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SUMMARY AND INTERPRETATION OF UNDERGROUND DEVELOPMENT IN NATURAL GRASSLAND COMMUNITIES

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INTRODUCTION

Root development in grassland has been studied many years. A survey of the underground plant parts in the Palouse Prairie of southeastern Washington was made in 1913-14. The work was continued under the auspices of the Carnegie Institution of Washington in the prairies and plains of central North America. Investigations were made at more than 25 stations in Colorado, Kansas, Nebraska, and South Dakota, from the Missouri River to the Rocky Mountains. Roots of practically all of the grassland dominants were examined, many in different communities. The total number of root systems examined was about 1,500 and the results were published in 1919-20. The objectives of these early studies were to ascertain the general relationships of roots to soil and to each other as regards spread, depth, and degree of development in the same community and in different and widely separated communities. They were exploratory.

Extensive studies on the structure of grassland communities were continued. Root systems were further examined as supplementary to Experimental Vegetation (1924), Plant Competition (1929), The Prairie (1934) and various other studies. The great drought of 1933-40 in both prairie and Great Plains offered an exceptional opportunity to ascertain the responses of native plants to extremely adverse environmental conditions. The role played by root systems in endurance of and recovery from drought was thoroughly investigated. Meanwhile notable contributions on root studies had been made by Sperry on Illinois prairie (1935), Albertson on the hard lands of west-central Kansas (1937), Tolstead on the Sand Hills (1942) and Hopkins on the Loess Hills of Nebraska (1951). In all these studies the trench and pick method was employed. "While the trench method is slower and more tedious than that of root washing, it has so many advantages and gives such superior results that the additional effort is amply justified" (Sperry, 1935).

With the rapid development of soil science and much emphasis on the role of grasses in soil formation and stabilization, a distinct need arose for a better understanding of the intimate relations of roots and soil. A new method was devised—the monolith method—for securing a representative sample of an entire root system (Weaver & Darland 1949). By this method a section of soil may be obtained from a trench wall to the depth of the grass roots without disturbing the root patterns. Usually a sample 12 in. wide and 4-6 ft in depth is taken to a thickness of 3 in. in the trench wall. When soaked for many hours, the soil may be gently washed away. The root system remains without vertical displacement. The number of roots, degree of branching, distribution and weight at any depth or in any soil horizon may be ascertained. By this method many dominant grasses and the soil in which they grew have been restudied, more carefully and completely.

With a renewed interest in the ecology and physiology of root distribution of grasses in their relations to soils and removal of tops in grazing, the following summary and interpretation has been written. The past half-century has offered advantages for the study of natural grasslands and their environments which the future can not offer because of over-grazing, too frequent mowing, use of herbicides, reseeding, etc., and especially plowing. Indeed the eastern prairies were almost destroyed before they were investigated by ecologists.

This study includes the True Prairie of the western third of Iowa, which extends westward to about 98°30′ west longitude in Nebraska, and the Mixed Prairie of the Great Plains, westward and southwestward to the Rocky Mountains in Colorado. Communities of grasses of lowland and upland prairie will be presented first and then those of the hard lands, loess hills, and sand hills of the Great Plains. The usual root habits of several dominants are shown in community charts for each of the several major plant communities as they occurred on well-developed and stabilized soil. These furnish a basis for the comparison of other grasses of the same or different communities. An attempt is made to relate the community root habit to the soil conditions and aerial environment under which the vegetation developed.

The physical or chemical causes of variations in root development in certain soil types are considered as well as the relation of root development to removal of tops, as in frequent mowing or various degrees of grazing.

Both common and scientific names of grasses are according to Hitchcock & Chase (1950) revised Manual of the Grasses of the United States.

GRASSLAND SOILS

The well-drained and well-developed zonal soils of the grasslands of Nebraska, Kansas and Colorado comprise chiefly four great groups. These are the Prairie soils of the humid grasslands, the black earths or Northern Chernozems of the subhumid grasslands, the Chestnut or Northern Dark-Brown soils of the semiarid grasslands, and, farther westward, the still lighter-colored Northern Brown Soils. Associated with each of the zonal soils are other soils (intrazonal). Some are young with only the beginnings of soil development (azonal soils), some have excessively developed claypan subsoils (Planosols), and still others are poorly drained and marshy but without claypans (Wiesenboden) (*cf.* Marbut 1935, Kellogg 1936).

True Prairie occurs mostly on zonal Prairie soil but it extends westward on Chernozems for many miles. Prairie soils are very dark brown in color, rich in organic matter, especially in the upper portion, moderately to strongly acid in reaction, and well supplied with nutrients necessary for a luxuriant development of grass. They have been leached to the extent that they do not have a horizon of calcium carbonate.

Chernozem soils occupy the most humid part of the drier region having soils with a calcium carbonate horizon. These deep, black soils are, owing to the luxuriant growth of grasses, high in content of organic matter distributed deeply throughout. They are neutral in reaction and even more fertile than Prairie soils, but productivity is less because of decreased precipitation.

Both Prairie soils and Chernozems are rich, deep, and fertile. Silt loams prevail with unusually good texture and structure. There are nearly always enough large pores to insure adequate drainage and good aeration and enough small ones to offer an adequate water-holding capacity. In various soil types under prairie grass total pore space usually composes about 50% of the soil volume. The mellow, granular topsoil (A horizon), enriched by untold generations of grasses and forbs, extends usually to depths of 12 to 18 in. Beneath is a zone of higher clay content and lighter in color (B horizon) which extends to a depth of about 3 to 4 ft. Underlying the solum is the parent material of the C horizon. It is often yellowish or at least lighter in color than the solum, partly because of its lower content of organic matter and partly because it is rich in lime. Except for rock outcrops, the parent material extends many feet in depth. Although lime has been eluviated from the A horizon and at least the upper portion of the B horizon, the soil (in this western area) is neutral or only slightly acid, since a constant supply of lime is brought to the surface by the grasses and deposited there when they die (*cf.* Thorp 1948).

Dark-Brown and Brown Soils are described later together with the Mixed Prairie vegetation which they support.

UNDERGROUND PARTS OF GRASSES OF LOWLAND TRUE PRAIRIE

The two types of grassland of greatest importance and widest extent in true prairie are those characterized by little bluestem and big bluestem, respectively. Prairie of the wetter or more moist lowlands is dominated by grasses that are quite different from those typically forming upland communities. A description of the 3 major prairie communities of lowland and the 3 of upland, together with their composition and structure, has been recorded (Weaver & Fitzpatrick 1934). A more succinct statement may be found in North American Prairie (Weaver 1954).

A map showing the lowlands along the Missouri River and its tributaries, the smaller streams and ravines leading into them, and the well-watered lower slopes of hills, would include the portion of the area formerly dominated by big bluestem and other lowland grasses. Exceptions are woodlands, marshes, soil covered with water or deep deposits of sand. Almost pure stands of big bluestem *(Andropogon ge-*

rardi) occurred over extensive areas in which this grass alone composed 70 to more than 90% of the vegetation.

BIG BLUESTEM

Total basal cover of big bluestem, even in the best stands, averaged only about 13% of the soil surface. Growth is rapid; a dense stand of foliage 3 ft high is produced by midsummer. Then stout stems, each with 9 to 10 leaves, extend upward; the mature flower stalks in late summer reach heights of 6 to 10 ft.

The very abundant roots of mature plants extend downward almost vertically. A few may run off somewhat obliquely before turning downward. They are rather coarse (1-3 mm in diam.) and tough. Although well supplied with laterals 2-6 in. in length, branching is not so profuse as on roots of upland grasses. Depths of 6 to 7 ft are usually attained.

Figure 1 and the following community charts show the average number of roots in an inch width of soil as ascertained at each foot in depth in the trench wall and from soil monoliths taken from many different trenches. Where the roots are too numerous in the upper soil to be shown in the drawing, this is indicated in the legend. Root depth of each grass is an average of 10 to 20 samples from widely separated sites in each of the plant communities illustrated. Relative size of roots of various grasses is also shown. Lateral spread of roots (the radial distance to which roots extend from the base of the plant) is shown as far as space permits. Only enough detail has been added to indicate the branching habit. Branches, as regard length, are drawn to scale. Intermixing of roots of plants (except in Fig. 4) has been avoided for the sake of clarity.

The rhizomes of big bluestem are coarse, usually 3-6 mm thick, much branched and frequently continuous for distances of 6-10 in. or more. Their general level is about 1 to 2 in. below the soil surface, but they are common to a depth of 4 in. The rhizomes alone form a rigid, coarse, open network, which is anchored by the multitude of coarse, branched roots arising from them. They are studded above by the abundant coarse stem bases 1-2 in. of which are buried in the soil. The whole stem-rhizome-root system forms a magnificent network for holding the soil against erosion by flooding (Fig. 2).

The amount of underground materials of big bluestem to a depth of 4 in. was ascertained in 24 widely distributed prairies. Each sample consisted of 0.5 sq m (5.38 sq ft) of soil, from which the underground parts were recovered by washing away the soil. The material was oven-dried at 100 C.

The portion of the true prairie examined extended from Guthrie Center and Creston, Iowa, approximately 75 mi east of the Missouri River, to Nelson, Nebraska, about 200 mi southwestward (Fig. 3). The silt loam soils are all deep and of high fertility. Rate of evaporation is increasingly greater from east to west, while other conditions favorable to growth, such as water content of soil, gradually decrease.

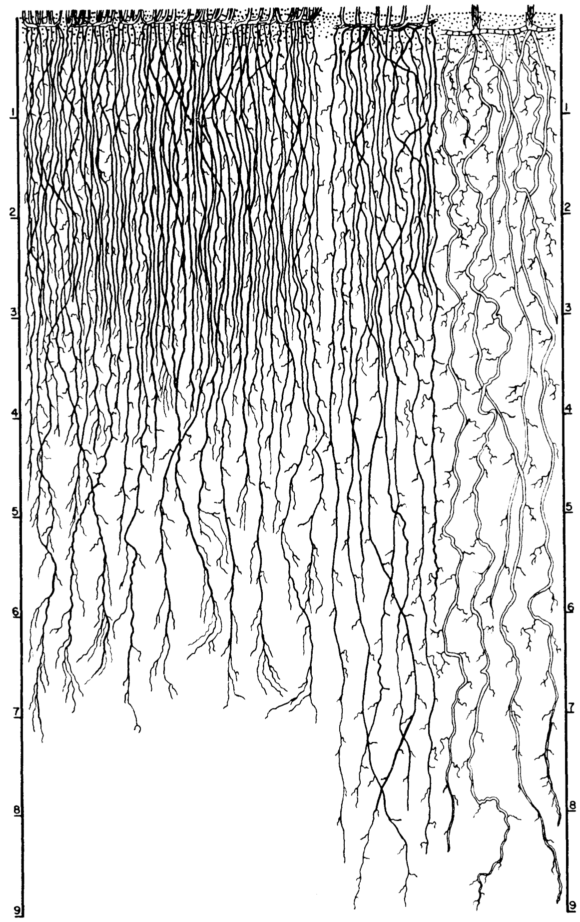

FIG. 1. Characteristic development of roots and rhizomes of grasses occurring in the big bluestem community. (Left) big bluestem *(Andropogon gerardi)*, switchgrass *(Panicum virgatum)*, and prairie cordgrass *(Spartina pectinata)* (right). Both vertical and horizontal scale in feet. The average number of roots in the first inch of soil in the trench wall is shown, except in the first 2 ft under big bluestem. Foliage height in midsummer is 3-4.5 ft and mature plants are 6-10 ft tall.

Yield data from stations with approximately equal rainfall were grouped and the average weights expressed in T/A. At the 6 Anita stations, mostly in southwestern Iowa, the rainfall averaged 32 in.; at the 8 Lincoln stations, in south eastern Nebraska, it was 29 in.; and at the Nelson stations, it was only 26 in. The yields of plant materials were 4.54, 3.54 and 3.17 T/A, respectively (Shiveley & Weaver 1939).

Average weight of roots occurring at 4 to 12 in. depth at Lincoln was about one-third the total weight of underground parts in the 0-4 in. level (4.1 T) or 1.35 T.

Root weight decreases rapidly with depth, especially below 24 in. However, the importance of the subsoil is demonstrated by the relatively great quantity of roots found there. An oven-dry weight of more than 300 lbs/A of grass roots often occurs in

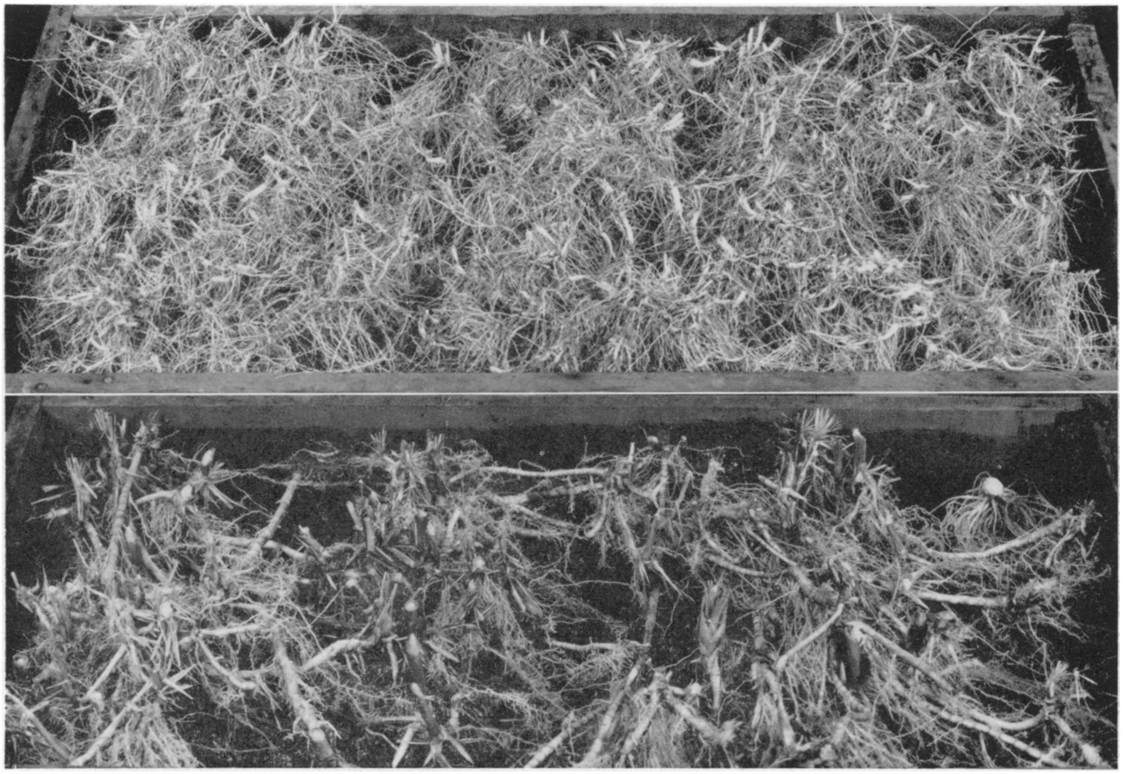

FIG. 2. (Upper) Underground parts of big bluestem from .5 sq m (5.38 sq ft) to a depth of 10 cm (4 in) from Union, Nebraska, after the soil was washed away. Note the uniform distribution of roots. (Lower) Roots and rhizomes of prairie cordgrass. Note wide spacing of stems as shown in Figure 1. Only 1% of the soil surface was occupied by stems, yet dense shade excluded nearly all other plants.

the fourth foot of bluestem prairie soil. These deeper roots probably absorb quite out of proportion to their small weight.

