches high. At a depth of 6.7 feet the very hard Pierre clay gave way to a layer of sand. The soil was fairly moist throughout. As at Yuma, the working depth of *Bulbilis* was about 4 feet, while the maximum depth of penetration exceeded 7 feet. For the sake of comparison the preceding data are brought together in table 7.

Study of these data reveals a number of interesting facts. The roots of buffalo grass, as regards working depth and maximum depth of penetration, are little affected apparently by environmental conditions. They are just as deep-seated in the short-grass plains as in the mixed or true prairie. One marked difference in root habit, however, should be emphasized. Plants examined in the less xerophytic grassland at Lincoln scarcely spread at all laterally. In the mixed prairies at Phillipsburg and at Ardmore the lateral spread in the surface soil was well developed, but not to such a marked extent as among the individuals growing at the various stations in the short-grass plains. The roots reach a working depth beyond the "hard pan," even where this is well-developed. "Hardpan" is thought to arise as a result of the water penetrating repeatedly only to a depth at which this harder layer is formed, thus not only washing down the finest soil particles but also causing them to be more or less firmly cemented together by the accumulated solutes carried downward. It has been shown that such a soil layer, more or less definitely differentiated and of variable thickness, does occur throughout much of the drier grassland area. But no case has ever been found by the writer among native species, and relatively few cases among crop plants, where the "hardpan" corresponded with the depth of root penetration. Usually roots penetrate it without profound modifications and it seems doubtful if it ever acts as a mechanical hindrance to root development. The soil here is certainly no more compact than the Pierre clay, through which roots penetrate with no apparent external modifications. The fact that native short-grass roots, together with those of many other species, are found regularly, and those of cultivated crops at least

TABLE 7.—*Root development of buffalo grass in prairie-plains-grassland formation.*

Station.	Community.	Soil type and condition.	Working depth.	Maximum depth.
			Feet.	*Feet.*
Yuma, Colo.	Short-grass plains.	Silt-loam. Dry throughout; powdery below 5 feet; poorly developed "hardpan" at 2.8 feet.	5.0	7.0
Burlington, Colo.	....do....	Silt-loam. Fairly moist to 3.5 feet, then very dry; poorly developed "hardpan" at 2.3 feet.	3.0	6.3
Sterling, Colo.	....do....	Silt-loam. Very dry throughout; "hardpan" at 2 feet.	3.6	5.5+
Limon, Colo.	....do....	Silt-loam (of swale). Fairly moist throughout; no "hardpan."	4.0	5.2
Do.	Mixed prairie.	Silt-loam with sandy loam below 1 foot. Very dry below 2.5 feet, no "hardpan."	3.0	4.5+
Phillipsburg, Kans.	....do....	Silt-loam. Well moist to maximum depth; no "hardpan."	3.3	6.0+
Ardmore, S. Dak.	....do....	Pierre clay. Fairly moist throughout; no "hardpan."	4.0	7.2
Lincoln, Nebr.	True prairie.	Silt-loam. Very moist; alluvial silt-loam soil.	3.5	6.1

often, below this layer should be sufficient to throw much doubt upon the too widely credited efficiency of "hardpan" in preventing water penetration. One of two things must occur: either buffalo-grass roots penetrate and develop normally several feet below the point where water is available for growth, or water reaches depths (at least at intervals) far beyond the surface 1.5 or 2 feet of soil. Very few published data are available on the water-content of short-grass plains soils. Shantz (1911) concludes from measurements taken at Akron from June 10 to September 10, and at Yuma, Colorado, for a shorter period, that "soil-moisture determinations in this type of land show that even during periods of more than normal rainfall available soil moisture is limited to a few inches of the surface soil." Alway (1919), using Shantz's data, has shown further that even during this season (1909) of excessive rainfall, the soil-water approached or reached the hygroscopic coefficient at depths of 0.5 to 1, 1 to 1.5 feet, and in the fifth and sixth foot at certain periods during the growing-season. However, until a long series of soil-moisture determinations are made at many stations throughout this region, we must accept the judgment of the plant as an indicator of available moisture at least periodically in the deeper soil layers.

Bouteloua gracilis.—This grama grass is a dominant not only in the short-grass plains, where it forms extensive consociations, but it plays an important part as a species in the layer of mixed prairie. It also occurs in alternes on the lighter soils of uplands in true prairie, where it may also often be found on areas of alluvial soil on bottom lands. From the standpoint of grazing, it ranks very high among the grasses, being equaled only by *Bulbilis dactyloides*.

The roots of this species have been described for a consocies growing as an alterne in a glacial deposit of very porous, coarse, sandy to gravelly loam soil on a ridge in the true prairie near Lincoln, Nebraska. The root system was found to be well-developed, great masses of fine roots occupying every cubic centimeter of soil to a depth of 1.5 feet. A few roots reached a maximum depth of 3.8 feet, although below 2 feet they were very sparse. Other groups of plants examined in two locations on alluvial soil showed a somewhat poorer development of the root system, but with a general distribution and depth very similar to those growing in the gravelly soil.

This grass has also been examined in the mixed prairie at Colorado Springs. The soil was well filled with fine rootlets to a depth of 2.5 feet, while in the next 0.5 foot they were still fairly abundant, some of the longer ones penetrating to a maximum depth of 4 feet. Further examinations of this species were also made in "adobe" soil in pure short-grass land about 25 miles southeast of Colorado Springs, where it was the dominant (plate 11, A). Roots were found to be very abundant to a depth of 3.3 feet, while several were traced to a maximum depth of 4.3 feet.

During 1919 still further examinations of this species were made at Sterling, Colorado, and Ardmore, South Dakota. At the former station (plate 2, A) the soil was quite filled with roots to a depth of 2.5 feet, while at 3.2 feet they were still abundant. The maximum depth of penetration was 4.2 feet.

At Ardmore, where grama was competing with wheat-grass and buffalo grass (p. 75), the roots were abundant to the working depth of 3.6 feet, while some were traced to a depth of 4.3 feet in the tenacious but moist Pierre clay.

A comparison of these data shows that grama-grass roots, like those of buffalo grass, are quite deep-seated. The working depth ranges from 1.7 to over 3 feet, while the maximum root depth in every case was between 3.8 feet and 5.8 feet. Little difference in root distribution was found in the several plant communities, except that the marked development of widely spreading surface laterals so common in the more arid portions of the grassland formation was not found in the true prairie. Here the specimens examined, like those of *Bulbilis*, spread but little in the surface soil.

Agropyrum glaucum.—This important dominant of true and mixed prairies has now been examined at five different stations in Nebraska, Colorado, and South Dakota. A complete description of its root habit, in both high and low true-prairie areas, may be found on page 18 (*cf.* fig. 3 and plate 12, B). The chief difference in its root habit in the true and mixed prairies, besides greater depth of penetration in the former is in the absorbing system near the soil surface. This is very much better developed in the drier mixed-prairie soils (*cf.* Weaver, 1919: 52). At both Ardmore, South Dakota, and at Limon, Colorado, where it grew in competition with *Bulbilis*, the latter station being on typical short-grass silt loam, the absorbing system in the surface soil was quite pronounced. In the Pierre clay at Ardmore the working depth was at 5.5 feet and the maximum root penetration 7 feet. At Limon this grass was only 1.2 feet tall and was not thriving, because of the keen competition with *Bulbilis* in the compacted silt-loam at the edge of a swale (plate 11, B). Here the working depth was only 4.3 feet and the maximum root penetration 5.2 feet. A correlation between the height of the tops and the root depth in the several communities (shown in table 8) is of particular significance, because similar general correlations have been determined for the root systems of crop plants.

TABLE 8.—*Development of Agropyrum glaucum.*

Station.	Plant community.	Height of plant.	Working depth.	Maximum depth.
		feet.	*feet.*	*feet.*
Limon, Colo	Short-grass plains	1.2	4.3	5.2
Ardmore, S. Dak	Mixed prairie	2.2	5.5	7.0
Colorado Springs, Colo	.....do	2.2	6.0	7.2
Lincoln, Nebr	True prairie (low)	2.7	7.0	8.0
Do	True prairie (high)	2.7	8.0	9.0

Gutierrezia sarothræ.—This perennial half-shrub forms societies throughout the plains region. In areas which have been greatly over grazed, or where the soil is rather poorly disintegrated, it often occurs in great abundance.

The plants examined in the *Bulbilis-Bouteloua* turf at Sterling, like those of *Aristida purpurea* and *Artemisia frigida* (pp. 42 and 83), were dwarfed specimens only 5 or 6 inches high. The numerous stems forming this woody half-shrub arose from tap-roots 4 to 8 mm. in diameter. Just beneath the soil surface the tap-root invariably gave rise to so many laterals (the largest being 2 or 3 mm. in diameter) that it diminished rapidly in size and at a foot in depth was frequently indistinguishable from its branches. Most of these laterals were found to spread horizontally in the surface 0.3 to 0.4 foot of soil to distances of 0.5 to 1.5 feet before ending, or, as is more usual, turning downward. Below 6 inches no large branches were given off, nor is the tap-root or its deeply descending branches furnished so abundantly with finely rebranched rootlets below a depth of 1.2 feet, as in the surface soil. Most of the many descending branches ended in the third or fourth foot and none was traced to a greater depth than 5 feet. In general, this root habit agrees very closely with that of the specimens excavated at Colorado Springs (Weaver, 1919:49). The chief difference is the greater root penetration (5 to 6.5 feet) and the wider surface spread of the laterals (0.3 to 2 feet) of the more robust plants at the latter station.

Petalostemon purpureus.—This species of prairie clover, like *P. candidus*, has a very wide distribution. Both form societies, being especially conspicuous in late summer. They are best developed in true prairie and are also abundant in mixed prairie, but seldom occur in the short-grass plains.

A very robust specimen, with a tap-root 2 cm. in diameter, was examined in the sandhills near Yuma. It gave off 10 branches, ranging from 4 to 7 mm. in thickness in the first 8 inches of soil. These spread widely in the shallow soil, as is characteristic of the species, before turning downward. Like the tap-root, the laterals taper very rapidly, and throughout their horizontal course give off an abundance of both large and small sublaterals. Upon turning downward, like the tap, they follow a more or less vertical course, but curve backward and forward through distances of from several inches to more than a foot. They taper so rapidly that below 1.5 feet none of the roots are usually more than 1 or 2 mm. in diameter. They soon become more or less threadlike, with small rebranched rootlets from a few millimeters to several inches in length. Many of the larger roots reached a depth of 5 feet, while the tap-root ended in the moist sand at a depth of 8.4 feet. The root habit was very similar to that found in the hard loam soil of the plains, except for the more profuse branching and greater depth of penetration. However, this was a much larger specimen than any found in the mixed-prairie habitat.

Lygodesmia juncea.—This composite is of frequent occurrence, often becoming ruderal, especially in drier situations throughout the prairie-plains grassland. It is especially interesting because of its xeroid-shoot habit. It has been examined both in the subclimax prairie near Peru, Nebraska, and in the mixed prairie at Colorado Springs. In the mellow loess soil at the former station the tap-roots were found to penetrate vertically downward to depths of 15 or 20 feet or more. The brittle, fleshy roots are usually 2 to 6 mm. in diameter and do not branch at all, except for tiny laterals less than a millimeter in thickness and an inch in length, which come off very sparingly at intervals of 6 to 12 inches. In the hard loam soil at the mixed-prairie station the depth of penetration of the two plants excavated was only about 6 feet. The root diameter was about 7 mm. Throughout its course the root was very much curved and twisted, nor did it penetrate directly downward. Several large, crooked, wide-spreading branches were given off, but practically no small ones.

This species was encountered quite frequently, not only among the native vegetation but also in excavating crop plants, among which it is often quite an abundant weed. The root habit varied somewhat between the two extremes above noted. In the sandy-loam soils the roots were less crooked and kinked and had fewer or no major branches, while in the harder soils, or layers of harder soil, these characters were more pronounced. Roots were found to penetrate well beyond a depth of 8 feet in two or three of the trenches dug at Burlington, Colorado, and also in the silt-loam at Colby, Kansas. Unquestionably this xerophyte is a deep feeder.

Andropogon scoparius.—Little bluestem ranks as one of the most important grasses of subclimax, true and mixed prairie. Its wide range can be largely explained by a consideration of its excellent and plastic root system, its methods of propagation, and its sod and bunch-forming habits. It is an economic species of much importance and warrants careful study.

This grass has been examined in two types of soil in the true prairies near Lincoln. In clay-loam soil with a clay subsoil several plants had a root depth of about 5.5 feet, while in a porous gravelly soil mixed with sand and underlaid with a rocky subsoil of decayed sandstone at a depth of 3 feet, none of the roots reached depths greater than 2.3 feet. Branching and lateral spread were much the same in both cases, but emphasized somewhat in the poorer soil type (Weaver, 1919: 5).

At Colorado Springs the surface portion of the root system was well developed, especially well-branched laterals spreading to 1 to 1.2 feet on all sides of the bunches in the surface 0.3-foot soil layer. Below and inside of these, at all angles to the vertical, the roots were very abundant. Most of them penetrated to about 3.5 feet, and the maximum depth of several roots was 6 feet.

During 1919 this species was excavated in the silt-loam soil of the mixed prairies near Phillipsburg. The roots were still very abundant at 4.5 feet and not a few reached a maximum depth of 5.2 feet. The roots occur in very large numbers, but are only 0.1 to about 0.8 mm. in diameter. Some spread laterally nearly parallel with the soil surface, but more often obliquely downward to distances of 1 to 1.2 feet before turning directly downward. These, with the more or less vertically penetrating roots, form a dense sod to a depth of about 2.7 feet. The surface soil layer is especially well occupied with dense masses of finely branched rootlets, but branching continues to the very root-tips. Many of these laterals are over 2.5 feet long and are rebranched to the third and fourth order. The root-ends formed a finely branched network or mat of roots 0.2 to 0.3 foot wide and about 1.5 feet long in the deeper soil, the branching mostly being confined to the one plane in the jointed subsoil.

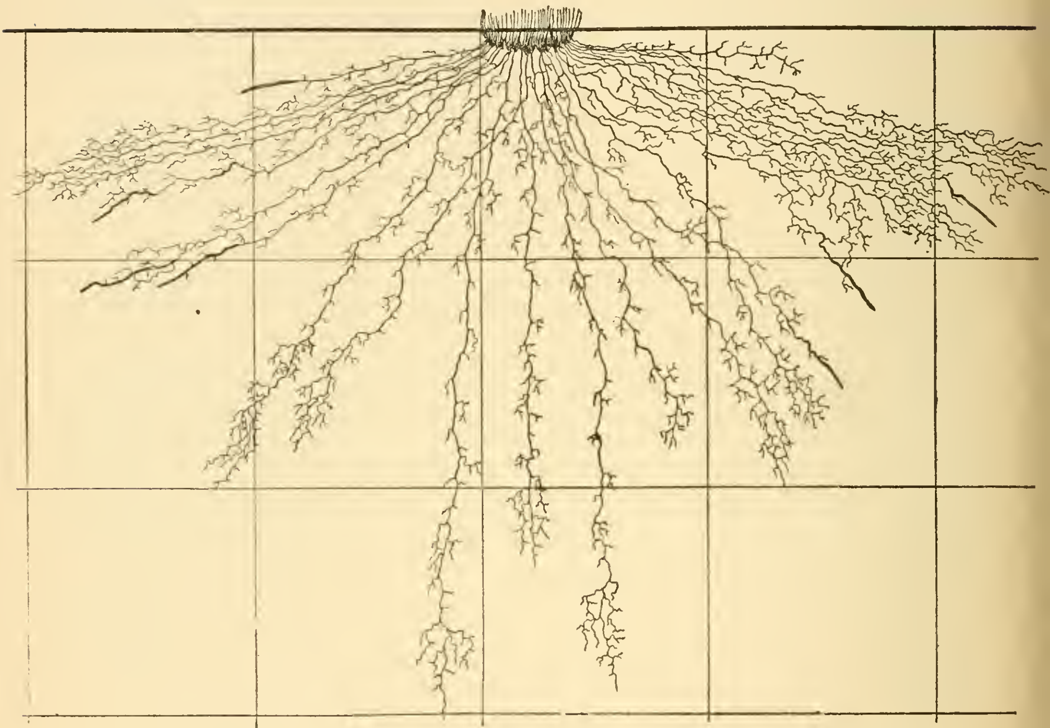


FIG. 28.—Root system of *Andropogon scoparius* excavated in the sandhills.

At Haigler, Nebraska, the plants were excavated in the sandhills. Three large bunches growing on a partly covered hillside were examined. Roots beneath the clumps were not at all abundant. Most of the roots ran off rather parallel with the soil surface or slightly obliquely for long distances, where they ended or finally turned downward. Numerous roots were traced to their enlarged, unbranched, growing-tips at a horizontal distance of over 2 feet from the base of the clump and in the first 0.8 foot of sand. Others are shorter and shallower. Still others turned more obliquely downward and extended well in to the third foot of soil. A few reached maximum depths of 3.5 feet, but they were rare below 3 feet. Branching was profuse, as already described. Figure 28 shows one of the plants excavated at this place. Its root habit reminds one strongly of that of *Aristida purpurea* when growing in the sand (p. 84). The enlargement of some of the root-ends was a frequently observed feature of several species of sandhills plants. The tip often rapidly and rather abruptly increases in size from 2 to 5 times its original diameter and may either end abruptly or gradually taper away again. The enlarged portion is often several inches long. These enlargements most often occur on the larger roots, and especially on those which are extending rapidly into new territory. Usually they are quite devoid of branches. They are apparently developed under normal conditions and seem to be due almost entirely to an increase in the growth of the cortical tissues. Waterman (1919) has observed the same phenomenon in *Juncus balticus* and other dune species about Lake Michigan and suggests the name "pioneer" or invading root-tip.

Further examination of this species was made at Yuma, Colorado, where in a valley of sandy loam it was dominant in a turf of short-grasses (plate 7, B). Here again the surface spread of the laterals was found to be very great. Large masses of roots ran out to distances of 1.3 to 1.7 feet or more in the surface 0.4 foot of soil. However, these widely spreading roots, which came off at all angles from the vertical, were supplemented by many more which penetrated vertically downward. These roots, like the soil in which they were growing, were intermediate in type between those described in nearly pure sand and those of clay-loam.

A final examination of this species was made on a hillside at Seneca, Nebraska, where the bunches were exceedingly well developed and where it was a dominant species (plate 8, A). The flowering stalks reached a height of 2.3 feet, and many of the bunches were 1.5 to 2 feet in diameter. They were composed of scores of individual stems, the old leaves and dead stems persisting for a number of years. This species has in size, duration, and abundance all the prerequisites of a dominant, and in fact is the bunch-grass of widest distribution and most controlling influence.

From one-half to two-thirds of the exceedingly well developed root system spreads laterally in the surface 1 to 1.5 feet of sand. Some roots ended at a depth of only 0.4 to 0.7 foot, but at a distance of 3.3 feet from the base of the clump. One root was traced to a horizontal distance of 3.8 feet from its origin. It ended with a well-branched tip at a depth of only 1.5 feet. Some penetrated laterally at various depths as far as 3.8 to 4.2 feet. All were well-branched, some of the deeper oblique roots sending up more or less vertical branches which ended near the surface. But while many of the roots ran out obliquely at all angles between the vertical and horizontal and thus furnished an excellent surface absorbing system, others penetrated nearly straight downward; these, with the oblique roots which often turned downward and reached a depth of several feet, provided for absorption in the deeper soil. Many of these well-branched roots reached depths of 6 or 7 feet, and some were found at a maximum depth of 8 feet. The working depth of most of these deeper roots was about 6.7 feet. Throughout, the root branching was very profound, the root-ends being unusually well supplied with branches.

It may be seen from these data that the root system of the little bluestem is always well developed but quite variable. Its extreme range in depth from 2.3 feet in poorly disintegrated subsoil to 8 feet in the sandhills is indeed remarkable and is equaled only by its marked variation in lateral spread, especially in the surface soil. In clay or silt-loam this is normally only about 10 or 12 inches, but as the substratum becomes sandier the lateral spread and proportion of roots in the shallower soil increase, reaching the maximum in the sandhills. Of all the plants examined, those at Seneca were the largest, the others, although old plants, having been either grazed or annually mown. This may account in part for the exceptionally great depth of the roots on the steep hillside at the former station, although repeated partial burial by the sand may also have been a factor. The great plasticity of the root system of this species is undoubtedly a factor accounting for its wide distribution.

Andropogon furcatus.—Like the preceding, this bluestem is also dominant among prairie grasses. Its smaller resistance to drought, which is shown both by its local and general distribution, can easily be understood when this taller and deeper but coarser-rooted species is compared with the shorter, finer-rooted and more profusely branched *A. scoparius.* While big bluestem occurs upon high prairies, it makes its best development in the draws and on lower land (plate 6, B, and figs. 11 and 13). It is an important mixed-prairie species, but does not extend into such dry areas as does *A. scoparius.* The root depth of the big bluestem has already been contrasted where the plants were growing on the high and low prairie at Lincoln (p. 41).

Further examination of this species was made at Phillipsburg, Kansas, where it occurs as a dominant among the tall-grasses (p. 75). The very abundant, rather coarse roots grow both vertically and obliquely downward, thoroughly occupying the soil and forming a dense sod. Some of the roots extend laterally in the surface 0.5 foot of soil to a distance of 0.7 to 1.2 feet before turning downward. The working depth is nearly 7 feet. The roots all branch profusely, the main laterals being mostly 0.2 to 0.5 foot in length. The ends of the roots are extremely well branched. Little difference was found in the root habit of these plants of the mixed prairies and those in the true prairie at Lincoln, except in greater depth of penetration. At Phillipsburg some of the deeper roots reached a level of 8.7 feet, while at Lincoln 6.8 feet was the greatest depth recorded for high-prairie species, those in the low prairie having a root system of even lesser extent (p. 41). However, in the mellow loess soil of the subclimax prairie at Peru, Nebraska, root depths of over 9 feet were recorded. A 4-months-old specimen, grown in alluvial soil on a lowland area near Lincoln, is shown in plate 18, A.

Artemisia filifolia.—The sand-sage is often a very important species in the structure of mixed-prairie vegetation in sandy areas. This is due both to its shrubby habit and its great abundance. It is indicative of a light type of soil with considerable moisture penetration. It rarely occurs on the more compact silt-loam soils.

Two large specimens were examined on a fairly well-covered area on a sandhill. The root system is dominated by a strong tap-root (plate 19, A), from which arise great numbers of long, profusely branched laterals. One tap-root was traced to a depth of over 8 feet. The strong, vertically descending, woody tap-root tapers gradually and uniformly. Some of the larger branches had a lateral spread of 4 or 5 feet and reached depths of 4 to over 6 feet. Most of the branches, both large and small, originated in the surface 3 feet of soil, and with their profuse laterals formed an extensive absorbing system in the surface 3 or 4 feet of sand. Little difference was found between these plants and those of the same species excavated near Colorado Springs (Weaver, 1919:73).

Muhlenbergia pungens.—This grass is a regular component of blowout communities and is not infrequently dominant. It is characterized by tufted stems which arise from rootstocks and form cushions or mats that lie close to the sand (plate 9, c) and by scabrous, narrow, rigid leaves.

This important sandhill grass was examined about 40 miles southeast of Colorado Springs, on the rim and grassy top of a blowout, where it was growing very abundantly. It was found to have a rather shallow but widely spreading root system, none of the roots penetrating the dry sand to a greater depth than 2.8 feet.

Careful examination of this species was made at Central City, Nebraska, in the extra-regional sand dunes. Here it was growing in the usual mats in pure sand on the side of a blowout. Fibrous roots, a millimeter or less in diameter, arose in clusters from the rather short, shallow rootstocks. Some penetrated rather vertically downward to maximum depths of 3.5 feet, and in fact the roots were abundant to a depth of 3.3 feet. Many others spread out laterally at all angles between the vertical and horizontal, some reaching distances of from 1 to 2 feet from the base of the plant and ending in the surface 2 or 3 inches of soil. All parts of the roots are furnished with multitudes of very fine absorbing laterals. While many of these are only a few millimeters long, others have a length of 6 to more than 12 inches. All are profusely and minutely branched, the larger ones to the third and fourth order. Even the tips are well supplied with branches. In a neighboring blowout other specimens were not so deep-seated. Roots were not abundant below 2.4 feet and the maximum penetration did not exceed 3.2 feet.

Other plants were examined at Haigler. One clump was excavated on the high, dry, rather vertical walled rim of a blowout. The bank was cut back about 2.5 feet. Some of the roots were found at a maximum depth of 4 feet and they were numerous at 3.3 feet. On the other hand, specimens examined in the grassy carpet of a fairly stable old blowout, only a few rods distant, were found to be shallower-rooted. None extended beyond 2.8 feet. The soil in the former situation was considerably drier, and this may account for the difference in root penetration.

Further examination of this species at Seneca confirms its shallow, widely spreading, profusely branching root habit. Here well-developed clumps were excavated in the loose sand of an old blowout. Practically all of the roots were found in the surface 1.8 feet of soil, only a few penetrating to a depth of 2.5 feet. The root habit of this species is fairly stable.

Aristida purpurea.—Wire-grass characterizes large areas of grassland throughout the Great Plains, especially where the soil is slightly sandy or where overgrazing or other disturbance has given it a foothold in competition with *Bulbilis* and *Bouteloua gracilis.* It is of very little grazing value, being eaten by stock only when other forage is scarce.

A complete description, accompanied by a drawing of this species as it occurs in the hard loam soil at Colorado Springs, has been given in "Ecological Relations of Roots," pages 46 and 47. Wire-grass has coarse, fibrous roots which spread 5 to 8 inches laterally, but do not branch profusely in the surface 4 inches of soil. The soil is filled with well-branched roots to a depth of 3 feet, at which level many terminate in much-branched tips, while others penetrate to a maximum depth of 4 feet or slightly beyond.

In the sandy loam at Limon the roots reached a depth of 4.2 feet and the root habit agreed in all respects with that at Colorado Springs, except that the roots in the surface layer of soil were somewhat better developed.

At Ardmore a group of well-matured plants about 1.1 feet tall was excavated. The Pierre clay soil was exceedingly hard and tenacious and underlaid at 4 feet with a layer of gravel and sand so closely cemented that it was picked away with considerable difficulty. Here the wire-grass roots reached a working depth of only 2.6 feet, although some penetrated 6 inches deeper.

Further examinations were made at Burlington and at Sterling, Colorado. At both stations only isolated groups of plants were found in the short-grass turf and the tops were much dwarfed, being only about 6 inches high. At Burlington the "hardpan" began at 1.9 feet and extended to a depth of 3.5 feet, below which the soil was mellow but powdery dry. In the soil of short-grass plains the "hardpan" is usually clearly demarked by its lighter color, due apparently to an accumulation of calcium and magnesium compounds. Here no roots of wire-grass extended below a depth of 2.8 feet. They were poorly developed throughout. At Sterling the lateral spread was about as described at Colorado Springs; no roots penetrated below a depth of 2.3 feet. It should be recalled that growth conditions on the rolling land here are even less favorable than on the level country at Burlington, as is indicated by the open mat type of vegetation (plate 2).

Aristida was further examined at Yuma, but this time in the sand. Several well-developed but somewhat isolated plants were found growing on a sandy ridge. The finer sand had been blown away and the plants were rooted in coarse sand which was firmly compacted. Three plants were excavated. On one medium-sized bunch, 3.5 inches in diameter, 189 roots were counted. Figure 29 shows a bisect about 4 inches wide through one of these clumps.

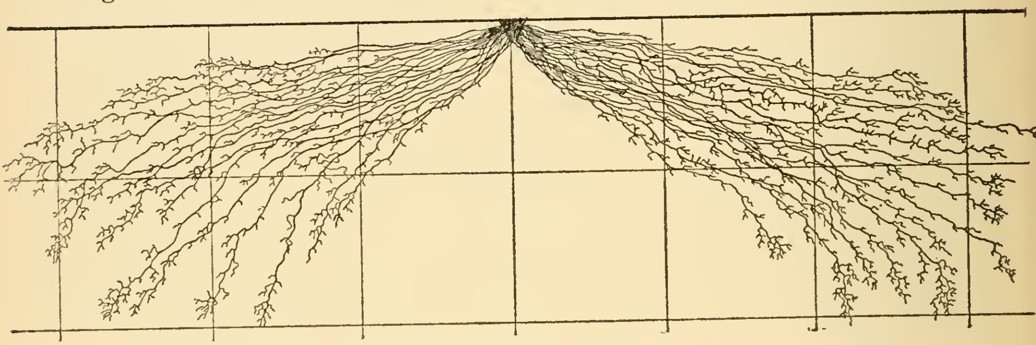


Fig. 29.—Bisect through the roots of *Aristida purpurea* growing in the sandhills.

This clearly illustrates the shallow root habit, the widely spreading roots, and the very abundant and relatively long lateral branches, the whole forming a very different root system from those growing in loam or clay. While there were practically no roots under the clumps, the lateral spread in the surface 0.5 foot of soil reached 2 to 3 feet, some of the deeper roots spreading even more widely. No roots were found below 2.5 feet, and practically the entire system was confined to the surface 2 feet of soil. Rebranched lateral rootlets were very abundant, some of the main laterals reaching a length of 4 or 5 inches, but they were mostly shorter. The root-ends were well-branched. A final examination of this species was made in a broad valley about a mile distant, where the compacted sand was somewhat intermixed, at least near the surface, with some black soil and humus. The area was dominated by *Andropogon scoparius*, with some *Aristida purpurea* growing in a short-grass turf of *Bouteloua gracilis*, *B. hirsuta*, and species of *Carex* (plate 7, B). The roots had a very wide lateral spread in the shallow soil. Some ran off nearly parallel with the soil surface at depths of only 2 to 6 inches for distances of about 2 feet. At 1.3 feet depth some exceeded 2 feet in lateral spread. The surface 1.5 feet of soil especially was filled with the coarse but well-branched roots of this species. Moreover, many of the roots (perhaps about a fourth of the whole root system) penetrated rather vertically downward, so that the soil below the plants was also well occupied.

From the above it is clear that the root habit of this species varies considerably with the environment. The wide lateral spread, especially in the surface 6 inches of soil, and the general root development was much more pronounced in every case where the species was excavated in a sandy substratum. Under these conditions the normal lateral spread of 0.4 to 0.7 foot in silt-loam or clay soil was extended to 2 or 3 feet; in fact, many of the roots ended in the surface foot instead of turning downward. A similar habit of other ecads when growing in sandy soil has already been pointed out (Weaver, 1919:110), and it will be shown that other species behave in this same way. In the mixed prairies at Colorado Springs and at Ardmore the roots penetrated a little deeper than at either Burlington or at Sterling, stations in the short-grass plains. A comparison of the root habit of buffalo grass and grama with that of wire-grass, especially with regard to lateral root distribution and branching in the surface soil, makes it clear at once why the latter can develop only poorly in undisturbed short-grass turf. Short-grasses begin to absorb at once from the surface soil after summer showers; wire-grass only to a small degree until water has penetrated more deeply. The root habit also explains why wire-grass often thrives on short-grass land that has been broken out and subsequently abandoned (*cf.* Shantz 1911: 41).

Psoralea tenuiflora.—This widely distributed legume occurs in nearly every association of the grassland formation. It is not only one of the most important herbs of the short-grass plains, but is also abundant in the mixed prairie. In less arid grassland, and especially in true prairies, it is represented by extensive societies of the more robust form, *Psoralea tenuiflora floribunda* (plate 5, B).

Several plants of this species have been examined, both in the mixed prairie at Colorado Springs and in the true prairie at Lincoln (Weaver, 1919). They are characterized by strong tap-roots and numerous large, widely spreading laterals, especially in the deeper soil. Frequently the tap-root penetrates to depths of 1 or 2 feet before branching. Very little absorption occurs near the surface. Maximum depths of penetration of 8 to over 12 feet have been recorded. Although larger laterals may be quite abundant, these are only poorly branched.

A specimen with a tap-root an inch in diameter was excavated in the mixed prairie at Limon. The crown of the plant, as is often the case, was sunk 6 inches below the soil-level. Two small laterals originated just below the crown and two large ones at a depth of 1.3 feet. The latter were each 8 mm. in diameter (plate 19, B). These ran off obliquely on opposite sides of the tap-root, to distances of 4 and 12 inches respectively, before turning downward, each pursuing a course almost parallel with the vertically descending tap-root to a depth of 4.4 feet. At this level the tap-root gave off a lateral 5 mm. in diameter and then turned off horizontally, running parallel with the soil surface for 1.5 feet, but still retaining a diameter of 5 mm. Here it broke up into two nearly equal branches, one of which ascended more than 6 inches, while the other continued its course far into the wall of the trench. While no roots were traced to a greater depth than 6 feet, several were found in different trenches at this level which still maintained diameters of 4 or 5 mm., and from their vertically downward course it is very probable that they penetrated much deeper.

In the short-grass plains at Yuma a specimen with a crown 15 mm. in diameter was excavated from one end of the trench described on page 72. The bushy plant was nearly 2 feet high and in full bloom. In figure 30 the details of this root system may be seen. The absence of any laterals in the surface 1.7 feet of soil and the widely spreading but poorly branched deeper roots are very characteristic. The tap was traced to a depth of 9 feet, at which point it was still 4 mm. in diameter and running rather vertically downward. Plants of this species were rather rare in the closed buffalo-grass sod (plate 9, A).

At Phillipsburg, Kansas, several psoraleas in the mixed prairie were traced to the maximum depth of the trenches (about 8 feet), but many of the larger ones evidently penetrated much deeper. Here, as at Ardmore, the root habit was about the same as that already described. At the latter station roots were traced to a depth of 7 feet in the Pierre clay.

