A STUDY OF THE ROOT-SYSTEMS OF PRAIRIE PLANTS OF SOUTHEASTERN WASHINGTON

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A STUDY OF THE ROOT-SYSTEMS OF PRAIRIE PLANTS OF SOUTHEASTERN WASHINGTON

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I.

While carrying on a study of the plant formations and associations of semi-arid southeastern Washington in 1912–1914, it soon became apparent that for a proper understanding of the development and structure of these associations a knowledge of the root-systems of the more important prairie species was imperative. Consequently, during the fall, winter, and spring of 1913–1914, more than 350 root-systems of 25 of the most important ecological species were examined. This paper contains descriptions of these, together with a discussion of the conditions under which the plants grow.

The prairies of southeastern Washington, and their eastward extension into adjacent Idaho, occupy a position between the foothills of the Bitterroot Mountains on the east, and the sagebrush region of western Adams, eastern Franklin, and western Walla Walla counties, Washington, on the west. On the south they are bounded by that high upfold of the lava-rock known as the Blue Mountains. Northward the Spokane gravels, extending somewhat southward of Spokane, with their open growth of yellow pine, mark at once the general northern boundary of the exposed part of the great lava sheet and its accompanying prairie formation. As the great Columbian Plateau with its wind-moulded hills ascends to an altitude of 2700 feet near its eastern border, the precipitation correspondingly increases, and this reflects itself in a more highly developed type of prairie vegetation. In fact, the well-developed high prairies occupy a relatively narrow belt of 30–50 miles in diameter along the eastern edge of the plateau, while the area westward is char-
acterized by a very open type of Bunchgrass vegetation. Pullman, Washington, the base station, where these studies were carried on, lies 85 miles south of Spokane and in the midst of the best developed type of prairie.

THE FACTORS OF THE HABITAT

Since the supply of water in this region is the chief limiting factor to plant growth, we shall first consider the total amount of precipitation, with its seasonal distribution (which is of greater importance than the total), after which the water content of the soil will be considered.

Hemmed in on all sides by mountains, and especially cut off from the moist winds of the Pacific by the Cascades, the Columbian Plateau has a very low annual precipitation. In much of the area it is less than 10 inches, and even where the prevailing southwest wind, cutting through the mountain gap of the Columbia River and rising over the great High Plains, loses much of its moisture near the high eastern border, the annual precipitation is but 21 inches. In this semi-arid region where evaporation rates are very high, a knowledge of the distribution of rainfall and humidity is very important, for it is well known that scanty rainfall throughout the year, or relative dryness of the air and soil during the growing season, favors a sparse vegetation and the development of xerophytic forms. Since vegetation is not only an expression of present conditions, but to a greater extent a record of conditions that have obtained during a period of years; and since this record is not likely to be altered greatly by a year or two in which conditions may depart from the normal, a study of the precipitation in table 1 is instructive.

This table gives the mean monthly precipitation at Pullman covering a period of 22 years, and is very representative of conditions in the High Prairies.

It may be seen at a glance that over two-thirds of the precipitation occurs during the non-growing season, and that the

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1 The writer has under preparation a paper dealing in detail with the vegetation of the prairies of southeastern Washington together with the plant associations of the adjoining mountain-woodland formation.
light showers of July and August seldom have much influence on
the water content of the soil. We may compare the soils of this
region to a gigantic reservoir replenished mostly during the non-
growing season, and (as will be shown) rather thoroughly emptied
of its water during the summer. It is not the absolute rainfall
figures alone which furnish a criterion of climate, for the
maximum duration of the drought period constitutes a limiting
factor of the greatest importance. The great problem is the
extent to which soil water derived from the winter precipitation
is conserved through the weeks of drought. The rains in south-
eastern Washington are so gentle that there is practically no
run-off; and the silt-loam soils have a wonderfully retentive
power of holding the moisture. As pointed out by Shreve the
influence of rainfall upon the distributional and seasonal
activities of plants is obviously exerted chiefly through its power
to replenish soil moisture, and while rainfall is only mediate in
its relations to plants, soil moisture is immediate.