The rate of production of the large quantities of roots has been ascertained. Big bluestem was grown from seedlings to maturity without competition and under an environment favorable for its development. Fifty seedlings were grown in the field in each of 3 steel drums (58 gal., 3 ft. deep) placed in the soil. The first year the grass produced 48% of its mature root weight. The second year it added 34% more, and the third summer the remaining 18%. Thus, it reached approximately its maximum root development in 3 years. The underground materials produced were similar in amount to those ascertained earlier in typical mature stands in native prairie (Weaver & Zink 1946).

The length of life of individual roots of several grasses was ascertained by banding large numbers of young roots of each species. Narrow bands of aluminum or soft tin were used. All roots remained alive on big bluestem and switchgrass (*Panicum virgatum*) for a period of 2 yrs, and the loss by death was only about 20% for big bluestem at the end of the third growing season. This loss was almost negligible, since at this time an average of 882 roots per plant had been produced (Weaver & Zink 1946a).

Finally the rate of decay of roots and rhizomes in their natural environment when the plants were killed was ascertained. Relative resistance to decay varied with the species. Decomposition proceeded at about the same rate at all soil levels. Big bluestem and Indian grass *(Sorghastrum nutans)* decayed rather slowly. A few roots retained some tensile strength after 3 yrs. Switchgrass decayed somewhat more rapidly. Rhizomes of these and other grasses were neither more or less resistant to decay than the roots (Weaver 1947).

OTHER GRASSES

Indian grass is usually associated with big bluestem and like it is a sod former. Its abundance is variable, increasing southward, but over the central lowlands as a whole it composed only 1 to 5% of the grass population. The roots are not so coarse as those of big bluestem nor do they usually extend quite so deep, but they are often branched more abundantly.

Prairie cordgrass *(Spartina pectinata)* occurs in pure stands only in soils that are too wet and consequently too poorly aerated for big bluestem. The coarse stems of this sod-forming grass usually attain a height of 6 to 10 ft. Both rhizomes and roots of prairie cordgrass are much larger than those of big bluestem and they also occur at greater depths (Fig. 1). The coarse, woody, much branched rhizomes, form an open network in part or all of the first foot of soil (Fig. 2). The roots are usually 3-5 mm in diameter. They grow from the rhizomes and the

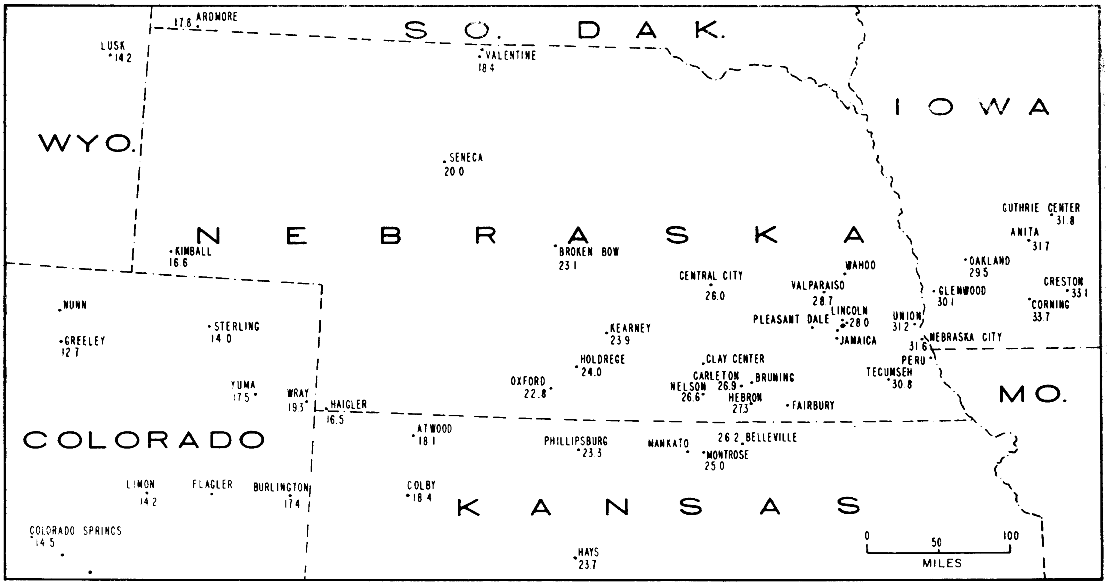

FIG. 3. General area of study showing stations where underground plant parts were examined. Figures indicate mean annual precipitation at the time the various studies were made.

base of the clumps and penetrate almost vertically downward, sometimes in a zigzag manner, to depths of 8-13 ft. The roots are clothed throughout with fine, rather short, poorly branched laterals. Branching is often profuse in the surface soil where recent deposits of soil have resulted from flooding. The weight of plant materials in the surface 4 in. of soil from 8 samples from Iowa and eastern Nebraska was about one-third greater than that of big bluestem.

Switchgrass, a tall, coarse, sod-forming species, forms extensive communities on lowlands where water relations are intermediate between those of prairie cordgrass and big bluestem. It is a warm-season grass and develops so rapidly that for a time it exceeds big bluestem in height. Height of foliage is 4 to 5 ft but the coarse stems with the large panicles extend 6 to 7 ft upward in late summer. The underground parts are somewhat intermediate between those of big bluestem and prairie cordgrass. Abundant, branched rhizomes 3-7 mm thick occur usually in the surface 3-6 in. of soil. The abundant roots (2-4 mm in diam.) extend almost vertically downward 8-11 ft but branch rather sparingly (Fig. 1).

Eastern gama grass (*Tripsacum dactyloides*), of similar growth habit to that of prairie cordgrass, occurs in southern Nebraska and southward. The plants tend to grow in large clumps. The yield of rhizomes and roots in the surface 4 in. of soil was twice that of prairie cordgrass and 3 times as great as big bluestem taken from the same prairie.

The root system of Canada wild-rye *(Elymus canadensis)*, unlike that of the preceding grasses, is shallow but wide-spreading. The roots are also much finer, 0.5 mm or less in diameter and well-branched. They are tough and wiry. Rhizomes, which are not abundant, vary from horizontal to oblique. Root spread on all sides of the plant may exceed 2 ft. All of the roots usually occur in the first 2.5 ft of soil. This plant, like switchgrass, has its best development where the soil-water relations are intermediate between those of big bluestem and prairie cordgrass, but it seems less well adapted and occurs in only moderate amounts.

The preceding are the most abundant of lowland prairie grasses. Indian grass is the nearest ecological equivalent of big bluestem. Other grasses occur in wet places in the big bluestem type.

DISCUSSION AND INTERPRETATION

Within this wonderfully fertile soil of good structure and aeration to great depths, water content plays a most important role in determining root habit. Available soil moisture and other physical factors of the environment have been measured continuously at Lincoln during the April to October growing season over a period of 13 yrs. A comparison of water relations in lowland with those of upland is pertinent here.

The upland soil (Carrington) is a deep, fertile, fine-textured silt loam of high water-holding capacity. It is circumneutral in reaction. The solum is 3 ft deep and the C horizon is many ft in depth. The lowland soil (Wabash) is a fertile, dark-colored, silt loam. The granular layer extends 7 in. deeper than that on the upland and the solum gives way to the massive layer at about 5 ft in depth. The mean annual precipitation, about 80% of which falls during the growing season, is 28 in. Water content in the surface 6 in. of upland soil became nonavailable for growth only twice during the 13 yrs (1916-1928). Water available for plant growth at greater depths was at no time exhausted. In general there was a gradual decrease in the supply with the advance of summer but this trend was frequently temporarily interrupted, especially in the second foot, by heavy rains. The available supply usually ranged between 5 and 15% at the depths (about 5 ft) occupied by grass roots. On the lowland, available water content was 3 to 10% greater in the surface foot and often 5 to 11% in excess of that on the upland in the deeper soil. A water table occurred at about 10 ft.

A similar study in 1932 of water-content of upland and lowland prairie on the flood plain of the Missouri River south of Union, Nebraska, gave even greater differences. Here big bluestem roots extended to a depth of 7 ft in Wabash clay loam. The water table occurred at about 10 ft. During this year of approximately average rainfall the surface 6 in. always had available water and at greater depths the amount was usually about 13% or more. Repeated sampling through many years revealed this to be about the usual condition, a continuous but rarely excessive water supply on lowland.

Growth in lowland prairie is rapid. Big bluestem elongates at a maximum rate of nearly 0.75 in./day and, like the other tall grasses, completes it vegetative growth late in July. Then the flower stalks begin to develop, often elongating 1.5-3 in./day, and the plants reach heights of 6-10 ft. Prairie cordgrass and sometimes Indian grass are taller, but switchgrass is often somewhat less in height. All except Canada wild-rye, which flowers in midsummer, are warm season grasses adapted to a long growing season.

This magnificent cover of grasses presents by midsummer a foliage surface of 5-10 A/A of soil. Since the grass roots are not only perennial but long-lived, the plants may absorb at all depths throughout the growing season. The abundant supply of water offsets the enormous losses by transpiration. The roots also take up sufficient nutrients to permit a yield of 3-5 T/A of forage annually. It is believed that lack of lateral spread of roots in the surface soil results in part from the abundance of moisture and partly from the network of rhizomes which distributes the roots widely and uniformly. Moreover, lowland soils are in general of a more uniform structure than are those of uplands. This, with their continuously higher water content, enables roots to penetrate through them easily and uniformly. The great depth that roots attain may be related to the usually increasing water supply with depth and the great demands of these tall grasses for water and nutrients. Many lowland soils have water tables within reach of very long roots.

It may well be that the continuously greater supply of water in the wetter habitats of switchgrass and especially prairie cordgrass is an environmental condition reflected in the more open network of rhizomes and fewer roots than those of big bluestem.

The amount of water absorbed and transpired in the big bluestem community must be very great. Yet only once (in 1934) during the past half century has drought in lowlands been observed to interrupt the growth of the grasses in late July. Then big bluestem was wilted and half dried. Switchgrass was almost as dry and even prairie cordgrass, discolored and dwarfed to less than half its normal stature, showed great distress. But these grasses were rarely killed where they were rooted in deep loam soils. The absence or lack of abundance of upland grasses is not due to unfavorable soil conditions but to the dense shade produced by big bluestem. When it is removed, they thrive.

UNDERGROUND PARTS OF GRASSES OF UPLAND TRUE PRAIRIE

Upland prairie is quite different from that of lowland. The grasses are nearly all bunch grasses of the mid-grass type, with heights ranging between 2 and 3.5 ft. Upland soils are not usually sufficiently moist to promote development of tall grasses, especially in competition with more xeric species.

Little Bluestem

Andropogon scoparius is the principal grass of the uplands. It forms not only the most extensive communities of upland but also occupies an area over the prairie as a whole many times as great as that dominated by big bluestem. It exceeds in abundance all other grasses combined, and usually constitutes 55% and sometimes 90% of the vegitation in this area. It ordinarily forms an interrupted sod of mats and tufts but large bunches prevail in drier places. The average basal cover is about 15%. The foliage varies in height in late summer from 7-12 in. on dry uplands but it is 15-18 in. in more favorable sites. Flower stalks vary in height from 1.5-3 ft. Usually it fruits abundantly only in wet years.

The mature root system consists of a vast network of roots and masses of finely branched rootlets, some more than 30 in. in length and branched to the third order. The largest roots have only about one-third the diameter (0.5 to 1 mm) of those of big bluestem. The soil beneath the crown and several inches on all sides of it is threaded with dense mats of roots to a depth of 4 to 5 ft (Fig. 4). The large number of roots in a 1-in. layer of trench wall below 2 ft is from an average of many counts. Actually some roots entered this layer from soil removed in digging the trench or from behind the exposed face of the trench wall. Approximately an equal number grew outward from it. This is difficult to illustrate, hence all of the roots are shown as if they grew only within this inch of soil throughout their entire length, as most of them did.

Stem bases and surface roots firmly bind the soil in the mats or bunches. Most of the space between bunches is also occupied by a dense network of roots.