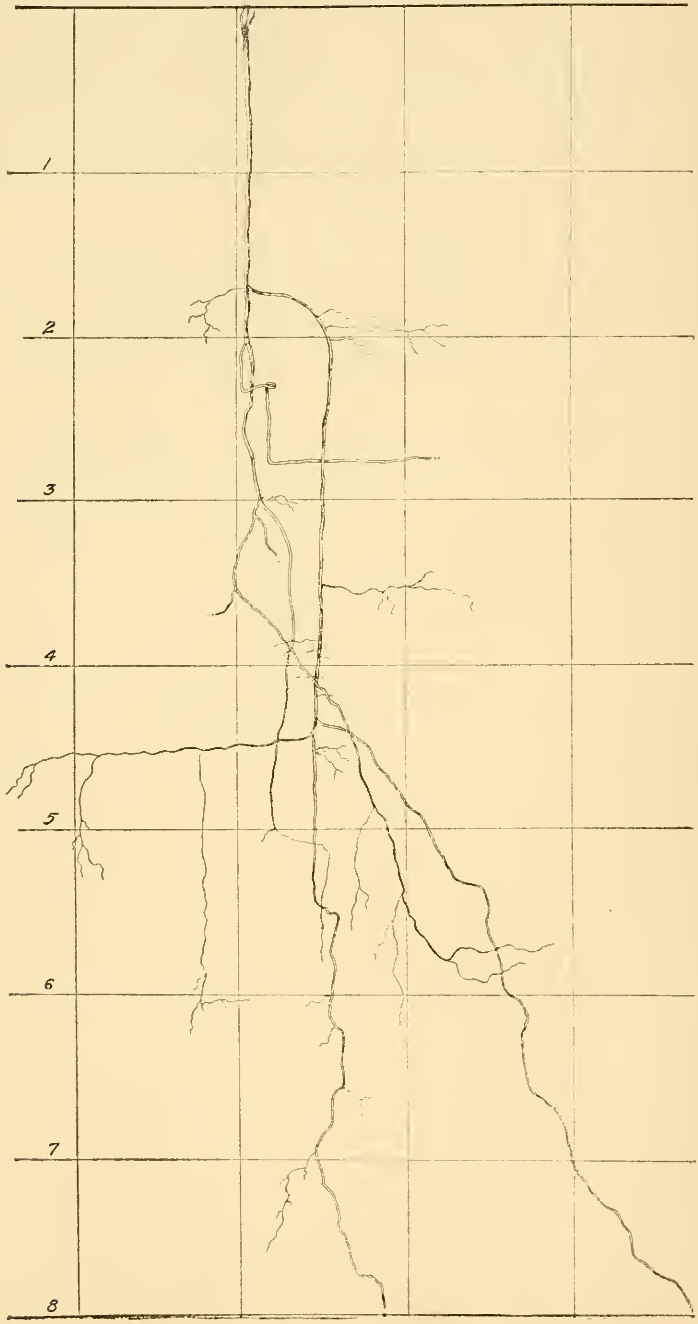


FIG. 30.—*Psoralea tenuiflora* in short-grass-plains association.

To summarize the data from the six widely separated stations in the three grassland associations: *Psoralea* has a deep tap-root with no provision for surface absorption, and in fact seldom branches in the surface foot of soil. The laterals are often large and wide spreading as well as deeply penetrating. The root system as a whole is not well supplied with fine absorbing rootlets. This is a stable species, little modified in root habit by varying conditions of the environment. Its presence is indicative of available moisture in the deeper soil.

Artemisia frigida.—This low, semi-woody perennial is especially well developed in the short-grass plains and mixed prairie. It frequently forms extensive socies when the natural vegetation is greatly disturbed, or in rocky or gravelly situations, especially near the mountains. It has been thoroughly examined at Colorado Springs. Arising from the base of the clustered woody stems, the strong tap-root descends vertically downward for a distance of 4 to 6 feet. Just below the soil surface many laterals originate. These run off either parallel with the soil surface or only rather obliquely with it for distances of 8 to 12 inches or more before turning rather abruptly downward. The smaller roots branch profusely and furnish the plant with an excellent absorbing system in the surface soil. Many of the well-branched laterals reach depths of 2 or 3 feet or more and are not infrequently as large in diameter as the tap-root.

In the dark sandy loam of the mixed prairie at Limon, roots of this plant were traced to a depth of from 3.7 to 3.9 feet. The root habit in every respect agreed with that at Colorado Springs. At Ardmore, the plant was found growing in Pierre clay underlaid at a depth of 4 feet with a very hard layer of gravel and sand, below which was a stiff sandy loam. Many of the roots ended with well-branched termini in the layer of gravel, although some penetrated even deeper. The general root habit, including the widely spread surface laterals, was characteristic, as was also the amount of branching in the clay, but the degree of branching of the roots in the gravel and sand was much more pronounced than usual.

Chrysopsis villosa.—This is a very widely distributed composite, which forms extensive societies both on the hard land and in the sandhills. Several specimens were examined in the mixed prairie at Limon. All had strong tap-roots which were woody to a depth of 1 or 2 feet. The diameters of these varied from 8 to 12 mm. Their course was almost vertically downward. The first 1.3 feet of the tap was abundantly supplied with small laterals, which ran out in a direction parallel with the soil surface for a distance of 0.2 to 1.5 feet. While many of the laterals are mere threads, others are 2 mm. thick. All are practically destitute of branches. Other laterals, usually not over 1.5 mm. in diameter, occur at various depths, but these are not at all numerous, and while they may run off horizontally or obliquely 1 or 2 feet from a vertical line with the tap-root, they are scarcely at all rebranched or provided with smaller absorbing rootlets. The absorbing system in the surface soil stands out strikingly and is characteristic of many species of dry grassland. The maximum depth of some of the smaller plants was about 5 feet, although others reached depths greater than that of any of the trenches (7 feet). With two exceptions the root habit was similar to that previously described in the hard loam soil at Colorado Springs (Weaver, 1919:117–119). The course of the tap-root was much straighter and not curved and kinked through distances of 1 or 2 inches of the fairly mellow sandy loam. Moreover, the root-tips and some of the laterals were branched to a greater degree, but as a whole the root system resembles closely that found in hard soil and is quite different from that of plants of the sandhills. Under the latter conditions the root system is much shallower and much more abundantly supplied with surface laterals. These are fairly well rebranched and the tap-root and main laterals, which branch and rebranch profusely, have a strong tendency to run obliquely or even horizontally rather than vertically as in the plains ecads (Weaver, 1919:118).

Carex pennsylvanica.—Because of its early growth and flowering habit, this sedge forms conspicuous societies in the prevernal aspect. It has a wide distribution throughout the grassland formation and where abundant (like *C. filifolia* and *C. stenophylla*) it affords considerable early forage before many of the grasses resume growth.

Several plants were excavated on a well-covered sandhill near Central City. The characteristic small plant tufts were connected by means of rhizomes. These are rather coarse, about 2 mm. in diameter and 1 to 10 inches in length. Some of the very abundant fibrous roots spread laterally in the sand at a depth of only 2 or 3 inches to distances of a foot or more before turning downward (plate 17, A.) The roots originate from the rhizomes as well as from the base of the clumps, and completely fill the soil to a depth of 2 feet. Many of the larger roots pursue an almost vertically downward course, reaching a maximum depth of 2.5 feet. All are well supplied with laterals, which, although usually not over an inch in length, are rebranched to the third and fourth order. These are exceedingly abundant in the upper portion of the root system, where they form tangled mats, but also extend to the well-branched tips, thus giving this sedge a wonderfully efficient absorbing system. The rhizomes and older roots are dark brown in color, while the younger ones are a light tan.

At Seneca a few roots of this species penetrated vertically downward to a depth of 2.9 feet, but the working depth was 2 feet. The lateral spread and profuse branching were identical with that just described.

At Colorado Springs, where this species was examined in the hard loam, the lateral spread was only 2 or 3 inches from the base of the tufts. The working depth was about 1.7 feet, although some roots penetrated to a depth of 3 feet. Branching was very similar to that found in the sandhills, but scarcely so profuse.

Redfieldia flexuosa.—This stout, perennial grass often reaches a height of 2 or 3 feet. It is the most abundant and important of blowout pioneers, and, while found mixed with other species, it is very frequently the only plant present in such situations (plate 9, c). While it is of very little grazing value, it is of great economic importance as a sand-binder. It has been excavated in the sandy region of central Colorado, about 40 miles southeast of Colorado Springs, together with *Calamovilfa longifolia*, *Andropogon hallii*, *Artemisia filifolia*, and numerous other species. Here it was found to have a widely spreading surface root system in addition to deeper-seated roots, some of which extended in the dry sand to a depth of about 5 feet.

At Central City they were again examined and, as pointed out heretofore, in a much more humid climate. Moreover, the sand of these dunes, being of local extent, is often slightly intermixed with darker soil. Several clumps of plants were excavated in the more open places on the slope of a large dune, otherwise well-covered with *Andropogon hallii*, *Calamovilfa longifolia*, and *Sporobolus cryptandrus* (plate 10, B). The tough, wiry, much-branched rhizomes are often many feet long. They may sometimes be traced for distances of 20 to 40 feet on the surface where the sand has been blown away. They extend in all directions, from parallel with the soil surface to vertically downward, and with the multitudes of tough, wiry roots originating from them and which likewise run in all directions, they form a tangle which is exceedingly efficient in preventing soil movement. The rhizomes are from 2 to 5 mm. in diameter, tipped with long, sharp-pointed buds. The roots are 1 to 4 mm. thick. They spread laterally 4 or 5 feet or more or penetrate downward to a working depth of about 5.5 feet. They were abundant still at 6 feet, while the deepest were found 0.8 foot lower. Throughout their entire course they are abundantly furnished with well-branched laterals, except the 4 to 6 inches near the growing tips of younger roots, the whole forming a very efficient absorbing system.

Calamovilfa longifolia.—This tall, coarse sand-reed, while of no great forage value, is an efficient sand-binder, and, like the preceding species, is important in holding the sand and thus permitting the entry of more stable vegetation. Not infrequently it invades with *Redfieldia* and other pioneers, but normally occurs somewhat later in the succession along with *Andropogon hallii.*

In the dunes at Colorado Springs the roots and rhizomes of this species formed mats in the loose sand to depths of 2.8 feet. Many of the deeper roots penetrate more or less vertically downward to a maximum depth of 5 feet; but in addition to these there are abundant laterally spreading surface roots.

This species was thoroughly examined at Central City. The plants were better developed, covered a larger local territory, and had apparently been in possession of the area for a much longer period (plate 10, B). The roots reached a maximum depth of 6.5 feet and many of them were found at a depth of 6 feet. As shown in plate 17, C, the tough, wiry, much-branched, and matted rhizomes were intermixed with the roots to a depth of about 2.5 feet. They are 2 to 4 mm. in diameter, clothed with long scales, and tipped with long, hard, sharp-pointed buds. Some of the rhizomes, which were probably at one time more superficial, were buried deeply in the shifting sand. The multitudes of tough, wiry, deeply penetrating roots may be seen in the bisect (plate 12, A), where the sand has been removed to a horizontal distance of about 2 inches. The great tenacity with which the abundant, short, but repeatedly branched laterals cling to the moist sand is clearly shown. There is only a small portion of the root system shown in the bisect, but at a depth of 3 to 4 feet. Where the grasses were at all thick, they held the trench-wall so well that little danger from caving was experienced.

At Haigler, in southwestern Nebraska, this species, with *Andropogon hallii,* was excavated in an old road in mixed prairie. The surface soil was very compact and hard in the first and second feet, but below this depth it was easily removed. It was quite moist to the maximum depth of the trench, about 11 feet. *Calamovilfa* roots were abundant to a depth of 8 feet. Some reached a maximum extent of 10 feet.

Finally, a further examination of the root penetration of the sand-reed was made in the sandhills at Seneca, Nebraska, while excavating *Ceanothus ovatus* (p. 57). Here the roots were found to reach a working depth of about 8 feet, the longest ending in the moist sand nearly a foot deeper.

Andropogon hallii.—This coarse, tall, yellowish-green grass occurs throughout the sandhills, where, like *A. scoparius,* it is a dominant in the bunchgrass subclimax. It forms close open bunches, with only a few characteristic large stems, 3 to 6 feet tall. Plants of this species have been excavated on a partially captured sand-dune southeast of Colorado Springs. Here it was found to possess a rather shallow, copiously branched, but only moderately deep root system. The lateral spread of the roots was 1.5 to 3 feet, while the maximum depth of root penetration was only 2.3 feet.

At Central City, a station of higher rainfall, the root penetration was much greater. Here it was excavated on a grassy hillside, where the elaborate system of rhizomes, lying at a depth of 1 to 6 inches, quite effectively held the sand from blowing. Of the large number of roots originating from these rhizomes, some spread obliquely at various angles below 15 degrees from the ground-line, reaching horizontal distances from the point of origin of 1 to 3 feet. Others penetrate rather vertically downward, ending mostly in the third foot of soil or somewhat deeper, a few reaching a maximim depth of 3.9 feet. The diameter of these rather coarse roots varies from 1 to over 2 mm. Throughout their entire course all were copiously branched with mostly short branches ranging from 0.5 to 3 inches in length. Not infrequently 6 to 9 of these bunches occurred on a single linear inch of root. Longer rootlets were rather rare, but these small branches were abundantly supplied with rootlets 4 to 8 inches long.

At Haigler, Nebraska, further examination was made in an old road where *Calamovilfa* was also excavated. The great depth of penetration was quite surprising. Numerous roots were traced to a depth of about 8 feet, while some penetrated 3 inches deeper. Many branches spread laterally in a more or less horizontal manner for distances of 3 to 12 inches. The soil was moist to a depth of at least 10 feet, extra moisture being afforded by run-off into the depression made by the roadway.

At Yuma, Colorado, a maximum depth of 7.3 feet was determined for this species (fig. 31). Here it was growing in a well-covered dune area. The surface roots, especially in the first 2 feet of soil, were exceedingly well clothed with fine laterals, as many as 30 to 50 occurring along a linear inch of one of the fibrous roots. Below this depth some of the branches were longer, often extending in a somewhat horizontal direction for distances of 4 to 8 inches or more. These, like the main roots, are well clothed with smaller rootlets. The final 6 to 12 inches of the growing roots are somewhat enlarged in diameter (2 to 3 mm.) and are destitute of branches. While many roots ended in the third and fourth feet, the soil was well filled to a depth of 6.5 feet. Indeed, even below 6 feet the soil is penetrated by a mat of roots whose profusely branched laterals rather completely occupy it.

Summarizing the data on the three sandhill grasses, *Redfieldia flexuosa*, *Calamovilfa longifolia*, and *Andropogon hallii*, we find that all three penetrate more deeply at all of the other stations than where first examined in the dune area southeast of Colorado Springs. At Central City, under a precipitation 75 per cent greater than in the former area, the root depth in every case was 1.5 feet or more deeper. But on the steep hillside at Seneca and in the sand at Yuma, as well as in the abandoned road at Haigler, the root depth of the sand-reed and the bluestem both exceeded that at Central City. At Haigler, the great penetration, which in fact was the deepest recorded, may be due to the excess of moisture collecting in the abandoned road. In the light of these further studies it seems not improbable that the roots of the plants near Colorado Springs were not fully developed. The life history of each of these species should be studied. Waterman (1919), after a study of seedling development on the sand dunes near Chicago, suggests that after "giving due weight to the possibility of moisture, oxygen-content, and penetrability of the sand as influencing factors,

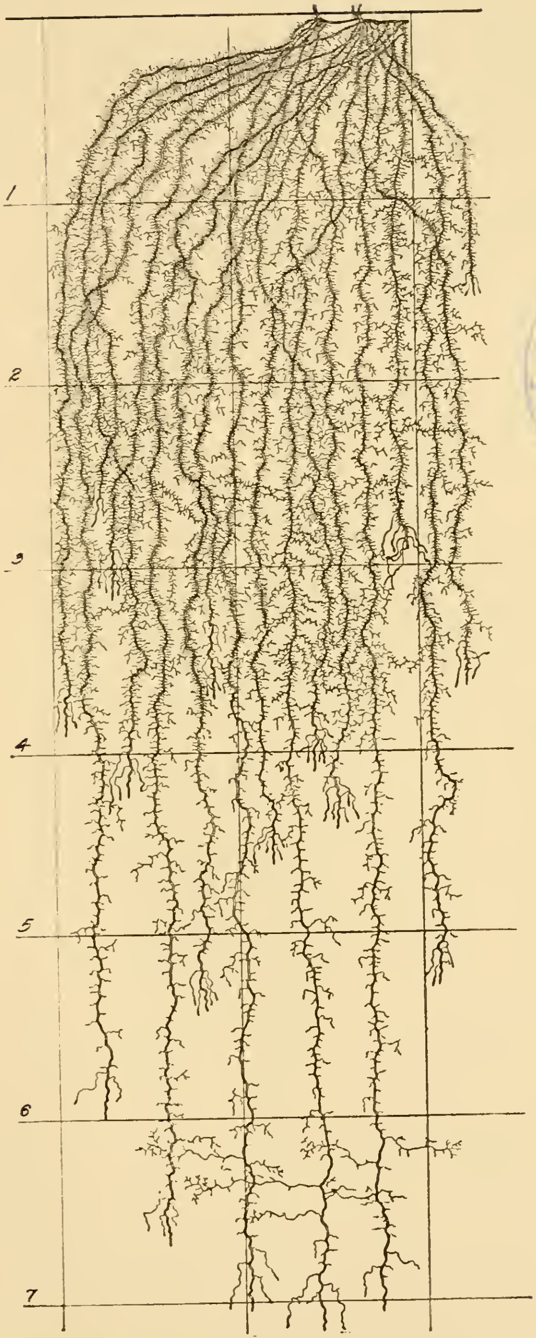


FIG. 31.—*Andropogon hallii* excavated in the sandhills.

the evidence seems to point conclusively to nutrient or at least chemical influences as the cause of variability in symmetry in the extension of roots under dune conditions." In more arid regions, at least, the evidence points to water-content as being the factor exerting the greatest control, although nutrients undoubtedly play an important rôle.

SUMMARY OF SHORT-GRASS-PLAINS AND MIXED-PRAIRIE SPECIES.

In order that a careful comparison may be made of the numerous species excavated in short-grass plains, and in hard lands and sandhills covered with mixed prairie, all of the species studied are listed in table 9, together with the extent of their root systems.

CONCLUSIONS.

An inspection of short-grass-plains species in table 9 shows that only two, *Opuntia polyacantha* and *Schedonnardus paniculatus*, may be said to be fairly shallow-rooted. All but one, *Psoralea tenuiflora*, are well adapted for water absorption in the surface soil, having a lateral spread of roots on all sides of the plant of about 0.5 to 1.5 feet. In this group the three dominants have the best-developed root system in regard to absorption both from the surface and deeper soils.

Of the 45 species in table 9 which were examined in the mixed prairie of sandhills, only four may be designated as shallow-rooted, but all of these have a widely spreading root system. Among the 23 species with roots of intermediate depth (which extended below 2 feet but seldom beyond the 5-foot level), only 4 have a root system which does not spread widely in the surface soil. In fact, the widely spreading superficial root habit is a pronounced group characteristic. Of the 18 species of deep-rooted sandhill plants, among which are 3 dominant grasses, all but 4 have widely spreading surface laterals in addition to the extensive deep-seated ones. In *Anogra cinerea*, *Asclepias arenaria*, and *Psoralea lanceolata*, the pronounced tap-root branches but little or not at all in the surface soil, while in *Pentstemon ambiguus* the numerous large branches are poorly fitted for surface absorption. Summarizing the group as a whole, only 9 per cent of the species have roots confined to the surface foot or two of soil, 18 per cent have few or no roots which carry on absorption in this area, while 73 per cent of the species are supplied with an absorbing system of such a character as to get water and solutes from both the shallower and deeper soil layers, many species having roots which extend as deep as the fifth to eighth foot of soil. These data on root penetration, obtained from the study of sandhills vegetation at 5 widely separated stations, emphasize the great depth reached by many species and considerably modify the tentative conclusions reached by the writer after studying the root development in a single area (Weaver, 1919:68). It now appears that the sandhills area near Colorado Springs, where the earlier studies were made, was in some respects rather exceptional. Either some of the plants excavated had not reached their maximum root extension or the deeper soil was much drier than is usual in the sandhills further eastward in Colorado and in Nebraska. This is an excellent illustration of the value of a broader field for study and the need of extensive ecological investigations before correct conclusions may be drawn. It is felt that the present broad survey supplies this need regarding the root habits of grassland vegetation.

Among mixed-prairie species on hard lands, only 4, including 2 cacti, are rather superficially rooted; 16 species are of moderate depth (2 to 5 feet), and of these only 3 are poorly equipped to carry on surface absorption. A group of an equal number of species, including 3 grasses, has roots which extend well below the fifth foot of soil, and many in fact to a depth of 7 to 9 feet. Of this number, 7 are adapted for absorption in soils mostly below the surface foot or two only. Thus 11 per cent of the mixed-prairie species of hard lands are shallow-rooted, 28 per cent have little or no provision for surface absorption, while 61 per cent are both fairly deep-rooted and well adapted to absorb water even when the surface soil only is moist.

In a comparison of mixed-prairie species of sandhills and hard land, the only marked difference as a group is the somewhat better development of the root system in the former habitat, especially as regards smaller absorbing rootlets. Indeed, the excellent development of surface absorbing laterals is equaled only by certain short-grass plains species. The general similarity in the root habit as regards position in the soil and depth of penetration of short-grass and mixed-prairie species is so marked that experimental studies now under way on the competition of the several dominants of the two grassland associations should throw much light upon the general problem of succession, and especially the causes of the present distribution of grassland dominants.

In a comparison of the root habits of plants in these three drier grassland habitats with those of true prairie, two characters stand out rather strikingly. In true-prairie species, probably due to a more constant supply of water in the subsoil, the roots as a group do not spread so widely in the surface soil. Also, the depth at which the largest number of absorbing roots are found is usually greater. This condition is likewise clearly reflected in the root habits of cereal-crop plants (*cf.* Chapter VI).

In seeking a correlation of the root habit of plants of true prairies, of mixed prairie covering sandhills and hard lands, and of short-grass plains, with their respective environments, several ecological factors must be considered. The most important of these are water-content, aeration, soil temperature, texture, and chemical composition. An examination of the literature emphasizes the fact that relatively little work has been done either upon an intensive study of root systems or

TABLE 9.—*Root depth and surface lateral spread of species of the short-grass plains, sandhill mixed prairie, and mixed prairie in hard lands. All measurements given in feet.*

Species.	Maximum depth.	Working depth.	Lateral spread in surface soil.
Short-grass-Plains Species.			
Opuntia polyacantha	2.0	0.4	1 to 5.5 feet.
Schedonnardus paniculatus	2.0+	About 2.0	1 to 1.5 feet.
Aristida purpurea	2.3 to 2.8	2.0	0.5 to 0.7 foot.
Bouteloua gracilis	4.3	2.4 to 3.3	1.5 feet or more.
Bulbilis dactyloides	5.0 to 7.2	3.0 to 5.0	0.8 to 1.7 feet.
Gutierrezia sarothræ	5.0	3.8	0.5 to 1.5 feet.
Muhlenbergia gracillima	4.7	4.0	0.5 to 1.5 feet.
Psoralea tenuiflora	9.0+	7.0 to 8.0	None.
Sandhill Mixed-Prairie Species.			
Cyperus schweinitzii	2.3	1.7	1 to 3.5 feet.
Heliotropium convolvulaceum	2.1	1.5	0.5 to 1.7 feet.
Sporobolus cryptandrus	1.8	1.3	1.5 to 1.7 feet.
Tradescantia virginiana	1.6	1.3	1 to 2.5 feet.
Abronia fragrans	4.0	3.5	0.3 foot only; few laterals.
Allionia linearis	5.0	4.5	Little or none.
Aristida purpurea	2.5 to 3.5	2.0 to 3.0	2 to 3 feet.
Bouteloua gracilis	2.3	2.0	0.8 to 2.1 feet.
Bouteloua hirsuta	3.3	1.7	1 to 1.5 feet or more.
Carex pennsylvanica	2.9	2.0	1 foot or more.
Commelina virginica	3.2	2.5	1 to 2.3 feet.
Erigeron bellidiastrum	3.2	2.5	0.7 to 1.7 feet.
Eriogonum annuum	5.3	4.0	1 to 2 feet or more.
Euphorbia petaloidea	2.3	2.0	0.3 to 1 foot.
Gilia longiflora	4.4	2.5	0.4 to 2 feet or more.
Haplopappus spinulosus	5.0	4.3	0.7 to 1 foot in first 0.5 foot.
Liatris squarrosa	2.8	2.3	Usually none in surface soil; 1.5 to 2 feet in first foot.
Meriolix serrulata	4.5	4.0	None.
Mentzelia nuda	5.3	5.0	None.
Muhlenbergia pungens	2.8 to 4.0	2.4 to 3.3	1 to 2 feet.
Panicum scribnerianum	3.9	3.0	About 0.5 to 0.7 foot.
Paspalum setaceum	3.8	3.2	1 to 2 feet.
Petalostemon villosus	5.0	3.5 to 4.0	1 to 2.5 feet.
Redfieldia flexuosa	5.0 to 6.8	4.0 to 5.5	2 feet or more.
Stipa comata	2.9	2.5	0.8 to 1.5 feet.
Tradescantia occidentalis	3.0	1.8	1 to 1.5 feet.
Thelesperma gracile	3.8	2.8	2 to 2.5 feet.
Andropogon hallii	2.3 to 8.3	1.8 to 7.0	1.5 to 3 feet.
Andropogon scoparius	3.5 to 8.0	3.0 to 6.7	1.3 to more than 3 feet.
Anogra cinerea	9.0+	7.0 to 8.0	Few or no roots in surface soil.
Artemisia canadensis	8.0+	5.5 to 6.0	1 to 2.5 feet.
Artemisia filifolia	9.0+	6.0 to 7.0	2 or 3 feet.
Asclepias arenaria	8.0+	6.0 to 8.0	None.
Calamovilfa longifolia	5.0 to 10.0	3.0 to 8.0	1 foot or more.
Ceanothus ovatus	12.0+	8.0 to 10.0	0.5 foot to over 3 feet.
Chrysopsis hispida	9.0+	5.0 to 7.0	1 to 2 feet or more.
Chrysopsis villosa	6.9	About 5.5	1.5 to 2 feet.
Croton texensis	8.0	4.0 to 6.0	0.5 to 1.5 feet.
Eriogonum microthecum	10.0+	8.0 to 10.0	Usually not over 0.5 to 0.7 foot, few surface laterals.
Ipomœa leptophylla	10.0+	10.0+	Surface foot of soil for many feet on every side of plant contains many roots.
Onagra biennis	6.8	4.0 to 4.5	1.7 to 3 feet.
Pentstemon ambiguus	10.0+	About 8.0	0.5 to 1.5 feet.
Pentstemon angustifolius	6.0	4.0 to 5.0	0.8 to 2.3 feet.
Petalostemon purpureus	8.4	5.0 to 6.0	1 to 2 feet or more.
Psoralea lanceolata	9.0+	8.0 to 9.0	Usually no surface laterals.

Table 9.—*Root depth and surface lateral spread of species of the short-grass plains, sandhill mixed prairie, and mixed prairie in hard lands. All measurements given in feet*—cont'd.

Species.	Maximum depth.	Working depth.	Lateral spread in surface soil.
Hard Land Mixed-Prairie Species.			
Kœleria cristata	2.2	1.2	0.7 to 1.0 foot.
Opuntia camanchica	2.9	0.3	0.5 to 6 feet, few roots below 0.3 foot except anchorage roots.
Opuntia fragilis	1.3	0.7	1 to 1.3 feet, many within 0.3 foot of surface
Ratibida columnaris	2.0	2.0	0.5 to 1 foot, very abundant rootlets.
Abronia fragrans	3.6	2.8	Little or none.
Allionia linearis	5.5	4.5 to 5.0	Do.
Andropogon scoparius	5.2 to 6.0	4.0 to 4.5	1 to 1.2 feet, abundant.
Aristida purpurea	3.1 to 4.3	2.6 to 3.0	0.4 to 0.7 foot, not profusely branched.
Asclepias verticillata pumila	3.8	2.0 to 3.5	0.7 to 1 foot but usually at depths of a few inches.
Astragalus drummondii	4.3	3.5	Widely spreading laterals below 0.3 foot.
Astragalus microlobus	5.2	4.5	Little or no surface absorption.
Bouteloua curtipendula	5.5	4.0	1 to 1.5 feet.
Bouteloua gracilis	4.0 to 4.3	3.0 to 3.6	1.5 feet or more.
Bulbilis dactyloides	5.0 to 7.2	3.0 to 4.0	0.8 to 1.3 feet.
Carex filifolia	5.2	4 0	2 to 2.7 feet.
Carex pennsylvanica	3.0	1.7	Only 0.2 to 0.5 feet.
Eriocoma cuspidata	3.2	2.3	0.7 to 1 foot.
Muhlenbergia gracillima	4.6	2.3	0.5 to 1.5 feet.
Senecio aureus oblanceolatus	3.3	2.5	0.3 to 1 foot.
Stipa comata	5.0+	3.5	1 to 1.2 feet; roots 0.3 to 1 foot. Very abundant.
Agropyrum glaucum	7.2	5.5 to 6.0	0.7 foot or more, roots very abundant.
Andropogon furcatus	8.7	6.8	0.7 to 1.2 feet, roots abundant.
Aragallus lambertii	8.0	7.0	Little, 0.3 foot only.
Argemone platyceras	12.2	8.0 to 10.0	None.
Artemisia frigida	6.0 to 7.8	3.0 to 4.0	0.7 to 1 foot or more, roots abundant.
Chrysopsis villosa	13.0	7.0 to 10.0	0.7 to 1.2 feet.
Eriogonum jamesii	7.3+	7.0	Often 2 or 3 feet, surface laterals numerous.
Euphorbia montana	7.5	7.0	Little or none.
Gutierrezia sarothræ	6.5	4.4	About 2 feet; laterals very abundant.
Lithospermum linearifolium	10.0	8 0	Very little absorption in first 2 feet of soil.
Lygodesmia juncea	7.0+	5.0 to 7.0+	No surface absorption.
Petalostemon candidus	5.5	4.5	Little; usually no surface laterals.
Petalostemon purpureus	6.5	5.0	0.7 to 1.5 feet, laterals well developed.
Psoralea tenuiflora	12.2	6.0 to 8.0	None.
Stipa viridula	11.7	8.0 to 9.0	1 to 1.5 feet or more; roots very abundant.
Yucca glauca	7.0	2.0	20 to 32 feet; roots most abundant at depths of 0.5 to 1.5 feet.

upon the effects of the environment upon their development. Until very recently (Cannon, 1913*a*, 1915; Waterman, 1919), intensive studies of root systems along both morphological and physiological lines have been made mostly by European investigators (*cf.* Kroemer, 1903; Tschirch, 1905; Von Alten, 1909). The chief records of the influence of the soil environment upon root extension and development are mainly incidental to other investigations. The rôle played by soil temperature has been discussed on page 34 in comparing mixed and true prairie environment. While its ecological importance has been emphasized, in the absence of further quantitative data we must for the present accept its influence in the development of grassland vegetation as of minor importance. The extension of the grassland associations throughout such wide areas of latitude with little change in their floristic composition would seem sufficient evidence to warrant this conclusion.

Soil aeration, which is closely connected with water-content and soil texture, is an important factor in root development. As shown by Livingston and Free (1917), the exclusion of oxygen from the roots of certain species interferes with the respiration of the protoplasm of the root-cells, resulting in the death of this protoplasm and the consequent failure of the roots to function as water-absorbers for the plant. The cessation of water intake is soon followed by progressively lessened turgor of the shoot and leaves and finally by wilting and death. Cannon and Free (1917) have shown that roots of various plants respond quite differently to variations in the composition of the atmosphere. An increased air-supply to the roots of certain species favors root-branching and probably accelerates root-growth. Their results indicate that plants growing in well-drained soil are much more sensitive to the composition of the soil-atmosphere than those from poorly drained and poorly aerated habitats.

The soil-atmosphere is important not only as affecting directly the respiration of the roots of higher plants and consequently their normal functioning and development, but it also plays a part in the life activities of both aerobic and anaerobic micro-organisms of the soil. These in turn alter its chemical composition, and this indirectly influences both root and shoot development. The deficiency in soil aeration and its bearing upon problems of agriculture and forestry have been clearly presented by Howard and Howard (1917) and Hole (1918). To grasp its full ecological significance, as a factor affecting root habit, and one always to be considered along with soil-moisture, it should be borne in mind, as is pointed out by Cannon and Free (1917) that different species may have great differences in the oxygen requirement of their roots and may show responses which may be quite as specific and significant as responses to temperature and to available water. It seems probable that one of the beneficial effects of heavy rains, aside from the increased water-content, especially in heavy soils, is the increased oxygen-supply to plant roots, rain-water being a solution highly charged with oxygen and having a markedly stimulating effect upon growth. (*Cf.* Russell and Appleyard, 1915; Richards, 1917.) However, the importance of aeration in the soils of the semiarid regions under discussion would undoubtedly be much less than in more humid areas.

Aside from water-content, the chemical composition of soil, especially in studying root development in sandhills species, should be given careful consideration. Since the early work of Nobbe (1862), Stohmann (1862), and Höveler (1892), Benecke (1903) and Tottingham (1914) have done perhaps the most comprehensive work with solutes. As pointed out by Waterman (1919), such work on the whole has been done chiefly on the roots of seedlings, and it seems doubtful whether the results would have been the same with mature plants. Benecke's "hunger etiolation" theory, where scarcity of nutrients had a tendency to increase root-length, is supported by the findings of Höveler, who grew plants in alternating layers of sand and humus. However, Seelhorst (1902) concludes, after counting the number of roots found in fertilized and unfertilized patches of soil, that plants strongly fertilized not only produce stronger roots, but also roots penetrating to lower levels. These and other experiments with soil nutrients show differences in length and weight of roots, but offer no definite evidence as to the causes of root extension. Waterman (1919), working with seedlings in the sand dunes about Lake Michigan, concludes that, after "giving due weight to the possibility of moisture, oxygen-content, and penetrability of the sand as influencing factors, the evidence seems to point conclusively to nutrients or at least chemical influences as the cause of variability in symmetry in the extension of roots under dune conditions." Among all the roots examined by the writer, in various sandhill areas, not a single instance of marked variability in symmetry of a mature root system was encountered. Nor can the widely spreading more superficial part of the root system, characteristic of most sandhills species, be accounted for in this manner, for the habit is almost equally developed among species on the hard lands. However, as Waterman suggests, there is a strong contrast between the pure dune-sands with which he worked, in which, except for calcium carbonate, mineral salts are practically absent, and organic matter so rare and scattered that as a general factor it is practically negligible, and the Nebraska-Colorado sandhills, where large quantities of desirable mineral nutrients are present, needing only the addition of water to make them available for plant use. The luxuriant growth of the natural vegetation of sandhills regions, as well as of ruderal species where favorable soil-moisture is found, emphasizes the paramount importance of the latter factor.