SOILS AND SOIL MOISTURE

The prairie soils of the region have originated from the de-
composed underlying basalt. By the action of water, and
especially by the prevailing southwest wind, the prairie topography
has been moulded into rounded hills which reach a height of 100
to 360 feet, and resemble sand dunes. The soil is usually many
feet deep, and only along the canyons of streams is the lava-rock
exposed. The wind has drifted much surface soil and humus

\[\text{TABLE 1} \]

<table>
<thead>
<tr>
<th></th>
<th>Precipitation at Pullman (in inches)</th>
</tr>
</thead>
<tbody>
<tr>
<td>October</td>
<td>1.70</td>
</tr>
<tr>
<td>November</td>
<td>3.41</td>
</tr>
<tr>
<td>December</td>
<td>2.66</td>
</tr>
<tr>
<td>January</td>
<td>2.55</td>
</tr>
<tr>
<td>February</td>
<td>2.18</td>
</tr>
<tr>
<td>March</td>
<td>2.02</td>
</tr>
<tr>
<td>April</td>
<td>1.50</td>
</tr>
<tr>
<td>May</td>
<td>1.84</td>
</tr>
<tr>
<td>June</td>
<td>1.20</td>
</tr>
<tr>
<td>July</td>
<td>0.57</td>
</tr>
<tr>
<td>August</td>
<td>0.68</td>
</tr>
<tr>
<td>September</td>
<td>1.29</td>
</tr>
<tr>
<td>Total</td>
<td>14.52</td>
</tr>
<tr>
<td>Total</td>
<td>7.08</td>
</tr>
</tbody>
</table>

\[\text{Shreve, Forrest, Rainfall as a Determinant of Soil Moisture. Plant World, 17: 9-26, 1914.}\]
material from the exposed south and southwest slopes and de-
posited it upon the steeper north and northeast leeward slopes.
Table 2 gives the mechanical composition of the first foot of
soil on a northeast and southwest slope respectively.

As is characteristic of dry regions, the transition from soil to
subsoil is not well marked, although the lighter colored subsoil
appears much nearer the surface on exposed than on sheltered
slopes. The humus content of the soils of north hillsides is
greater at all depths to 5 feet, in some cases more than 12%
greater, than on the exposed slopes, as was shown by six sets
of humus determinations made for each foot of soil on the two
slopes, respectively. This combination of more clay and more
humus on the north and northeast slopes reflects itself especially

<table>
<thead>
<tr>
<th>TABLE 2</th>
</tr>
</thead>
</table>

**Mechanical composition of the first foot of prairie soils on a southwest and a northeast slope respectively**

<table>
<thead>
<tr>
<th>STATION</th>
<th>FINE GRAVEL 2.00 TO 1.00 MM.</th>
<th>COARSE SAND 1.00 TO 0.50 MM.</th>
<th>MEDIUM SAND 0.50 TO 0.25 MM.</th>
<th>FINE SAND 0.25 TO 0.10 MM.</th>
<th>VERY FINE SAND 0.10 TO 0.05 MM.</th>
<th>Silt 0.05 TO 0.005 MM.</th>
<th>CLAY 0.005 TO 0.000 MM.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Southwest slope</td>
<td>0.00</td>
<td>0.60</td>
<td>0.60</td>
<td>0.40</td>
<td>23.58</td>
<td>73.30</td>
<td>1.49</td>
</tr>
<tr>
<td>Northeast slope</td>
<td>0.40</td>
<td>0.40</td>
<td>0.90</td>
<td>1.50</td>
<td>33.16</td>
<td>53.50</td>
<td>10.03</td>
</tr>
</tbody>
</table>

in the increased water-holding capacity of the soil. An average
of six determinations gave a mean water-holding capacity of
56% (based on dry weight at 104°C.) for the first foot of
soil on north slopes, as compared with 48% on south
slopes. This margin of 8% is rather an important difference
in favor of the soils on the protected slopes, since the wilt-
ning coefficients of the two soils differ but little. These sub-
stratum differences are pointed out here since it will be shown
later that certain plants are quite confined to moist north and
northeast hillsides.