Samples of sod were taken to a depth of 4 in. in 22 upland prairies where little bluestem alone formed 88 to 98% of the vegetation. Annual precipitation at the three groups of stations—Anita, in western Iowa, and Lincoln and Nelson in southeastern Nebraska—was 32, 29, and 26 in., respectively. The yields of plant materials in these silt loam soils were, in the same order, 3.15, 2.60 and 2.34 T/A. (Fig. 5). Correlation between the average dry weight and the mean

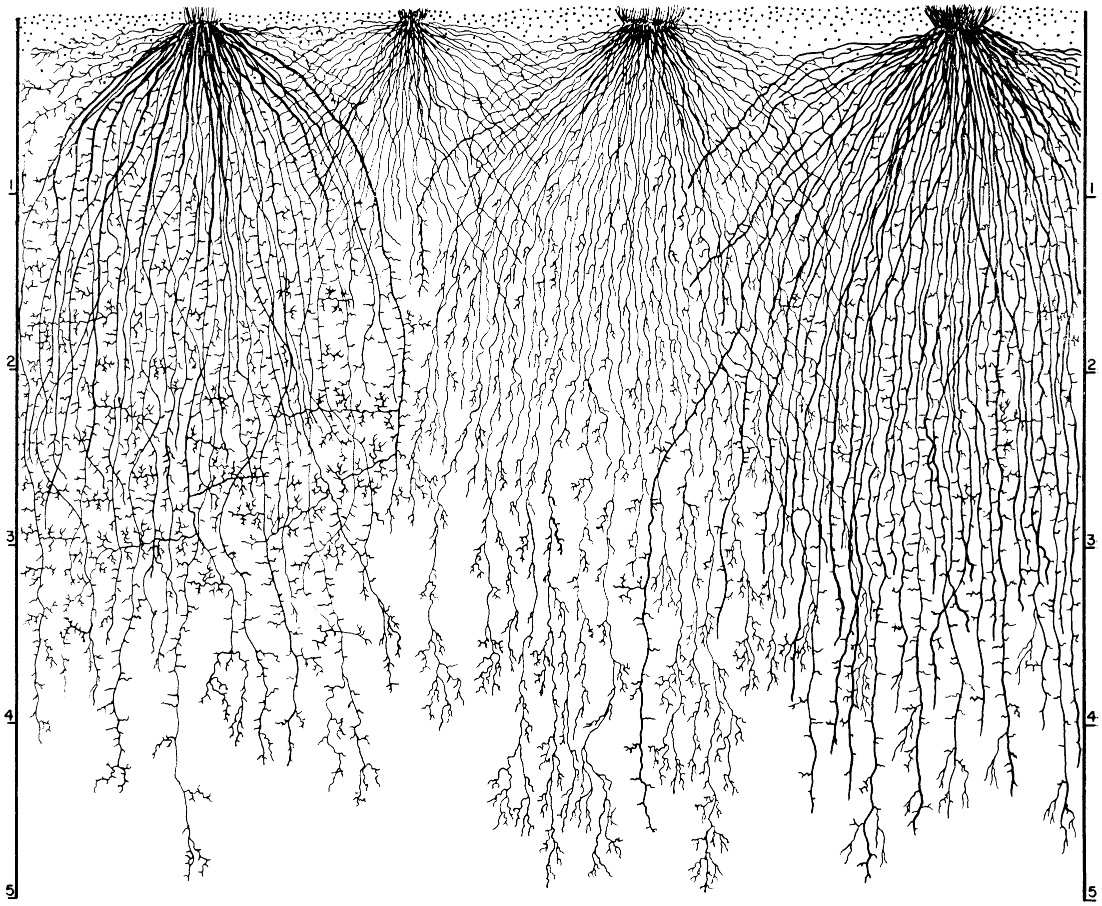

FIG. 4. Characteristic development of roots of 3 upland bunch grasses as they occur in the little bluestem community or in their own communities. From left to right are needlegrass *(Stipa spartea)*, interstitial Junegrass *(Koeleria cristata)*, little bluestem *(Andropogon scoparius)*, and prairie dropseed *(Sporobolus heterolepis)*. Average number of roots in the first inch of soil in the trench wall is shown except in the first 2 ft. Scale in feet, height of foliage by midsummer is 1.5-2.5 ft; flower stalks extend upward mostly 2.5-3.5 ft.

annual precipitation at each station was found to be very significant. Coefficient of correlation of the little bluestem was .642, of the big bluestem series, already described, .673. Volume of these materials was also determined. Statistical treatment of the data from each series showed that the correlation between volume and weight was very significant. Coefficients of correlation were .870 and .874, respectively (Shively & Weaver 1939).

These are samples of the furrow slice that the breaking plow clove neatly from the surface of the soil. The pioneer walked behind the plow in a clean, cool, moist path of richness. The furrow slice was a long, almost unbroken strand of turf, each one laid smoothly against the former one. A study of the binding network of roots showed that a single strip of Iowa prairie sod, 8 in. wide, 100 in. long, to a depth of 4 in. is bound together with a tangled network of roots having a total length of more than 20 mi (Pavlychenko 1942).

The average weight of roots occurring at 4-12 in. depth at Lincoln was one-third the total weight of underground parts in the surface 4 in. (3.3 T) or 1.1 T/A. Root weight nearly always decreases rapidly with soil depth. That from a foot-wide monolith in silty clay loam decreased from 85.8% in the first 6 in. to 5.3 in the second, and then, foot by foot, from 5.0 to 2.3, 1.4 and 0.2%.

Stem bases and roots of bluestems constituted about 10% of the total organic matter in the upper 6 in. of soil. The amount decreased gradually to 3-4% in the second 6 in. to 1% in the fourth foot under little bluestem in an upland (Lancaster) soil. A similar gradual decrease under big bluestem in a lowland (Wabash) soil was ascertained to a depth of 7 ft. Below the surface 6 in. of soil in native grassland, there has been found an approximate linear relation between the amount of root material and the amount of soil organic matter in the various soil horizons (Weaver, Hougen & Weldon 1935). This indicates that organic materials had accumulated in larger quantities at those depths where the roots had been most concentrated. Extensive early studies by Alway & McDole (1916) have shown that in grassland soils

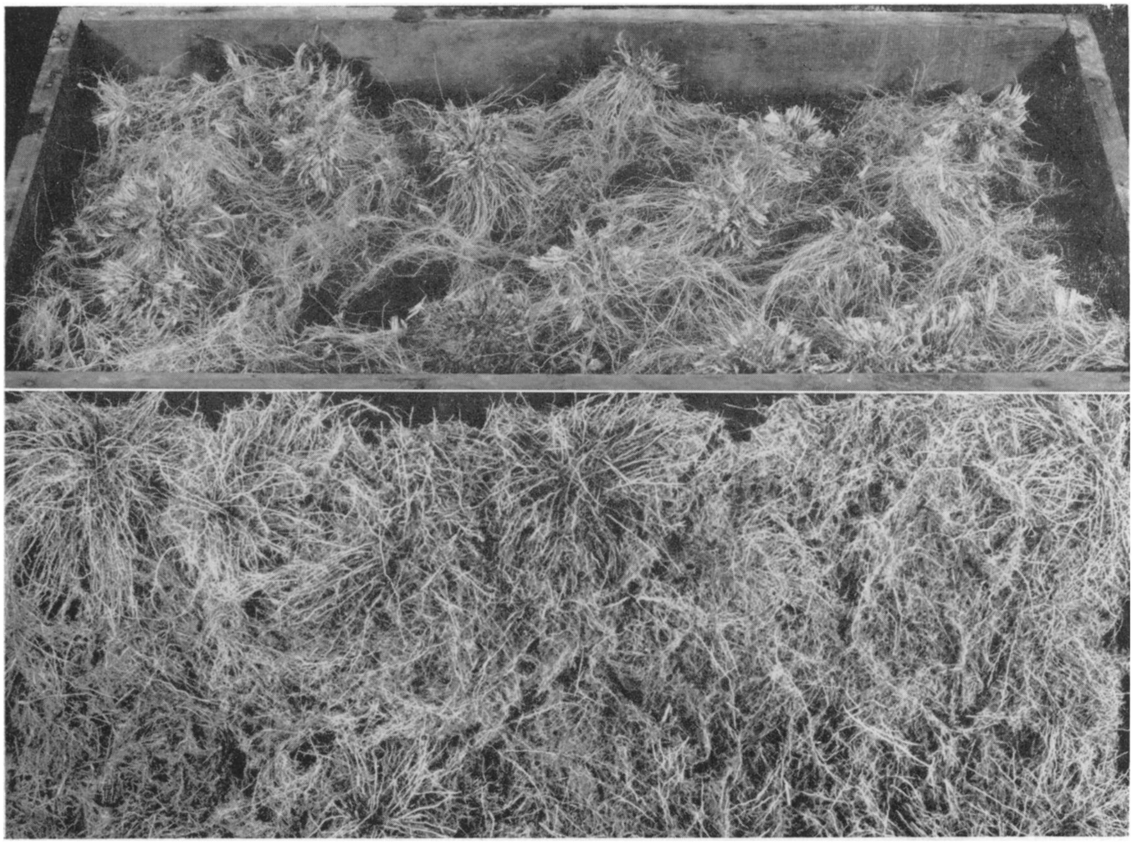

FIG. 5. (Upper) One-half sq m of underground parts of little bluestem *(Andropogon scoparius)* to a depth of 4 in. at Nelson, Nebraska, a drier type of true prairie as is shown by the pronounced bunch habit. (Lower) Part of a similar area of underground parts of needlegrass *(Stipa spartea)* to 4 in. depth at Lincoln. The sod mat is inverted.

the nitrogen and organic matter decrease regularly with depth, the bulk of the organic matter being confined to the surface foot (Russel & McRuer 1927).

NEEDLEGRASS

Stipa spartea often occurs intermixed with little bluestem but it is also a dominant of a second upland community. The bases of the widely spaced, usually circular bunches vary from 1-4.5 in. in diameter. Basal cover is only about two-thirds that of little bluestem. It averages only 11%. Foliage varies from 1.5-3 ft in height and flower stalks range from 2-4 ft.

The root system of mature plants usually reaches depths of about 4.5 but sometimes 6 ft. Numerous, profusely branched, smaller roots occupy the surface soil, spreading horizontally or mostly diagonally downward to a distance of 8-18 in. The longer roots give rise to many laterals which divide into fine branches in the deeper soil. Careful examination of the usual prismatic structure of the B horizon (subsoil) reveals patterns of root branching as indicated in Fig. 4.

The average weight of roots at 4-12 in. depth at Lincoln was 48% (0.89 T) of that of underground parts in the 0- to 4-in. level (1.87 T).

Total length of roots of needlegrass occurring in the 0.5 sq m sample, partly shown in Fig. 5, was ascertained by Pavlychenko (1942) to exceed 11 mi.

PRAIRIE DROPSEED

Sporobolus heterolepis is another bunch grass of uplands which intermixes somewhat with little bluestem and needlegrass but also forms limited communities of its own. This warm-season grass produces circular bunches from less than 0.5 ft. to 1.5 ft in width. Foliage height is mostly 8-18 in. and flower stalks are 2.5-3 ft high. The root system is very similar to that of little bluestem, but the roots are coarser and branch somewhat more horizontally. Roots spread 1-2 ft in the upper soil but many extend vertically downward 4-5 ft (Fig. 4). The average dry weight of plant materials in the surface 4 in. is considerably greater than that of needlegrass, and also greater than that of little bluestem.

BIG BLUESTEM

Big bluestem occurs commonly on uplands. On lower and midslopes it not only shares dominance with little bluestem but also regularly forms 5-20% of the grass cover in the little bluestem type of uplands except on the drier hilltops and ridges. On upland it usually occurs in the bunch form and height is considerably reduced. Roots were 1-2 ft less in depth than on lowland and some also spread outward in the upper soil. The main roots were usually much finer and better branched, and somewhat more of the root weight occurred near the surface of the soil. Root habits of this grass have been studied in ten soil types.

OTHER GRASSES

Side-oats grama (*Bouteloua curtipendula*) is a common but rather minor constituent of upland prairie. It is far more abundant in mixed prairie westward where its root habits will be described. The rather fine well-branched roots spread 1-1.5 ft laterally and attain depths of 4-5.5 ft.

Junegrass (*Koeleria cristata*) has a shallow but exceedingly well-developed root system. From the base of the small bunches some of these very fine roots, scarcely exceeding 0.2 mm in diameter but much branched, spread horizontally or obliquely to about 8 in. Others penetrate nearly vertically downward, but usually only 15-20 in. (Fig. 4). It is a drought evader, profiting by early growth, summer dormancy, and autumnal development. Its life span is shorter and it is less persistent than most grasses.

Penn sedge (*Carex pennsylvanica*) is a low-growing rhizomatous plant which absorbs chiefly in the first 2 ft of soil, but sometimes to 3 ft. Roots of Scribner's panic grass (*Panicum scribnerianum*), another low-growing species, spread widely throughout the surface 2-3.5 ft of soil.

Kentucky bluegrass (*Poa pratensis*), an introduced rhizomatous plant, has spread widely since the cessation of prairie fires and under the practice of annual mowing. It has a wonderfully well-developed root system. The fine, thickly branched, thread-like roots form dense mats especially in the surface 1.5 to 2 ft of soil. The longest are sometimes 3 ft deep.

Western wheatgrass (*Agropyron smithii*), sand dropseed (*Sporobolus cryptandrus*), blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*) were species of minor importance before the 7-year drought. They are all dominants of mixed prairie for which the root systems will be described. The decrease in stature of lowland grasses (switchgrass, Canada wild-rye, and Indian grass) where they have migrated along ravines often halfway up the hills, is marked. This is accompanied by an increase in lateral spread of surface roots and the production of networks of branches.

Except for a few upland grasses and sedges, the diagram in Figure 4 mirrors faithfully the root habits in upland prairie communities.

EXPERIMENTS WITH UNDERGROUND PARTS

When one examines a diagram of the roots, as in Figure 4, he may wonder about the actual number in the surface soil, their tensile strength, and their effect on holding the soil in place. The number of main roots has been ascertained by Pavlychenko (1942) on representative samples of sod of several prairie grasses selected by the writer as representative of average conditions. In the upper 10 cm of soil they occurred in decreasing numbers (to the nearest hundred per 0.5 sq m 5.38 sq ft): *Poa pratensis* 16,300; *Agropyron smithii* 11,500; *Bouteloua gracilis* 5,800; *Stipa spartea* and *Sporobolus cryptandrus* 4,400 each; *Andropogon gerardi* 3,500; and *A. scoparius* 3,400. He also ascertained that the tensile strength, expressed in grams, of the main roots of each species in the above order was 273, 849, 757, 981, 821, 1,712 and 1,171. Thus, the very fine roots of Kentucky bluegrass showed the least tensile strength and the coarse ones of big bluestem the greatest.