As regards soil-texture, it seems clear that its chief influence on root development is through water-content and aeration (*cf.* Hunter, 1912), although mechanical resistance exerts some effect upon root structure. The effects of compact soil upon penetration is shown not only by the tortuous courses pursued and the distortions of the roots themselves, but also by their modified branching. Roots of many species show a marked increase in their output of branches upon leaving the compact soil and entering earthworm burrows. This difference is probably due largely to increased aeration. In soils with a subsoil of alternating layers of sand and clay, a striking distribution of laterals was observed. They often occurred abundantly near the bottom of the sandy layers and in the clay strata when the latter, acting as a rather impervious layer, had retained much soil moisture (*cf.* Cannon, 1913*a*).

In "Ecological Relations of Roots" fairly close correlation was established between the water-content of soils and the root distribution of plants on gravel-slide, half gravel-slide, and in forest communities, as well as in the chaparral of southeastern Nebraska and the grassland association in the Pacific Northwest. Further studies in the grassland formation confirm the conclusion that water-content is the dominant factor. That different species respond differently to similar environmental conditions, and that the reactions in certain cases are specific and apparently controlled by heredity, have likewise been pointed out. Of 10 polydemic species, each growing in at least 2 different habitats, 7 showed very striking changes in their root habits, adapting their absorbing organs to conform with the stratum of moisture-supply, 2 made practically no change, while 1 exhibited only moderate differences of root development (Weaver, 1919: 121). Summarizing the present study of plant ecads, we find that practically all of the species examined under distinctly different conditions showed marked changes in root development, either in surface lateral spread, depth of penetration, or output of branches. *Bulbilis dactyloides* and *Bouteloua gracilis*, while showing no consistent differences in depth of penetration, have a much more marked surface lateral spread in the drier grassland communities. *Andropogon furcatus*, *Agropyrum glaucum*, *Andropogon scoparius*, and *Aristida purpurea* showed considerable difference in both depth of penetration and, the last two especially, in surface lateral spread. In hard lands this is quite clearly correlated with water penetration, while in sand the remarkable lateral spread of *Andropogon scoparius* and *Aristida purpurea* may also be considerably influenced by soil nutrients. *Gutierrezia sarothræ* and *Artemisia frigida* showed a somewhat poorer root development under the more unfavorable growth conditions of short-grass plains than in mixed prairie. *Psoralea tenuiflora* retained a fixed habit under widely varying conditions of soil-moisture and soil-texture. *Petalostemon purpureus*, *Lygodesmia juncea*, *Artemisia frigida*, *Chrysopsis villosa*, and *Carex pennsylvanica* all showed a somewhat more pronounced output of branches when growing in a sandy substratum than when grown in soils of firmer texture. These branches were also often more widely spreading, especially in shallower soils. *Artemisia filifolia* and *Muhlenbergia pungens*, species examined only in the sandhills, showed only slight variations, but *Redfieldia flexuosa*, *Calamovilfa longifolia*, and *Andropogon hallii*, all sandhill dominants, in general showed greater depth of penetration where the precipitation was actually greater or where the topography or other local conditions were such as to supply an unusual amount of soil-moisture. Convincing evidence on the relation of root distribution to soil-moisture in these semiarid regions may be found in Chapter VI on the development of cereal-crop plants.

It should be noted further that root-length, closeness of branching, etc., may have different causes and effects in different species or under different conditions and consequently a different meaning to the plant. The remarkable constancy of the specialized root habit of such species as *Asclepias arenaria* and *Mentzelia nuda* (where the tap-root is the dominant feature) is worthy of note. The retention of this habit under sandhill conditions, where 85 per cent of the species show the apparently much more efficient generalized absorbing system, strongly suggests their relation to an ancestral habitat or condition of growth. As shown by Cannon (1911:94), plants with generalized roots (where both laterals and taps are well developed) are aided in their distribution by their root plasticity, while those of the specialized type are restricted because of their rigidity. It may be noted that none of the plants with highly specialized root systems are dominants, but rank only as subdominants and, with the exception of cacti, are of no great importance.

The relation of root development to the various factors and the proper evaluation of each demand a long series of ecological-physiological investigations of a very intensive nature. A knowledge of the exact position of root systems in various soils and descriptions of root habits of native vegetation and crop plants under field conditions is an essential prerequisite to such studies. It was with this purpose in mind that the writer has carried out the investigations here recorded.

VI. THE ROOT SYSTEMS OF CEREALS.

The detailed study of the root systems of cultivated plants has been grealty neglected in the past, in spite of the importance of the root in the utilization of water and solutes in the soil. Comparatively too much attention has been devoted to the above-ground portion of the plant, and it has been all but forgotten that a large part of every crop consists of the root system, which is of great importance in determining yields, although out of sight. Except for the early work of King (1892), Headden (1896), Goff (1897), Ten Eyck (1899, 1900, 1904), and Shepherd (1905), at the Wisconsin, Colorado, Kansas, and North Dakota Agricultural Experiment Stations, respectively, a study of the literature shows that the work done on the extension and development of root systems in the United States has been surprisingly little. The excellent work by Miller (1916) on the root systems of corn and the sorghums, and by Howard and Howard (1917) on the root development of agricultural plants in India, are conclusive evidence of the great wealth of both purely scientific and practical values to be obtained from a thorough investigation of root habits. A summary of the literature on the root systems of agricultural plants has recently been made by Miller (1916*a*), to which the reader is referred. The purpose of these studies is primarily to find the relation between the root development of crop plants and the native species and to determine what correlations, if any, exist between the two. In this way a much broader basis for the use of the natural vegetation as an indicator of crop possibilities can be established. A knowledge of root habits should help us to select and breed varieties better adapted to the various regions delimited by the natural vegetation, since the chief limiting factor to crop production is soil-moisture in the grassland area west of the Missouri.

ROOT DEVELOPMENT IN TRUE PRAIRIE.

The root development of rye, *Secale cereale*, was first examined in the sandy soils near Central City, Nebraska. On page 64 it has been pointed out how continued overgrazing initiated the blowing of the sandy soil, which, as a result of successive movements, is often somewhat stratified, and how it is being reclaimed by growing rye and other crops, which more or less efficiently prevent soil movement (plate 10, A).

The development of the rye, both tops and roots, varied greatly with the type of soil, the stand being thin, the stalks short, and the root system meager in pure sand. Two areas were carefully selected typical respectively of the better and poorer development of the crop On both the crop was drilled at the rate of 56 pounds per acre early in September of 1918. The plants were examined on June 6, 1919, when in full bloom. A long trench was dug just within the field, where the stand was thick and the stalks 6 feet in height (plate 20, A). The soil was plainly stratified. The surface 1.3 feet of nearly pure sand was underlaid by 1.3 feet of dark-colored sandy loam. Below this, pure sand occurred to the water-level at a depth of 7.5 feet.

From the base of a single clump 15 to more than 40 roots originated (plate 12, C). Most of the roots were 0.5 mm. or less in diameter, but rather tough and easily excavated. While a few ran off obliquely, most of them penetrated rather vertically downward, the soil being filled with dense masses of roots to a depth of at least 3 feet. The lateral spread, which was often more or less parallel with the soil surface, did not exceed 1.2 feet; many of these shallower roots ran obliquely so as to reach their greatest horizontal spread at a depth of 0.5 to 1 foot. Here they either ended or turned vertically downward. The surface soil was especially well supplied with roots, many of which ended at a depth of 0.4 to 1.2 feet. However, the roots were fairly abundant to a depth of 6 feet, while not a few reached a maximum depth of 7.7 feet. All of the roots were extremely well branched, but the branches were mostly only 1 or 2 inches or less in length. They were very fine, but well furnished with secondary laterals (*cf.* fig. 34). In the deeper soil the roots were somewhat larger in diameter, and while abundantly branched, the branches were coarser and not so well furnished with minor branchlets. No differences were noted in the root development in passing from one soil layer to another. The soil was quite moist throughout, probably as a result of the recent heavy rains.

Other plants were examined in another portion of this area at about the same level and only a few rods distant, but where the soil to a depth of at least 7 feet was composed of pure sand. Here the rye was thin and only 3.3 feet in average height. The maximum root depth was 4.6 feet. The general root habit was about the same as that described, a cubic foot of soil containing approximately only half as many roots. Roots were not at all abundant below 2.8 feet, but the soil was fairly well occupied to this depth. Below 3.3 feet there were practically no roots and only 2 or 3 were traced to the maximum depth indicated.

The root system of rye was further examined at Lincoln, Nebraska. Both the common rye and a variety known as "Rosen" rye, which were growing in adjoining fields, were studied. They were growing on a deep, black silt-loam underlaid with a somewhat clayey subsoil. The land had been tilled for many years. The preceding crop was spring wheat. The field had been plowed to a depth of 4 inches and the rye sown late in September. Although the stand appeared poor in the fall, yet at the time of harvest the yield was estimated at 40 bushels per acre; the common rye reached an average height of 5.5 feet, while the "Rosen" variety was about a foot taller. The crop had been harvested at the time of these examinations.

The roots of both crops reached a maximum depth of 5 feet in the hard clay subsoil, but only relatively few roots penetrated so deeply. Those of the common rye had a working depth of 3.9 feet, while the absorbing level of the "Rosen" variety was about 3.7 feet. The soil was fairly moist to the maximum depth of excavation, about 5.5 feet. The roots were exceedingly well branched to the working depth. In fact, branching is usually better developed in rye than in wheat or oats when growing in the same soil type and under the same conditions of moisture. This is one reason why rye is adapted to drier climates than wheat and will thrive on poorer and sandier soils than any of the other cereals (*cf.* Miller, 1916, on corn and sorghums). In this connection the work of Nobbe (1869) is interesting. He compared, measured, and counted the roots of winter wheat and rye plants 55 days old and grown in soil. He found that the roots of the first to the fourth order numbered 16,000 in rye and 10,700 for wheat. The combined lengths of these roots measured 118 and 82 meters respectively.

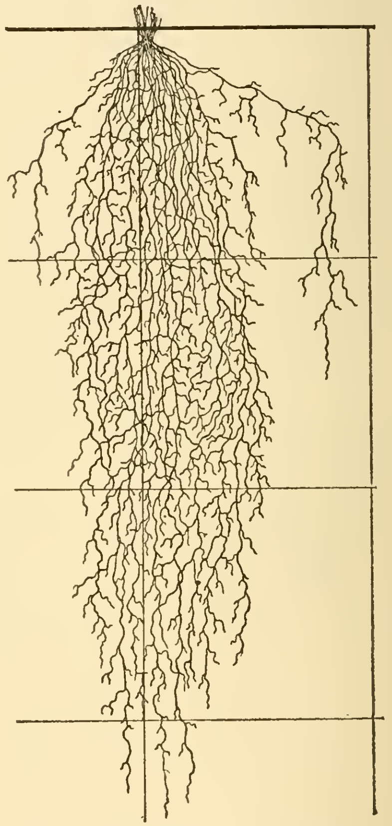


Fig. 32.—Root system of *Avena sativa* grown in moist silt-loam soil.

The root system of oats, *Avena sativa*, was also examined at three different stations at Lincoln. Two of these stations were in the crop plats adjoining the high and low prairie stations respectively, while the third was in the experimental fields of the State University farm. White Kherson oats were examined at each place, but the soil types were very different. The crop plats adjoining the low prairie were on rich, black, alluvial soil known as Wabash silt-loam, which was underlaid with a rather tenacious subsoil of clayey texture. A full description of the mechanical and chemical composition of the soil, together with its water-content through the growing season, is given on pages 140 and 141.

The oats, following a crop of potatoes, were sowed quite thickly on April 24, after the soil had been plowed to a depth of 4 or 5 inches. On July 8 the oats were quite ripe. The stalks averaged 3 feet in height and the well-filled heads indicated an excellent yield. The deepest roots penetrated the wet, sticky subsoil to a depth of 3.4 feet, but only a few reached this depth. However, they were very abundant to the working level of 2.6 feet. The maximum lateral spread was somewhat less than a foot, most of the roots penetrating more or less vertically downward or running obliquely downward at such angles that surface laterals were rare. The great masses of roots, their lateral spread, copious branching, and depth of penetration are shown in figure 32. The upland plats, located on a level tract of land about half a mile distant and about 80 feet higher, were on a rather shallow Marshall silt-loam underlaid at a depth of about 1.2 feet with heavy loess. Physical and chemical analysis of the soil, together with its seasonal water-content, may be found on page 140. Here the preceding crop had been Sudan grass. The soil was double-disked to a depth of 4 or 5 inches just preceding planting on April 24. White Kherson oats were sowed at the same rate as in the preceding case. On July 8 the grain was very ripe, had an average stem-height of 2 feet, but was only about two-thirds as thick as that on the lower plat. The soil was fairly moist, but not wet all the way down (see table 19). Some of the roots had reached a maximum depth of 4.1 feet, while a working depth of 3.1 feet was determined.

The White Kherson oats examined in the fields at the State University farm were a crop in the four-year rotation scheme, being preceded by corn and followed in succession by winter wheat and red clover. They were planted on April 1 at the rate of about 56 pounds per acre. Although the field was quite level, the soil was found to be somewhat variable. In the trench dug in the oat field, the black Marshall silt-loam was underlaid at a depth of 2.3 feet with a compact subsoil of loess intermixed with clay. It was quite moist at all depths examined. The crop had reached an average height of about 2.8 feet. The roots were examined on August 12, several weeks after the grain had been harvested. While some reached a maximum depth of 3.8 feet, the average working depth was determined at 3.2 feet.

The root system of Turkey Red winter wheat, *Triticum æstivum*, was also studied in this same field on a plat about 100 feet distant. Here the dark-colored silt-loam at a depth of 2.3 feet intergraded into a very hard tenacious subsoil of clay intermixed with chalky spots and streaks below 4 feet. The wheat, which had been preceded by oats, was sown at the rate of 75 pounds per acre on September 19. At the time of harvest it had reached an average height of about 3.3 feet. Roots were excavated on August 12. The working depth was at 3.2 feet; not many roots penetrated below 3.5 feet, although a few had a maximum penetration of 4.7 feet. The abundance of roots, amount and length of branching, as well as the depth of penetration, are quite variable for all of the smaller cereals in different soil types and when grown under varying degrees of water-content. Following is a typical example of Turkey Red wheat roots when grown in moist silt-loam.

This field was sown at the rate of 60 pounds per acre early in October and on land farmed for many years. A crop of wheat had been grown the preceding year. The moist, fertile silt-loam was very similar to that described for the low-lying oat plats (p. 102). *Spartina cynosuroides*, *Andropogon furcatus*, and *Panicum virgatum* formed a border about the field. At the time of harvesting, about July 1, the abundant crop had an average height of about 3.8 feet. About a week later the roots were examined. From the base of the plant great numbers of long fibrous roots originated. Most of these penetrated rather vertically downward, others ran obliquely downward, but seldom reached a greater horizontal distance than 6 or 8 inches from the base of the plant; while still others ran off somewhat parallel with the soil surface for short distances before turning downward. The working depth was found at approximately 4.4 feet, while the maximum root depth was 6.2 feet (fig. 33). Beginning just below the surface and extending to a depth of 4 feet, numerous laterals, several inches in length, with countless smaller ones, all profusely branched, ran off in all directions and fairly filled the soil. These light-colored roots showed very plainly in the black soil. They were covered with dense mats of root-hairs, the rootlets intercrossing in the jointed subsoil in such a manner as to give a cobwebby appear-

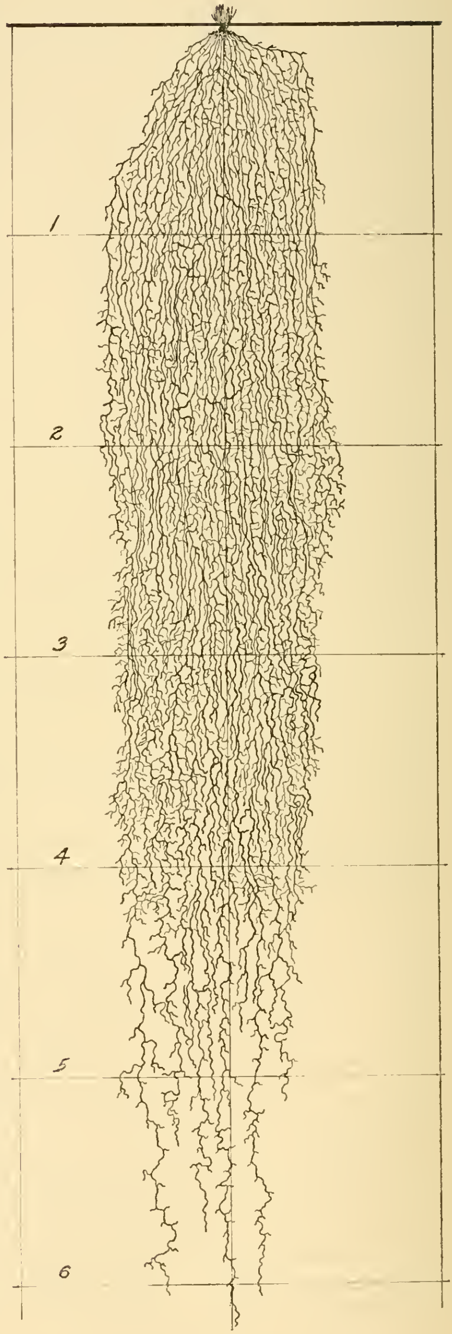


FIG. 33.—Root system of *Triticum æstivum* grown in moist silt-loam soil.

ance. It is quite impossible to show these finer roots and all of their branches in the most carefully planned drawing. Below 4 feet the roots were much less abundant. They were well-branched in the moist, jointed soil, but often only in one plane, and clothed with root-hairs. The last 6 inches of the deeper roots were poorly branched and the laterals were only a few millimeters in length.

A third examination of Turkey Red winter wheat was made about 2 miles north of Lincoln, on a high level tract adjoining the prairie area where the base station was maintained (p. 28). The soil consisted of dark-colored Marshall silt-loam, which had been broken only 4 years. At a depth of about 1.5 feet it intergraded into a very deep, rather mellow loess subsoil. Except for the first 0.5 foot, it was quite moist to a depth of many feet. The wheat, which had been drilled in the corn on September 29, was about 3.5 feet high at the time of harvest, the first week in July (plate 21, B). The stand was good and the yield estimated at 40 bushels per acre. The root system was exceedingly well developed. Many roots ran off obliquely, but usually for only small distances, seldom extending more than 4 to 6 inches horizontally from the base of the plant. While the main course of the bulk of the roots was rather vertically downward, they often meandered from this course, sometimes with rather sharp turns, and ran off obliquely or even parallel with the soil surface for distances of 2 or 3 inches. Roots were fairly abundant to a depth of 4.9 feet. Quite a few penetrated to 7 feet and the maximum root-depth was 7.3 feet. The root branches were short, mostly less than an inch in length, in the first 2 feet of soil. Many of the roots were about 0.5 mm. in diameter. Near the ends they frequently ran 2 to 5 inches without branching, but were densely clothed with root-hairs. At the 13 stations where wheat roots were examined, none reached depths greater than those here recorded. The greater root extent in the mellow loess soil agrees entirely with the greater root development of certain native grasses grown under similar conditions. For example, *Andropogon furcatus*, ordinarily with roots from 5 to 7 feet deep, reached a maximum depth of 9.3 feet in the mellow loess soil at Peru, Nebraska (Weaver, 1919:15).

Near Fairbury, Nebraska, about 50 miles southwest of Lincoln, but still in the typical true-prairie region, further examinations of cereal-crop roots were made. The natural plant cover, relatively large areas of which still remain intact, indicates growth conditions like those at the base station. Turkey Red wheat, sown about September 15, and preceded by a similar crop, was examined 4 miles northwest of Fairbury on a high, level area. The soil was a black, silty clay-loam, dry to a depth of 0.7 foot, but otherwise moist and sticky. Below 3.5 feet it became less clayey and lighter in color. In the spring the ground had been exceedingly wet. At the time of harvest the wheat averaged 3 feet in height and the estimated yield was 15 bushels per acre. The roots had a working depth of 3 feet and a maximum depth of 4.1 feet.

On a hillside in an adjoining field, the roots of rye were excavated. The crop was planted during the first week in September in a field where a similar crop had been grown the preceding year. The dark silty clay-loam gave way at a depth of about 0.8 foot to a tenacious clayey subsoil underlaid at a depth of about 5 feet with sand and gravel. Barnyard manure spread over the surface had induced a rank growth. The rye was thick and about 4.5 feet tall. The roots reached a working depth of about 4.7 feet, while the maximum penetration was 0.5 foot greater.

The following example of root behavior is illustrative, although soil conditions are hardly typical. Rye planted from the same lot of seed and at the same time as the preceding field, but upon low-lying land subject to overflow, was examined. The preceding crop was oats. In both cases, as in all the soil described in the true-prairie region, except where otherwise indicated, the land had been broken and cultivated for many years. The alluvial soil of mellow silt-loam extended to a depth of 3 feet. This was underlaid with a thin sheet of sandy loam which at 3.5 feet gave way to pure sand. The rye at the time of harvest had reached an average height of 3.8 feet. The working depth of the roots was approximately the same as the height, 3.9 feet; none extended below the 4.2-foot level. They were very abundant to 3.9 feet, at which depth most of them ended rather abruptly in the sand.

On a gently sloping hillside in an adjoining field, the roots of White Kherson oats were examined. The crop, which had been harvested, was 3 feet high and formed a thick stand on the rich black silt-loam which extended to a depth of over 7 feet. The estimated yield was 50 bushels per acre. The preceding crop was corn. The ground had been plowed and the oats sown early in March. Except for the surface 10 inches, which was quite dry, the soil was moist to the maximum depth examined. The plants had well-developed root systems, with a working depth of 4.2 feet and a maximum root penetration of 5.3 feet.

A final examination of the roots of cereal crops in the true prairie was made about 25 miles north of Lincoln and 4 miles south of Wahoo, Nebraska. In the level upland area, where the trenches were dug, the Marshall silt-loam was underlaid at a depth of about 2 feet with a loess subsoil, although of a more compact type than that described at Belmont (p. 105). A field of Yellow Kherson oats, which had been preceded by corn and which was disked during the first week of April, was examined. Although the stand was good and the plants of about the normal height (3 feet), a hailstorm had considerably reduced the yield. The high fertility of the soil was indicated by the rank growth of *Andropogon scoparius*, *A. furcatus*, *Agropyrum glaucum*, *Amorpha canescens*, and other native prairie species along the roadway. The roots reached a working depth of 4.1 feet, to which level they were very abundant. A maximum depth of 5 to 5.3 feet was found for several of the longer ones. Minor modifications in numbers and length of branches, etc., occur in different soil types, but they are of varying degrees of distinctness and difficult to describe. In general, it may be stated that where root penetration of oats, wheat, or rye is marked, as in the cases described, the surface root system, although well developed, is usually not so extensive nor so profoundly branched as in more arid regions, where the entire system is confined to the surface 1.7 to 3 feet of soil.

Wheat of the Turkey Red variety was examined in two separate fields adjoining the oats. The soil was of the same type and showed no great variation. In one field, where the crop, preceded by oats, had been planted about the middle of September, the plants were 3 feet high at harvest, but the yield was reduced because of hail. The roots had a working depth of about 3.6 feet, to which level they were quite abundant, while the maximum depth of penetration was 5 feet. In the other field, roots of wheat were examined in one end of a large trench which was dug primarily for the purpose of excavating the roots of red clover, *Trifolium pratense*, (p. 138). Here the maximum root penetration was the same as that already recorded, but the working level was about 3 inches deeper.

The following investigations of the root habits of the smaller cereals in true prairie grassland at Fargo, North Dakota, and at Manhattan, Kansas, are of much interest here.

Ten Eyck (1899) described the root development of a variety of Scotch Fife wheat planted April 14 and examined August 2 on land at Fargo, North Dakota, that had been cropped 12 years. "Most of the main roots run almost vertically downward, sending out numerous small feeders, which practically occupy the soil to a depth of 4 feet, which was as deep as the sample was taken. I think it is safe to affirm, however, that many roots penetrated a foot or two deeper." It should be added that the water-table, when the sample was excavated, was only 6.5 feet below the surface. He found the roots of oats similar to those of wheat, but "roots are more numerous and a little larger and coarser and extend fully as deep as those of wheat." (The ends of both plants were broken off at 4 feet depth.) The "mat or network of fibrous roots near the surface is much the greater in oats." The oat plants were 109 days old, 3.2 feet high, and the heads fully filled. The soil was a very fertile, deep, black loam underlaid by a compact heavy loam. The following year (1900) he examined wheat at the same station 80 days after planting and found the roots had reached a depth of 3 feet and had a horizontal spread of 9 inches on every side of the plant.

Shepherd (1905), in reporting root investigations at the same station, states that while root growth of cereals seems to vary considerably during different years, wheat roots reached the normal depth for this station, which is somewhat more than 4 feet, while oat roots are about 4 feet long normally. He washed out the roots of winter rye growing in the fertile loam soil. On July 7 the roots had reached a depth of only 3 feet, "the supply of roots being lighter than commonly found by this station for cereals." He suggests that "in this northern latitude, where the ground freezes deep in the winter, it is probable that the soil is too cold, at a depth greater than 3 feet, prior to July 7, to prove a suitable zone for cereal plants."

Ten Eyck (1904) working at Manhattan, Kansas, states that the roots of Red Winter wheat planted on October 11, at maturity on July 7, reached a depth of fully 4 feet in the hard subsoil underlying the fertile compact loam. Fine, fibrous roots extended to the very surface of the ground. The deeper slender roots did not branch much, and he estimated that the absorbing surface of the roots was greater in the first foot of soil than in all the lower soil. He describes oat roots excavated from a fine compact loam with a rather clayey subsoil. The roots were examined July 11, 103 days after planting in drills 8 inches apart. Several of the main roots were washed out to a depth of 4.5 feet and a few extended even deeper. The larger side-roots interlaced between the drill rows within 2 inches of the surface.

The preceding data, which will be summarized at the end of the chapter, are sufficient to warrant the conclusion that crop plants, like their native predecessors in prairie soil, are deeply rooted.

ROOT DEVELOPMENT IN SHORT-GRASS PLAINS.

Examinations of the root development of the smaller cereals were made at six typical stations in the short-grass plains. It has been pointed out on page 13 that in this plant association tall-grasses and most of their accompanying herbaceous societies are not present because of the light, unevenly distributed precipitation, which, with the high run-off from the compact silt-loam and the high evaporating power of the air, result, normally in a low available water-content. Moreover, the short-grasses, especially *Bouteloua gracilis* and *Bulbilis dactyloides*, being able to complete their growth and mature seed in a short period, compete successfully with the slower developing prairie species, the combined result of all these conditions being the almost entire absence of the latter, except perhaps very locally and in the most favorable situations. Consequently the short-grass vegetation indicates an entirely different set of environmental conditions than the tall-grass prairies, as is shown also by the development of crop plants.

Near Yuma, Colorado, and in a level field adjacent to one covered with a close sod of buffalo grass (described on p. 72), the roots of Turkey Red wheat and winter rye were examined. The rye land had been broken for only two years, the wheat land for about four. Both had been cropped the preceding season with sorghum and corn respectively. The rye was drilled at the rate of 30 pounds per acre about the last week in September. The wheat was drilled late in August and at the same rate. Both came up well in the fall. At the time of harvest the rye averaged 2.3 feet in height and the wheat only 2.1 feet. The roots were excavated on July 20. The very compact, chocolate brown silt-loam was well filled with the abundant much-branched wheat roots to a depth of 2.1 feet, while a few reached a maximum depth of 2.3 feet. The rye roots reached a working level of 2.2 feet, while some penetrated about 0.6 foot deeper. The soil was less compact than that in the unbroken sod (plate 9, A), and was fairly moist to a depth of 6 feet. At 3.6 feet occurred the grayish layer locally known as "hardpan" (*cf.* p. 75).

The open-mat type of buffalo and grama sod near Sterling, Colorado, has already been described (p. 42; plate 2, A). Five miles northwest of Sterling, the soil on which a field of Turkey Red wheat was growing consisted of a stiff loam slightly intermixed with sand. It was chocolate brown in color and very uniform to a depth of 2.8 feet, where there was a layer of gravel with some pebbles an inch in diameter, the whole considerably intermixed with sand and rather firmly cemented together, probably with compounds of calcium and magnesium. At the time of examination on July 21, several weeks after harvest, the soil was quite moist to the layer of gravel, which throughout its extent of about 10 inches was very dry, as was also the underlying sand. The soil had been farmed for 7 years and cropped with wheat during 1917 and 1918. The 1919 crop was quite thick, and gave a good yield, the plants at maturity standing 2 feet high. Many profusely branched roots, with long, widely spreading laterals, penetrated the soil to a working depth of 2.7 feet. Only a few roots entered the hard, gravelly layer, and these penetrated it only a little. It is interesting to note that in this dry subsoil the old roots of buffalo grass were easily identified. They were traced about a foot through the sandy layer and probably extended much deeper.

At Flagler, Colorado, about 100 miles east of Colorado Springs, the vegetation is also of the short-grass type. Here, again, mats of buffalo grass alternate with those of grama, leaving many intervening bare areas. Buffalo grass is somewhat more abundant than the grama and takes complete possession of low areas ("buffalo wallows"), where the run-off water from melting snows or heavy rains collects and stands. *Muhlenbergia gracillima*, *Festuca octoflora*, *Aristida purpurea*, and in disturbed areas *Schedonnardus paniculatus* occur more or less abundantly over the level or slightly rolling lands. These are accompanied, usually sparingly, by *Psoralea tenuiflora*, *Gutierrezia sarothræ*, *Opuntia camanchica*, *O. polyacantha*, *O. fragilis*, *Chrysopsis villosa*, *Artemisia frigida*, and *Plantago purshii*. In rougher land as along small canyons, the greater water penetration is indicated not only by a greater abundance and better development of most of the above herbs, but also by the appearance of *Stipa comata*, *Agropyrum glaucum*, and *Liatris punctata*.

A field of rye about 3 miles northwest of Flagler was examined on August 5, and about 3 weeks after it had been harvested. The crop had grown on land broken out for 25 years. Following a crop of wheat, the rye had been drilled the first week of September, after disking the wheat stubble, at the rate of 30 pounds per acre. It came up well in the fall, and although somewhat thin of stand, promised a good yield. During the blossoming period, about the first of June, freezing weather, accompanied by snow, cut the yield to only 10 bushels per acre. The plants had an average height, when ripe, of about 2.1 feet. The soil was of the usual chocolate-colored silt-loam type, and somewhat columnar in structure, to a depth of 2.5 feet, where a grayish "hardpan" 0.7 to 0.9 foot in thickness was in evidence. Soils of arid regions are uniformly high in their percentage of lime and usually also of magnesia, and this quite independently of the underlying formations being calcareous or otherwise (Hilgard, 1911:374). Alway (1916:414) states that in western Nebraska areas the carbonates, which are practically absent from the first foot or two of soil, are distributed throughout the subsoil mass instead of being segregated in the form of concretions, as is characteristic in more humid areas. Frequently they constitute 3 to 6 per cent of the weight of the soil (Alway, 1919). Below this harder layer the soil became lighter in color, dry, and very mellow. Below 1 foot it was uniformly moist to the working depth of the roots, which occurred at 2.3 feet. The roots were very abundant to this depth, very few extending deeper, although some were found to penetrate to 2.8 feet.

Red spring wheat was examined in a field only a few rods away on old land previously cropped with corn. The wheat had been disked late in March at the rate of about 45 pounds per acre. This resulted in a fairly thick stand. The crop reached an average height of 2.5 feet. The only difference in soil structure was the depth of the "hardpan"; here it occurred somewhat nearer the surface (at 2.3 feet). This shallower depth may have been due to surface-soil blowing, for great ridges of wind-blown silt had half buried the wire fence between the two fields. The roots reached a working depth which corresponded to the depth of moist soil (about 2.5 feet), only a very few extending 3 or 4 inches deeper.

About a mile eastward, a field of Yellow Kherson oats was examined on land that had been broken for over 5 years. It was drilled on April 2, following a crop of corn, the land having been plowed to a depth of 0.5 foot. The silt-loam was very hard and dry near the surface, while at 1.6 feet in depth a "hardpan" was encountered, below which dry soil again occurred. Aside from cropping effects, the water-content of the soil, even in adjacent level fields, is frequently considerably varied by greater or less accumulations and subsequent melting of drifts of snow (*cf.* p. 116). The oats had an average height of 2.2 feet, which was 0.5 foot greater than the working depth of the roots; only rarely did roots extend to 1.9 feet.

About 1.5 miles further eastward, and just north of Flagler, a field of Turkey Red wheat growing on sod was examined. The land had been broken in the spring of the preceding year and the wheat was drilled in September. The straw was very short, the maximum height scarcely exceeding a foot, while considerable grain was left in the field, being too short to be caught by the header. The roots were developed very much as if growing in a large flowerpot, for the soil was moist only to a depth of 1.3 feet, where a very tenacious "hardpan", 0.8 foot thick, occurred. Below this the soil was less compact but powdery. The dense masses of compacted roots practically all ended at a depth of 1.4 feet; only a very few penetrated slightly deeper.