Studies of the water content of these soils have been carried
on since the spring of 1912. It will be unnecessary to burden
the reader with all of the data and graphs obtained, and only
enough will be given to make plain the seasonal march of soil
water. In figure 1 are graphs giving the march of soil water
from April 25 to September 25, 1913, on a typical northeast and
southwest prairie slope, respectively. The ordinates represent percentages of soil moisture in the first 10 inches of soil, on the dates indicated by the abscissae. The rainfall between the intervals of readings is also shown in inches, each ordinate representing 0.1 inch. The horizontal solid and broken lines show the wilting coefficients of the soils on the northeast and southwest slopes respectively. The greater amount of moisture on the northeast slope (in some cases being twice that of the southwest slope) may be noted at a glance; while the fact that the soil on the exposed slope reached its wilting coefficient about July 15, and more than five weeks before similar conditions obtained on the sheltered slope, is significant. Records for the fall of 1913 were discontinued when the rains of late September replenished the moisture of the parched soil. In 1914 these 10-inch soil moisture determinations were made only at longer intervals and with the object of determining the time at which the wilting coefficient was reached. The water contents on the dates of these determinations are indicated by the light lines (fig. 1), the solid line representing soil moisture on the northeast slope. The rainfall for June, 1914, being approximately normal (and not 1.6 inches in excess of the mean, as in 1913) the wilting coefficient of these soils was reached much earlier than in the preceding year. An examination of these determinations together with the rainfall records at Pullman, shows that at no time after June 28 and until September 14 was there water available for plant growth in the first 10 inches of soil on the southwest slope. Only 0.13 inch of rain fell in July, none in August, and the light showers of the first 13 days of September gave a total precipitation of only 0.33 inch.

The autumn and winter rains replenish the water lost during the long period of drought and in the following spring the soils again show a maximum water content. Soil moisture records obtained at 6 inches and 12 inches respectively, at the prairie stations on the two slopes from October 15, 1912, to January 1, 1913.

Samples of 100–150 grams of soil were invariably taken in duplicate, dried in an oven at 100–104°C., and the water content calculated in percentages on the basis of the dry weight.
1913, well illustrate this process. On October 15 the north-side soil had a water content of 17.4% and 23% at 6 inches and 12 inches respectively, while that on the south slope had only 11% and 12% at the two depths. The graphs show a general increase of water content (except for a trough in late November)

![Graph showing soil water content](image)

and on January 1 the water content had increased to 31% and 41% respectively, on the north slope, and 28% and 28% on the south slope.

It is apparent from these data that prairie plants must obtain their water from greater depths than 10 inches, at least during the dry summers. In fact, some of these plants penetrate to a
depth of 12 or 13 feet, while most of them get the bulk of their water from the second to the sixth foot of soil. Consequently a consideration of soil moisture at these depths is imperative for a proper understanding of root environment. These deeper soil water determinations (many to a depth of 8 feet) were taken at intervals from December, 1912, to August, 1914. Samples were taken in duplicate from separate holes. Figure 2 (solid lines) shows the march of soil water from early spring until late summer of 1914, on a southwest slope. It is apparent that there was still a downward movement of water at depths of 4 and 5 feet after April 18; but from June 3 to August 15 the soil moisture was gradually depleted at all depths to 5 feet. The heavy horizontal bars give the wilting coefficients at the depths indi-
cated. On July 6 no water was available in the second foot of soil and only a small margin over the wilting coefficient was present at 3 feet. The broken line indicates that on December 13 of the preceding winter the soil was drier at 3, 4 and 5 feet respectively, than at any other time indicated. The fall rains had not then penetrated beyond 2 feet. While excavating root-systems during the fall, winter, and spring, an excellent

![Graph showing soil water content](image)

Fig. 3. Graphs showing the march of soil water to a depth of 5 feet on a northeast slope from April 18 to August 15, 1914, and the water content of the soil on December 6, 1913.