The main roots exert considerable binding effect upon the soil. But, as Pavlychenko (1942) points out, "their chief significance, however, rests in their ability to produce multitudes of branches. These penetrate the soil in all directions and come into contact with the smallest soil particles. Unlike main roots, they are composed largely of young, actively absorbing tissue." Their tensile strength has also been ascertained; in little bluestem, for example, it varied from 31 gm for branches of the first order to 2 gm for those of the third. Of all the underground parts of the preceding, rhizomes of little bluestem and roots of big bluestem exhibited the greatest tensile strength. Tensile strength is involved in resistance to frost heaving, especially of seedlings but its main value is that of resistance to soil erosion. Poorly anchored plants, but not those of native prairie, may be pulled up during grazing. The binding of soil by roots as well as the process of granulation continues under the action of long-lived and regularly renewed growth of roots of prairie grass.

The binding power of underground plant parts and their resistance to erosion have been ascertained by a series of experiments (Weaver & Harmon 1935). Similar soils without living roots or with only the roots of weeds, when placed under the same conditions of erosion, were washed away in only a small fraction of the time required to erode the prairie sod when the grasses were cut at the soil surface and removed. Even the best growth of field crops is far inferior to the native bluestems in preventing the soil from washing away (Kramer & Weaver 1936). Once the prairie was destroyed, the deep, thick topsoil (A horizon) of Iowa, protected for thousands of years by prairie sod, lost about one-third of its original depth during a single century under cultivation. Moreover, depletion of mineral nutrients is making necessary additions of fertilizers. Unlike prairie plants, cereal crops take more from the soil than they put back into it.

An examination of roots in Figure 4 indicates that there must be very great competition between plants for water and nutrients. This is entirely correct. As has been shown repeatedly, production of any prairie grass may be increased and often doubled simply by removing other grasses from a few feet on all sides of it (Clements, Weaver & Hanson 1929). These long-lived, perennial root systems may absorb water at all times except in winter when the soil is frozen, often to a depth of 8 to 18 in. Although some new roots are developed each year, it is believed that the bulk of the root system undergoes very gradual change.

Although no studies on the activities of native grasses in fall and winter have been made, the number, length, and absorbing area of roots of winter wheat were ascertained at 10-day intervals during the fall and at longer intervals during winter and spring. The development of both roots and shoots fell into three rather distinct periods, temperature being the controlling factor (Weaver, Kramer & Reed 1924).

It has been shown experimentally that from early spring until the middle of May, soil with needlegrass loses 2 to 3 times as much water as that under the later-growing little bluestem (Weaver & Albertson 1943). During summer absorption by needlegrass is less than that of bluestem, but it increases again in autumn. Upland grasses depend entirely for their water supply upon precipitation. In a series of extensive studies approximately 200 samples of prairie sod were collected from 24 stations distributed over a region extending several hundred miles from east to west. More than 10 tons of soil were removed from prairies of Iowa, Nebraska, Kansas, and Colorado, and transported to Lincoln. A comparison of the yields of 67 samples from upland in true and mixed prairie in relation to precipitation is of special interest. The mixed prairie stations were from Hays, Kansas, northward to Holdrege, Nebraska (Fig. 3). Mean annual precipitation at the Anita, Lincoln, Nelson and Holdrege station groups was 32, 29, 26 and 23 in., respectively. If weights of the Anita group are considered as 100%, those from the other stations were 80, 73, and 64%, respectively. Here again there was a close correlation between yield of underground parts and precipitation.

The rate of production of the large quantities of roots of little bluestem has been ascertained. Plants were grown from seedlings to maturity under conditions described for big bluestem. The first year it produced 56% of its mature weight, which it attained at the end of the second summer; the underground materials produced were similar in amounts to those found in typical mature stands in native prairie.

Although blue grama is far more abundant in mixed prairie, its rate of production underground was also ascertained with these studies on the bluestems at Lincoln. It reached its maximum development the second growing season, producing 64% of this weight the first summer. With both little bluestem and blue grama, yields of the controls allowed to grow a third year did not exceed the weight attained the second summer.

The weights of roots alone (minus stem bases and rhizomes) produced in these experiments amounted to approximately 5.5 T/A in big bluestem, 2.7 in little bluestem, and 1.6 in blue grama. These amounts might be expected after 3 years' growth of full stands of similar grasses cut annually for hay (Weaver & Zink 1946).

Roots of little bluestem and blue grama were among the 3,400 roots of young plants banded to determine their length of life. After 2 years about 66% of the banded roots were alive. By the autumn of the third year the number had decreased to 10 and 45%, respectively, for the two species. These losses were almost negligible, since the total number of roots per plant was now very large (Weaver & Zink 1946a).

Rate of decay of roots and rhizomes of little bluestem and western wheatgrass left in the soil when the grasses were killed was similar to that of big bluestem. A period of 3 or 4 yrs was required for complete disintegration. The most resistant to decay were blue grama, side-oats grama, and buffalo grass. Here much undecayed material remained and some roots of each species retained moderate tensile strength after 3 yrs. It is of interest that roots of Sudan grass and smooth brome grown for one summer disintegrated as far in 1 yr as did many perennial native grasses in 3 yrs (Weaver 1947).

Discussion and Interpretation

In upland prairie differences in soil horizons are more pronounced and exert greater effects upon root distribution than those of lowland. As a result of the processes of development, the mellow surface 16-18 in. of soil has a granular structure. Much of the colloidal clay has been eluviated into the B horizon. This granular structure has resulted from alternate wetting and drying, repeated freezing and thawing, a high humus content and the favorable effects of root activities. Roots penetrate this granular layer easily, they spread widely and branch repeatedly. This rich layer has the greatest number of roots, and they can be separated from the soil with little difficulty.

In the subsoil or B horizon the clay content is higher and much of the lime has been leached. Here the soil often has a prismatic structure. The vertical prisms are often 2-3 in. in diameter and 8-12 in. in length, with vertical cracks between them when the clay shrinks in drought. Penetration of roots is much more difficult and branching is often less pronounced in the prismatic layer of soil. Here the rootlets are mostly appressed to the surfaces of the prisms where penetration is easy, water enters more readily, aeration is best, and nutrients apparently more concentrated. Fewer roots penetrate through the prisms. Roots of grasses are removed from this horizon, which is usually 1.5-3 ft deep, with much more difficulty than from the granular layer above or the massive layer below, where there is less clay. Lime occurs in amounts sufficient to give the parent materials a mellow structure. In Figure 4 the effects of the B horizon upon the branching of roots of needlegrass are indicated. Other effects of soil structure on roots will be shown elsewhere.

The finer and much more branched roots of plants of upland seem better adapted to penetrate and absorb water and nutrients from the drier and more compact soil than the coarser roots of the tall grasses of lowlands.

In the deep fertile soils of the prairie, with its favorable climate for the growth of grasses, water content of soil and rate of water loss influence root development of underground parts perhaps more than any other environmental condition. Precipitation varies from about 23 in. in the west-central portion to about 33 on the eastern border of the area under consideration. Nearly 80% falls during the growing season and long periods of severe drought are not common.

Alway, McDole & Trumbull (1919) found the surface 2-3 ft of upland prairie at Lincoln dried to near the point of unavailable moisture on only three occasions in the 6 yrs, 1906 to 1912. From 1909 to 1912 the moisture content of the first foot of the prairie soil was reduced to the hygroscopic coefficient only once.

Results of a 13-year study of soil moisture in upland (1916-1928) have already been presented in comparison with that on lowland.

Available soil moisture was ascertained at 3 groups of stations (3 widely distributed prairies in each) during the dry year (1940), which was the last year of the 1933-40 drought, and the moderately wet year, 1941. In 1940, at the western Iowa stations, rainfall was sufficient to keep the soil continuously moist to a depth of 6 ft, except for a moderate midsummer drought. In the drought-damaged bluestem prairies of eastern Nebraska, severe drought began in midsummer and available soil moisture was exhausted to a depth of 5 ft. In the mixed prairie on the High Plains of western Kansas, where the cover of vegetation had been reduced to about 10% normal, drought began in May. Usually the surface foot of soil alone had available water, but only temporarily and at widely separated intervals.

In 1941 in Iowa, water content was available for growth to a depth of 6 ft, at least until August. There was moderate drought in late summer at one station. In eastern Nebraska prairies both rainfall and soil moisture were less, but the general pattern of water distribution was the same. In the soil of the western Kansas stations, an excellent supply of available soil moisture usually prevailed. These data are illustrative of water content of soil which has been determined regularly in both true prairie and mixed prairie over a long period of years.

Extreme environmental conditions to which prairie vegetation near Lincoln was subjected in midsummer, 1943, and from which it has recovered were as follows. The average daily maximum temperature increased week by week from 88° to 111°F, and average day temperatures ranged upward from 77° to over 100°. The average daily minimum humidity over a period of 6 weeks did not exceed 22% and it was as low as 15%. Minimum humidity of 3-5% was recorded on some afternoons. The rate of evaporation was often twice and sometimes nearly 3 times as great as that recorded in prairie during the 3 preceding years. Water for growth became unavailable to 3 ft in depth in July and to 4 ft in August, and less than 2% water was available in the fifth and sixth foot (Weaver, Stoddart & Noll 1935).

During the years of great drought (1933-40) it was repeatedly observed that death of plants was directly correlated with depth of the root systems. The first to succumb were the more shallowly rooted plants. In true prairie these were Junegrass, Kentucky bluegrass and Scribner's panic grass. On uplands big bluestem persisted in small amounts where little bluestem died. Death resulted when no available water occurred to a depth of about 4 ft. Through its deeper roots big bluestem continued to absorb enough moisture from 1-2 ft of moist soil below this level to maintain life.

On the Great Plains marked changes in root habits resulted from drought. Roots of blue grama and buffalo grass were profoundly reduced in numbers, spread, and depth of penetration. Often only 10% or less of the former number occurred in the upper soil, lateral spread was usually not more than a third normal, and living roots were usually confined to the first 8-12 in. of soil. The reaction of each of the most important grasses of both prairie and plains to severe drought has been described (Weaver & Albertson 1943).

During the last years of the great drought of the 30's current rainfall in true prairie moistened only the upper 2-2.5 ft of soil. Below, a dry layer of soil with no water available for growth extended downward to as much as 5.5 ft. This condition was common over most upland, eastern Nebraska prairies. In areas badly denuded by drought, much soil between the widely spaced relics was almost free from living roots. Depths of roots of invading western wheatgrass, sand dropseed and big bluestem were confined by the dry layer to the upper 2-2.5 ft of soil. During the following years of heavy rainfall when the soil was again moistened deeply, the grass roots extended to their usual depths.

Growth of vegetation begins slowly in April, when the cool-season grasses and sedges resume activity. Early in June they attain a foliage height of 1-2 ft. Flower stalks of needlegrass and western wheatgrass may add 8-18 in. to this height. Early in May little bluestem attains a height of 3-4 in. and late in July about 1.5 ft. Flower stalks then elongate rapidly and reach a height of 2-2.5 ft. The average percentage of little bluestem by weight during 3 yrs was 2% in April, 26 in May, 36 in June, and 21 in July. The 13% increase of weight in August and 2% in September consisted almost entirely of flower stalk production (Flory 1936). Development of other warm-season grasses—prairie dropseed, big bluestem and side-oats grama—is very much the same. These warm-season grasses overwhelmingly predominate. Thus, the cover of grasses, as on lowland, develops steadily in summer and fruition extends into autumn. This cover differs from that of lowlands in that it is composed almost entirely of bunch grasses, it is a little less than one-third as high, and the yearly production of forage is only about half as great.

Since the bunches and tufts of grasses are spaced several inches distant, a lateral spreading from the base of the clump into the soil below these interspaces would be expected. Moreover, the great demands for water from this rich, deep but somewhat drier subsoil promotes deep rooting and extensive branching. Just as the coarsest and most poorly branched roots of grasses occur in moist to wet lowlands and the finest and most extensively branched ones occur in dry mixed prairie (as will be shown), in these less xeric upland prairies an intermediate condition prevails.

The soil (solum) is somewhat shallower than on lowlands and it depends entirely upon precipitation for its renewable water supply since the water table is far beyond the depths of the longest roots.

Experiments extending over a period of several years on upland prairies near Lincoln have shown that average daily water losses during the growing season ranged from 19 to 32 T/A (Flory 1936, Fredricksen 1938). Thus, the soil reservoir is more or less depleted of water and made ready to absorb the precipitation from subsequent showers. The frequently low soil moisture content of late summer and fall results in part from the luxuriant growth of the plant cover and an enormous expenditure of water, and only partly from a lack of rainfall.

UNDERGROUND PARTS OF GRASSES OF MIXED PRAIRIE OF HARD LANDS

Over the vast extent of mixed prairie, a large number of grasses of great abundance occur. Hence the communities are more numerous than in true prairie. They have recently been described by Weaver & Albertson (1956). Only a few of the grasses of great abundance in true prairie extend far westward over the Great Plains. Most mixed prairie grasses are of a more xeric kind. In general, tall grasses are not found except on sandy soil and sand hills, and they are different species from those of lowland true prairie. They will be considered separately.

As precipitation decreases and evaporation increases westward, the vegetation becomes sparser and less luxuriant, soils become lighter in color and decrease in depth. West of the Chernozems, Dark Brown Soils and Brown Soils have developed. Vegetation on the Dark Brown Soils while not luxuriant is still well-developed, especially the underground parts. The zone of lime accumulation decreases in depth compared with that in Chernozem. The B horizon, with less humus, is lighter brown and contains the calcium accumulations. The lime zone becomes still shallower in the Brown Soils where it may occur at 8-12 in. depths. This zone varies from a few to 18 in. or more in thickness. When it is moist, roots easily penetrate through it. The fertile Dark Brown Soils and the best Brown Soils are used for wheat production, despite the hazardous climate. Grazing predominates over the more rolling terrain of the area of Brown Soils.

Organic matter decreases gradually westward as follows: Anita Iowa stations 7.1%, Lincoln stations 6.1, Nelson stations 5.4, Phillipsburg stations 4.4, and Burlington stations 2.7%. Soil nitrogen decreases similarly from .308%, .271, .248, .198 to .130%. These decreases occurring under approximately the same mean annual temperature (48.6-50.2° F.) are due partly to the smaller amount of vegetation from which organic matter is formed and partly because it is more rapidly oxidized, both the result of an increasingly more arid climate (Shively & Weaver 1939).