From these four soil examinations, none of which were made more than 3 miles apart, it is clear that the depth of the "hardpan" varies considerably. This frequently greatly hinders the penetration of moisture and gives rise to "spotted" soil conditions. Indeed, when the land is broken and farmed, local variations in the height and luxuriance of the crop are often very evident, even in the same field. Shantz (1911:47)has shown that in short-grass plains the run-off, even on slopes having the same inclination and in areas only a few feet apart, may be five times greater in one place than in another. The areas of greater moisture penetration were marked by a growth of *Psoralea tenuiflora*. When the land is broken these moist spots would have a marked effect upon crop growth. Corn growing in "buffalo wallows" is frequently a foot higher than that in the surrounding fields. However, it should be stated here that this is the only case out of 15 examinations made throughout the short-grass plains where the crop was so shallow-rooted. Continued farming, with the use of proper methods of dry-land agriculture, providing the rainfall is sufficient to warrant the initial breaking of the sod, should lead to the disappearance of the "hardpan" and consequent deeper moisture and root penetration. Under natural conditions, as has been repeatedly pointed out in preceding pages, practically all species of the short-grass plains examined (except the cacti, which possess water-storage organs) have extensive roots which easily penetrate below the "hardpan" layer and often many feet into the drier soil. Available moisture must be present, at least during certain periods, to a considerable depth. This may occur only during wet years of a climatic cycle. Whether living roots are to be found in the deeper subsoil only during each successive wet period or whether they continue to live but absorb little or no water throughout the dry periods of several years (assuming that available water is entirely exhausted), remains to be determined.

The root development of the smaller cereal crops was also examined at Burlington, Colorado. This station is about 10 miles west of the Kansas-Colorado State line and in the midst of great stretches of short-grass plains of which *Bulbilis dactyloides* forms the consociation. The natural vegetation has been described on page 74, in connection with the description of the roots of buffalo grass, which were examined in an area adjoining the fields of crop plants. This whole area, lying about 7 miles northeast of Burlington, was quite level.

A field of mixed oats (Yellow Kherson in part) and one of Turkey Red wheat were examined. In both fields the small grains were the second crop. The first crop after breaking on the oat land was millet, while on the wheat land a crop of sorghum had been raised. The soil was disked and harrowed and the wheat was drilled about October 1. After similar preparation of the soil in the spring, the oats were drilled on April 16. The fields were visited June 29, 1919. The oats had just finished blossoming and were in the milk stage. The wheat was somewhat more mature, the kernels being in the dough stage of development.

In both fields the stand was good; the oats averaged 2.2 feet and the wheat about 2.5 feet in height. The trenches were dug after completing work on the natural vegetation, and the much greater ease with which the tilled soil at all depths could be excavated was very pronounced. Indeed, the soil was quite moist to the maximum depth examined (7.5 feet), being easily molded into firm lumps with only slight pressure of the hand. No "hardpan" was in evidence, the soil being mellow throughout and easily spaded. Similar conditions were found in adjoining fields of rye and barley, growing on land that had been broken for 3 years. This is in sharp contrast to conditions in the native sod, where the hard, compact soil was powdery below a depth of 3.5 feet. An examination of the rainfall records shows that an excess of nearly 3 inches over the normal precipitation had occurred the preceding December and 4.3 inches in June. It is probable the run-off was very much higher from the sod than in the fields of grain.

The oat roots were found to be very abundant to a depth of 4 feet; the working depth for the wheat was about 2 inches less. The maximum depth of oat-root penetration was 5.3 feet, while several wheat roots were traced to 5.4 feet in depth. At 5 feet the soil contained enough moist clay to stick to the spade. Roots of both *Lygodesmia juncea* and *Bulbilis* were found extending well below the level reached by the roots of crop plants. They are easily distinguishable from the thicker, more watery, fragile root-ends of oats and wheat, which are thickly beset with root-hairs to which the soil clings tenaciously. Although both wheat and oats had well-branched root systems, the latter had more numerous branches, and most of these were of larger diameter.

A field of rye, the third crop following sorghum and barley, was next examined. The preparation of the seed-bed was similar to that already described. At the time of examination the plants averaged 3.5 feet in height and were just entering the dough stage. Soil-type and soil-moisture were practically identical with those in the adjacent fields. This is true also for a field of barley where roots were excavated. Many rye roots were found at a depth of 5 feet, the working depth being about 4.3 feet. The maximum depth attained by several roots was 6 feet.

A field of barley, *Hordeum vulgare*, of an undetermined variety, was next examined. It also was growing on land which had raised but two preceding crops, sorghum and rye. On June 29, the crop, drilled late in April, averaged 2.5 feet in height and was in the dough stage. The average working depth of the roots was 4.2 feet and the maximum root depth 5.7 feet, which was slightly greater than that of oats or wheat. The roots were well-branched and spread to 12 inches laterally in the surface 2 to 4 inches of soil.

At Colby, 50 miles east of the Colorado-Kansas State line, wheat, oats and rye were examined at the Colby Experiment Station. Here the surface 2 feet of soil was the fine, fertile Colby silt-loam underlaid with a light-colored clay. Mechanical analysis shows that it is rather uniform at all depths reached by crop plants. From the rather limited examination of the vegetation, it is believed that this station lies in the short-grass plains, although near their eastern boundary. *Bouteloua gracilis* and *Bulbilis* predominate and are accompanied by *Schedonnardus paniculatus*, *Festuca octoflora*, *Aristida purpurea*, *Psoralea tenuiflora*, etc. The short-grasses form a close sod. *Agropyrum glaucum* occurs in moist ravines and often in disturbed areas, as along roadsides. The excellent development of grama grass, which was 1.5 to 1.7 feet in height, together with the fine growth of wheat-grass (2.5 to 3 feet high) and the luxuriance of the weeds, were indicative of the favorable season for growth.

A field of oats (variety unknown) was examined growing on land which, as in the other field, had been broken for a number of years. It was planted on April 17, at the rate of 32 pounds per acre (the preceding crop being barley), and harvested for hay on July 12. The stand was quite thick, and the average height about 2.8 feet. The roots were examined on August 7. In digging the trench a harder soil layer was found extending from 1.9 to 2.6 feet in depth. Below this the dry, mellow, light-colored clay subsoil occurred. Only the surface 2 feet of soil were quite moist. The roots reached a working depth of 2.5 feet; they were quite abundant to 2.8 feet, while the maximum depth of penetration was 3 feet.

Less than half a mile away, in this level area, the roots of winter wheat were excavated. It was a variety of Turkey Red known as Kansas Red or Kanred. It had been planted, following a crop of wheat, on September 12 and harvested on July 4, the plants reaching an average height of about 3.2 feet. The rich black loam extended to a depth of 2 feet and broke out with rather a columnar structure. At 2.1 feet occurred well-formed "hardpan" nearly a foot thick, below which was the dry, light-colored, loose subsoil. The working depth of the roots was found to be 2 feet, none extending deeper than 2.3 feet.

A field of rye was also examined. Following a crop of milo, it was planted on September 19 at the rate of 56 pounds per acre. It came up very well in the fall, and reached a height of about 3.5 feet, when it was plowed under for green manure on May 27, just when it was in the late flowering stage. A rather pronounced "hardpan" occurred at 2.3 feet. Below this level the subsoil was streaked and colored with magnesium or calcium compounds to a depth of 4.4 feet. This layer extended much farther below the 2-foot level than in either of the preceding fields. The roots had a working depth of 3 feet, while some reached a maximum extent of 3.6 feet.

Finally the roots of spring wheat were examined. Corn had been grown on the ground previously. The wheat was planted March 12. It was of good stand, with an average height at harvest of about 2.6 feet, but the yield was only 12 bushels per acre. The soil was in all respects similar to that in the adjoining field of winter wheat, only it was moist to a depth of at least 7 feet. Indeed, it was so wet that it stuck to the spade and at any depth could easily be pressed into a very coherent lump. The "hardpan" was so thoroughly moist that it could not be distinguished from the surface soil. The root development readily responded to the presence of the moist subsoil and reached a working depth of 3.4 feet. It may be noted that this is 1.4 feet deeper than the working depth of the winter wheat, which, under similar growth conditions, is usually of greater extent than the former. The difference in maximum penetration is even more marked, being only 2.3 feet for winter wheat and 4.4 feet for spring wheat. The cause of the excess of soil moisture in this field was due to seepage from a large irrigation reservoir about 150 feet distant from the place of root excavation.

These data throw some light upon the root penetration of native grasses, legumes, and other species of the short-grass plains vegetation. Most of these deep-rooted species are plants with periods of life and growth of extended duration. During wet phases of the climatic cycle it seems almost certain that water must penetrate far into the subsoil. Becoming gradually moistened and finally thoroughly wet, the "hardpan" offers little resistance to the downward penetration of water. At the Colby Experiment Station it has been shown conclusively that under cropping conditions the water-content varies to a depth of at least 6 feet, and similar conditions occur at Burlington, Colorado. Further study, now that we are certain of the deep rooting habits of short-grass-plains species, will in all probability show this to be the case in native vegetation.

A final examination of the root development of crop plants in short-grass land was made at Limon, Colorado, 70 miles east of Colorado

Springs. Here the typical grass cover of *Bulbilis* and *Bouteloua* on the harder silt-loam alternates with the mixed-prairie cover on the sandy loam (*cf.* p. 66). Winter wheat, spring wheat, and rye were all examined on land that had been broken for only two seasons. The winter wheat and rye had both been preceded by corn, having been drilled about the middle of September. The spring wheat was also preceded by corn. At the time of these examinations, on June 25, the winter wheat was just coming into the dough stage, while the spring wheat had just begun to blossom. The former had an average height of 1.8 feet, the latter of only 1.7 feet (plate 22, A). The surface 10 inches of soil consisted of a fine silt-loam underlaid by 1.7 feet of dark chocolate-colored clay, which, although moist, because of its somewhat jointed structure, broke out in lumps. At 2.5 feet depth the soil became somewhat chalky and sandy, while 10 inches deeper it gave way to a very fine yellow sand. It was very dry below 2.5 feet. The average working depth of the winter wheat was found at 2 feet. The roots were abundant to this depth. Some roots were found deeper, even penetrating a little into the dry sand. Unlike the roots of the dominant native grasses, those of wheat do not run so parallel with the soil surface, although they take an oblique direction downward at such an angle that at a distance of 5 to 8 inches from the base of the plant they may be only 3 to 5 inches deep. The root system was well developed and profoundly branched, the branches often being 2 or 3 inches in length. Although the surface soil was much more mellow in the field of spring wheat, due to the disking of the ground before drilling the wheat in the spring, the water penetration was no greater. The working depth was 2 feet, below which the soil was dry and no roots penetrated beyond. The lateral spread and degree of branching were about the same as that already described. Under both crops the roots of native plants were found extending 7 feet deep and may have penetrated even deeper.

The field of rye was about a quarter of a mile distant. The ground was level and the soil almost identical with that just described, but the water penetration was not so great. The crop was in the flowering stage and about 2.3 feet in height. The roots had a working depth of 2 feet, below which few or none penetrated. They had a wide lateral spread, reaching horizontal distances of 0.8 to 1.3 feet or more on either side of the plant at a depth of 0.2 to 0.4 foot. All of the roots were exceedingly well branched and were especially abundant in the crevices of the somewhat jointed soil. The rather limited root penetration shown by these crops on land formerly covered by short-grass vegetation is in striking contrast to the deeper-rooted ones on the lighter soil type in adjacent fields, as indicated by mixed prairie. Moreover, where rainfall is sufficient to support a growth of mixed-prairie species on hard lands, a far better development of crop plants is found.

ROOT DEVELOPMENT IN MIXED PRAIRIE.

Mixed-prairie vegetation indicates growth conditions more favorable than those in short-grass plains, but a water-content somewhat less than that found in true-prairie areas. Frequently, because of edaphic conditions, tongues of mixed prairie extend far into the short-grass-plains association or occur as alternes in it. In general, the possibilities of crop production on mixed prairie are much greater and a correspondingly better root development may be anticipated.

At Limon, Colorado, 1.5 miles distant from the fields already described (p. 115), an examination of the roots of oats and winter wheat was made on land formerly covered with and now adjacent to mixed prairie. In both fields the soil consisted of about a foot of dark-colored sandy loam, below which it became lighter in color. It was almost identical with that described on page 74, where native plants were excavated. The oat land had been broken for 4 years, the wheat land for about 8 years. The preceding crops were corn and pinto beans, respectively.

The White Kherson oats had been drilled late in April; on June 26 it was well headed and had a good color, but the straw was only 1.5 feet high. The maximum root penetration was 4 feet and the average working depth 3.2 feet. Below 2 feet the soil was very moist to a depth of at least 6 feet. This excess moisture was probably due to the blowing of the snow from the field of wheat on a gentle west slope and its accumulation in this field, lying on a slope somewhat north of east.

The winter wheat was 1.8 feet high and in blossom. It had been drilled about November 1, but did not come up well until spring. The soil, which was of a somewhat sandier type than that in the oat field, was dry throughout and the wheat was beginning to roll a little from lack of moisture. The surface spread of laterals was from 0.4 to 0.8 foot on all sides of the plant, while the maximum depth of penetration was 4 feet. However, the working depth was 3 feet, a foot greater than in adjacent areas of short-grass land.

About 12 miles southeast of Yuma, Colorado, rye roots were excavated from the sandy soil which formerly was covered with mixed prairie. The native vegetation in an adjoining area of this rather level tract, where certain deep-rooted native plants were excavated, is described on page 58. The rye land had been farmed for several years, the crop of the preceding year also being rye. The seed was sowed late in September at the rate of 56 pounds per acre. It came up well in the fall, but was of very thin stand and only 2.7 feet high at the time of harvest, 10 days before this investigation was made on July 19. The sandy soil, which was rather uniform throughout, and quite dry to a depth of 2.5 or 3 feet, became gradually more moist and was wet at a depth of 5 feet.

The roots spread laterally in the surface 0.5 to 0.8 foot for distances of 0.4 to 1.3 feet before ending or turning downward. The first 4 to 6 inches of roots at the base of the plant were almost woolly with dense masses of root-hairs to which the sand clung tenaciously. The roots soon began to branch, with delicate, hairlike branches 0.5 inch to 3 or 4 inches in length, some being even longer. They ran off in all directions, even obliquely upward, and were fairly well rebranched to the second order. The main roots, which were rather tough, appeared like coarse threads. The branching in the first 2.5 feet of soil was not so profuse as at greater depths. Here great numbers of fine, poorly rebranched, threadlike laterals occurred to the ends of the roots at a depth of 4 or 5 feet. They were mostly 0.5 to 2 inches in length, but frequently several inches long. In places as many as 10 to 30 were found on a single inch of the root. The working depth was 4.2 feet, and no roots were found below 5 feet. After several root systems were examined on the four walls of the long trench, a drawing (fig. 34), was made to show, as nearly as possible, all the root characters described.

At the United States dry-land experiment station at Ardmore, South Dakota, some examinations of the roots of crop plants were made in correlating their development with those of the roots of the mixed prairie. A description of this mixed prairie may be found on page 67 (*cf.* also plate 3, A, B). Since the soil, even on this rather level area, is far from uniform, it will be necessary to point out the variations in the two fields examined.

In the field of Turkey Red wheat the very hard, tenacious, brownish-black Pierre clay gave way at a depth of 3.7 feet to a poorly disintegrated gravelly sand intermixed with some clay. The degree of compactness of this soil should not be overlooked. The writer has excavated roots in scores of places in many different States, but in no other soil (once through the surface foot) has greater difficulty been experienced in excavating a trench preliminary to examining the roots. It is quite remarkable how roots can penetrate soils which are so compact even when quite moist.

This land had been broken for 7 years and had lain fallow the preceding season. Wheat was seeded at the rate of 45 pounds to the acre on September 9. It came up well in the fall, and when harvested, about July 10, it had an average height of 2.6 feet. The yield was estimated at 30 bushels per acre (plate 22, B). Roots were very abundant to a depth of 3.3 feet, some penetrating entirely through the clay and 0.3 to 0.4 foot into the gravelly sand beneath. The soil was quite moist to the maximum depth excavated, about 5 feet.

About 100 yards from this trench, another was dug in a field of oats. The variety is known as "Sixty-day" oats and is very similar to the White Kherson. This crop followed one of corn, the soil having been disked and the oats seeded at the rate of 48 pounds per acre on April 2.

The stand was thick, the plants averaged about 2.5 feet in height, and promised a good yield. At the time of this investigation the crop had been harvested. The surface 2.2 feet of Pierre clay was much drier than in the field of wheat. At this depth there was a layer of coarse

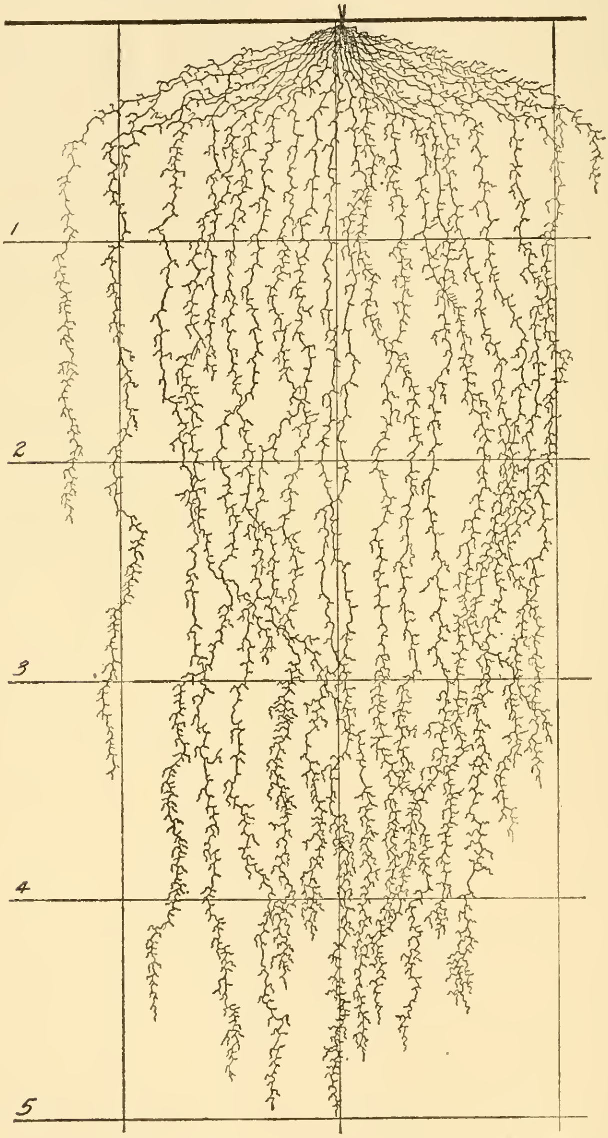


Fig. 34.—Root system of *Secale cereale* grown in sandy soil.

sand intermixed with pebbles and some small rocks. It soon gave way to gravelly soil intermixed with somewhat alternating streaks of sand and clay. The yellowish-brown sand was quite dry, but the underlying strata of clay and sand were fairly moist and to the depth of the trench (about 5 feet) easily formed a lump with slight pressure of the hand. The oat roots had a working depth of only 2.7 feet, while the maximum penetration was 3.2 feet.

A field of rye was examined in the mixed prairie near the base station at Colorado Springs. A description of the natural vegetation of this area may be found on page 36. The hard loam had been broken for only two seasons. The first crop was millet. The rye was sown about the middle of November. As is often the case in dry-land cropping, the stand was thin (plate 20, B). On June 23, when it was examined, the crop averaged 3 feet in height and was past the blossoming stage. Many of the abundant fibrous roots spread obliquely outward, so that at 5 to 10 inches horizontally from the base of the plant they were only 6 to 8 inches deep. Here most of them turned abruptly downward. In fact, most of the roots took a more or less obliquely downward course, relatively few descending vertically. The main roots were cordlike, quite tough, and rather easily excavated. The branching was not so pronounced as that described for rye growing in the sand at Central City (p. 100) and Yuma (p. 116). The roots showed a marked tendency (as is the case with so many native species) to follow the soil crevices and branch in one plane only. Indeed, in such places of greater water-content and better aeration, they showed their maximum development. The working depth was determined at 3 feet, although the maximum root penetration was about 4.7 feet. Below 4.3 feet roots were scarce.

At Phillipsburg, Kansas, 90 miles east of Colby and well within the mixed-prairie region (fig. 14), wheat and oat roots were again examined. Both crops were growing on land that had been broken for 10 years. The preceding crop was corn. The Turkey Red wheat had been drilled in the corn on September 20 and the Texas Red oats about the middle of March. On June 27, at the time of this investigation, both crops were rapidly ripening and were harvested about a week later. The stand was thick; the wheat averaged 3.8 feet in height and the oats about the same. The soil is a dark-brown clay-loam to a depth of 1.7 feet, below which level it is somewhat sticky, although when wet it maintains a dark-brown color, to a depth of 4.3 feet. At greater depths it becomes lighter in color and more clayey in texture. It was thoroughly moist to a depth of at least 8 feet. The oat roots reached a maximum depth of 4.8 feet and were fairly abundant at this depth. The older roots on the first 2 feet of soil were usually tougher and smaller in diameter than the remaining deeper portions. In the deeper soils the roots may extend for several inches and give off scarcely a single branch, while at other levels short laterals, 2 to 25 mm. in length, are quite abundant. These laterals are seldom rebranched. The wheat roots were abundant to a depth of 4.8 feet, while a few extended to the extreme depth of 5.7 feet. The ends of the wheat roots, especially the last 1.5 feet, were much more branched than those of the oats.

Mankato, Kansas, lies still 60 miles farther east than the last station and the unbroken land shows some exceedingly fine mixed prairies. It lies near their eastern border, the rainfall being sufficient for an abundant development of the tall-grasses and many accompanying herbaceous societies, but not sufficient for these to entirely dominate the short-grasses. *Bulbilis dactyloides, Bouteloua gracilis, B. hirsuta,* etc., normally form a layer in most places below the taller grass dominants, and while sometimes absent they are sure to reappear on hillsides, often in equal or greater abundance than the former. Where overgrazing has occurred, the tall-grasses drop out more or less completely and the area becomes carpeted with buffalo grass and grama, the former usually predominating (plate 3, c). Of the tall-grasses, *Agropyrum glaucum* frequently occurs in pure stands (plate 12, B), but is still more frequently a part of a mictium. *Andropogon furcatus, A. scoparius, Kœleria cristata, Bouteloua curtipendula, Elymus canadensis,* and in moister areas *Panicum virgatum,* are all abundant. *Stipa comata* is absent. *Amorpha canescens, Kuhnia glutinosa, Petalostemon* spp., *Psoralea tenuiflora,* and many other subdominants abound. The vegetation was exceptionally well developed because of the high water-content.

A field of White Kherson oats was examined 6 miles northwest of Mankato, on a broad, flat hilltop, growing in Colby silt-loam. Although the surface foot of this dark-colored soil was so dry that it came out in great lumps, below this it was very moist to a depth of more than 6 feet. At 1.8 feet depth the characteristic whitish-streaked layer of "hardpan" was encountered, but this, too, was thoroughly moist and of no firmer texture than the soil above or below it. The silt-loam subsoil was dark-colored to more than 5 feet. The land had been farmed for several years; the preceding crop was corn. The oats were disked in at the rate of 40 pounds per acre about the middle of May. The stand was even and fairly thick and the crop at harvest time 2.8 feet in height. Roots were examined on August 8. The working depth was determined at 3.5 feet and the maximum root penetration at 4.6 feet.

About 2 miles further west a field of Turkey Red wheat was studied on fairly level land which had been cropped for 30 years. Wheat had grown on this land the preceding season. The stubble had been plowed to a depth of 6 inches and the winter wheat drilled in at the rate of 60 pounds per acre early in September. At harvest time, July 4, the grain was 2.8 feet tall, quite thick on the ground, and the yield was estimated at 20 bushels. The soil was heavier and contained more clay than that just described. It was moist nearer the surface but quite dry at about

4.6 feet depth. The wheat roots had a working depth of 3.2 feet, a few extending 0.5 foot deeper.

In an adjacent field a crop of rye had been grown. It had been drilled in the corn at the rate of 2 bushels per acre on September 1. It had a great abundance of straw, which averaged 4.2 feet in height, but the heads did not fill out well. As in all of these fields, the dry surface soil was very hard and filled with cracks often half an inch wide. These were especially pronounced in the rye. However, at 0.7 foot depth the soil became moist, and this condition prevailed through the "hardpan" at 3.5 feet and to all depths examined. The soil was similar to but less clayey than that in the wheat. The working depth of the rye roots was 3.8 feet, although some extended 0.8 foot deeper.

SUMMARY.

For comparison these data on root development and height growth of the cereal crops are summarized in table 10. A statement of grain yield would also have been very desirable had it not involved either an amount of work incommensurate with its value or the inclusion of data furnished by a number of farmers and ranchmen. Moreover, as is well known, local conditions at the time of blossoming or when the grain is maturing often materially affect, if indeed they do not largely determine the yield. Undoubtedly the vegetative development is the best criterion for our purpose.

A study of table 10, which records the development of rye, shows striking relationship between the growth of the crop and the degree of xerophytism of the plant association. Not only the height of tops and the working depth of the roots, but also the maximum root-depth, increases consistently from short-grass plains through mixed prairie to true prairie. In fact, this was found to be the case with oats and also with wheat. Except for the greater development of both roots and tops at Burlington (a phenomenon which is clearly related to an unusual local moisture-supply) the averages for rye would have been much less in short-grass plains. Through this association the maximum root penetration, not only for rye but also for the other cereals, is clearly related to the depth of water penetration. The root penetration in mixed prairie in all three soil types was markedly greater than in short-grass plains. Likewise, the height of tops, with the exception of the crop grown in pure sand, and the working root depth were greater in every instance but one in true-prairie soils than was the average development under mixed-prairie environment.

Using oats as the indicator, the average differences are just as consistent even if not so great. The shorter growing period of this crop probably accounts for these smaller differences. Here, again, the averages of root depth in short-grass plains are increased by the greater root penetration at Burlington.

TABLE 10.—*Development of rye, oats, and wheat at various stations in the grassland formation.*

Station.	Variety of crop.	Soil.	Height of tops.	Working depth.	Maximum depth.
RYE.					
I. Short-grass plains:			*feet.*	*feet.*	*feet.*
Yuma, Colo	Winter	Silt-loam [1]	2.3	2.2	2.8
Flagler, Colo	.....do	.....do.[2]	2.1	2.3	2.8
Burlington, Colo	.....do	.....do.[3]	3.5	4.3	6.0
Limon, Colo	.....do	.....do.[2]	2.3	2.0	2.0
Colby, Kans	.....do	.....do.[4]	3.5	3.0	3 6
Averages			2.7	2.8	3.4
II. Mixed prairie:					
Yuma, Colo	Winter	Very sandy loam	2.7	4.2	5.0
Colorado Springs, Colo.	.....do	Sandy loam	3.0	3.0	4.7
Mankato, Kans	.....do	Silt-loam [5]	4.2	3.8	4.7
Averages			3.3	3.7	4.8
III. True prairie:					
Central City, Nebr	Winter	Very sandy loam	6.0	5.0	7.7
Do	.....do	Pure sand	3.3	2.8	4.6
Lincoln, Nebr	.....do	Silt-loam	5.5	3.9	5.0
Do	Winter Rosen	.....do	6.5	3.7	5.0
Fairbury, Nebr	Winter	Clay-loam	4.5	4.7	5.2
Do	.....do	Alluvial	3.8	3.9	4.2
Averages			4.9	4.0	5.3
OATS.					
I. Short-grass plains:					
Flagler, Colo	Yellow Kherson	Silt-loam [6]	2.2	1.7	1.9
Burlington, Colo	.....do	.....do.[3]	2.2	4.0	5.3
Colby, Kans	Unknown	.....do.[7]	2.8	2.5	3.0
Averages			2.4	2.7	3.4
II. Mixed prairie:					
Limon, Colo	White Kherson	Very sandy loam	1.5	3.2	4.0
Phillipsburg, Kans	Texas Red	Silt-loam	3.8	4.0	4.8
Ardmore, S. Dak	Sixty-day	Pierre clay	2.5	2.7	3.2
Mankato, Kans	White Kherson	Silt-loam [8]	2.8	3.5	4.6
Averages			2.7	3.4	4.2
III. True prairie:					
Lincoln, Nebr	White Kherson	Alluvial silt-loam	3.0	2.6	3.4
Do	.....do	Silt-loam	2.0	3.1	4.1
Do	.....do	.....do	2.8	3.2	3.8
Fairbury, Nebr	.....do	Clay-loam	3.0	4.2	5.3
Wahoo, Nebr	.....do	Silt-loam	3.0	4.1	5.3
Averages			2.8	3.4	4.4

[1] "Hardpan" at 3.6 feet.
[2] "Hardpan" at 2.5 feet.
[3] No "hardpan" found.
[4] "Hardpan" at 2.3 feet.
[5] "Hardpan" at 3.5 feet.
[6] "Hardpan" at 1.6 feet.
[7] "Hardpan" at 1.9 feet.
[8] "Hardpan" at 1.8 feet.

Table 10.—*Development of rye, oats, and wheat at various stations in the grassland formation*—continued.

Station.	Variety of crop.	Soil.	Height of tops.	Working depth.	Maximum depth.
WHEAT.					
I. Short-grass plains:			*feet.*	*feet.*	*feet.*
Yuma, Colo	Turkey Red	Silt-loam [1]	2.1	2.1	2.3
Sterling, Colo	do	do.[5]	2.0	2.7	2.8
Flagler, Colo	Red Spring	do.[4]	2.5	2.5	2.8
Do	Turkey Red	do.[6]	1.0	1.4	1.5
Burlington, Colo	do	do.[3]	2.5	3.8	5.4
Colby, Kans	Kanred	do.[7]	3.2	2.0	2.3
Limon, Colo	Turkey Red	do.[2]	1.8	2.0	2.8
Do	Spring	do.[2]	1.7	2.0	2.0
Averages			2.1	2.3	2.7
II. Mixed prairie:					
Limon, Colo	Turkey Red	Very sandy loam	1.8	3.0	4.0
Ardmore, S. Dak	do	Pierre clay	2.6	3.3	4.1
Phillipsburg, Kans	do	Silt-loam	3.8	4.8	5.7
Mankato, Kans	do	do	2.8	3.2	3.7
Averages			2.8	3.6	4.4
III. True prairie:					
Lincoln, Nebr	Turkey Red	Silt-loam	3.3	3.2	4.7
Do	do	Alluvial silt-loam	3.8	4.4	6.2
Do	do	Silt-loam	3.5	4.9	7.3
Fairbury, Nebr	do	Clay-loam	3.0	3.0	4.1
Wahoo, Nebr	do	Silt-loam	3.0	3.6	5.0
Do	do	do	3.0	3.8	5.0
Averages			3.3	3.8	5.4

[1] "Hardpan" at 3.6 feet.
[2] "Hardpan" at 2.5 feet.
[3] No "hardpan" found.
[4] "Hardpan" at 2.3 feet.
[5] Gravel layer at 2.8 feet.
[6] "Hardpan" at 1.3 feet.
[7] "Hardpan" at 2.1 feet.

For wheat the different environmental conditions have most profoundly affected its development. Spring wheat at Flagler and Limon have been included under short-grass plains, since their development was quite similar to that of winter wheat. An examination of table 10 shows that the data are fairly consistent throughout, except at Burlington, Colorado, and in the mixed prairie at Phillipsburg, Kansas. At the latter station the excess of precipitation above the normal is pronounced (table 11), and the resulting increased water-content reflects itself in the development of both wheat and oats. The general relation of root penetration to the depth of moist soil rather than to the "hardpan" should be noted.

In the absence of water-content data there is given in table 11 a comparison of precipitation at the different stations during several periods. The values of average mean annual precipitation are small for this

TABLE 11.—*Precipitation at the several stations.*

Station.	Mean annual.	July 1918 to July 1919.	January to July 1919.	Variation from normal.
I. Short-grass plains:				
Yuma, Colo	17.4	20.2	7.5	....
Burlington, Colo	17.2	21.7	9.5	+2.8
Colby, Kans	17.0	22.5	10.1	+1.6
Sterling, Colo	18.1	....	6.7	....
Limon, Colo	13.4	[1]13.8	2.4	[1]−3.3
Averages	16.7	21.4	8.4	....
II. Mixed prairie:				
Phillipsburg, Kansas	22.9	28.7	14.9	+3.6
Ardmore, S. Dak	17.8	16.7	8.4	....
Colorado Springs, Colo	14.6	....	3.4	−3.7
Averages	18.4	22.7	8.9	....
III. True prairie:				
Central City, Nebr	26.1	25.9	14.3	+1.4
Lincoln, Nebr	27.5	29.3	16.2	+2.2
Fairbury, Nebr	29.8	33.4	19.6	+4.0
Wahoo, Nebr	31.7	[2]26.6	13.9	[2]−0.2
Averages	28.8	29.5	16.7	....

[1] March reading missing. [2] February reading missing.

study. Nor is a knowledge of the annual precipitation for the year during which the crops were grown of great worth. The precipitation for the period of January to July 1919, together with the variations from the normal, are of greater interest. However, as pointed out by Chilcott and Cole (1917), the uncertainty of the distribution of rainfall rather than the total average quantity received is the factor that makes crop production over the Great Plains hazardous. Shantz (1911:29) emphasizes the fact that the average annual rainfall alone gives almost no idea of the conditions favorable or unfavorable for crop production, for crop failures sometimes occur during the years with the greatest annual rainfall. The great amount of run-off and the high evaporation rates in short-grass plains are factors to be kept constantly in mind in evaluating efficient rainfall. That water-content and not soil fertility is the chief limiting factor in crop production in this grassland formation should again be emphasized. In fact, because of the fertility of the soil, cultivated crops on short-grass land usually make such an excellent growth in spring and early summer that the very rapidity and luxuriance of growth exhaust the water-supply all the more rapidly during the drier intervals of summer, and thus accentuate the drought.

In order to compare the relative development of cereal crop plants somewhat more directly, the averages of growth of tops and roots are given on the percentage basis in table 12, where growth in the true prairie is considered unity. It may be noted that rye shows the greatest extremes in height of tops, and wheat in root-depth, in the three communities, while oats show the least. General correlations between precipitation and plant association are apparent in every case.