opportunity was offered to study the rates of penetration. The water penetrated very slowly and at about equal rates on all slopes. By October 18 only the surface layer of 8 inches was wetted, and in late March the wet soil reached a depth of not more than 4 feet. The dotted graphs in the figure indicate the soil moisture on the northeast slope. Aside from the lower
temperatures and greater humidity of the north slopes, the actual amount of moisture available to these soils is important in explaining the observed differences in moisture content. The same agency that has so profoundly affected the topography, namely the wind, also drifts over to the sheltered slopes much snow, which upon melting adds to the soil water. Two examples will suffice. In February 1914, exposed prairie slopes had a blanket of snow from 5–8 inches deep, while on the sheltered slopes at the same time drifts 48–52 inches in depth were measured. The second, while an extreme case, is illustrative. During February

| TABLE 3 |

The march of soil water on a northwest and south slope respectively. 1914

<table>
<thead>
<tr>
<th>Depth</th>
<th>MAY 22</th>
<th>JULY 6</th>
<th>AUGUST 15</th>
</tr>
</thead>
<tbody>
<tr>
<td>0&quot;-6&quot;</td>
<td>N.W....</td>
<td>23.4</td>
<td>15.2</td>
</tr>
<tr>
<td></td>
<td>S........</td>
<td>12.5</td>
<td>11.1</td>
</tr>
<tr>
<td>6&quot;-12&quot;</td>
<td>N.W.....</td>
<td>25.7</td>
<td>13.7</td>
</tr>
<tr>
<td></td>
<td>S........</td>
<td>17.9</td>
<td>11.4</td>
</tr>
<tr>
<td>At 2'</td>
<td>N.W.....</td>
<td>27.0</td>
<td>18.9</td>
</tr>
<tr>
<td></td>
<td>S........</td>
<td>19.9</td>
<td>12.6</td>
</tr>
<tr>
<td>At 3'</td>
<td>N.W.....</td>
<td>30.2</td>
<td>23.7</td>
</tr>
<tr>
<td></td>
<td>S........</td>
<td>20.2</td>
<td>13.2</td>
</tr>
<tr>
<td>At 4'</td>
<td>N.W.....</td>
<td>27.2</td>
<td>24.9</td>
</tr>
<tr>
<td></td>
<td>S........</td>
<td>22.0</td>
<td>17.3</td>
</tr>
<tr>
<td>At 5'</td>
<td>N.W.....</td>
<td>24.3</td>
<td>21.3</td>
</tr>
<tr>
<td></td>
<td>S........</td>
<td>22.4</td>
<td>19.6</td>
</tr>
</tbody>
</table>

and March, 1913, while only 1 foot of snow lay on the south and southwest slopes, the protected northeast slopes were covered with drifts of well packed snow from 10–13 feet deep.

In figure 3 is shown the march of soil water similar to that in the preceding figure, but for soils of a northeast slope. Here again, the downward movement of water at 3 to 5 feet after April 18 is apparent, as is also the gradual depletion of soil water at all depths to 5 feet. Likewise, the broken graph indicates conditions similar to those explained for the corresponding graph in figure 2. On August 15, no soil water was available above the 2-foot level. If the graphs in this figure are compared with the corresponding graphs in the preceding, it may be readily
seen that in all cases, except on July 6 and at a depth of 5 feet, a higher water content was maintained in the soils on the northeast slope.

In order to further check these deep soil water conditions samples were again taken in duplicate on the northwest and south slopes of another prairie-covered hill. These findings, indicated in table 3, check very closely with the preceding, and the striking difference between soil water content on the two hillsides at all depths is well shown.

It may also be noted that at each determination the soil at any depth was much drier than at the same depth at the preceding determination. On the south slope, it is interesting to note that without exception the soil moisture increased with depth, and that the same condition maintains in most cases for north-side soils. Thus, it may be seen that topography with soil texture is the great middleman that distributes the soil moisture to fill the gigantic earthen reservoir, which again is largely emptied during the following growing season. The common farm practice in the Palouse region of alternating season after season the growing of wheat with summer fallow, is a method of storing the moisture from one year for use in the growth of the next year’s crop.

TEMPERATURE

The observations on the temperature of the soil consist of two series of readings, namely, of a continuous one by means of a thermograph and of a very large number of readings of thermometers. The thermograph records are at a depth of 4 inches (April 22 to June 9, 1913) and 3 inches (June 5 to August 15, 1914) respectively, on a southwest slope. Comparative temperatures on the northeast slope were taken at frequent intervals. The other thermometer readings are mostly for depths of 1 foot, and a number of readings were made at each foot to depths of 8 feet.