The greater percentage of Plains' soils consist of clay loams, silt loams, and sandy loams, often referred to in the literature as "hard lands," which, of course, they are not, in contrast to the sandy soils ("soft lands") which have little or no cohesive properties. However, hard lands, when dry, become very compact and often a pick is necessary to remove the soil. These soils are frequently moist to a depth of several feet; the water below 12-18 in. is not removed by evaporation but only by absorption through plant roots.

Over the Great Plains wind movement is more frequent and much greater than eastward, humidity is relatively low, day temperatures and evaporation are high, and periods of summer drought are frequent. Nutrients have not been leached from the soil and plant growth is controlled largely by available soil water.

Transition from true to mixed prairie occurs gradually over an ecotone about 50 mi in width at 98°30′ W longitude (Weaver & Bruner 1954). Mixed prairie is limited on the east by soil moisture from 25 in. or more of precipitation. This is sufficient to support a continuous growth of mid-grasses under which a short-grass understory is kept out by the dense shade. Rainfall decreases to about 15 in. near the mountain border, about 400 mi westward.

Important changes from true to mixed prairie are reduction in height and volume of vegetation without decrease in average root depth. Changes in the plant cover are from more mesic to distinctly more xeric species. Sod-forming species become common in the understory; among mid grasses the bunch habit prevails. In drought and cold their foliage cures on the stems and retains its value for forage.

The term short grass applies to grasses and sedges only 5-18 in. tall, such as blue grama, hairy grama (*Bouteloua hirsuta*), buffalo grass, and thread-leaf sedge (*Carex filifolia*). Moreover, it applies only to the plant parts above ground, since short grasses usually root as deeply as mid grasses. It is important to note that both have an equal opportunity to absorb water and nutrients at the several soil depths.

BUFFALO GRASS

Buchloë dactyloides is a warm-season, sod-forming grass with foliage 4-5 in. high and flower stalks 4-8 in. tall. Roots are much finer than those of most plains grasses. They are less than 1 mm in diameter but tough and wiry. They are very numerous and occupy the soil thoroughly. Many spread almost horizontally 6 to more than 18 in. in the surface 6 in. The bulk of the main roots pursue an almost vertically downward course to depths of 4-6 ft. Very fine thread-like branches occur in great abundance (Fig. 6). Roots have been examined in many soil types in

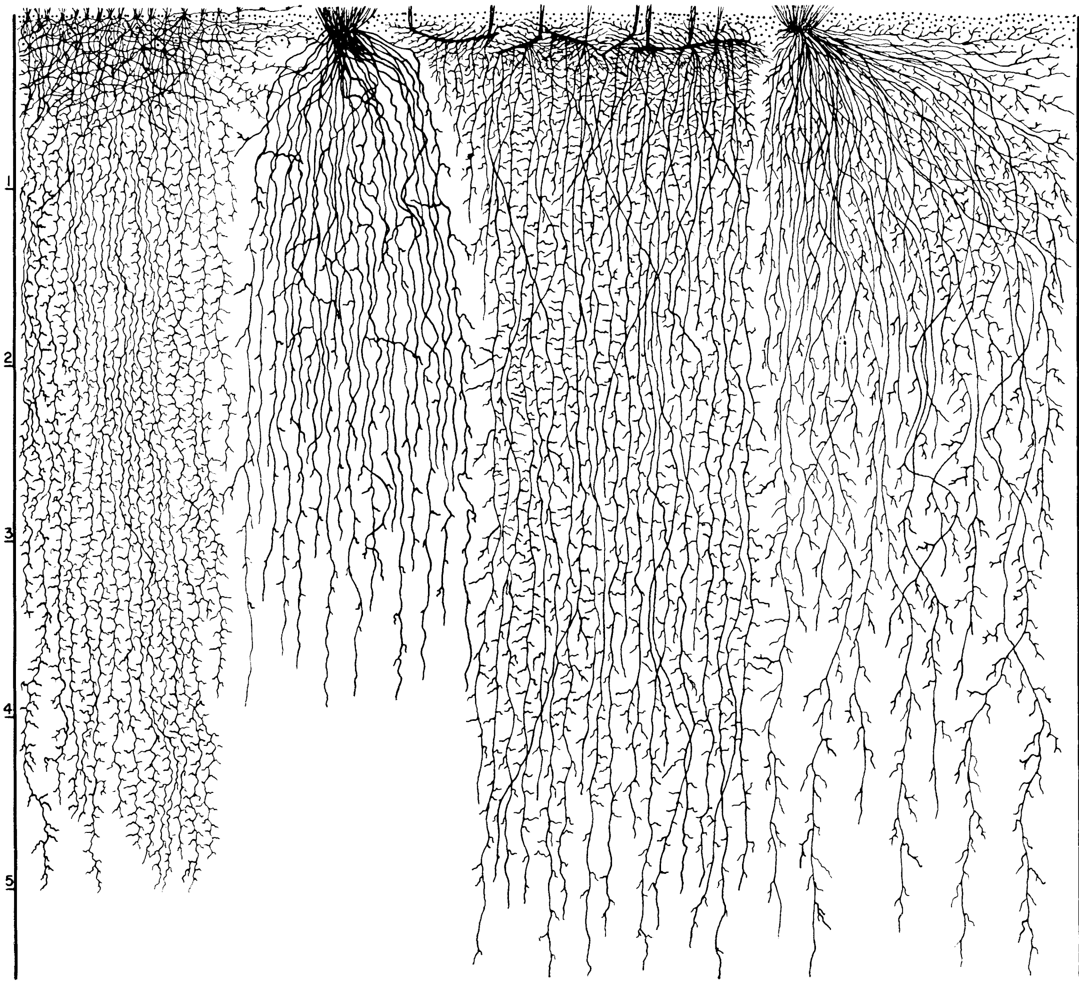

FIG. 6. Representative root systems of dominant grasses of mixed prairie communities as they occur in an in.-thick layer of soil in a trench wall. From left to right are buffalo grass (*Buchloë dactyloides*), purple three-awn (*Aristida purpurea*), western wheatgrass (*Agropyron smithii*), and side oats grama (*Bouteloua curtipendula*). The average number of roots is shown throughout, except the fine ones of western wheatgrass in the surface soil. Scale in feet. Height of foliage ranges from 4-18 in. and flower stalks are usually 5 in. to 2.5 ft tall.

the hard lands of the Great Plains at widely separated stations.

Sod produced by buffalo grass is dense, tough, and resistant to erosion. When cut a few inches deep into strips 12-15 in. wide, it can be rolled in the manner of bluegrass sod.

The root system developed so rapidly that seedlings presented a network of roots in the first 2 ft of soil at the end of the first summer and some roots were a foot deeper. The efficiency of the primary root alone is remarkable. A single seedling in 2 months tillered profusely, produced a leafy stolon 5 in. long and 137 leaves with a total area of approximately 20 sq in. Water and nutrients were absorbed by a hair-like seminal root, the others being constantly removed (Weaver & Zink 1945).

Root distribution to 4 ft in Holdrege silt loam on upland and a Chernozem Wabash silt loam of lowland was very similar. Approximately 70% by weight occurred in the first 6 in. and 11.5% in the second. Then foot by foot at increasing depths it was 11, 4, and 3%.

BLUE GRAMA

Bouteloua gracilis is the most drought resistant of all the plains grasses in the Nebraska-Kansas-Colorado region (Mueller & Weaver 1942; Weaver & Albertson 1943). Like buffalo grass it has small leaves which develop near the soil surface. Foliage height is 3-5 in. and flower stalks are 8-14 in. high. The tufts are closely grouped and a basal cover of 60-80% is attained in good stands. Roots of blue grama are so similar to those of buffalo grass that they are almost indistinguishable. The wonderfully developed network of shallow roots and their spreading habit are the same. Thus, the bare places between the mats of both blue grama and buffalo grass, which are of usual occurrence, are normally as well occupied by roots as the soil beneath the plants. Both plants are thus

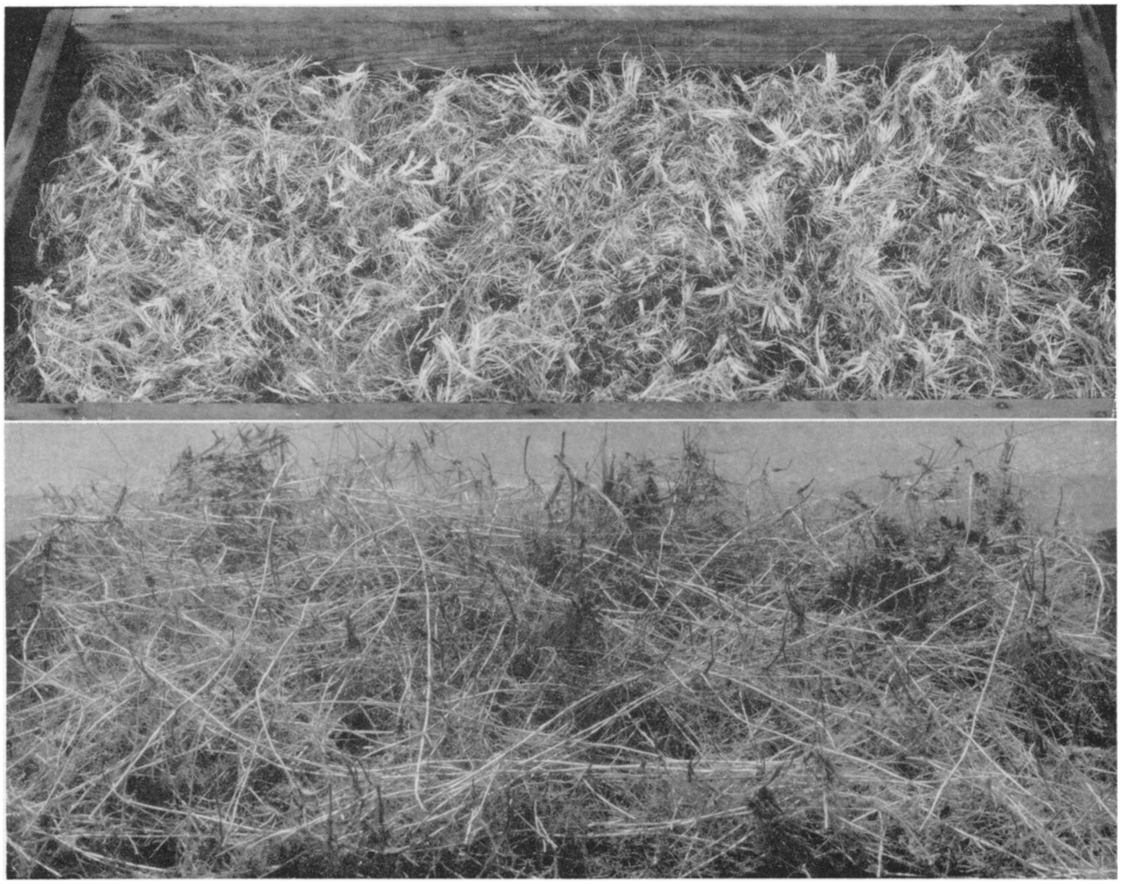

FIG. 7. (Upper) Underground parts of an excellent stand of blue grama *(Bouteloua gracilis)* in .5 sq m of surface soil in mixed prairie at Phillipsburg, Kansas. (Lower) Invasion of western wheatgrass into big bluestem sod. The soil was washed away from this .5 sq m area, revealing the dead underground parts of the former dominant (black) and the shining white rhizomes of wheatgrass at Belleville, Kansas.

able to benefit from water furnished by light showers. Under the increased precipitation of true prairie eastward, this wide spreading of lateral roots rarely occurred. At the many stations in mixed prairie where root depth was ascertained, it ranged between 4-6 ft.

A comparison was made of 36 samples of (0.5 sq m) of underground parts to 4 in. depth. They were taken at groups of stations from Lincoln to Colorado Springs. No consistant differences in dry weights of either blue grama or buffalo grass in the several areas were found. Yields averaged about 2 T/A. The almost continuous network of stem bases and fine roots in the first 4 in. of soil under a good stand of blue grama is shown in Figure 7.

From monolith samples of blue grama in mixed prairie, it was ascertained that about 79% of the weight of underground parts occurred in the first 6 in. of soil and 10% in the second 6-in. layer. The second foot yielded 7%, the third about 3% and the fourth only 1%.

PURPLE THREE-AWN

Aristida purpurea, a bunch grass 12-20 in. tall, has somewhat coarser roots than blue grama. Some extend outward 5-8 in. before turning downward; others grow directly downward to depths of 4 ft and some to 5 ft. There was little branching in the surface 4 in. of soil. Usually the root system lacks the abundant laterals so pronounced on short grasses. This grass is also less drought resistant than buffalo grass and blue grama (Fig. 6).

WESTERN WHEATGRASS

Agropyron smithii is one of the few sod-forming species. This cool-season grass is 2-3 ft tall in good years, but is much dwarfed by drought. The extensive, much branched, tough rhizomes are 1-2 mm thick. They occur within a few inches of the soil surface. From these and the bases of the plants many roots run out somewhat horizontally in the surface 12-18 in. of soil (Fig. 6). They are profoundly branched to the third and fourth order and thus furnish an excellent surface absorbing system. Other roots extend obliquely and still others almost directly downward. Depth of penetration varies with soil from 5-7 ft. The roots are branched throughout.

Roots were examined in many places in 4 states. The chief differences in the root habit of this grass in both upland and lowland true prairie, as compared with mixed prairie, were the lack of an extensive surface absorbing system and the greater depth of penetration (8-9 ft).

Extensive studies in true prairie of eastern South Dakota, Nebraska and Kansas have shown that wheatgrass composed scarcely any part of this grassland. Only the great losses sustained by the bluestems and the bare areas thus produced made possible the remarkable spread of wheatgrass (Fig. 7). But in mixed prairie it has always been widely spread, and with an understory of short grasses, chiefly buffalo grass, it dominates wide areas, especially on heavy compacted soil. The vitality of the rhizomes and their resistance to drought is remarkable (Mueller 1941).

The amount of underground parts of wheatgrass in the surface 4 in. of soil at mixed prairie stations near Burlington, Colorado, was 2-2.2 T/A.