TABLE 12.—*Relative development of cereal-crop plants*[1] *and relative precipitation in the several grassland associations.*

	Short-grass plains.	Mixed prairie.	True prairie.
Rye:			
Height of tops	56	66	100
Working depth	69	92	100
Maximum depth	65	90	100
Oats:			
Height of tops	85	94	100
Working depth	79	95	100
Maximum depth	77	94	100
Wheat:			
Height of tops	64	85	100
Working depth	61	93	100
Maximum depth	51	80	100
Mean annual precipitation	58	64	100
Precipitation from July 1918 to July 1919	73	77	100
Precipitation from January to July 1919	50	53	100

[1] In order to secure greater accuracy in percentages, these results were obtained directly from the field notes of root depths given in feet and inches. Table 10 gives the measurements to the nearest tenth of a foot.

These data, which agree with those of other investigators, emphasize the depth at which crop plants distribute their roots, when grown under favorable climatic conditions as indicated by true prairies, where the subsoil is moist. Such studies must lead to a revision of the current ideas of the depths at which crop plants carry on absorption, especially when nearing maturity (*cf.* p. 139). The smaller development of both aerial and underground portions of crop plants in mixed prairie and their still poorer development in the short-grass plains is to be expected, but the correlation has not heretofore been worked out. Shantz (1911) has given certain correlations between root development of native species and water-content as affected by soil type in eastern Colorado, but his findings of root-depths in short-grass lands appear quite erroneous. The close correlation between the poorer development of root and shoot of a given crop as less favorable growth conditions occur is marked. Such a relation has also been found for *Agropyrum glaucum* (p. 78). These results greatly increase the exactness of the use of natural vegetation as indicators and throw much light upon agricultural practice.

VII. ROOT DEVELOPMENT OF CROP-PLANT ECADS.

A number of crop plants were grown under two distinctly different sets of environmental conditions near Lincoln, and their root development followed throughout the growing season. The plants experimented with were alfalfa, *Medicago sativa;* sweet clover, *Melilotus alba;* brome grass, *Bromus inermis;* orchard grass, *Dactylis glomerata;* meadow fescue, *Festuca elatior;* oats, *Avena sativa;* sorghum, *Andropogon sorghum;* sunflower, *Helianthus annuus;* white clover, *Trifolium repens;* and red clover, *Trifolium pratense.* They were grown in plats 5 feet square with an uncropped area of 2.5 feet between each plat. The plats, which were in duplicate on each site, were arranged in three rows in a rectangular field. Care was taken to plant the taller crops, such as sunflowers, sorghum, and oats, in such a position as not to shade the adjoining crops. The plats of spring wheat, timothy, and bluegrass were accidentally injured or did poorly and were abandoned (plate 23). All the plats and intervening areas were kept free from weeds. While 25 square feet is too small an experimental area for a study of crop production, it was sufficiently large for root examination, and it is believed that near the center of the plats the roots developed under normal field conditions. Moreover, the space between the plats was ample to prevent root competition between crops, at least during the first season's growth, except in the case of the widely spreading roots of sunflowers, where many times this intervening space is necessary. In fact, the adjoining plats of timothy and bluegrass were abandoned because of the severe competition of the sunflower (fig. 37). One of the experimental fields was located at the edge of the flood-plain of Salt Creek and adjoining the base-station area of typical low prairie described on page 39. The other was approximately a mile distant and about 80 feet higher. It was located on a broad, level hilltop of silt-loam and adjoining the area of typical upland prairie described on page 36. In the two areas the experimental plats were exact duplicates in location within the area, time and amount of seeding, etc. In both areas the soil had been cultivated for many years. In the lower area the crop of the preceding year was potatoes; in the upland it was Sudan grass. The upland seed-bed was prepared by double disking the soil to a depth of 4 or 5 inches on April 23, the lowland by plowing to the same depth at the same time. All of the crops except cane were planted by hand and in measured amounts in each plat on April 24. In every case each crop was sowed at approximately the normal field rate of seeding for eastern Nebraska. An exception to this was the sunflower, one plat of which was seeded very thick and the other much thinner in each area, for the purpose of a study of root competition. At the time of planting, both fields were in excellent tilth, the subsoil was moist (table 19), and as a result of frequently recurring rains the crops all came up in excellent shape. The sorghum was planted on May 27. The stand was thick and the plants made an excellent growth.

A detailed discussion of the environmental conditions under which the two sets of crops were grown, including soil type, water-content and mechanical and chemical composition of soil, evaporating power of the air, etc., is given after the description of their development. These data are then correlated with the root development of the natural vegetation on the adjoining areas.

Alfalfa (Medicago sativa).—The first examination of alfalfa roots was made on June 1, 38 days after planting. In the lower plats the plants averaged 6 inches in height, in the upper ones they were only half so tall. The root system of alfalfa is simple and easily excavated. Usually the plant sends a single strong tap-root almost vertically downward, deep into the soil. The tap-root gives off some branches along its course, but these are relatively few and usually small. The roots in the lower field were very abundant to a working level of 0.7 foot, some of the longer ones reaching depths of 1.3 to 1.6 feet. In the upper plats, notwithstanding the smaller above-ground parts, the roots were abundant to a depth of 0.8 foot, some deeper ones penetrating to 1.4 to 1.7 feet. At this time the tap-roots were only 1 or 2 mm. in diameter. Laterals were especially well developed in the surface 6 inches of soil, some spreading rather horizontally for a distance of 2 or 3 inches or even more.

The root development was again examined on July 8. At this time the plants in the lower field were 1.1 feet in average height and those in the upper plats about 0.9 foot. Alfalfa in both plats was rather badly discolored by an attack of *Pseudopeziza medicaginis* so that at this time the plants in one of the duplicate plats in each field were mown close to the ground and the forage removed. In the lower plats the roots were abundant to 3 feet. The black silt-loam was thoroughly moist to this depth. Some of the roots extended quite through it and into the underlying wet, sticky, yellowish clay, reaching a maximum depth of 3.6 feet. A typical specimen, excavated at this time, is shown in figure 35. This well illustrates the dominance of the tap-root, the paucity of laterals below the first foot of soil, the occurrence of nodules at considerable depth, and the rather direct downward course. In the upland plats roots and bacterial nodules were fairly abundant in the clay-loess subsoil to a depth of 3.3 feet, which was the working depth of the plants. Several of the longer roots extended to the 4.3-foot level. The tap-roots were fairly well branched in the surface 8 to 10 inches of soil. As in the lower plats, they varied from 2 to 4 mm. in diameter. Differences in number and length of branches in the two areas were not pronounced, probably both being slightly greater in the upland soil.

A third examination of alfalfa roots was made on August 18. In both cases the plants from which the tops were cut on July 8 were examined. In the lower field these were 8 inches tall, and some were in blossom. In the upper one they were only 6 inches high and not so well developed, the crop having suffered from dry weather following the cutting on July 8. In the lower plats the maximum root-length was 5 feet, and several plants had attained this. The maximum root-depth on the upland soil, which was also reached by several plants, was 4.2 feet. At this time examination was made of the adjacent uncut plat, which had completely recovered from the fungus attack. Here the plants were thick, about 1.1 feet high and in every way well developed. The roots, 116 days after the seed was sown, had reached a maximum depth of 6.3 feet. These data are summarized in table 13.

The lower plats were adjacent to a field of alfalfa in which the plants were 2 years old. The upper part of the field had been seeded on July 5 at the rate of 14 pounds per acre, the seed having been harrowed in between the rows of corn. The lower portion was seeded August 6, at the rate of 17 pounds per acre, after a crop of potatoes had been plowed out and the ridges harrowed down.

A long, deep trench was dug in this field and the roots thoroughly examined during the first week in June. No other plants were present and the soil was occupied entirely by the roots of alfalfa. Of a large number of plants examined, the tap-roots were 5 to 10 mm. in diameter. Just below the crown and to a depth of 1.5 feet, the roots are well supplied with a great abundance of small laterals, usually less than a millimeter in diameter. These often run off parallel with the soil surface for a distance of 1 to 12 inches or even more.

TABLE 13.—*Development of alfalfa.*

Age of plants.	Lower plats.		Upper plats.	
	Height of tops.	Depth of roots.	Height of tops.	Depth of roots.
days.	*feet.*	*feet.*	*feet.*	*feet.*
38	0.5	1.3 to 1.6	0.3	1.4 to 1.7
75	1.1	3.6	0.9	4.3
116	[1]0.7	5.0	[1]0.5	4.2
116	....	....	[2]1.1	6.3

[1] Cut July 8. [2] Uncut.

Other branches run more obliquely downward, usually making wide angles with the tap. They are well supplied with secondary laterals, few of which are more than 2 or 3 inches in length, while many are much shorter. All of the rootlets, but especially those in the surface 2 feet of soil, were abundantly supplied with nodules 2 or 3 mm. long and 1 to 1.5 mm. in diameter. Indeed, these occurred to the maximum depth of root penetration, about 12 feet. The tap-roots tapered rather rapidly, so that at a depth of 2 feet the diameter was seldom greater than 1 to 3 mm., while below 9 feet none of the roots were more than a millimeter thick and usually much less. The general course of the root is vertically downward. While many ended at depths of 7 to 10 feet, others extended to the water-level at a depth of 12 feet, where they terminated with little branching. Not infrequently the main root ran for distances of 2 to 5 inches in the deeper soil, giving off few or no branches. Branches more than an inch in length were rare in the deeper soil and usually they were very much shorter. The roots showed a marked tendency to branch only in the crevices of the deeper soil, and here the branching was confined to one plane. These laterals ended abruptly, and were poorly rebranched. As a whole the tap-root predominates throughout and typically it branches but little, many plants penetrating deeply without giving off any large laterals. One of the roots, which penetrated to the water-level at 12 feet, is shown in two sections in plate 16, B. Since the roots are light tan in color, they show plainly in the black silt-loam. Their abundance and habit in the first 3.5 feet of soil is illustrated in the bisect in plate 15, A. Here the soil was carefully removed from about the roots in the face of the trench to a horizontal depth of about 4 inches and the roots taken in their natural position. Unfortunately, the tops, which were about 1.3 feet high, were trampled down in the process of digging the trench.

The presence of earthworm burrows in the deeper, stiff, clayey subsoil is significant. These, with the countless small holes left at all depths, even to 12 feet, upon the death and decay of older alfalfa roots, are very important in aiding soil aeration (*cf.* Weaver, 1915: 243). It would seem that the excellent development of other crops upon old fields of alfalfa, sweet clover, and red clover, the roots of which all penetrate deeply, aside from the increased nitrogen supply in the soil, must be benefited also by its better aeration. The fertilizing effect of the deeper portions of these root systems must be below the reach of most crops.

One part of this field of 2-year-old alfalfa extended over a rather steep hillside and to the crest of the hill. For the purpose of comparison, a large number of roots were excavated on the hilltop. It was discovered, after considerable labor had been expended in excavation, that subsoil conditions were far from typical for the region, but nevertheless the results were of much interest.

The surface 1.2 feet of clay-loam was dark in color and rather rich in humus. Below this was a subsoil of stiff yellow to slate-colored clay about 2 feet thick. This was somewhat intermixed with streaks of decomposed Dakota sandstone which modified its tenacity. Below 3.2 feet the clay became very hard and much jointed, roots being largely confined to these joints. It was intermixed with pockets and streaks of chalk, the latter sometimes being an inch in diameter. The soil was so hard, and especially the deeper soil, that it was removed with considerable difficulty. Its glacial origin was shown by pebbles, often 2 or 3 inches in diameter, which occurred throughout; however, these were nowhere very abundant. A large number of plants from the hilltop and valley were compared. The tap-roots had about the same diameters, varying from 5 to 10 mm., but a marked difference in branching habit was at once apparent; the plants on the hilltop were very much more abundantly supplied with both large and small laterals in the surface 1 to 1.5 feet of soil, while those on the lowland rarely had laterals more than 1 to 2 mm. in diameter (in fact, branches more than a millimeter in diameter were rather rare); the plants on the upland were abundantly supplied with branches 1 to 4 mm. thick and much more numerous smaller ones. In the latter habitat the first 6 to 8 inches of the tap-roots gave rise to branches two or three times more abundant than did the plants in the valley. These differences are shown in plate 13, c, where typical specimens were selected from a very large number excavated at each place of examination.

While the smaller, well-branched rootlets in the drier upland soil ran off laterally to a distance of only a few inches, some of the larger ones ran off obliquely in the surface 1.5 feet of soil to horizontal distances of about 1.5 feet, where they turned downward. Some of these larger laterals ultimately reached depths of 5 or 6 feet. Not infrequently they divided up into large branches, which, with numerous small ones, often only a few inches in length, furnished the plant with an absorbing system especially well developed in the surface 2 feet of soil. The deeper roots pursued a much more tortuous course than those in the valley. Many roots were found at a depth of 5.5 feet, which was the average working depth. Not a few extended to depths of 6 to 7.5 feet and one specimen was traced to 8.8 feet. All but the deepest roots were very well branched, especially in the last 1.5 feet of their course, with both long and short branches. The latter were mostly 1 to 4 inches in extent. In the deeper soil, branching was largely confined to one plane in the joints of the clay. This root habit should not be confused with rather rare cases in the lowland soil, where the tap-root had been destroyed, or for other reasons was not so much in evidence. At a depth of a few inches to several feet it may divide into two or more branches which take on more or less the character of the tap-root, and, spreading very little, pursue an almost vertically downward course. The plants on the hilltop were in a good, even stand and were almost as thick as those on the low ground, while the tops were equally well developed. These differences in root habit namely, a deep tap-root with no major branches and relatively few smaller ones in one habitat, and a pronounced wide-spreading shallower root system with a smaller development of the tap-root in the other,

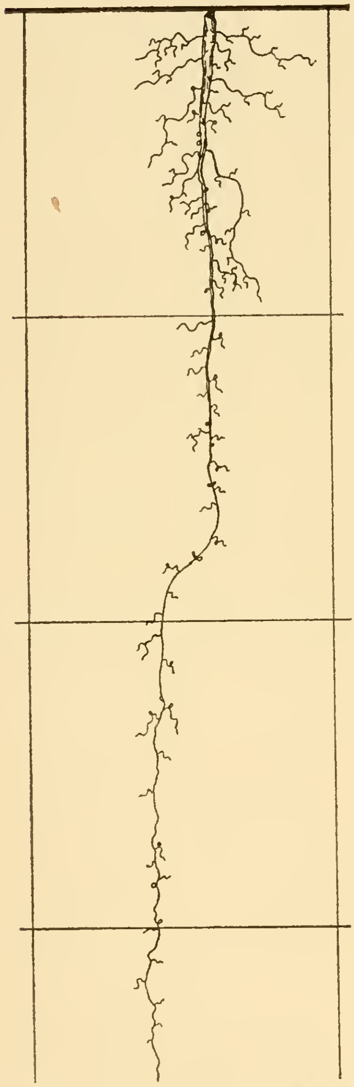


Fig. 35.—Root system of *Medicago sativa*, 2.5 months old.

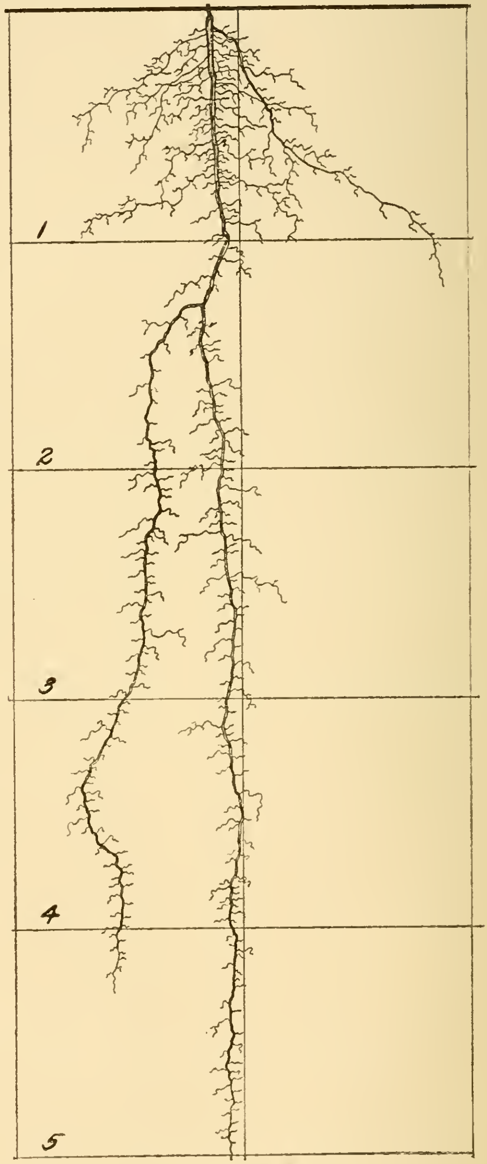


Fig. 36.—Root system of *Melilotus alba* about 4 months old.

must be attributed to soil conditions with their resultant effect upon water-content, soil solutes, and perhaps aeration. Which of these or what combination of these is the controlling one can be definitely answered only by a series of experiments carried on under conditions where the effect of each factor can be evaluated.

In this connection, the results of certain other investigations are of interest. Headden (1896) excavated alfalfa roots in three different counties in Colorado in soil varying from sandy loam to heavy clay. He stated:

"They show a marked permanency in type of development in a simple tap-root, running down from 3 to 5 feet and then sending off a few side roots, or rather dividing into a few branch roots of about equal size and length. These branches do not as a rule deviate more than a few inches from the course pursued by the tap-root before division. I have in no case found a system of small roots starting out below and near the crown, extending laterally for several feet and then turning downward. The tap-root is often perfectly smooth, save for wart-like excrescences on it caused by symbiotic micro-organisms."

Six-year old plants on stiff clay soil near Fort Collins were found to penetrate to a depth of 11.8 feet in one instance and to 12.3 feet in another. In speaking of the effect of age on roots he states: "I have seen many roots of 6-year-old plants smaller than roots of other plants which we knew to be only 9 months old." He also says that 7 feet is as deep as a large percentage of alfalfa plants penetrate in our soils. He cites cases of yearling plants penetrating to a maximum depth of 3.8 feet in fine prairie loam, while a 9-months-old plant was found with a root-length of 9.4 feet. "These differences in development of roots are no greater than I have often found and I see no satisfactory explanation for facts."

Cottrell (1902) has followed the tap-roots of 8-year-old alfalfa in stiff "hard-pan" soils in Kansas to a depth of 10 feet without finding an end. "The roots extend 15 to 30 feet and more in depth in fairly good soil."

Ten Eyck (1904) excavated 3-year-old alfalfa roots on an upland loam at Manhattan, Kansas. Several roots were traced to a depth of 8.5 feet.

Sweet clover (Melilotus alba).—An examination of the development of the roots of sweet clover was made on June 13, when the plants were 49 days old. The crop in both areas was growing very well, but the plants in the upper plats were only 3 inches in average height as compared with a height of 10 inches for those in the valley soil. The pronounced development of the tap-root may be seen in plate 17, B, which shows two typical specimens from each site. The main roots pursued an almost vertically downward course; those in the upland reached a working depth of 1.3 feet, and those on lowland soil 1.8 feet. The maximum depth of root penetration attained on the two sites were 1.3 and 2.6 feet, respectively. The roots were exceedingly well branched throughout their course, even to their tips. The branches were small and mostly 2 inches or less in length, although some had reached a length of 5 or 6 inches. Of the numerous plants examined, the light-colored tap-roots had a diameter of only 1 to 3 mm.

On August 18 the roots were again examined. The plants in the upper plats were 1.5 feet in average height and in excellent condition, some of the tallest reaching a height of 2 feet. Those growing in the lower plats were likewise in a flourishing condition, with an average height of 1.8 feet and a stem diameter of 5 or 6 mm. The root development of a typical specimen from the lower plat is shown in figure 36. The tap-roots here were seldom over 6 mm. thick and usually only 4 or 5. They pursued a more or less vertically downward course, the tap-root tapering rapidly. The deeper roots of many plants reached the 5-foot working level, but few penetrated beyond, and these for a distance of only 0.2 to 0.3 foot in the moist soil. The main roots were only poorly supplied with major branches, rarely more than two occurring on a single plant. These were about 2 mm. in diameter and originated at any depth from 4 inches to 3 feet. Their usual lateral spread, extent, and degree of branching are well shown in figure 36. However, some rather marked differences in the degree of development of major laterals were found. The above description, as usual, is for roots developed near the center of the plats. Those nearer the periphery, where competition was much less keen, were not only larger in both top and root diameters, but there was also a much greater development of large lateral branches, in some cases approaching that of the specimen shown in plate 18, B. This is a somewhat isolated plant one year old and excavated near Central City (see p. 23). Waldron (1911: 409) reports a a similar condition in the development of alfalfa roots in plat experiments. Throughout its course the tap-root and its larger branches are furnished with many small lateral branches, varying in length from a few millimeters to several inches. Only the tan-colored roots originating in the surface 2 feet of soil were at all well rebranched. The younger, glistening white roots of the deeper soils branched not at all or only poorly, except where they occurred in the crevices of the jointed subsoil. Here, perhaps because of better aeration, they rebranched somewhat profusely, the delicate rootlets with glistening white hairs contrasting markedly with the dark-colored soil. Nodules were of frequent occurrence to depths of 3 or 4 feet.

Several of the sweet clover plants in the upper plats reached maximum depths of 6.5 feet. The tap-roots had diameters ranging from 4 to 9 mm. The lateral roots were not well developed in the surface soils, but were much better developed in the deeper moist loess subsoil, rather large laterals often arising at a considerable depth. Often the last 8 inches of the root was entirely destitute of branches. Clusters of nodules, 5 to 9 mm. in diameter, were not infrequent in the first 2.5 feet of soil, while below this depth many smaller ones occurred. These data are summarized in table 14.

TABLE 14.—*Development of sweet clover.*

Age of plants.	Lower plats.		Upper plats.	
	Height of tops.	Depth of roots.	Height of tops.	Depth of roots.
days.	*feet.*	*feet.*	*feet.*	*feet.*
49	0.8	1.8 to 2.6	0.3	1.3
116	1.8	5.3	1.5	6.5

Brome-grass (Bromus inermis).—On July 10, a preliminary examination of the development of the roots of brome-grass was made. The plants in the lowland plats were 1.2 feet high and in excellent growth. In the upland plats the stand was much poorer and the plants had attained an average height of only 0.5 foot. In the low moist soil the roots were abundant to a working depth of 2.3 feet, a few reaching 3.4 feet; in the upland plats the working depth was practically the same, although many roots penetrated deeper.

A final examination was made on August 20, when the grass was nearly 4 months old. At this time the lowland plants averaged 1.3 feet in height, although some had put forth flowering stalks, which, of course, were much taller. Only about half a stand was present in the upland area, no flowering stalks had yet developed, and the plants were only 6 inches in average height. This grass spreads by rhizomes and forms a dense sod. The roots form a close growth, filling the soil to a depth of about 2 feet. The dark-brown roots, only 0.5 to 1 mm. in diameter, are densely clothed with hairs and a great network of fine, well-branched rootlets. These are several inches in length, while the tertiary branches are 1 or 2 inches long and very numerous. Some lighter-colored roots were intermixed with the brown ones. These are younger, shorter, and often less branched, and take on the darker color and other typical root characters when more mature. Below 2 feet in the lighter colored subsoil at the lowland station the roots were very much less abundant. In fact, at a depth of 1.5 feet they began to thin out considerably, but were quite abundant to the working depth at 2.7 feet, while some extended 1 to 2 feet deeper. The working depth of the roots in the upper plats was 2.3 feet; the soil was very well filled with roots to a depth of 2 feet, although, of course, they were not so abundant as in the lower plats, where the stand was better. A number were traced to a depth of over 3 feet and a few to the maximum depth of 3.8 feet. Shepherd (1905) reports the roots of 3-year-old brome-grass at the North Dakota Agricultural Experiment Station at Fargo to be about 4 feet long.

Ten Eyck (1900), working at the same station, found brome-grass, planted in the spring and examined July 18 of the following year, had reached a depth of over 4 feet and formed a good sod. At two years of age the roots were found to a depth of 5.5 feet, the whole soil to this depth being fully occupied by its roots. Five-year-old brome-grass from a lower, more poorly drained area had roots only about 4.5 feet in length. At Manhattan, Kansas (1904), he found three-year-old brome-grass roots penetrating through 4.3 feet of soil to the solid limestone rock below.

Orchard grass (Dactylis glomerata).—This grass was not excavated until July 10, when it had reached heights of 5 and 12 inches respectively in the upper and lower plats. An excellent stand and good growth characterized the grass in the lower area; that on the upland was much thinner, but of a healthy appearance. Notwithstanding the great difference in above ground development, the working depth of the roots at the two stations differed but little. It was 2.3 feet for the lowland plants and 2.2 feet for the upland. In the former area the maximum depth of root penetration was 3.1 feet, in the latter about 2.8.

On August 26 the roots of the orchard grass in the lower plats were again examined. The surface soil was literally filled with a great mass of tan-colored fibrous roots to a depth of nearly 2 feet, below which level they became fewer in number, but were abundant to a depth of 3.2 feet. The roots are tough and rather coarse. They are well furnished with laterals 1 to 3 inches or more in length, which are themselves branched to the second order. The ultimate rootlets are very fine. In the deeper soils the branching was rather largely confined to one plane in the crevices. Some of the delicate roots reached a maximum depth of 4.4 feet. Orchard grass grows in tufts or bunches and does not form a continuous sod. The plants in the upland plats had developed so poorly that they were not further examined.

Ten Eyck (1904) describes the roots of this grass excavated at Manhattan, Kansas, and states that those of a two or three year old specimen reached a depth practically the same as the extreme height of the grass, which was 3.5 feet.

Meadow fescue (Festuca elatior).—The root development of this important forage grass was first examined on June 13 in the lowland plats. The plants had an average height of 8 inches. The working depth of the root was 1.5 feet, although some extended to a maximum depth of 2.3 feet. The grass in the upland plats was of a very thin stand and grew so poorly that the roots were not examined. But on August 18, when the plants in the lower plats were nearly 4 months old, the root development was again recorded. At this time the grass was 8 to 10 inches in height, but had sent up no flowering stalks. The roots had a working depth of 3 feet, although some penetrated 0.7 to 1 foot deeper. To a depth of 1.5 feet the soil was quite filled with great masses of the brown roots, which are only slightly less abundant at 2 feet. They are very fine, the largest being scarcely a millimeter in diameter, while many are only one-fourth that size. They originate from the base of the plant in great numbers, 6 to 24 or even more from a single stem. While most of the roots pursue a course somewhat obliquely to almost vertically downward, others spread laterally more or less parallel with the soil surface or obliquely outward 3 to 6 inches before turning downward. They are exceedingly well furnished with threadlike laterals ranging from a few millimeters to several inches in length, all of which are branched and profusely rebranched, ending in hairlike termini. Many of the roots did not reach the general working level; others penetrated far beyond. The 6 to 8 inches of root-ends are not so well branched and are hairlike. To insure certainty of maximum depth, as usual the trench was undercut 6 to 12 inches below the deepest roots.

Oats (Avena sativa).—The roots were first examined on June 12, which was 49 days after the crop was planted. At the lower station the plants had reached an average height of 1.8 feet. The roots were abundant to a depth of 2.3 feet, while a very few penetrated to the maximum depth of 3.3 feet. At the upland station the plants averaged 1.3 feet in height. They had a working depth of 2.1 feet and a maximum penetration of 2.8 feet. A description of the mature plants has been given on page 102. At the lower station they reached a height of 3 feet at maturity, at the upper station only 2 feet. At the lower station the working depth and maximum depth were 2.8 and 3.4 feet respectively, while they were 3.1 and 4.1 feet on the upland soil.

Sorghum (Andropogon sorghum).—The plats of sorghum, of the Black Amber variety of the "sorgo" group, which were planted on May 27, were given a careful examination 3 months later, on August 26. On both sites the crop was thick. In the lower plats it averaged 4.4 feet in height, while some stalks were 4.6 feet tall and had a maximum diameter of 12 mm. The plants were all in seed. The sorghum on the upland was slightly above 3 feet in average height, the largest stalks having a diameter of 10 mm. and a height of 4.3 feet. It was in the late flowering and seeding stages. This plant has tough, fibrous roots, 3 or 4 mm. in diameter at their origin and often a millimeter thick at a depth of 4 feet. They are of a grayish white color, those near the surface being strongly tinged with red and the deeper, younger roots glistening white. They originate in large numbers and completely occupy the hard, dry soil beneath the plants. Branches from 0.5 to 3 inches long are exceedingly abundant and are quite well rebranched. In the more mellow surface soil these branches spread somewhat widely in all directions, but in the hard, jointed subsoil the branching was confined largely to the crevices and was in one plane. The abundant, ultimate branches are hairlike, shining-white, and exceedingly delicate. Not infrequently they occur in clusters of 3 to 5 on a millimeter of root-length. Often they form cobweb-like mats covered with root-hairs in the deeper soil crevices. As a whole, the absorbing system of sorghum is very efficient and so well distributed throughout the soil that it can thoroughly exhaust it of its available water for plant growth. In both plats the roots reached a working depth of 4 feet. The maximum root penetration was also the same, about 4.5 to 4.7 feet. It is interesting to note that Miller (1916) found that the root systems of related groups, Blackhull kafir and

Dwarf milo, reached depths of 6 feet and had a maximum lateral spread of 3.7 feet. These plants were grown at Garden City, Kansas, from May 26 to September 3, in rows 3.7 feet apart, in sandy loam which had been well irrigated the preceding autumn.

Sunflower (Helianthus annuus).—Sunflowers, of the Russian variety, were seeded at two different rates, one plat thick and the other thin, in both the lowland and upland areas. On June 2 the plants in the lowland area had an average height of 1.3 feet and a working root-depth of about 1.5 feet. The maximum root penetration at this time was 2.2 feet. In the upper plats the plants were 0.8 foot tall. Many roots were found at a depth of 0.9 foot, while the deepest ended in the clay subsoil at the 1.3-foot level. At this time many plants were removed from the plats with the thin stand, but competition among plants in the thick stand was permitted to continue. On June 11 the thinning was again repeated until only about 8 plants were left in the thin stand on the area of 25 square feet. The crowded condition of the plants in the unthinned plats at this time is shown in plate 23, A. A month later a trench was dug and 3 of the sunflowers in the thin stand in the lower plats were carefully excavated. The extent of the root system of these plants, which were only 2.5 months old, was quite surprising. They were 6.5 to 7 feet in height, had a stem diameter at the base of 1.2 to 1.5 inches, and each was furnished with 35 to 40 large, active green leaves. The flower-heads were fairly well formed and a week later the plants would have been in blossom. Since all agreed in general root habit and extent, only one will be described.

The major portion of one of these root systems is shown in figure 37. The roots occurred in such great numbers that it was quite impossible to show them all in the drawing without confusion, and for this reason the front portion of the crown and swollen part of the tap-root, with their accompanying roots, were removed before the penciled draft was made in the field. It may be seen that the bulk of the roots lie in the surface 1.5 feet of soil. The enlarged tap-root gives off so many laterals and tapers so rapidly that at a depth of 8 to 10 inches it is only 4 to 5 mm. in diameter and in fact no larger than some of the major branches. It penetrated rather straight downward to a depth of nearly 5 feet. In the surface 0.5 foot of soil 28 large laterals originated. Some of these ran off obliquely, at various angles with the tap, spreading rather widely, and reached depths of 2 to more than 3 feet. Numerous others took a course more or less parallel with the soil surface and ran off to distances of 3 or 4 feet, where they ended in the surface 0.5 foot of soil, or, more rarely, turned downward. One large lateral was traced to a distance of 5.5 feet from the base of the plant, but at no point did any of its branches reach a greater depth than 0.7 foot. Many of the large laterals had a diameter of 5 to 8 mm. They gave off few or no large branches, but were thickly clothed with smaller ones. They tapered very slowly and were quite coarse to their tips. The surface 0.8 foot of soil, especially the first 2 feet on all sides of the plant, was so densely filled with great masses of branched and rebranched roots of all sizes that they formed a network. Indeed, a more profoundly developed absorbing system can scarcely be imagined. Not only were roots less abundant, but the branching also was poorer below the first foot. However, even in the third foot, glistening white but poorly rebranched rootlets were quite abundant. These were seldom more than an inch or two in length.

On August 18 the sunflowers were again examined. At this time the 10 plants remaining in the upland plat of thin planting were 6.2 feet in average height, the tallest reaching a height of 6.9 feet, and an average diameter of 24.7 mm. In contrast to this, the 7 remaining sunflowers on the lower, thinly planted plat had an average height of 6.9 feet and a diameter of 33.4 mm. One of the tallest plants was 8.3 feet high. They were in seed, some having flower-heads 8 inches in diameter.

The number and size of the plants in the thickly planted area in each site is summarized in table 15:

TABLE 15.—*Development of sunflowers.*

Group.	Number of plants.	Average height.	Average diameter.	Remarks.
Upper plats:		*feet.*	*mm.*	
1	8	6.0	22.4	Maximum height 7.5 feet; some of the plants in full bloom. (1 and 2)
2	12	5.3	17.2	
3	50	4.4	8.8	
4	46	3.0	5.1	Many smaller dead and dried plants not counted.
Lower plats:				
1	20	7.5	24.8	A few 8 feet tall; some of the plants had seed nearly ripe. (1 and 2)
2	27	6.5	19.0	
3	15	5.7	18.5	
4	58	3.0	12.0	Many half dead; a few shriveled plants not counted.