Weight of underground parts in the surface 6 in. averaged 55% of the total. The second 6 in. yielded 15% and the second foot 16%. The remainder was in the deeper soil. Thus, the root-weight of this drought-evading grass is more deeply placed than that of most other species.

SIDE-OATS GRAMA

Bouteloua curtipendula is a very drought resistant, warm-season, mid grass. It usually occurs in small to wide bunches and attains a height varying from 1.5 to more than 2 ft. Roots are not so fine as those of buffalo grass or blue grama, but about 1 mm in diameter. Many roots spread outward 1-1.5 ft in the surface 2-4 in. of soil. Others run obliquely or nearly vertically downward. All are extremely well branched, mostly with rootlets 1-3 in. long. Depths of penetration of 4.5 to 5.5 ft were attained (Fig. 6).

NEEDLE-AND-THREAD

Stipa comata is a cool-season grass which occurs on both hard land and sand. The bunches are small, usually only 1-3 in. in diameter, and not closely spaced. Plants vary in height from 1-3 ft. This grass has a widely spreading, deep, and exceedingly well-branched root system. The main roots are about 1 mm in diameter. Many have a lateral spread of 14 in. in the surface 6 in. of soil and 18 in. in the first foot. To a depth of 2.5 ft the main roots are only a few mm apart and the interspaces are well filled with horizontal, well branched rootlets. Many roots extend into the fourth and fifth foot of soil.

OTHER GRASSES

Thread-leaf sedge *(Carex filifolia)* is grass-like in appearance and habit. It grows in dense bunches 4-6 in. in width and has about the same stature as blue grama. The tough, black, wiry roots bind the soil more firmly than most grasses. They are a mm or less in diameter but occur in enormous numbers. They seldom descend vertically but run obliquely away from, as well as under, the plant to distances of 2-2.5 ft. They are profusely branched and end in brush-like mats. Many roots crisscross at various angles and reach depths of 4 ft. A few are 5 ft deep.

Green needlegrass *(Stipa viridula)*, a bunch former 1.5-3 ft high, has a root system very similar to that of needle-and-thread.

The soil beneath bunches of sand dropseed *(Sporobolus cryptandrus)* and at least 12 in. on all sides is filled with a vast network of small roots and masses of finely-branched rootlets to a depth of 3-4 ft. Some roots extend even deeper. This mid grass attains a height of 1.5-2.5 ft.

The widely distributed Junegrass has been described. In mixed prairie the plants are shorter and the bunches small. But the widely-spreading, rather shallow root system changes but little, except to branch more profusely in the surface soil.

Roots of ringgrass *(Muhlenbergia torreyi)* occupy the soil to depths of about 4 ft. Galleta *(Hilaria jamesii)*, a xeric, sod-forming grass, also has a root depth of about 4 ft.

Thus, each of the dozen grasses described (except Junegrass) fits well into the diagram representing Great Plains grasses. All attained root depths of at least 4 ft in the many soil types in which they were examined.

OTHER STUDIES IN HARD LANDS

Root systems of a large number of grasses in 3 communities at Hays, Kansas, have been described by Albertson (1937). Soil profiles and root depths in each community are given. In the short-grass (blue grama and buffalo grass) type of the drier uplands, grasses with foliage heights of 3-5 in. were rooted 4-5 ft deep. In the little bluestem community of moist, rocky hillsides, where the foliage of little bluestem was 8-16 in. tall, the grasses were rooted 3-5 ft deep. Heights of 2-3 ft were attained by mature tall grasses growing on lower slopes and in ravines, which received runoff water. Root depths of 5-6 ft were attained by big bluestem, switchgrass and western wheatgrass.

Extensive, earlier studies have been made by Shantz (1911) in the hard lands, sandy loam soils, and sand of eastern Colorado. He studied the natural vegetation as an indicator of the capabilities of land for crop production.

DISCUSSION AND INTERPRETATION

A comparison of the amount and time of available soil moisture in the Great Plains with that in true prairie and factors contributing to a drier atmosphere will aid in understanding the greater xerophytism of plants of mixed prairie and their root relations in shallower and drier soil.

Altitude increases from about 1,500 ft on the Plains eastern border to about 5,500 ft near the mountains in Colorado. This shortens the growing season a few weeks. Nights are cool but days are hot. Soil temperatures at Colorado Springs (June 5 to August 5) showed extreme variations in the 24-hr period from 60° or 70° F to 90° or 95° or even more at 4 in. depth. Not infrequently the surface soil (0.5 in. depth) ranged from 55°-60° F in early morning to 120°-125° 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 soil combine to increase the day soil temperatures greatly over those of true prairie. However, it seems quite certain that water content of soil and air, and not temperature, is by far the most important factor in root development.

The fine textured soils have a high water-holding capacity. Considerable moisture is held from late fall, winter, and early spring before transpiration losses from vegetation become great. Absorption of rain falling in short, heavy showers is relatively inefficient both because of high runnoff and great loss by evaporation. When the supply of stored moisture is exhausted vegetation undergoes long periods of summer drought.

Water content of soil in prairie and plains, with other environmental factors, was ascertained at Lincoln, Nebraska, and in mixed prairie at Phillipsburg, Kansas, and Burlington, Colorado, during 3 years of rather normal precipitation. Rainfall is 5 in. less at Phillipsburg and 11 in. less at Burlington than the 28 in. at Lincoln.

In 1920, at Lincoln, a sufficient amount of water to promote good growth was available at all depths at all times. At Phillipsburg, July and early August were periods of drought and at times, of actual water deficiency. Available water supply was favorable at Burlington until June, but after this time marked deficiencies were of frequent occurrence.

In 1921 at least 5 and usually 8-10% available water existed at all times to depths of 4 ft at Lincoln. At Phillipsburg the nonavailable point was approached once in July and twice in August; no water was available to a depth of 4 ft in late summer. At Burlington no water was available at any time for growth in the third and fourth foot of soil, and after June 30 it was depleted repeatedly in the first and second foot.

In 1922 the season was fairly favorable for growth, except the latter part, when severe drought occurred at all stations, though it was relatively less marked at Burlington. A margin of 5-11% available water existed at all times to a depth of 4 ft at Lincoln. At Phillipsburg drought began late in June and continued throughout the summer. There was often no water available to a depth of 4 ft at Burlington. The soil in spring and early summer was, as usual, quite moist, but deficiencies were marked and almost continuous after the middle of June.[1]

The value of water content to the plant, however, is not determined entirely by its quantity but also by the rate of loss both through the plant and by surface evaporation. These in turn are controlled by humidity as affected by temperature, wind, etc., all of which are more or less integrated in evaporation. Evaporation was lowest at Lincoln and highest at Burlington, where it was 2-2.5 times as great. During the 3 growing seasons, conditions for plant growth in respect to rainfall, soil water, temperature, humidity, wind, and evaporation were most favorable at Lincoln, intermediate at Phillipsburg, and least favorable at Burlington.

The weekly record of available soil moisture to 5 ft in depth in mixed prairie at Hays, Kansas, extends (except for 1 yr) from 1935 to 1954, inclusive (Weaver & Albertson 1956). Also some earlier determinations are available (Albertson 1937; Weaver 1919).

The combined differences of lower rainfall, drier soil, greater evaporation, and less favorable temperatures for growth in mixed prairie are reflected both in the vegetational cover and root habit.

In mixed prairie, it was early ascertained that water relations of soil and air were controlling in plant development, other factors being merely contributory (Weaver 1924; Clements & Weaver 1924). For example, root development of winter wheat in the fertile silt loam soils in 20 fields from true prairie throughout western Kansas and eastern Colorado was ascertained. Average depth of roots was 5.3 ft and average lateral spread in the surface soil was 6 in. under a precipitation of 26-32 in. They were 4.2 ft and 9 in, under 21-24 in. of rain, and 2.3 ft and 12 in. in Colorado where precipitation was 16-19 in. Tops were proportionately smaller. Similar results were obtained with a variety of grass crops grown experimentally at Lincoln, Phillipsburg and Burlington (Weaver 1920).

The greatly increased branching habit of the shorter but more widely spreading roots in dry land is readily produced experimentally. For example, corn, with similar hereditary characters, was grown in moist, rich, loess soil with an available water content of 19 and 9%, respectively. After 5 weeks the first lot had a total root area 1.2 times greater than that of leaves and stems. Root area in the drier soil was 2.1 times greater than the tops. In the more moist soil primary branches furnished only 38% of the total root area, but 75% in the drier soil. Thus, a low water content, within certain limits, stimulates increased root branching (*cf.* Jean & Weaver 1924).

All of the Great Plains grasses are notably successful under the semiarid environment. The numerous cool-season grasses—needle-and-thread, western wheatgrass, Junegrass, thread-leaf sedge and others—begin growth early with the spring rains but may become semidormant in dry midsummer and thus evade the drought. They renew growth in autumn. The three grama grasses and buffalo grass are warm-season plants but they are extremely drought resistant. They endure long periods of dormancy, renew growth when rains come, and produce seed in early summer, late summer, or in fall.

This greater ability to cope with drought was revealed on a magnificent scale during the 1930's when grasses of true prairie were so sorely depleted. Not only the short grasses but also side-oats grama, western wheatgrass and sand dropseed spread over the drought-bared areas and flourished on the scanty precipitation during the drought years.

Volume of vegetation in mixed prairie is much less than that of true prairie and by weight annual forage production is normally half and often far less than

[1] Physical and chemical analyses of these soils and tables of water content may be found in "Experimental Vegetation" (Clements & Weaver 1924).

half as great. The grasses are wonderfully adapted to benefit from light rains. Water is absorbed at all soil levels and used as soon as possible for forage production. Root development in proportion to that of tops is greatly increased over that of true prairie. Root extent of short grasses and sedges is 4-16 times as great as plant height. That of mid grasses is 2-4 times as great. This grassland flora can adapt itself to dry cycles as well as to moist ones, a property not possessed by the plant cover substituted by agriculture.

UNDERGROUND PARTS OF GRASSES OF MIXED PRAIRIE OF LOESS HILLS

One physiographic section of the Great Plains is known as the Loess Hills. It must be given special attention for here the vegetation, although not different from that of the hard lands, is much more deeply rooted.

An area of loess hills several thousand square miles in extent lies southeast of the Nebraska sand hills and some loess hills extend southwestward near Holdrege, Nebraska, and Atwood, Kansas. Extensive studies of the origin of this loess by Lugn (1935) and Condra, Reed & Gordon (1947), have been summarized by Reed for the writer (Weaver & Bruner 1948). These loess depositions correlate with interglacial time; and wind, correlated with other factors, was the major force in the genesis of this loess.

The soils have developed from loess. Both soil and parent material to great depths are mellow and easily penetrable to both water and roots. Well developed soils of the upland are predominately of the Holdrege series, but over parts of the area the immature, light-colored Colby soils occur. They are approximately neutral in reaction. Both soils are very fine-textured. The degree of aggregation is very low. Organic matter is about 4-5% in the surface foot, and nitrogen 0.11-0.19%. The friable, dark-grayish-brown silt loam (A horizon) is about 12 in. deep in the Holdrege type. The subsoil (B horizon) of silty clay loam extends to a depth of 3 ft or more. The lime layer of this Chernozem occurs often between 3-6 ft in depth.

Mean annual precipitation is 23-24 in., nearly 80% occurring between April 1 and September 30. In May and June, drought is uncommon, distribution of rainfall in July is less favorable, and during August and September long periods of drought often occur. These are the conditions of soil and water supply for root development.

Depths of penetration of roots were reported by Weaver & Bruner (1948) as follows: buffalo grass 6.3 ft, blue grama 7, big bluestem 7.5, and western wheatgrass 10.3 ft, all from upland soils. Hopkins (1951) found that blue grama reached depths of 6.5 ft, little bluestem 8, side-oats grama 8, and big bluestem 10 ft. Even Junegrass added a foot to its usual root depth, extending downward to 2.5 ft. A somewhat similar increase in depth of various forbs was also noted; several species had root depths of 21 ft. Tomanek & Albertson (1957), working in loess hills at Atwood in northwestern Kansas, noted very similar or even greater depths of root penetration.

The great depth of rooting in loess may be attributed to both physical and chemical conditions of the substratum. Water penetration is greater than on hard land. The percentage of readily soluble phosphorus in the organic matter is unusually high and may be a factor in promoting deep root growth. Effect of phosphates in promoting root growth in length and number of branches has long been known.

UNDERGROUND PARTS OF GRASSES OF SAND HILLS

Many areas with sandy soil or sand hills occur in every state in the Great Plains. The largest lies in central Nebraska where wind-blown, sand-hill topography extends over more than 18,000 sq mi. Some hills reach a height of more than 150 ft. Mixed prairie vegetation on sand is subjected to the same aerial environment as that of surrounding hard lands. Wind is one of the most important environmental factors of sandhill vegetation through its effect on shifting the sand. Geological evidence reveals that sand habitats have existed in this region since early Tertiary times.

Because of wind erosion, little soil development has occurred. The hills are composed mostly of fine-grained sand of a light-yellow color. The sand on the tops of dunes has a coarser texture than that on the sides and adjacent dry meadows. This is the result of the selective action of wind erosion. The finer sands contain sufficient silt to give them a light-gray color. Very little organic matter occurs in dune sands, but in the more stabilized dry meadows at their base small quantities of humus are present in the surface soils, which are classified under the Valentine soil series. Hygroscopic coefficients are 0.7-1.3% except the harder Valentine soils where they range from 3-3.5%.

Vegetation on sand presents several communities from blowouts and drifting sand to well stabilized grassland. Plants grow thickly only in the valleys. Vegetation is sparse on the hillsides and very thinly spread on the hilltops. "Communities characteristic of the true prairie (in its western extension) dominate the upper portions of the wet meadows and form a narrow zone of transition between the mesophytic, tallgrass communities at slightly lower levels and the less mesophytic, tall grasses of the dunes" (Tolstead 1942). Special attention will be given to the dominant grasses of stabilized climax communities. Many species are found only on sand, and those also common to hard lands often have modified root habits in sand.

Extensive studies have been made in the several communities and at various stations with rainfall varying from 15 to 20 in. or more. The earliest examination, 40 mi southeast of Colorado Springs, Colorado, was made in poorly vegetated, low sand hills. Mean annual precipitation was 15 in. but in some dry years it was only 8 in. This study revealed much shallower root development than that of similar plants in stabilized vegetation at Yuma, Colorado, Valentine, Haigler, Seneca, and Central City, all in Nebraska where mean annual rainfall varied from about 17-26 in. (Fig. 3).