The root development in the middle of the thickly planted areas was thoroughly studied. In the lower plat it was found that the roots were not at all abundant below the surface foot of soil and they were very scarce below 2 feet. The soil in this plat was exceedingly dry and hard when compared with adjacent areas. Even the largest sunflowers in the area had very much more poorly developed root systems than those of the thin planting shown in figure 37. Not only were there far fewer laterals, but they were much less extensive and more poorly branched. A few tap-roots of the larger plants were traced to a maximum depth of 3.8 feet. In the upper plats the roots were even more poorly developed. Few occurred below 10 inches. The laterals were not so widely spread as in the plants in the lower plats. Several of the larger tap-roots ended at a depth of about 3 feet, but one with an unusually large diameter was traced to the 4.6-foot level. It gave off no large branches below 10 inches, although short ones occurred nearly to the tip. The last foot of the root, which was 1.5 mm. thick, had no branches, but was densely covered with root-hairs. It appears from this experiment that just as competition between individual sunflowers growing close together inhibits the normal development of the above-ground parts, it affects the roots in a similar manner (Weaver, 1918: 279). The plants in the upper plats which had the poorer stem development also had a poorer root-growth. Of the lowland plants, those in the crowded area had a much poorer stem and root development than those in the thinly planted plat. Under the latter condition in both areas the numerous lateral roots obliqued downward to a much greater extent and reached greater depths than those in the thick planting. Even the dominant individuals in the crowded areas matured earlier and dried up more rapidly than their larger, deeper-rooted neighbors in adjoining plats.

White clover (Trifolium repens).—On July 11 the plants of white clover were 3 and 5 inches high in the upper and lower plats respectively. In the latter habitat the tap-roots were 2 to 2.5 mm. in diameter and penetrated to a working level of 2.5 feet. This was the same depth determined for plants growing in the upland soil. In general, the root-habit was not greatly unlike that of red clover. The stand on both sites was poor and further studies were not made.

FIG. 37.—Root system of *Helianthus annuus* about 2.5 months old.

Red clover (Trifolium pratense).—The first examination of the roots of red clover was made on July 10, at a time when the plants in the lower and upper plats were 1 and 0.8 foot in height respectively, and in full bloom. As usual, numerous plants were examined on each site. In the lowland soil some tap-roots with a diameter of 5 mm. were traced to a depth of 3.6 feet. The strong tap-roots penetrated almost vertically downward, but tapered so rapidly that at a depth of 6 to 8 inches they were seldom more than a millimeter thick. Beginning 3 to 4 inches below the soil surface and to a depth of 1.5 feet, numerous branches were given off. Some of these extended laterally for distances of 8 to 12 inches before turning downward.

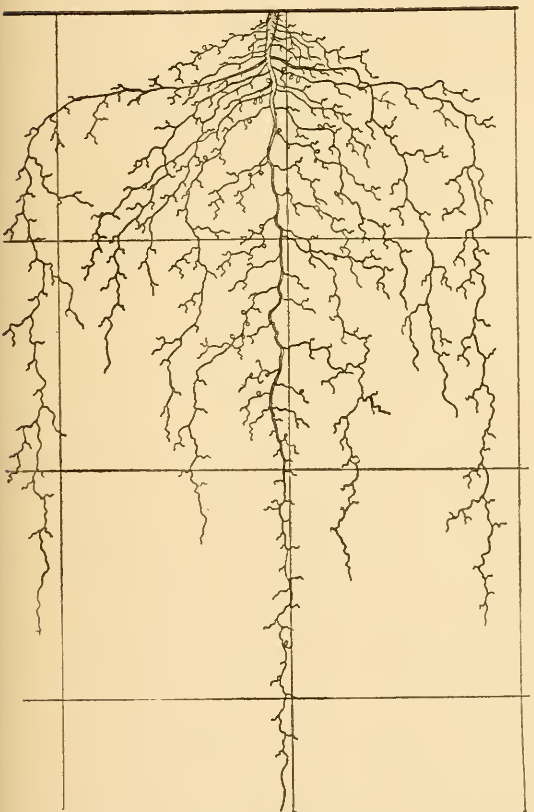


Fig. 38.—Root system of *Trifolium pratense* about 2.5 months old.

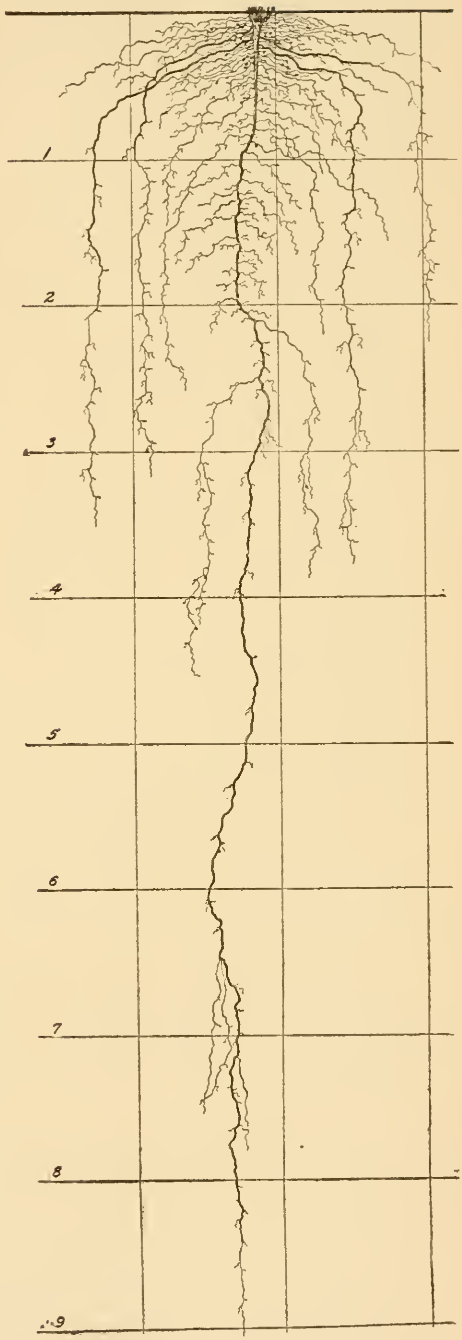


Fig. 39.—Mature root system of *Trifolium pratense*.

They then ran rather straight downward, branching repeatedly. On both the larger and smaller branches tubercles occurred to a depth of about 3 feet. The amount of branching and the extent of the root development of this 2.5-months-old plant is shown in figure 38. Plants in the upland soil were not so deeply rooted. Many roots were found at 2.5 feet depth; some penetrated about 0.5 foot deeper.

On August 18 red clover roots were again examined. In the lower plats the plants were 1.1 feet high, some were still blooming, others were developing seed, and all were in a very healthy condition. From 3 to 13 stalks occurred on a plant. Three plants with tap-roots 5 to 7 mm. in diameter were traced to a depth of 4.5 feet. None were found penetrating deeper. The tap-root tapered so rapidly that at 9 inches depth it was only 1 mm. thick. In the surface 8 inches of soil it gave off 10 major branches ranging from 1 to 2 mm. in diameter. These ran off to distances of 4 to 12 inches in a direction either rather parallel with the surface or only slightly obliquely before turning nearly vertically downward. Like the tap-root, they tapered rapidly, some reaching a depth of 3 to 4 feet. In addition to these branches, the 12 inches of the tap-root, and especially the first 6 inches, were covered with a great network of roots only 0.5 mm. or less in diameter but 1 to 7 inches long. Like the larger roots, many of them spread rather laterally in the surface soil. They were poorly rebranched. Below the first foot no large branches occurred, although in some plants it was noted that the tap-root sometimes broke up into two rather equal parts. Short laterals arose throughout the course of the root and only a few millimeters apart to a depth of 3 or 4 feet. These varied in length from only 0.5 inch to several inches. The younger roots are glistening-white and fill the joints of the deeper soil with a network of rootlets. Other roots are more hairlike and run for an inch or two, giving off practically no branches. Near the tip the laterals are very short. The tap-root is prominent throughout and in general has a vertically downward course.

In the upland plats the plants were 10 inches high and in blossom, but none had formed seed. Their development in every way was poorer than at the lower station. There were fewer stalks per plant and the largest tap-roots were only 5 or 6 mm. in diameter, while on most of them the roots were smaller. Several plants were traced to their greatest depth at 4 feet. None penetrated deeper. The root habit was similar to that described, but the larger laterals were often fewer.

Hays (1888) gives the development of red clover plants when grown at the experiment station of the University of Minnesota in a "hollow" in rich drift soil of clay, sand, and loam. The roots reached depths at the ages of 1, 2, and 5 months of 7, 22, and 68 inches respectively. In all the plants examined the large laterals were very abundant and many were of equal size and penetrated as deeply as the tap-root.

The development attained by mature root systems of clover plants is indicated in the following description. They were excavated in a fine 6-year-old meadow near Wahoo, Nebraska. The deep, fertile, silt-loam was underlaid to a depth of at least 10 feet with a fairly compact loess subsoil. The soil was quite moist throughout. Many of the plants examined had strong tap-roots 10 to 12 mm. in diameter, but they tapered off rapidly and at a depth of a foot were seldom more than half this thickness. However, the tap-roots were dominant and ran nearly straight downward to depths of 8 or 9 feet. In fact, one root penetrated to the 10-foot level. A great mass of fine rootlets arose from the crown and first few inches of the tap-root, and, running off laterally for distances of 6 to 8 inches, quite filled the surface soil. Also, a few larger branches, ranging from 2 to 3 mm. in diameter, arose in the surface foot of soil and ran off horizontally or obliquely for 0.5 to 1.5 feet before turning downward. These ultimately reached depths of 3 or 4 feet. Below the surface 1.5 feet lateral roots were more sparse. Near the root-tips, and especially in the deeper soil, the branches were threadlike, and ran for several inches without rebranching. A typical mature root system may be seen in figure 39.

SUMMARY OF CROP PLANTS.

These data on root development in the two sites are summarized in table 16:

TABLE 16.—*Development of crop plants.*

Kind.	Age of plants.	Lowland plats.			Upland plats.			Ratio of root development in relation to height growth between lowland and upland plants based on—	
		Height of tops.	Working depth.	Maximum depth.	Height of tops.	Working depth.	Maximum depth.	Working depth.[1]	Maximum depth.[1]
	days.	*feet.*	*feet.*	*feet.*	*feet.*	*feet.*	*feet.*		
Alfalfa	38	0.5	0.7	1.3–1.6	0.3	0.8	1.4–1.7	1 : 2.25	1 : 2.11
Do	75	1.1	3.0	3.6	0.9	3.3	4.3	1 : 1.31	1 : 1.46
Do	116	[2]0.7	....	5.0	[2]0.5	....	4.2	....	1 : 1.11
Do	116	....	....	....	[3]1.1	....	6.3	....	....
Sweet clover	49	0.8	1.8	2.6	0.3	1.3	1.3	1 : 2.53	1 : 1.72
Do	116	1.8	5.0	5.3	1.5	5.8	6.5	1 : 1.43	1 : 1.51
Brome grass	77	1.2	2.3	3.4	0.5	2.3	3.0	1 : 2.33	1 : 2.05
Do	118	1.3	2.7	4.7	0.5	2.3	3.8	1 : 2.19	1 : 2.05
Orchard grass	77	1.0	2.3	3.1	0.4	2.2	2.8	1 : 2.23	1 : 2.14
Oats	49	1.8	2.3	3.3	1.3	2.1	2.8	1 : 1.36	1 : 1.21
Do	75	3.0	2.6	3.4	2.0	3.1	4.1	1 : 1.68	1 : 1.78
Sorghum	92	4.4	4.0	4.7	3.0	4.0	4.7	1 : 1.47	1 : 1.48
Sunflower	39	1.3	1.5	2.2	0.8	0.9	1.3	1 : 1.08	1 : 1.08
Do	116	[4]7.5	1.0	3.8	[4]6.0	0.8	4.6	1 : 1.04	1 : 1.49
White clover	78	0.4	2.5	3.0	0.3	2.5	....	1 : 1.66	....
Red clover	77	1.0	3.0	3.6	0.8	2.5	3.0	1 : 1.00	1 : 1.00
Do	116	1.1	....	4.5	0.8	....	4.0	....	1 : 1.15

[1] In order to secure greater accuracy in the ratios, these results were obtained directly from the field notes where measurements were given in feet and inches. Table 16 gives the measurements to the nearest tenth of a foot. In the ratios the root development in relation to height growth at the lowland station is designated as unity.
[2] Cut July 8. [3] Uncut. [4] Average maximum height.

CORRELATION OF CROP-ROOT DEVELOPMENT WITH THAT OF NATURAL VEGETATION.

An examination of table 16 shows that with all of the crop plants, except three, the root penetration was as great or greater on the upland, while the root development in relation to the aerial part was consistently greater than in the lowland. This relation, which agrees with the root development of certain native species (p. 41), holds true whether we determine the ratio from maximum root penetration or from working depth. In seeking a cause for these differences, several possibilities present themselves. Chief among these are the composition of the soils and the moisture relations of the habitat.

Mechanical analyses of the soils are given in table 17, together with the moisture equivalents computed from the mechanical composition by the formula of Alway and Russel (1916: 842). These data show that both soils are fine-textured, being composed mostly of silt and clay. A study of the table shows that they are remarkably similar.

TABLE 17.—*Mechanical analyses of soils.*

Depth of sample.	Coarse gravel.	Fine gravel.	Coarse sand.	Medium sand.	Fine sand.	Very fine sand.	Silt.	Clay.	Moisture equivalent.
Upland plats:	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
0.0 to 0.5 foot....	0.0	0.0	0.3	0.5	1.6	19.8	48.6	29.2	31.4
0.5 to 1.0 foot....	.0	.0	.2	.6	1.3	16.7	52.4	28.8	31.8
1 to 2 feet........	.0	.0	.1	.2	0.8	16.7	55.6	26.6	31.5
2 to 3 feet........	.0	.0	.1	.1	0.5	19.0	57.9	22.3	30.1
Lowland plats:									
0.0 to 0.5 foot....	.1	.4	2.2	1.8	5.0	25.0	41.3	24.3	27.7
0.5 to 1.0 foot....	.3	.7	2.1	2.2	5.0	25.4	38.8	25.8	27.9
1 to 2 feet........	.2	.3	1.3	1.5	3.7	21.4	40.8	31.0	30.6
2 to 3 feet........	.0	.1	0.4	0.5	1.7	19.2	43.4	34.7	32.9

Table 18 gives the chemical composition of representative composite samples of soil at various depths from the two areas. A study of the table shows that the soils at the two stations are not strikingly different. It should be noted that the lime content is about the same in both fields. However, the greater amount of volatile matter and the greater nitrogen content at all depths indicate more favorable conditions for growth in the lowland plats, and this probably accounts in part for the more rapid growth and better development of the crops in this field.

TABLE 18.—*Chemical analyses of soils by digestion with hydrochloric acid (sp. gr. 1.115) for 120 hours.*

Depth of sample.	Insoluble residue.	Soluble salts.	Volatile matter.	Iron and aluminium oxides.	Calcium oxide.	Magnesium oxide.	Phosphorus pentoxide.	Nitrogen.
Upland plats:	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
0.0 to 0.5 foot........	76.87	17.12	6.01	13.20	0.68	1.19	0.13	0.159
0.5 to 1.0 foot........	75.70	18.58	5.72	14.25	.70	1.32	.12	.134
1.0 to 2.0 feet........	76.17	19.08	4.75	14.72	.75	1.68	.12	.079
2.0 to 3.0 feet........	77.86	18.46	3.68	14.03	.86	1.69	.15	.045
Lowland plats:								
0.0 to 0.5 foot........	79.34	12.96	7.70	9.57	.68	.75	.13	.218
0.5 to 1.0 foot........	79.63	13.66	6.71	10.27	.63	.77	.10	.187
1.0 to 2.0 feet........	78.11	15.83	6.06	12.11	.64	1.01	.08	.135
2.0 to 3.0 feet........	74.78	19.82	5.40	15.20	.76	1.27	.09	.082

The evaporating power of the air, while not measured in the crop plats,(where indeed the crops in each plat would probably have caused a different evaporation rate) was recorded in adjoining areas of upland and lowland prairie (p. 37). Figure 12 shows that evaporation on the upland, due largely to greater wind movement, is constantly higher. During the driest period of the summer (July 7 to August 18), the evaporating power of the air on the upland was 64 per cent greater. This difference in evaporation, which must greatly accelerate transpiration, together with a somewhat lower water-content of the subsoil, go far towards explaining these differences in crop development. An inspection of table 19 shows that, while no constant difference exists in

TABLE 19.—*Water-content of soils in excess of hygroscopic coefficient in upland and lowland crop plats at Lincoln.*

Date.	0.0 to 0.5 foot.		0.5 to 1.0 foot.		1.0 to 2.0 feet.		2.0 to 3.0 feet.		3.0 to 4.0 feet.	
	Upper plats.	Lower plats.	Upper plats.	Lower plats.	Upper plats.	Lower plats.	Upper plats.	Lower plats.	Upper plats.	Lower plats.
May 5	21.8	21.1	18.9	20.0	......	......	......	......	......	......
May 27[1]	11.9	14.0	10.1	15.0	15.5	16.4	......	11.1	......	11.7
June 13	......	......	17.8	17.1	16.5	19.4	16.8	18.0	......	......
July 1	12.1	12.3	16.1	11.1	......	......	......	......	......	......
July 8	5.2	1.6	6.8	4.1	7.3	10.1	9.7	10.0	14.1	15.4
July 14	3.3	1.9	10.1	5.5	13.4	17.2	10.0	......	......	......
July 28[2]	2.7	0.9	3.0	1.7	7.7	10.8	13.4	9.4	16.0	18.7
Aug. 11	......	......	17.5	13.6	18.6	15.0	8.8	8.2	12.6	14.8
Aug. 26	17.4	19.3	13.9	2.0	10.6	5.2	11.7	15.3	6.0	10.6
Hygroscopic coefficient	9.8	10.0	10.9	9.6	10.1	9.2	10.0	11.1	10.3	10.8
Wilting coefficient	14.4	14.7	16.0	14.1	14.8	13.6	14.7	16.3	15.2	15.9

[1] The soil had been no drier at any time since May 5.
[2] Surface soil had deep cracks, no rain had fallen for about two weeks.

relative wetness or dryness of the soils in the first 3 feet, below this depth the subsoil at the lowland station has a constantly higher water-content. The samples were taken, as usual, with a Briggs soil-tube, in the plats of spring wheat, timothy, and bluegrass which grew poorly (p. 126). Care was taken to secure samples for the different determinations from similar plats in the two sites. In the plats with normal plant-growth it is not improbable that the water-content was lower and thus differences in the water relation accentuated. Judging relative temperatures in the two areas from data obtained from adjacent lowland and upland sites (p. 38, and plates 4, B, and 6) it is believed that only small differences in either soil or air temperature occurred. We may conclude then, at least tentatively (for work must be carried on for several years before generalization may be made), that differences in root development in the two areas are due to the water-content of soil and air and probably also to differences in the amount and distribution of nutrients.

Aside from the relative differences in development in the two areas, the rapid growth and great depth of root penetration of crop plants should be emphasized. Using again the natural vegetation as the indicator of conditions for agricultural practice, the rotation of short-rooted and densely-rooted crops with those of longer and more spreading root systems should prove advantageous, if, indeed, under intensive agriculture two such crops might not be grown on the same area at the same time (*cf.* Rotmistrov, 1914).

It seems certain that under growth conditions of the less arid portions of the grassland formation, many crop plants absorb both water and nutrients from the deeper soils, at least when they are approaching maturity and often when the surface water-content is nearly or quite depleted. We should keep clearly in mind that water and solute absorption at different stages in the life of the plant does not depend upon the total root-mass or surface, but is determined by the size of the functioning parts. If the older roots in the surface soil become suberized or cutinized, absorption would be confined to the younger, deeper portions. This knowledge of root structure and function is quite essential in selecting crops for drought resistance, as well as in the proper use of water for irrigation, in determining different methods of tillage, the application of fertilizers, and other farm practices (*cf.* Vorob'lev, 1916). A determination of the actively absorbing portions of the root system will throw much light upon the ability of a plant to adapt itself to adverse environment. The extent and difficulties of the problem are equaled only by their interest and importance.

VIII. SUMMARY.

This study, which is in part a continuation of the investigations recorded in "Ecological Relations of Roots," but also includes an investigation of the root development of crop plants, was undertaken with the following aims: (1) to increase our knowledge of the root habits of dominant and subdominant plants growing under a wide range of climatic and edaphic conditions; (2) to determine more fully the root distribution and root competition of the individual species in relation to other species of the community; and (3) to find the root relations of grassland communities as units of vegetation. Further aims were: (4) to determine the relation of the root habits of plants in various communities to their successional sequence; (5) to ascertain the correlation of the root development of cereal-crop plants with the different grassland associations, thus rendering more exact the indicator value of various native species used in classifying land for different types of agricultural practice or for purposes of grazing only; and finally (6) to obtain some knowledge of the root development of crop plants when grown under different environmental conditions. For the proper setting of these studies "Ecological Relations of Roots" forms the background.

Investigations have been carried on at more than 25 stations in Colorado, Kansas, Nebraska, and South Dakota, from the Missouri River to the Rocky Mountains. A study of practically all of the grassland dominants has been completed; many of them have been examined repeatedly in more than two associations; this, with the study of important subdominants, has brought the total number of root systems excavated and examined up to about 1,500, including those of about 150 grassland species. More than 80 examinations of the root systems of crop plants have been made in widely varying soil types and conditions of growth.

The trench or pit method was used in excavating roots, the soil about the root systems being removed with appropriate apparatus from the face of the trench and the roots photographed either in place or against a suitable background. In many cases drawings of the root systems were made to scale as they were uncovered. The quadrat-bisect method has also been employed to show the root systems of communities and of crop plants in place and thus to exhibit their inter-relations in detail.

The grassland formation, because of pronounced climatic variations, especially in rainfall and evaporation, has been differentiated into several associations (Clements, 1920), of which three are considered here. True prairie (*Stipa-Kœleria* association) is characterized by a luxuriant growth of many species of tall, sod-forming grasses and numerous societies of tall herbs. This association constitutes the portion of the climax grassland with greatest rainfall and merges into the subclimax prairie eastward. In central Kansas and Nebraska it gives way to mixed prairie. Short-grass plains (*Bulbilis-Bouteloua* association) are covered with a sparser growth of a few sod-forming short-grasses and fewer herbaceous societies. This association constitutes that portion of the formation with the smallest precipitation, greatest run-off, and highest rate of evaporation. Its typical expression may be seen in western Kansas and eastern Colorado. With an increase in rainfall or with more favorable edaphic conditions it gives way to mixed prairie. Mixed prairie (*Stipa-Bouteloua* association) differs from true prairie in the practically universal presence of one or more of the short-grasses or sedges as a lower layer under the taller prairie species. Here tall-grasses are intimately mixed with the shorter ones. The precipitation over this association is intermediate between that of short-grass plains and true prairie. Mixed prairie forms a distinct belt of vegetation in central Nebraska and Kansas between true prairie and short-grass plains; it recurs along the mountain front in Colorado, and often as alternes governed by edaphic conditions, especially in short-grass plains (Clements, 1920).

The root systems of 43 species of plants have been examined in the true prairie of eastern Nebraska; 17 of these were grasses. All of the dicotyledonous plants were found to extend well beyond a depth of 2 feet, while the roots of 6 grasses were confined to the surface 2 feet of soil. Four of the grasses and 5 other species were found to penetrate well below the second foot of soil, but seldom deeper than 5 feet. The remaining species, including 7 grasses, 4 of which are dominants, have roots which reach depths greater than 5 feet—in fact, most of them penetrate to distances of 7 to 9 feet and a few to a maximum depth of 13 to 20 feet. Thus, 14 per cent of the typical prairie species examined were shallow-rooted, 21 per cent had roots of intermediate depth, while 65 per cent were very deeply rooted. The roots of prairie species are grouped into about three more or less definite absorbing layers, many of the deeper-rooted species having few or no absorbing roots in the first few feet of soil. The layering of the roots reduces competition, and, since available moisture is present throughout the subsoil, permits the growth of a larger number of species. However, no relation between layering and seasonal activity is apparent. The period of most active growth and flower production of plants rooted at various levels occurs synchronously, and, like the successive development of aerial parts of different species in time and space above ground (which results in seasonal aspects), probably equalizes the demands upon the habitat, distributing them throughout the growing-season. True-prairie species as a community emphasize depth of penetration and widely spreading, deep laterals.

This is in sharp contrast to the usual root habit of plants of the more xerophilous grassland associations, which, apparently because of drier subsoil and a consequent greater dependence for moisture on the surface soil layers, show, in addition to great depth of penetration, a highly developed root system for absorption in the surface soil. True-prairie species in lowland areas usually show a greater shoot and less root development than when growing in upland soil. This seems to be a response to the uniformly higher water-content of air and soil in the lowland.

A comparison of the factors affecting growth in the true prairie at Lincoln, Nebraska, with the mixed prairie at Colorado Springs, Colorado, reveals the fact that conditions in the former habitat are more favorable in every respect. At Lincoln the mean annual precipitation is 28.6 inches, at Colorado Springs only 14.6. Run-off is greater, and hence the rainfall is less efficient at the latter station, because of the more compact soil. At both stations the soil is fertile and very deep, and water-content of soil and air is the limiting factor of plant-growth. Soil-moisture studies at Lincoln from 1916 to 1919, together with those for other periods (Alway *et al.*, 1919) show that there is a constant supply of water in the subsoil even during the driest years, and normally water is available at all depths. Water-content determinations at Colorado Springs during 1918 and 1919 show that the available soil-moisture at all depths is much less and that frequently the first foot of soil has no water available for growth, while data from other mixed-prairie areas (Alway *et al.*, at McCook, Nebraska) indicate that during dry phases of the climatic cycle the available water supply is exhausted to a depth of 3 or 4 feet.

The evaporating power of the air is much higher in the mixed prairie than at Lincoln, frequently being twice as great and sometimes reaching 45 to 60 c. c. per day. In true prairie the average daily evaporation throughout the growing-season scarcely exceeds 22 c. c. and a maximum of 35 c. c. is seldom reached.

The mean day and night temperatures throughout the growing-season are, with few exceptions, more favorable for plant development in the true prairie, while the fluctuations between day and night extremes are much less at Lincoln. In the mixed prairie these range from 35° to 40° F., the temperature varying from 90° to 95° F. in the shade in the afternoon to 50° to 60° F. in the morning. Even greater temperature extremes occur in the surface soil in the mixed prairie, ranging from 55° to 60° F. in early morning to 120° or 125° F. in the afternoon. These habitat differences affect not only the abundance and height-growth of the species, but also profoundly modify the root development.

Among the 36 species of plants examined in the hard lands of mixed prairie at Colorado Springs, in north central Kansas, and western

South Dakota, only 4, including 2 cacti, are rooted in the surface 2 feet of soil. Sixteen species, including 10 grasses and sedges, reach a depth of 3 to 5 feet, while a similar number, among which are 3 grasses, extend their roots well below the fifth foot and many to a depth of 7 to 9 feet, but none were found deeper than 13 feet.

Of 45 species excavated in mixed prairie of the Colorado-Nebraska sandhills, only 4, including 1 grass, have shallow root systems; 23 species, of which 8 are grasses, have roots reaching depths of 2 to 5 feet; while 18, including 3 grass dominants, have root systems which extend beyond a depth of 5 feet; in fact, many are 8 to 10 feet deep. Thus the root-depth of the sandhills species is very similar to that of the hard lands. Of all the species examined in the two habitats, only 10 per cent have roots confined to the surface 2 feet of soil, 48 per cent have roots which are of moderate depth (2 to 5 feet), and 42 per cent are deep-rooted. Compared with species of true prairie, those of mixed prairie are not as deep-seated. Among sandhill species especially it is quite usual to find the branches most numerous and best developed in the surface 3 or 4 feet of sand. Unlike true-prairie species, however, plants in mixed prairie have usually developed a very efficient, widely spreading absorbing system in the surface soil. Thus, in hard lands, 72 per cent and in sandhills 82 per cent of the species are well provided with wide-spreading surface roots. Of the remaining species none are dominants and only a few are subdominants of considerable importance. Those on hard lands are often found growing in places especially favorable for water penetration (*cf.* Shantz, 1911). This widely spreading, surface-rooting habit is apparently a response to the relatively low water-content of the deeper soil and to moisture in the surface soil being frequently replenished by showers during the season of growth. In sandhills, where it is often most pronounced, it may possibly be accentuated by a low supply of certain soil nutrients. However, the habit is of quite as wide occurrence among species of the short-grass plains.

Among the 8 dominants and subdominants excavated in short-grass plains of Colorado and western Kansas, only 2 are shallow-rooted, while but one, *Psoralea lanceolata*, usually extends to a depth much greater than 5 feet. The dominant grasses are all of intermediate root-depth. All the species except *Psoralea* show a marked development of the surface-spreading root-habit. The poor development of root-layers, so marked in true prairie, is closely related to the much lower water-content. Roots of *Bulbilis* or *Psoralea* extending below 4 or 5 feet suffer little or no competition for water which is undoubtedly present, at least during wet phases of the climatic cycle. As a community, short-grass-plains species are more shallow-rooted than are those of mixed prairie, while the latter are less deeply rooted than are species of true prairie. While 65 per cent of true-prairie species reach depths beyond 5 feet, this occurs among only 42 per cent of mixed-prairie species, whether in hard lands or sandhills, and is found only in 13 per cent of the species examined in short-grass plains. This correlation between depth of root penetration and efficient rainfall in the three plant associations is fundamental.

Of the numerous factors affecting root development in the grassland formation, water-content is the one of controlling influence. In "Ecological Relations of Roots," page 110, it has been shown that the root habit of polydemic species is usually profoundly modified when plants are grown under distinctly different conditions, and that in general the root position conforms strikingly with the distribution of water-content, although a few stable species were found which showed little or no variation. Further studies of ecads show that practically all the species examined, many under a wide range of environmental conditions, revealed marked changes either in surface lateral spread of roots, depth of penetration, or output of branches. These changes were correlated in nearly every instance with changes in water-content of the soil.

Soil texture exerts a direct influence upon root development, but modifies it most profoundly through water-content and aeration. Roots often show tortuous courses and modified branching in growing through layers of hard soil, but no "hardpan" was encountered where mechanical resistance was so great that roots could not penetrate. Those of many species show a marked increase in their output of branches when growing in less compact soil or upon leaving a compact soil layer and entering a more mellow one, and especially upon entering ancient burrows of earthworms or rodents. This difference is probably largely due to increased aeration. In soils with a subsoil of alternating layers of sand and clay, striking differences in branching occur.

The general characters of the root systems of species are often as marked and distinctive as are those of the aerial vegetative parts. Although the root system may be profoundly modified when subjected to different environmental conditions, it still retains the characteristic impress of that species in its usual habitat. The root systems of different species of the same genus, while often somewhat similar, may be of entirely different types.

Cereal crops grown at many stations in short-grass plains, mixed prairie, and true prairie showed marked differences both in shoot and root development. Root-growth was greatest in true prairie (100 per cent), least in short-grass plains (51 to 79 per cent), and intermediate in mixed prairie (80 to 95 per cent). Certain local variations were directly correlated with an increased water-content. Similar correlations of root and shoot development of native grasses have been determined. Thus, crop plants, like the majority of native species, have the most extensive roots in true prairie, where the subsoil is constantly moist and the evaporating power of the air is not extreme.

The root development of crop-plant ecads grown in plats on upland and lowland areas was found to be greater on the upland in most cases and uniformly so in relation to shoot development. This correlates with the root development of certain native species in similar habitats. The variations in plant behavior appear to be a response to differences in evaporating power of the air and water-content of soil, although differences in the abundance and distribution of nutrients probably also play a part.

A knowledge of the development, position, and competition of roots is indispensable in explaining the phenomena of succession. Since root position so clearly reflects the moisture conditions of the soil, especially when interpreted in its community relations, a study of the root habits of plants greatly increases our knowledge of the value of various species in indicating lands of agricultural or non-agricultural value, and aids us in selecting the kind of crop to be most profitably grown, as well as in determining the proper methods of tillage. A study of the root development of crop plants in the various plant associations renders more accurate our interpretation of the indicator significance of the natural vegetation. The great depth reached by crop plants under the true-prairie environment indicates that they, like many native species, must rely largely upon the deeper portions of their root systems for water and solutes when approaching maturity, and especially during periods of drought. This suggests the problem of determining the actively absorbing areas of plants at various stages throughout their development. The applications of such knowledge to agricultural practice are patent.