Sand Bluestem

The 3 most abundant tall grasses are sand bluestem, *(Andropogon hallii)*, sand reed *(Calamovilfa longifolia)* and blowout grass *(Redfieldia flexuosa)*. All are equipped with strong, extensive rhizomes. Sand bluestem forms loose open bunches with only a few coarse stems in each bunch. Thus, the basal cover is always small. The stems reach heights of 3-5 ft when flowering occurs after midsummer. The rhizomes, 4-9 in. long, elongate in spring and produce new stems and roots while the older rhizomes and roots slowly decay. Thus, there is a constant, if slow, migration. The outward spreading of the roots and the method of branching is shown in Fig. 8.

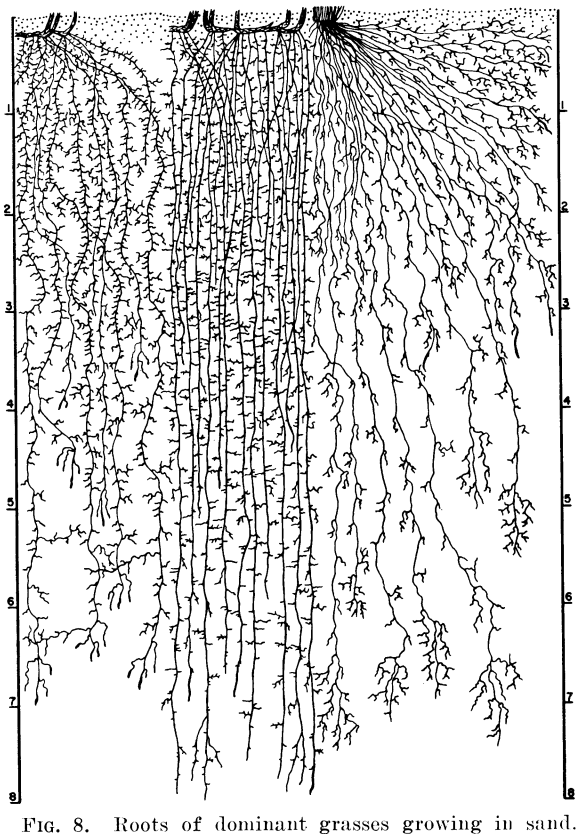

Fig. 8. Roots of dominant grasses growing in sand. From left to right they are sand bluestem *(Andropogon hallii)*, sand reed *(Calamovilfa longifolia)*, and little bluestem *(Andropogon scoparius)*. Average number of roots in an in. layer of soil in a trench wall is shown from the shallowest to the greatest depth. Scale in feet.

Depths varying from 6-10 ft have been recorded in the many places where it and the following species were examined. The root branches, short and rebranched to the third or fourth order, are indeed numerous, sometimes 80/in. of main root.

Sand Reed

Stems of sand reed usually arise singly from the strong root stocks and thus produce very open vegetation. The large panicles are held aloft 3-4.5 ft when flowering occurs in July to September. Long, mostly vertically descending roots arise from the coarse rhizomes on plants in stabilized vegetation, but others may spread widely (Fig. 8). Where the plants have been subjected to shifting sand, roots and rhizomes may be intermixed in dense mats to a depth of 2-3 ft. Root depth varies greatly, from 4.5-10 ft. Main roots are clothed throughout with multitudes of short, well-branched roots, that extend outward 1-3 in., mostly in a horizontal direction. Some roots, only 2-3 mm in diameter, end in starch-laden tips which are sometimes 8 mm thick. These occur on several other grasses growing in sand.

Blowout Grass

Redfieldia flexuosa is at home in shifting sand. It is found rarely in stabilized vegetation. The usually sparse and small clumps of a few stems each are connected by coarse, tough rhizomes which are 10-40 ft in length. The depth at which they occur depends upon the degree of burial by shifting sand—sometimes to 3-4 ft. Often they are exposed to great lengths on the sand surface. Whether horizontally, obliquely, or vertically placed, they produce numerous long roots densely clothed with short branches, which extend horizontally outward to vertically downward, some to depths of 5 ft or more. Thus, this pioneer adjusts itself to life in the shifting but moist soils of the sand dunes, where it forms very open but often nearly pure stands. The flexuose culms are 2-3 ft tall.

Sandhills Muhly

Muhlenbergia pungens is a mid grass with strong but short rhizomes. It forms bunches 5-15 in. wide and may aggregate into large clumps. The tough, wire-like roots occur in clusters; some penetrate almost vertically downward to depths of 3-3.5 ft, others run off nearly horizontally a foot or two on all sides of the bunch, while the remainder pursue obliquely downward courses. Thus, a large volume of sand is occupied by roots. This grass forms open communities which replace blowout grass but in turn it is replaced by the more deeply rooted sand reed, sand bluestem and little bluestem in fully stabilized places.

Little Bluestem

Root habit of little bluestem differs from that in true prairie in three ways. The main roots are less abundant, they spread more widely, especially in the surface soil, and penetrate more deeply in the sand (Figs. 4 & 8). In clay or silt loam the lateral spread of roots of little bluestem is normally only about 1 ft, but as the substratum becomes sandier the lateral spread and proportion of roots in the shallower soil increases. A maximum lateral spread of 3 ft may be attained. Its extreme range in depth from 3-4 ft in rock-filled soil to 8 ft in sand hills is indeed remarkable. The great plasticity of the root system is undoubtedly a factor accounting for its wide distribution.

OTHER GRASSES

Needle-and-thread *(Stipa comata)* has a root habit in sand not greatly unlike that described in hard lands. It has a wider lateral spread in the deeper sand and the main roots frequently break up into 3-5 profusely branched laterals. Depths of 4-5 ft are attained in stabilized vegetation.

Blue grama often roots 4.5 ft deep in sand; hairy grama *(B. hirsuta)* is much more shallowly rooted.

Sand lovegrass *(Eragrostis trichodes)* grows in widely spaced bunches on north slopes of dunes where it is protected from drying southerly winds. According to Tolstead (1942) the roots spread about 2 ft on all sides of the bunch in the surface foot but total depth did not exceed 2 ft. Junegrass and sun sedge *(Carex heliophila)* are also shallowly rooted.

From these typical examples of rhizome habit and root development, it may be concluded that, except for relatively few species, the usual root depth, lateral spread and nature of branching is well illustrated by the species shown in Fig. 8.

OTHER STUDIES IN SAND HILLS

A study of the root systems of various sand-hill communities and the environment under which the vegetation has developed has been made by Tolstead (1942), with findings in close agreement with those of the writer. He states that "the highly diversified and well developed vegetation of the dunes points to a great age and an early historical development of the sandhill flora." The tall sand-hill grasses are entirely characteristic of sand-hill habitats. Root habits in the several communities resulting from succession and degeneration are described.

DISCUSSION AND INTERPRETATION

Almost all the rainfall immediately enters the sand. After the storm, evaporation dries out the surface sand with great rapidity but to a slight depth only. An excellent mulch is formed by the layer of dry sand, which greatly retards further evaporation. Except in extreme drought, the sand at a depth of a few inches is nearly always moist. The efficiency of sand in absorbing rainfall without loss by runoff and in almost entirely preventing evaporation is the compensating factor which permits the growth of tall grasses.

Although growth of the dominant grasses occurs throughout the summer, and in dry years somewhat according to the occurrence of rain, flowering occurs in mid and late summer or autumn. Water loss from the sparse cover is undoubtedly much less than from upland true prairie. During summer there is probably little loss of water due to its penetration beyond the depth of the roots of the tall, postclimax grasses.

Tolstead found that pioneer vegetation in blowouts and communities in early phases of development were slow to deplete moisture. It was available throughout the growing season at depths beyond 2 ft. But xerophytic grasses in well developed communities with large leaf and root surfaces readily absorbed available moisture throughout the 4- to 5-ft levels and endured long periods of drought. He concluded that the quantity of available moisture is the most important single environmental factor in determining the composition of the plant cover.

Ecological relations of the dominant grasses can be interpreted only after their underground relationships are understood. The tall grasses have stems widely spaced on their rhizomes and roots also are well spaced. In the several surface feet of sand they compete for water with more shallowly rooted species, such as hairy grama and sand dropseed, but they also absorb water at greater depths. During long periods of drought they may rely chiefly upon the deeper water supply. Although many sand-hills dominants thrive when grown in rich loam soil, they are unable to withstand competition of tall and mid grasses of true prairie growing in the sand-hill meadows. Moreover, most of them are too mesic to endure the severe competition of climax grasses of the hard lands.

The tall grasses, sand bluestem, sand reed and blowout grass, all have rhizomes. Sand-hill muhly, a mid grass, also has strong rootstocks. Little bluestem and needle-and-thread are bunch grasses, but like the preceding species their roots extend deeply into the sand. Other important bunch grasses are sand lovegrass and sand dropseed. They are less deeply rooted. The short grasses, blue grama, hairy grama, and sun sedge, occur in the understory. Buffalo grass does not thrive in sand and occurs only rarely. The tufts and bunches of all the preceding grasses are so widely spaced in the several communities that basal area of vegetation is usually less than 5% except in compacted soil. Forage yield is much less than that of upland true prairie where 4 to 7 A support one animal unit. In the sand hills 17 A per animal unit are required.

ROOT-SOIL RELATIONS IN VARIOUS SOIL TYPES

Knowledge of the soil as a medium for growth of roots has increased very greatly in the past 30 yrs. Absorption of both water and nutrients at great depths has been adequately demonstrated (Crist & Weaver 1924, Hunter & Kelly 1946). Moreover, it has been found that during the period of heading and ripening of seed the deeper portions of the root system often absorb most actively. The monolith method, now widely used, permits the studying of the intimate relations of roots and soils and of measuring root production quantitatively at various soil levels. With a better understanding of the relationships of one soil type to another, and especially the greater accuracy and detail with which soil profiles are now described, it is possible to understand more fully the relationships between roots of grasses and the soil in which they grow.

The solum (A & B horizons) is especially important in root development, since most of the changes resulting from the growth of grasses throughout the centuries have occurred here. But roots of many grasses and especially perennial legumes, composites and others, extend far into the C horizon as well. A deeply penetrating root system encounters numerous environments. Each may affect the nutrient, water, and air supply as well as the ease or difficulty of root penetration. The effects of these environments on a single representative root system, as revealed by the monolith method, afford an excellent opportunity for a study of problems relating to root distribution.

Approximately 50 monoliths with roots of 12 species of grasses from 16 different soil types have been studied and described in three general areas. One was in the vicinity of Lincoln near the Prairie soil—Chernozem boundary in eastern Nebraska. Another was 65 to 125 miles southwestward in Chernozem soils; the third was in the loess hills in central Nebraska where both Chernozem and Dark-Brown soils are found. Thus, root systems were obtained from many soils of widely different profile characteristics. Marked differences in root habit of the same species of grass growing in different soils were observed. Soil profile descriptions and photographs of roots taken from them are filed with the Soil Conservation Service of the U. S. Department of Agriculture, Lincoln, Nebraska (Weaver & Darland 1949, Weaver & Voigt 1950).

Examples of Root Habits in Azonal Soils

A usual root depth of western wheatgrass in Zonal Prairie soil or Chernozem is 7-8 ft. Near Bruning, Nebraska, in Scott silty clay loam with a very compact claypan at 5-41 in. in depth, the root system occurred entirely in the first 31 in. of soil. In a well-drained Rendzina soil, near Belleville, Kansas, where the clayey subsoil overlaid unweathered limestone, roots extended downward only 38 in. In the loess hills near Kearney, Nebraska, roots penetrated the Colby silt loam, a Zonal Chernozem soil, to 10 ft. But on a hillside where the topsoil had been washed away and the fertility level was low in the thin, poorly developed new A1 horizon, the few roots produced by the dwarfed plants were only about 4 ft deep. Roots of blue grama responded in a similar manner in this azonal soil.

Buffalo grass in Holdrege silt loam of upland and in Wabash silt loam of lowland extended its roots downward to 6 and 6.5 ft, respectively, and produced more root-weight on the lowland. Root weight decreased with depth as is usual for all grasses in zonal soils. But in Sherman silt loam on a nearby hillside where there was a buried A horizon at 17 in. depth, there was an increase in weight in the second foot of soil over that in the second 6 in. This was probably due to the buried A horizon of an old soil.

Purple three-awn in zonal soil spread but little in the surface soil but distributed its roots below the plant to depths of about 4 ft. But in azonal loess soil only a few roots extended downward and 95% by weight ran outward horizontally in the surface 6 in. of soil, some to a distance of 3.5 ft. Since the soil was easily penetrable and moist several ft in depth, the response was undoubtedly due to a nutrient deficiency (*cf.* Voigt 1951).

Differences in soil compaction, water content, and amount of clay and nutrients, often cause marked differences in root development. The marked effects of soil upon root habits is especially pronounced where vegetation develops on intrazonal soils. These are soils with one or more horizons overdeveloped and in marked contrast to "normal" or zonal soils. Soils with claypans furnish excellent examples. In the Crete silty clay loam soil on a hillside near Lincoln, roots of western wheatgrass had three very different habitats. The A horizon, 14 in. thick, consisted of a black, mellow, well granulated silty clay loam. Here root development was similar to that in a zonal soil; about 500 main roots and their network of branches occurred in a foot-wide monolith 3 in. thick (Fig. 9).