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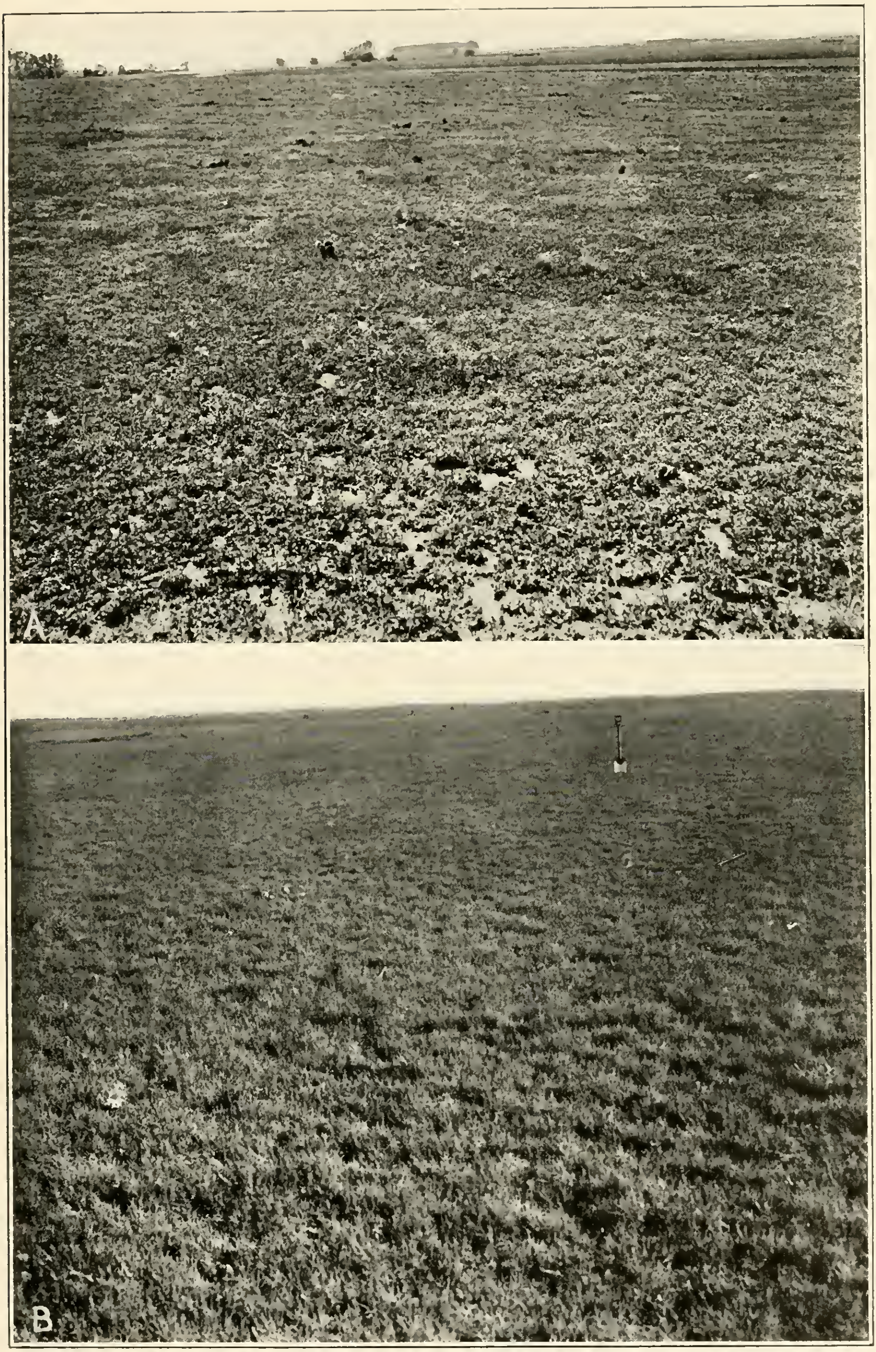
A. True prairie near Lincoln, Nebraska, dominated by tall-grasses and with many herbaceous societies.

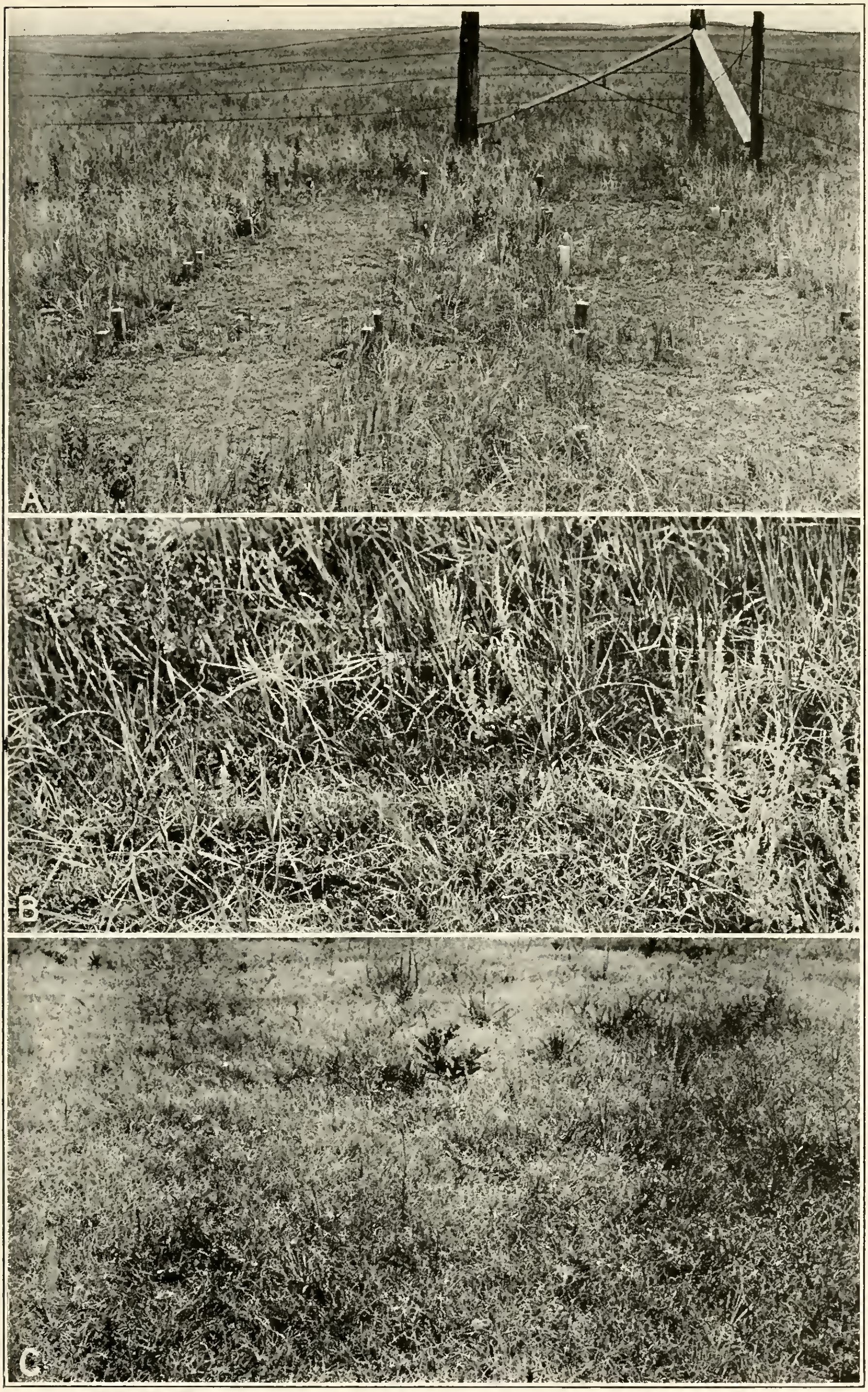
B. *Kœleria cristata* in true prairie, eastern Nebraska, in June.

C. *Stipa spartea* and *Solidago rigida*, Minneapolis, Minnesota.



A. Open mats of *Bulbilis dactyloides* and *Bouteloua gracilis*, Sterling, Colorado.

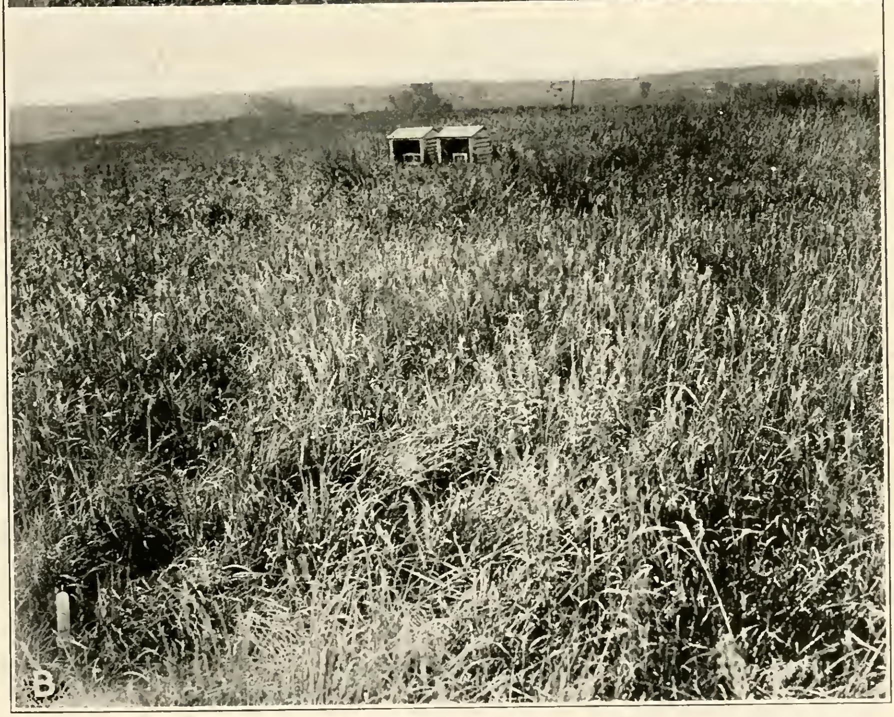
B. Closed mat of *Bulbilis dactyloides* in the short-grass-plains association, Burlington, Colorado.



A. *Agropyrum glaucum* in mixed prairie, Ardmore, South Dakota.

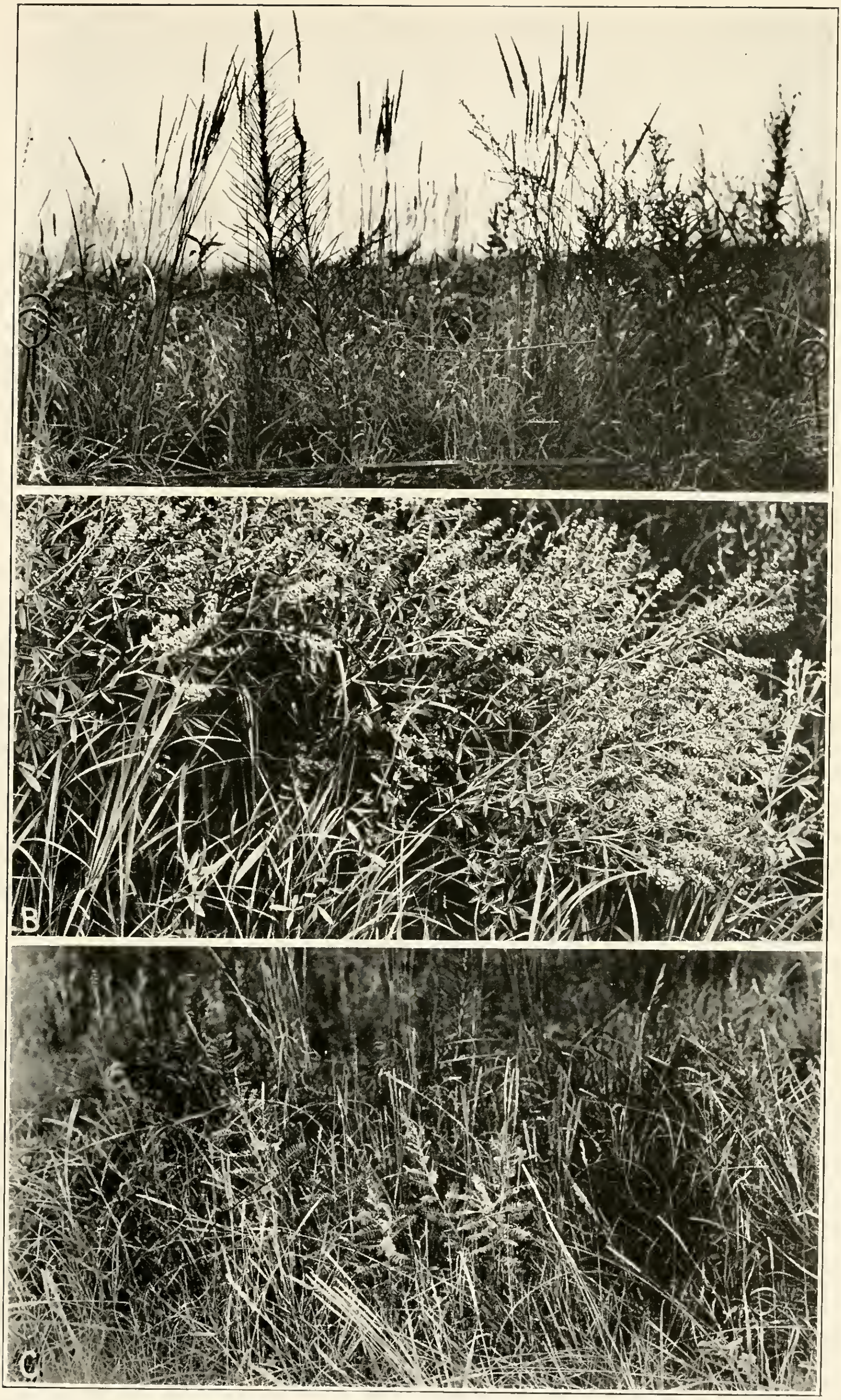
B. *Bulbilis dactyloides* layer in *Agropyrum* consociation Ardmore, South Dakota.

C. Mixed prairie, Mankato, Kansas. *Bulbilis dactyloides* and *Bouteloua gracilis* dominating as a result of overgrazing.



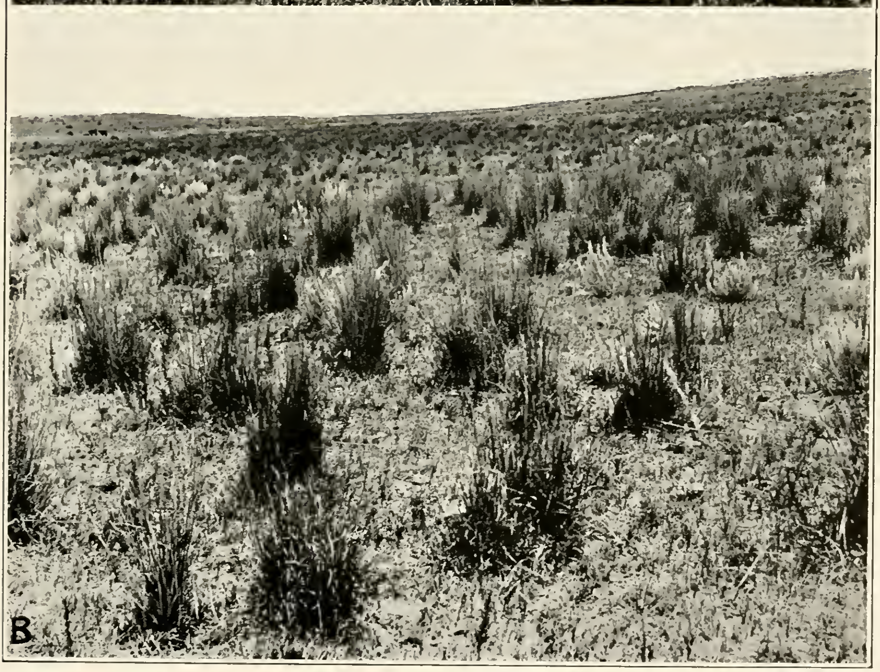
A. Station in the mixed prairie at Colorado Springs, Colorado, in an overgrazed area, photographed shortly after it was enclosed in 1918.

B. Station in the upland prairie at Lincoln, Nebraska.

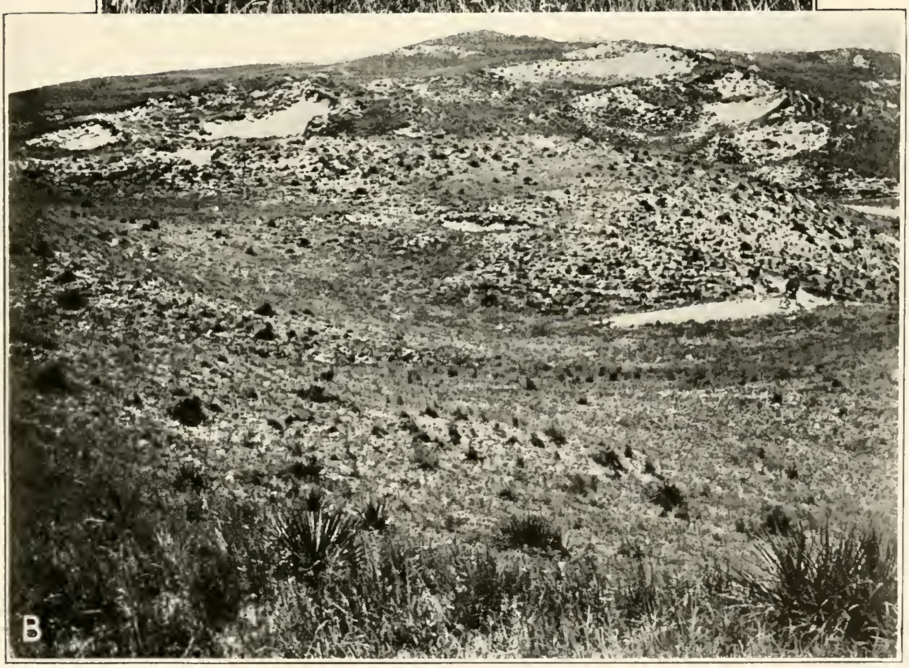


A. View along edge of an upland prairie quadrat where the bisect (plate A) was made.
B. Society of *Psoralea tenuiflora floribunda* in true prairie.
C. A meter quadrat in the upland prairie station at Lincoln.

A. Prairie near the lowland station at Lincoln, Nebraska.
B. *Andropogon furcatus* on low prairie.
C. *Panicum virgatum* on low prairie.

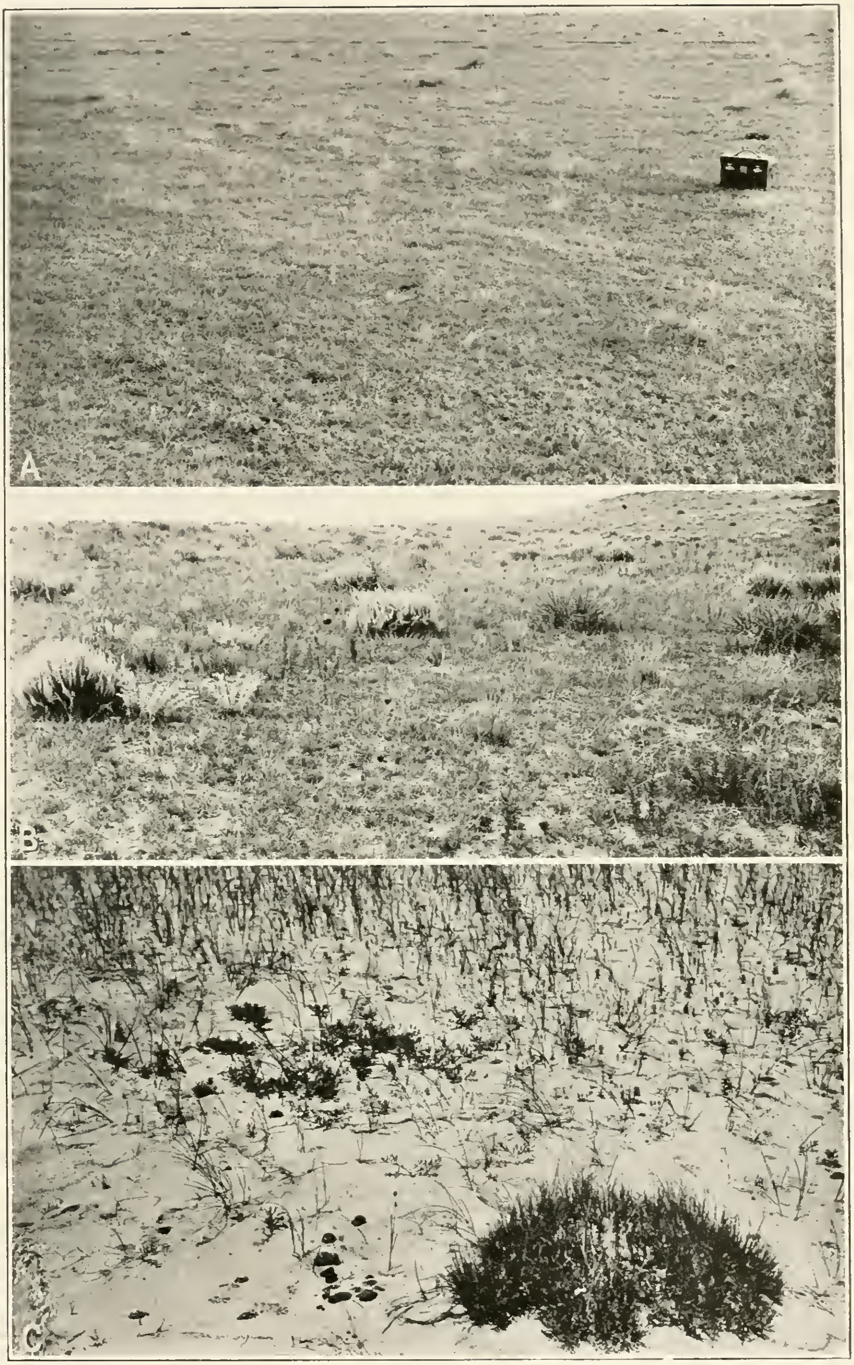


A. *Artemisia filifolia* and *Stipa comata* in mixed prairie at Haigler, Nebraska.
B. *Andropogon scoparius* in a turf of short grasses near Yuma, Colorado.



A. Sandhill at Seneca covered with mixed prairie. The most conspicuous species is *Andropogon scoparius*.

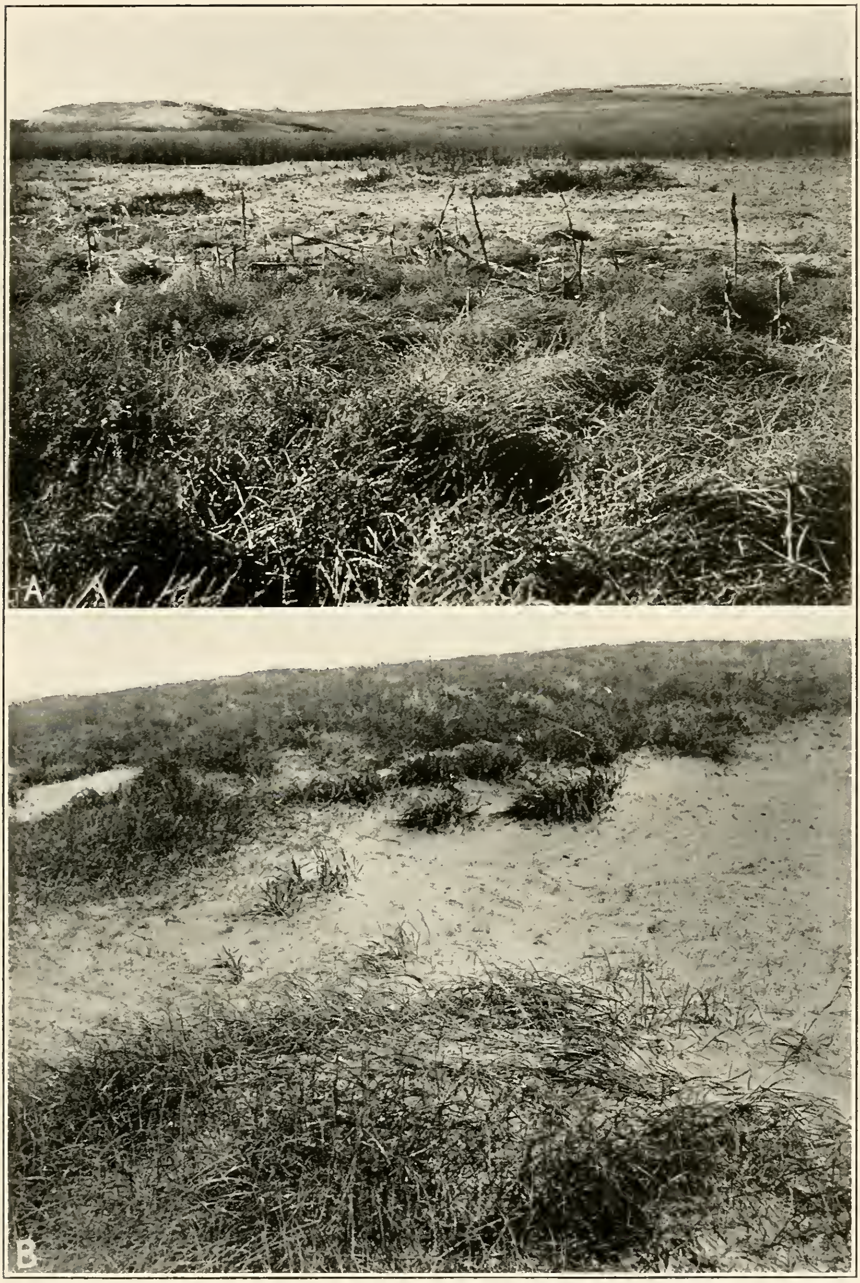
B. Typical view of sandhills, Seneca, Nebraska.



A. *Bulbilis dactyloides* on hard land, Yuma, Colorado.

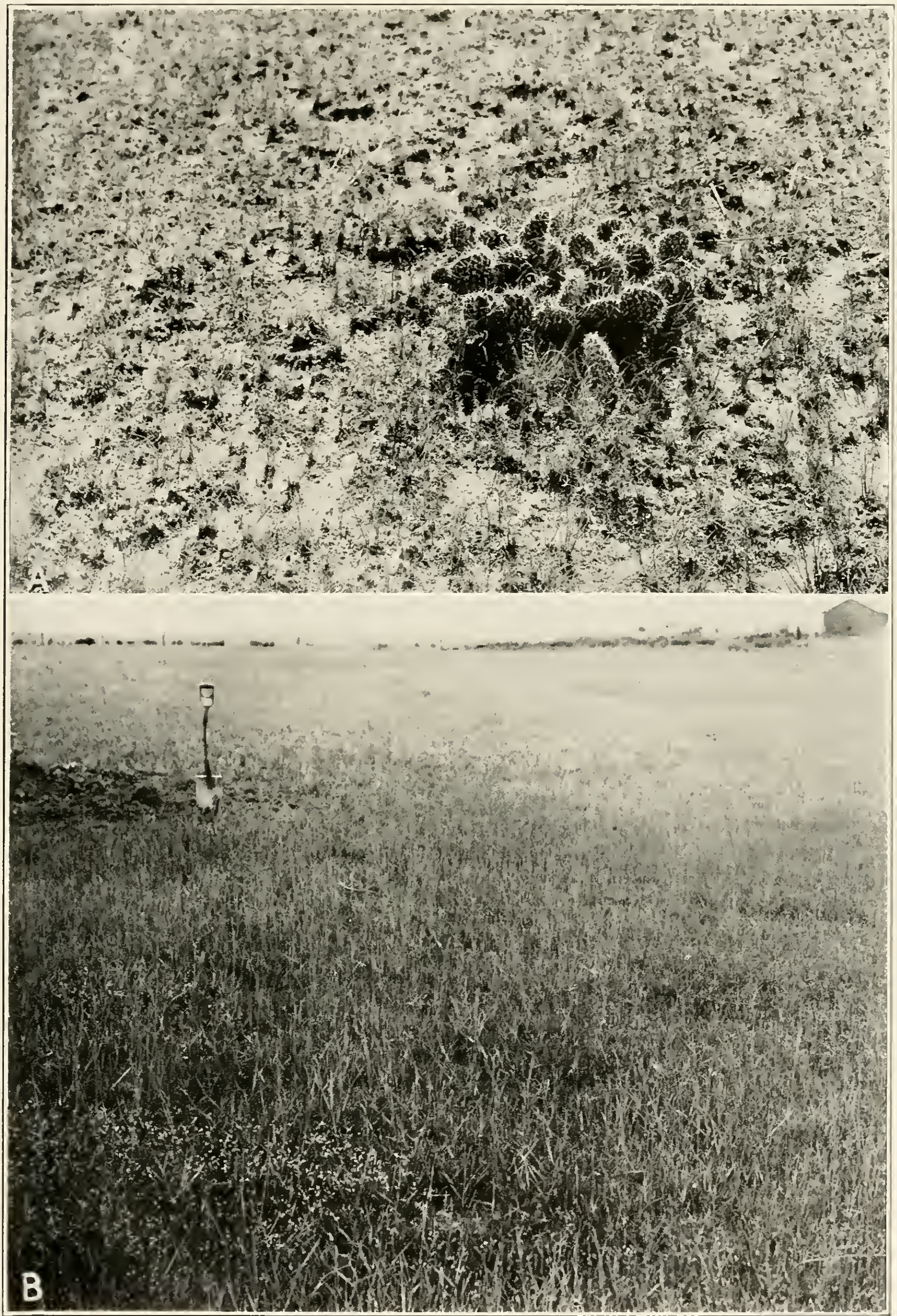
B. Mixed prairie in sandy loam soil near Yuma, Colorado.

C. *Redfieldia flexuosa* and *Muhlenbergia pungens* (in foreground) revegetating an old blowout near Yuma, caused by overgrazing.

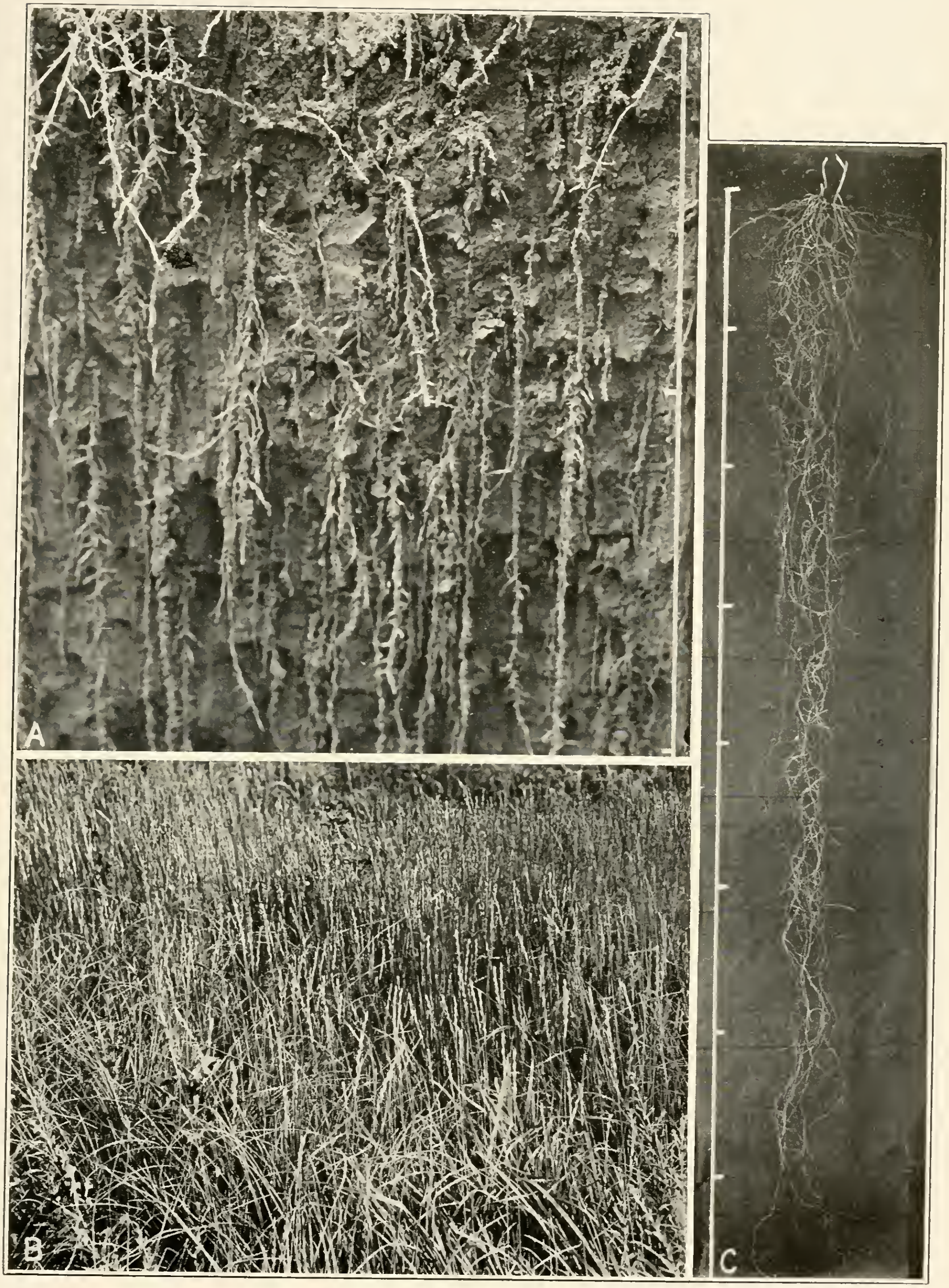


A. Overgrazed and wind-eroded sandy area near Central City, Nebraska, being reclaimed by cropping with rye. *Salsola tragus* in foreground.

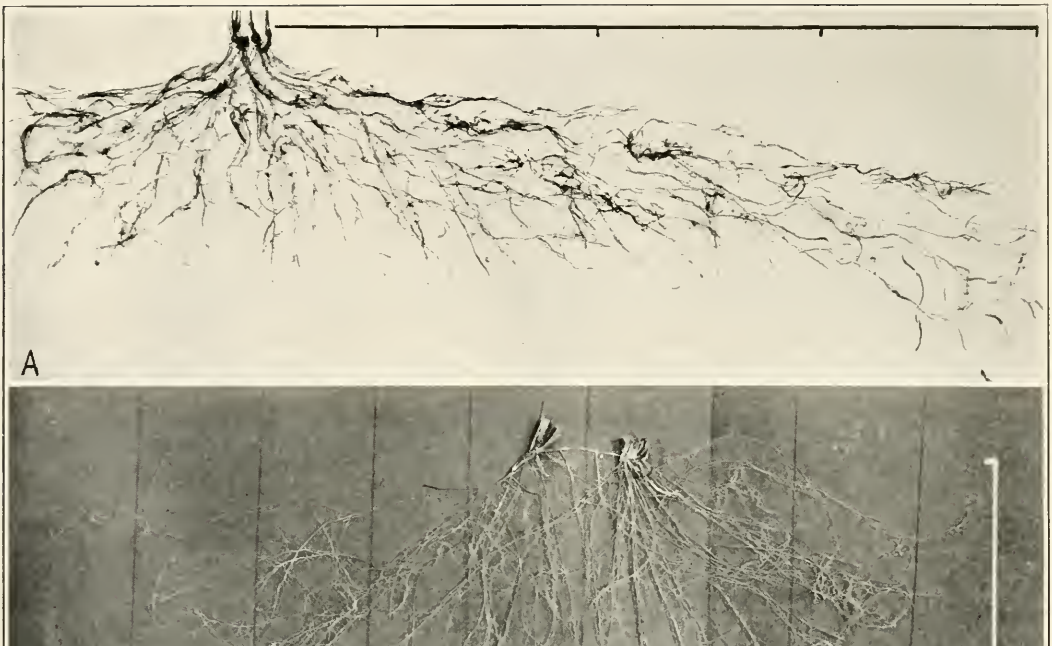
B. A sandhill in this area dominated by *Redfieldia flexuosa*, *Calamovilfa longifolia*, and *Andropogon hallii*.