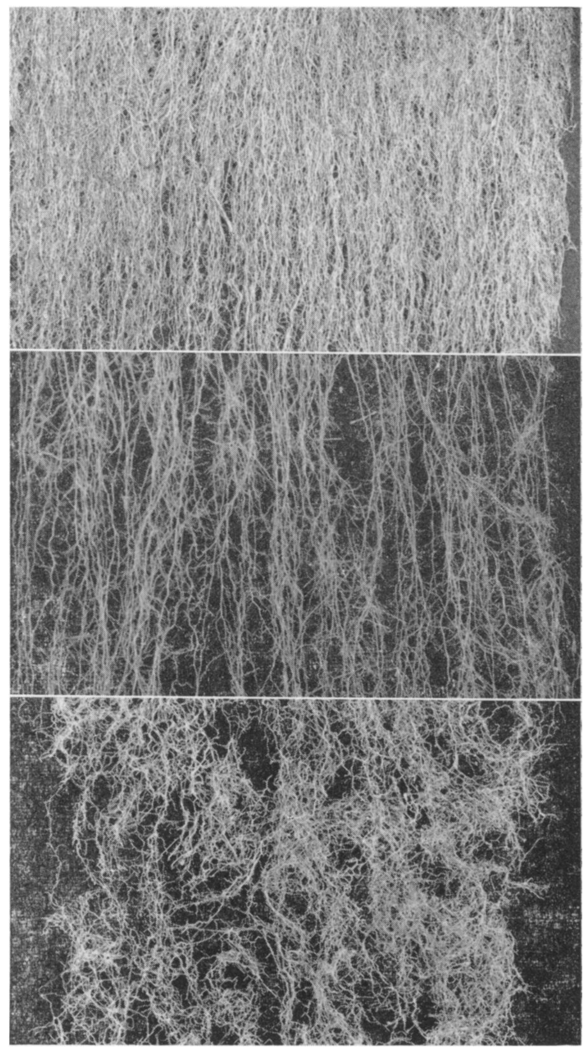

FIG. 9. Roots of western wheatgrass *(Agropyron smithii)* from a Crete silty clay loam soil with a claypan. They were in a foot-wide monolith 3 in. thick from the central portion of the A horizon (upper), the central part of the B horizon (middle), and the lower portion of the C horizon (lower). Roots are about one-fourth natural size.

A very distinct and abrupt transition to a blocky prismatic structure occurred in the B horizon, which was 16 in. thick. Clay content increased rapidly with depth. The vertical prisms were 8-12 in. long and 3-4 in. thick. The soil was very heavy and although moist it was removed only with great difficulty. Only about a third of the roots entered this claypan and the number that continued into the C horizon was only about half as great. Some roots penetrated downward through the prisms, despite their compact structure, but many grew downward on their surfaces and were attached to the soil only by their finer branches. Here they branched abundantly but only in one plane.

The C horizon consisted of loess, a silty clay loam of massive structure. It was mellow and moist and contained an abundance of lime, often in concretions. The soil broke up into blocky pieces. This offered a third environment for root development, and the type of root distribution was distinctly different from that in either the A or B horizon. The roots were often flattened on the faces of small blocks which cleaved in all directions; a few penetrated into the blocks. Thus, these white roots branched in all planes and, when freed from soil, appeared as a glistening white mass (Fig. 9). Often greater root development occurs below the claypan than within it. The root weight in this sample in the first foot of the C horizon was 30% greater than that in the lower foot of the B horizon.

SEGREGATING FACTORS INFLUENCING DISTRIBUTION

Although it is difficult to segregate the various physical and chemical factors that influence root penetration and distribution, yet it seems certain that the surface environment is only one set of conditions which influence root development. A study has been made of some physical and chemical properties of several prairie soils and related to the distribution of grass roots. Marked variations in profile characteristics, and abrupt boundaries between horizons, especially with regards to physical properties were found in Crete and Butler soils. "In a Butler soil near Carleton, Nebraska, limited root development of western wheatgrass in the upper region of clay accumulation was a feature of this profile. A reduction of branching was observed at a depth of 8 in. and extended to a depth of 20 in. Associated with this was a greatly reduced phosporus supply and a restricted pore space. Increased branching of roots in the lower B horizon (20-28 in.) was associated with an increased percentage of pore space and with a soluble phosphorus content of nearly 2.5 times that present in the region of restricted development. Root weight was one-third greater in the lower B horizon within the depth of 20-28 in., than the weight of roots from an equal volume of soil in the region of restricted growth" (Fox, Weaver & Lipps 1953).

Effects of different soil types on root distribution are often great. Roots of Kentucky bluegrass and blue grama were studied in a compact Carrington silty clay loam, and in a deep, well drained Judson silt loam, a type occurring between upland soils and alluvial bottom lands. The Carrington was an old soil developed on glacial soil before the Peorian loess was deposited upon it. The A horizon was 7 in. deep and the B horizon extended to only 22 in. The entire solum, though granular in structure, consisted of heavy silty clay loam. It was very compact and water penetration was poor. In the Judson soil the A horizon of the mellow granular silt loam was 20 in. deep and the granular silty clay loam of the B horizon 10 in. deeper. Silty clay then occurred to the depth of the solum at 4.5 ft. These two stations were only a few miles distant from Lincoln.

The differences in root penetration, 22 in. in Carrington and 48 in. in the Judson soil reflect wide differences in soil properties. Moreover, the bulk of the roots, about 82% by weight, were confined to the upper 7 in. in the first type. The deep A horizon (0-20 in.) of the Judson soil was filled with a great mass of roots with a total weight more than 3.5 times as great as that in the shallower soil.

"Total pore space in the 0-4 in. depth of the Carrington soil was somewhat less than at a similar depth in the Judson soil; but throughout the remaining depths, percentage of pore space and clay content in the two soils were not greatly different. The total nitrogen content of the Carrington was lower than in the Judson soil. Soluble phosphorus content was extremely low in the Carrington soil; and at a depth of 20-24 in., which marks the deepest penetration of roots, the level of phosphorus was only 10% of that at the same depth in Judson soil.

"The Judson soil was well supplied with mineral nutrients at all depths. Although the soil was slightly acid, the exchangeable bases were sufficient for plant nutrition and nitrification of organic matter. Total soil nitrogen was high and the phosphorus level in the surface soil was sufficient throughout the profile to promote excellent root development at all depths.

"In the Carrington soil, only the levels of calcium and magnesium appeared to be optimum for root growth. The soluble phosphorus content was extremely low. The exchangeable potassium was also very low . . . and it may have been a limiting factor in root growth" (Fox, Weaver & Lipps 1953).

ROOT DEVELOPMENT AND REMOVAL OF TOPS

One of the most important factors affecting root development of grass does not occur in the soil. It is frequent removal of parts above ground as in overgrazing. During the dry year of 1933 it was noticed that native grasses in long-overgrazed prairie protected during recovery were much more subject to wilting than were plants in adjacent prairie that had not been grazed. The leaves rolled or folded and many of the lower ones dried and lost their green color. The evidence pointed clearly to a meager or inefficient root system. Accordingly experiments on effects of frequent removal of tops on development of the root system were performed.

Large blocks of sod of 10 species of the more abundant prairie grasses were grown at Lincoln each in large, deep containers under favorable conditions. Grasses in one-half of the containers were clipped as if closely grazed about 7 times during the growing season. The clipped plants failed to produce new rhizomes and many of the old ones died. Roots developed very poorly in length compared with the unclipped controls. Both volume and dry weight of roots were greatly reduced, the average volume to 12% and the average dry weight to 10% of the controls. Moreover, the diameter of the roots was only about three-fourths, or less, than that of unclipped plants (Biswell & Weaver 1933).

When transplanted blocks of sod of various prairie grasses were placed under control conditions for study, it was ascertained that those which were clipped four times during the six weeks they were producing new tops developed few and sometimes no roots (Weaver & Darland 1947). In the Great Plains the grass roots were greatly affected by close clipping (Albertson, Riegel & Launchbaugh 1953). Many similar studies are discussed in the three papers just cited.

A prairie of 290 A near Lincoln had been grazed moderately but not uniformly for more than 50 yrs. The soil was Carrington silt loam, quite uniform throughout. After several years of study the 3 range-condition classes it presented—excellent, good and fair—were mapped. In the excellent class both big and little bluestem had not been harmed by too frequent and too close grazing. In the mid-grade (good) condition both grasses showed some overuse by more open bunches, less remaining stubble, and less debris from preceding forage crops. Some bluestems still persisted in the low-grade (fair) condition class which was nearer the water and salt supply and, consequently, most often grazed. They were in a much weakened condition.

A representative bunch of little bluestem and a sod of big bluestem were selected in each range condition class. Monoliths of the soil under each were procured and examined. The results showed a decrease in root weight of 55% in mid-grade and 75% in fair grade pasture. Root deterioration was from root tips upward toward the crown. Deterioration in big bluestem was about the same as that of little bluestem. Decrease in dry weight was 49% in mid-grade pasture and 76% in fair grade (Weaver 1950).

In poor pasture all bluestems had disappeared. They were replaced by Kentucky bluegrass and blue grama neither of which utilized the moisture and nutrient supplies to a depth greater than 2.5-3 ft.

Decrease in weight of total underground parts of grasses when little bluestem prairie had been reduced by overstocking to an early, a medial, and a late stage of degeneration has been ascertained. Samples from pastures in early, medial, and late stages of degeneration showed consistent decreases in underground plant materials. On upland, decreases in dry weight were 35, 40 and 72%, respectively, from the original sod in the surface 0-4 in. Similar decreases occurred at the 4-12 in. depth.

It has recently been shown that removal during the growing season of half or more of the foliage of various grasses—including switchgrass and blue grama—caused root growth to stop for a time after each removal (Crider 1955). "A single clipping that removed most of the foliage caused root growth to stop for periods ranging from 6 to 18 days. Stoppage occurred usually within 24 hrs and continued until recovery of the top growth was well advanced. . . . The percentage of roots that stopped growth varied in proportion to the percentage of the foliage that was removed. . . . Stoppage of root growth failed to take place . . . only when 40% or less of the foliage was removed."

Root-soil relations in various soil types and root development and removal of tops both illustrate the need of some understanding of differences between successional stages and stabilized or climax vegetation and especially that of zonal and azonal soils. It was only with the cooperation of the Soil Survey of the Soil Conservation Service at Lincoln, Nebraska, and the Department of Soils of the University of Nebraska that this part of the study was possible. The diagrams of underground parts in the several communities illustrated are believed to represent the usual plant development in each throughout the very extensive territory described. From the studies of others, notably Hanson & Whitman (1938), it may be that the patterns extend over even much wider grassland areas.

SUMMARY

Underground development in western Iowa, Nebraska, Kansas and eastern Colorado has been studied for a period of 40 yrs. The earlier work (1916-1927) dealt largely with the root systems of a large number of individual species in relation to soil and climate. In further intensive studies of the structure of prairie vegetation this background was employed in defining the root habits of various plant communities on fully developed and stabilized soils. Both soil and aerial environment determining root development were used in interpreting community root habits.

Studies of the effects of extreme drought, recovery from drought, and removal of herbage on root development have aided greatly in the interpretation. They also emphasized the value of a knowledge of the usual community root habit.

The sod-forming tall grasses of lowland communities of true prairie are of the greatest height (5-10 ft), have the greatest leaf surface, and produce the largest amount of forage. Their roots are coarsest, least well branched, but deepest. They are about as deep (7-10 ft) as the stems are tall. Roots do not spread widely just below the soil surface. All of the dominants, except *Elymus canadensis,* are warm-season grasses that grow all summer and flower late.

Upland mid grasses nearly all grow in bunches. They are of intermediate height (2-3.5 ft), leaf surface, and amount of forage production. Roots are

moderately fine, well branched, and moderately deep. They are about twice as deep (4-5.5 ft) as the stems are tall. They are fairly well spread and moderately dense just beneath the soil surface. Grasses from lowland when growing in upland are reduced in size and weight. The roots are somewhat finer and more branched but penetrate less deeply. There are several cool-season grasses on uplands which flower early but most are warm-season species, flowering late after a long season for growth.

Grasses of the hard lands of mixed prairie are the smallest in height, leaf surface, and amount of forage production. Mid grasses are usually 1.5-2.5 ft high and short grasses of the understory 4-15 in. Both groups are represented by bunch grasses and sod formers. Roots are finest, best branched, and about as deep as those of upland true prairie. But they are 2-16 times deeper than the stems are tall. They spread widely and form dense masses in the surface soil and nearly all are well branched throughout. When hard-land species grow in true prairie they increase in size and weight. The roots are often deeper, spread much less in the surface soil and branch less profusely. All of these grasses are extremely xeric. Many cool-season grasses and sedges may evade drought by early growth and flowering. Warm-season grasses may grow intermittently, when water is available. All can undergo deep drought-dormancy and revive when rains come.

The amount of roots, stem bases and rhizomes in the surface 4 in. of soil is greatest in lowland of true prairie (3.7 T/A), intermediate in upland true prairie (2.7 T/A), and least in the hard lands in mixed prairie (1.8 T/A). This cover of sod has protected the surface of the earth for centuries against violent physiographic change and has made possible the formation of soil.

Grasses of mixed prairie in the Loess Hills, under a precipitation of 23 in., are usually rooted 2-4 ft deeper than those in adjacent hard lands. This is due to deeper water penetration and perhaps also to a higher percentage of readily soluble phosphorus.

Postclimax tall grasses in sand grow higher (4-5 ft) than grasses of upland true prairie. The mid grasses equal or exceed in height those of mixed prairie hard lands. They are mostly warm-season grasses, but some cool-season species are common. Sand-hills grasses are characterized by moderately fine roots which spread widely in the surface, usually 1.5-3 ft, and penetrate deeply, mostly 4-7 ft. The roots have extremely numerous branches, often 15-75 per in., mostly only 0.5-3 in. in length, but longer ones may occur in the deeper soil. Branching of these fine rootlets often occurs to the third or fourth order. Grasses that grow both in sand and silt loam spread their roots more widely in sand but usually not so close to the soil surface. Several grasses found only in sand have excellent rhizomes. The cover of vegetation is more open and forage production is much less than that of upland true prairie but may equal or exceed that of plains hard lands.

Over much of the prairie and plains, because of good soil structure, slight leaching, and almost negligible fertilizer requirements, the quantity of water demanded by the richness of the soil usually exceeds the supply and thus water becomes the limiting factor to plant growth.

Grassland vegetation is adjusted to fit into periods of dry cycles as well as wetter ones. Reserves of food in crowns, rhizomes and roots are extensive and the ability to absorb water throughout a large volume of soil is excellent.

Soil-root relationships in various soil types are considered. A study of intrazonal and azonal soils by the monolith method has made clear some of the physical and chemical causes for root variations.

The extremely important relation of root development to removal of tops has been discussed, especially as it is affected by various degrees of grazing.

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