A. *Bouteloua gracilis* and *Opuntia polyacantha* in short-grass plains.
B. *Agropyrum glaucum* in competition with *Bulbilis dactyloides*, Limon, Colorado.



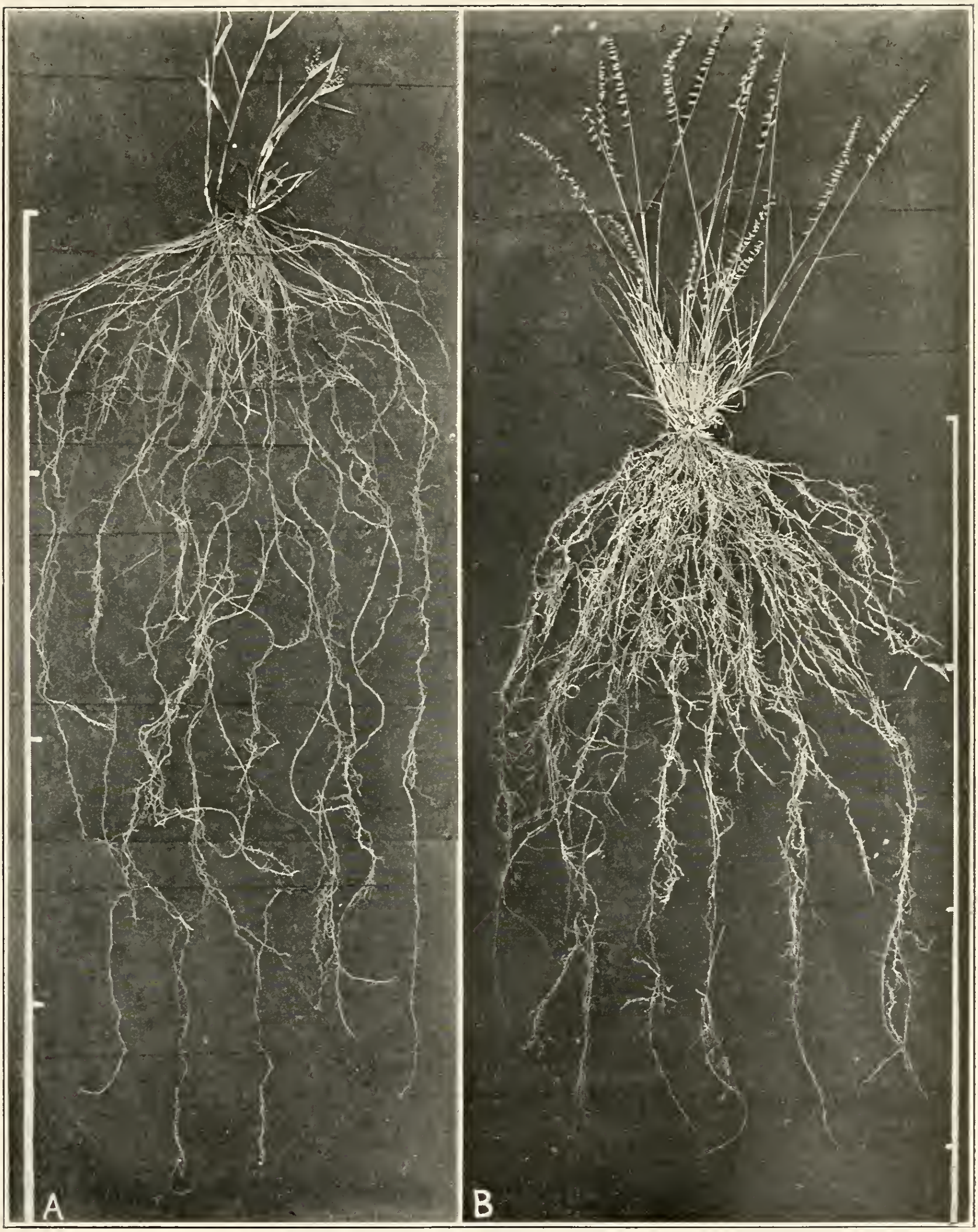
A. Roots of *Calamovilfa longifolia* in natural position at a depth of 3 or 4 feet.
B. *Agropyrum glaucum* in mixed prairie, Mankato, Kansas.
C. Root system in *Secale cereale* excavated in sandy soil.



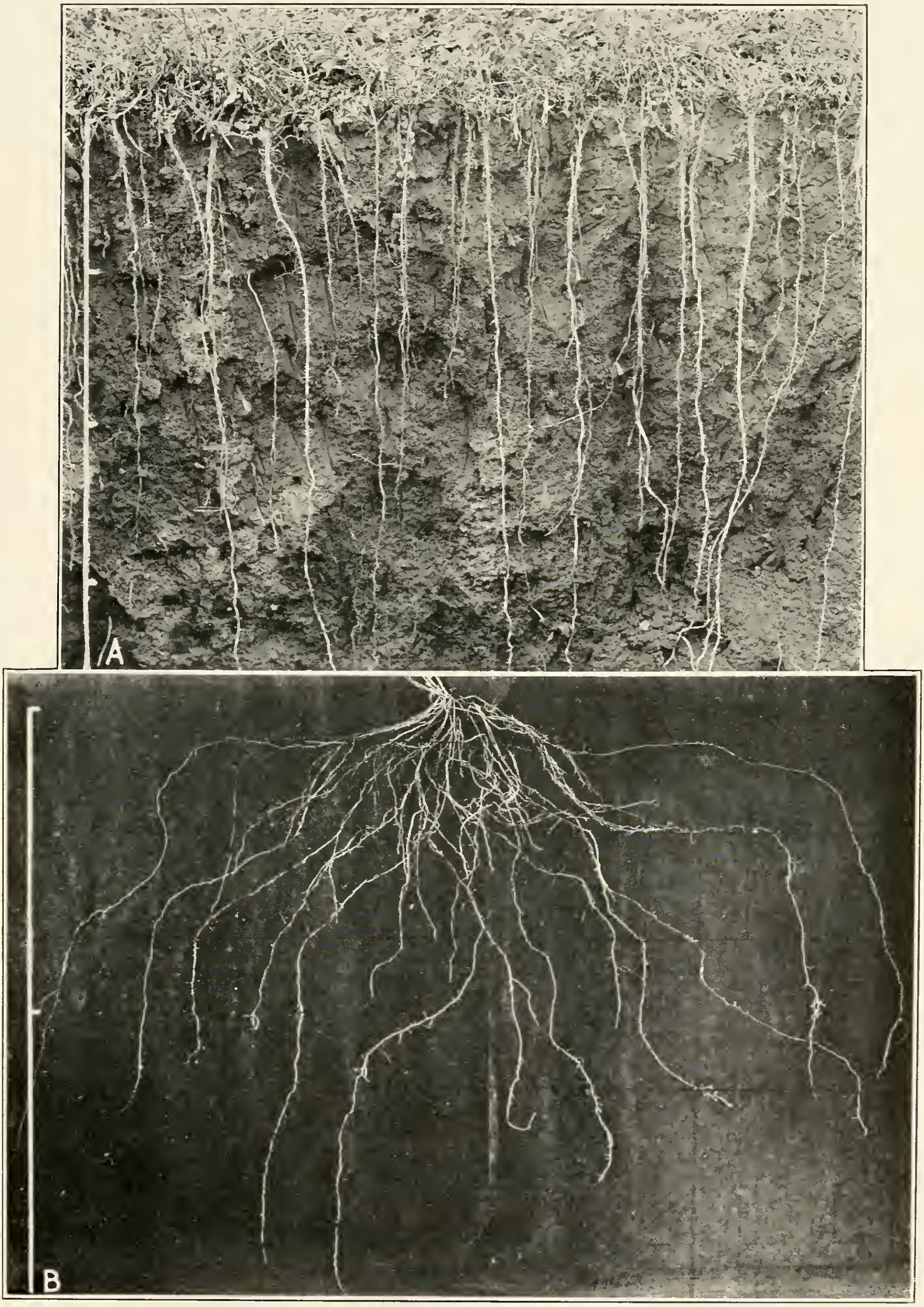
A. Root system of *Cyperus schweinitzii.*

B. Rhizomes and a portion of the root system of *Bouteloua curtipendula.*

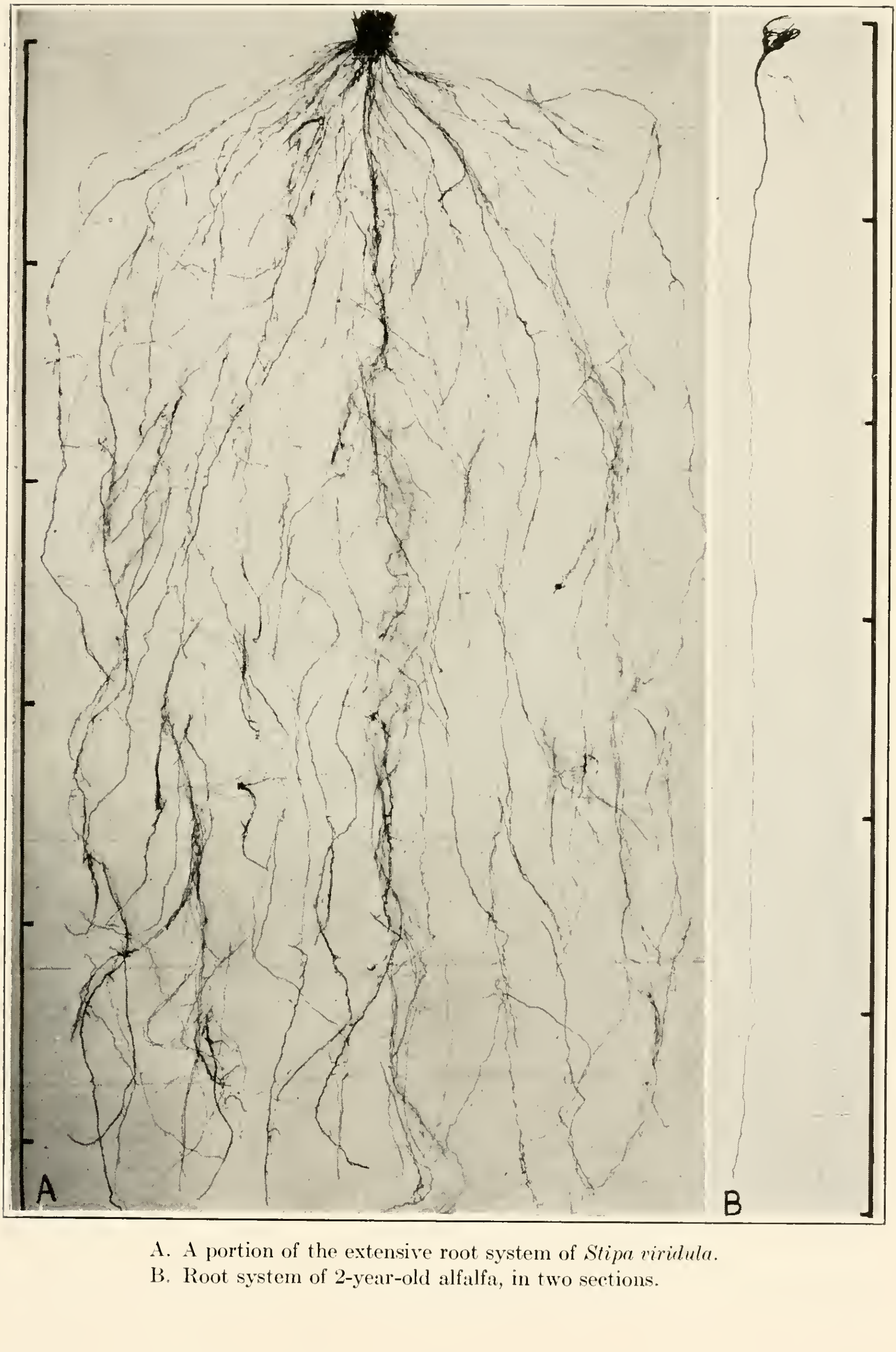
C. Portions of the root systems of alfalfa from lowland (left) and upland (right) areas.



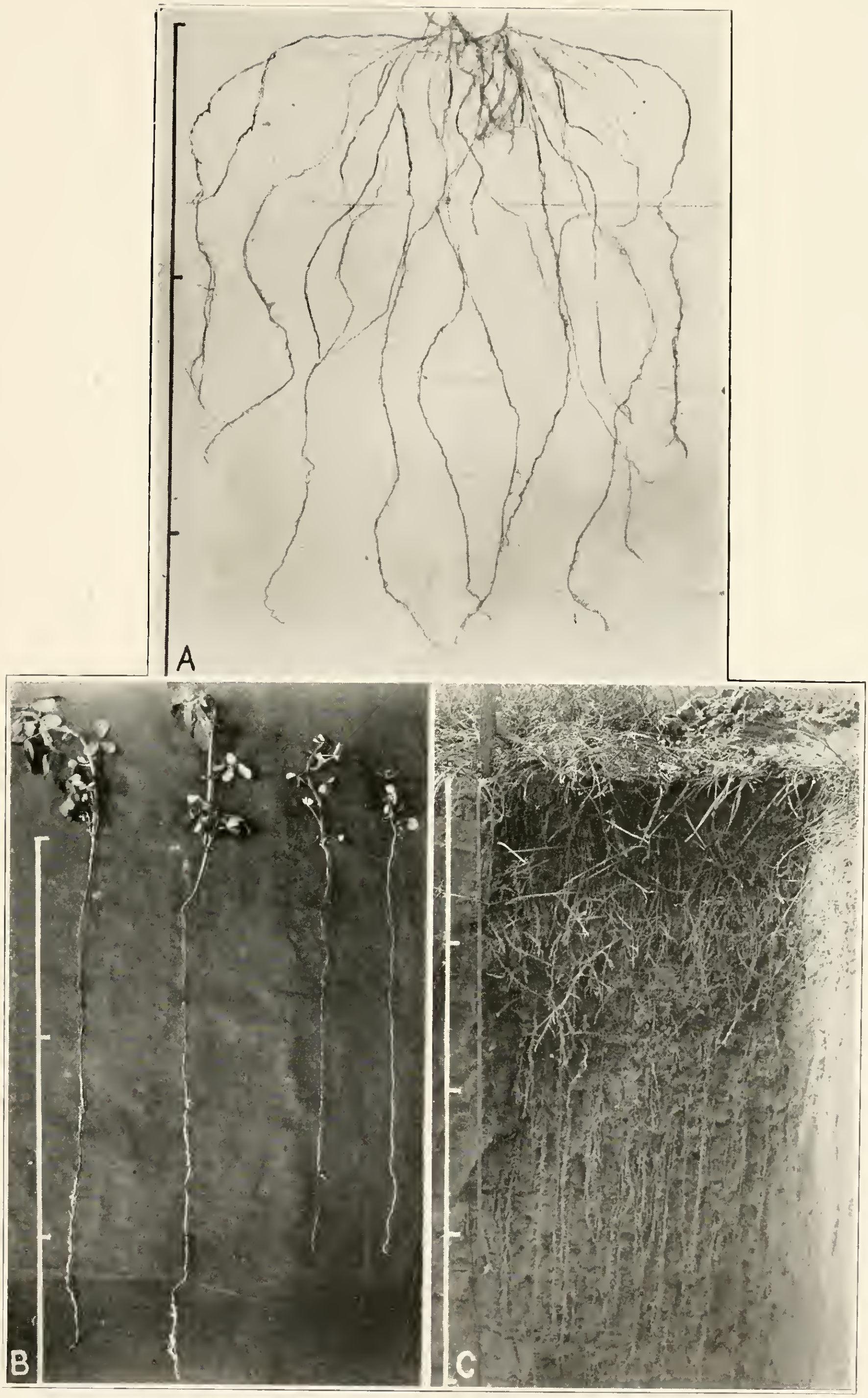
A. *Panicum scribnerianum.*
B. Four-months-old *Bouteloua curtipendula.*



A. Bisect showing roots of 2-year-old alfalfa.
B. Root system of *Bouteloua hirsuta*.



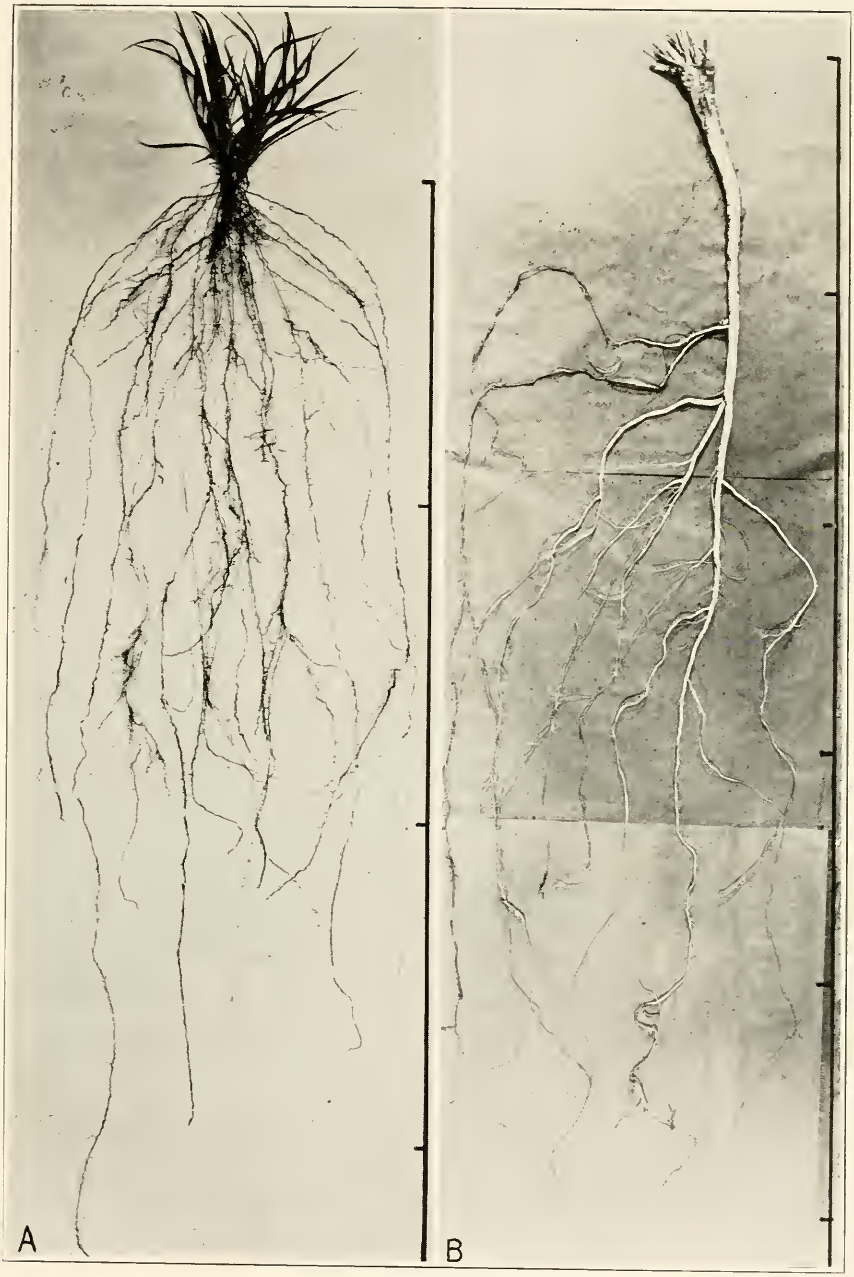
A. A portion of the extensive root system of *Stipa viridula*.
B. Root system of 2-year-old alfalfa, in two sections.



A. Root system of *Carex pennsylvanica*.

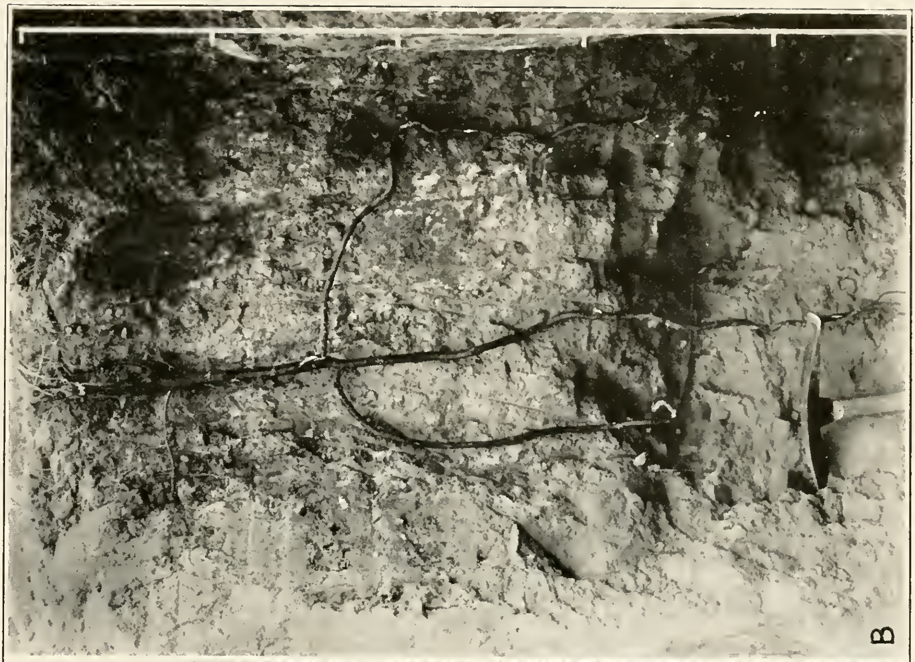
B. Plant of 49-day-old white sweet clover grown on lowland (left) and upland (right) plats at Lincoln, Nebraska.

C. Bisect showing roots and rhizomes of *Calamovilfa longifolia*.



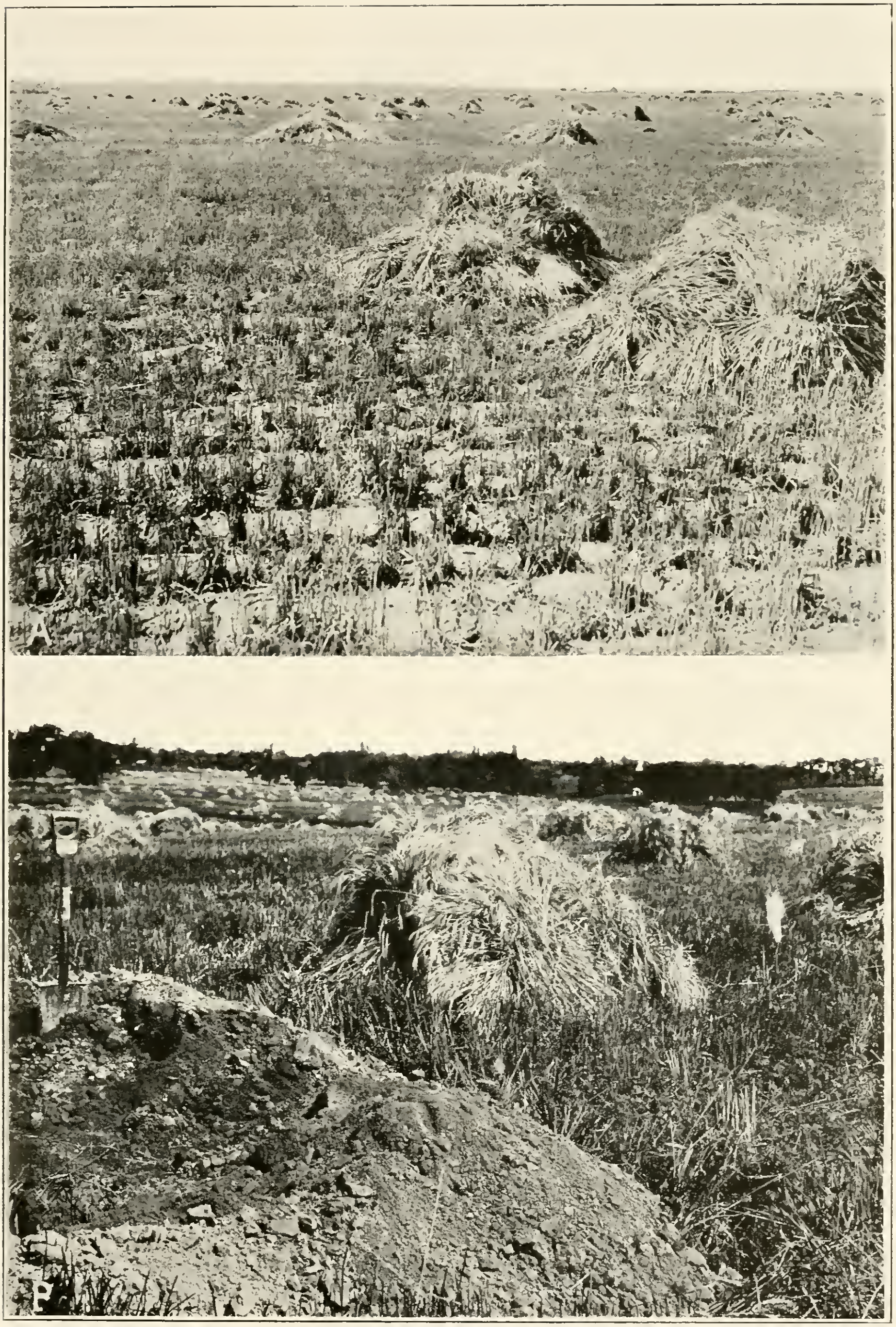
A. *Andropogon furcatus*, 4 months old.
B. One-year-old *Melilotus alba*.

A. *Artemisia filifolia* in sandy soil.

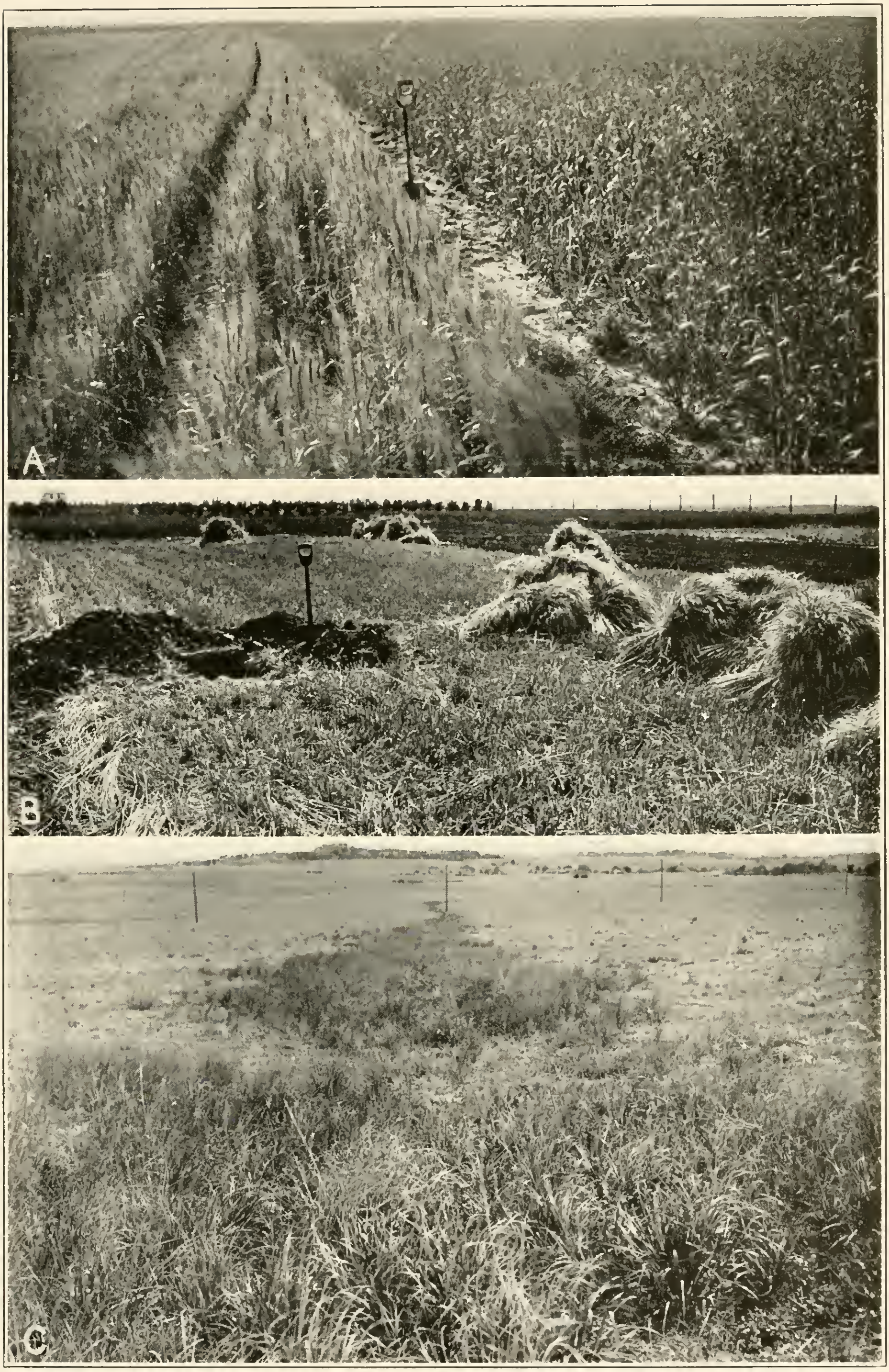


B. Portion of root system of *Psoralea tenuiflora*.

A. Rye grown in sandy soil to prevent wind erosion, Central City, Nebraska.
B. Rye on sod, Colorado Springs, Colorado.



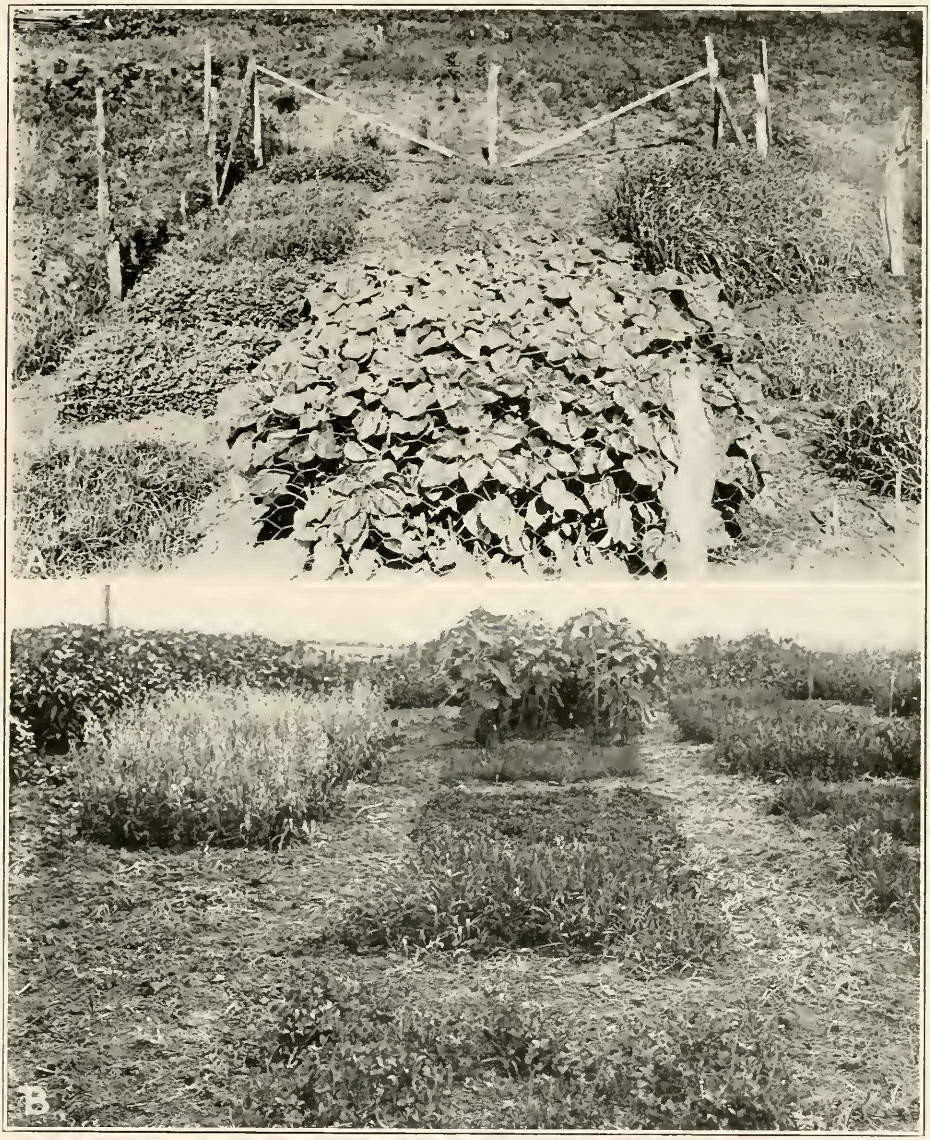
A. Field of wheat at Colby, Kansas, where roots were excavated.
B. Field of wheat at Lincoln, Nebraska, where roots were excavated.



A. Field of winter wheat (left) and spring wheat (right) on the hard land near Limon, Colorado.

B. Winter wheat on Pierre clay, Ardmore, South Dakota.

C. Consocies of *Stipa viridula* in an abandoned road.



A. Crop plats on lowland area, Lincoln, Nebraska.
B. Crop plats on upland area, Lincoln, Nebraska.

ROOT DEVELOPMENT IN THE GRASSLAND FORMATION

A CORRELATION OF THE ROOT SYSTEMS OF NATIVE VEGETATION AND CROP PLANTS

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