The thermograph records show an undulating line of which the curve crests correspond to the warmest period of each day, and the depressions to the coldest. The crests for any (7 day)
Fig. 4. Graphs showing the average weekly maximum and minimum soil temperatures (solid lines), and air temperatures for 1913 (first series), and 1914, on a southwest prairie slope.
record are remarkably uniform in height, as are also the depressions uniform in depth. The difference between the crests and the depressions is shown in figure 4 where the average weekly minimum and maximum soil temperature (solid lines) are recorded, since these are more important to plant growth than the mean. The differences between these averages increase from about 10°F. (at 4 inches depth) April to June, to about 24°F. (at 3 inches depth) in July and August. For purposes of comparison graphs representing the average weekly maximum and minimum air temperatures (at 3 inches above the soil surface and in the shade) recorded at the same station are also given in figure 4.

**TABLE 4**

Soil temperatures at a depth of 3 inches

<table>
<thead>
<tr>
<th>STATION</th>
<th>MINIMUM</th>
<th>TIME</th>
<th>MAXIMUM</th>
<th>TIME</th>
<th>RANGE</th>
<th>DAY</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>a.m.</td>
<td></td>
<td>p.m.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N.E. slope</td>
<td>63.5</td>
<td>5</td>
<td>75</td>
<td>3</td>
<td>11.5</td>
<td>July 27</td>
</tr>
<tr>
<td>S.W. slope</td>
<td>67</td>
<td>7</td>
<td>93</td>
<td>4</td>
<td>26.0</td>
<td>July 27</td>
</tr>
<tr>
<td>N.E. slope</td>
<td>59</td>
<td>5</td>
<td>71.5</td>
<td>3</td>
<td>11.5</td>
<td>July 28</td>
</tr>
<tr>
<td>S.W. slope</td>
<td>68</td>
<td>7</td>
<td>94</td>
<td>4</td>
<td>26.0</td>
<td>July 28</td>
</tr>
<tr>
<td>N.E. slope</td>
<td>61</td>
<td>5</td>
<td>73.5</td>
<td>3</td>
<td>12.5</td>
<td>July 29</td>
</tr>
<tr>
<td>S.W. slope</td>
<td>67</td>
<td>7</td>
<td>95</td>
<td>4</td>
<td>26.0</td>
<td>July 29</td>
</tr>
</tbody>
</table>

It is interesting to note that, while the soil temperatures at night were always warmer than those of the air, on many days during June, July, and August the air temperatures were lower than those of the soil.

Owing to the lagging of the soil temperature the maximum was not attained until about 4 p.m. and the minimum at 7 a.m. as compared with 3 p.m. and 5 a.m. respectively, for maximum and minimum air temperatures.

The seasonal march of soil and air temperatures varies inversely with the soil water. That is, the temperatures steadily become higher in proportion as the soils become drier. This condition occurred on both slopes, but the temperatures were lower and the extremes of variation less on the sheltered side. A single example of maximum and minimum soil temperatures on the two slopes and at 3 inches depth must suffice here.
The three days from July 27 to 29 were clear, and, judging from records of preceding and following days, quite typical. The daily maximum air temperature was reached somewhat earlier on the north than on the south slope, and was from 2°F. to 3°F. lower.

A comparison of a large number of temperature readings at 1 foot on the two slopes brings out the facts that at this depth the daily range of temperature is seldom over 1°F.; that the southwest-side soils are from 3°F. to 5°F. warmer in early spring than those of the north slopes, and that these differences may increase by late summer to 7°-10°F. Table 5 indicates these temperature differences of the soils of the two slopes to a depth of 5 feet, in early spring and in late summer. Undoubtedly the higher soil temperatures prevailing on the south side have much to do with the earlier seasonal activities of many plants.4

OTHER FACTORS

Just as the possible growth of the aerial parts of plants is affected by the extent of the development of the root system, conversely the environmental conditions to which the aerial parts are subject, especially as concerns their water relations, must reflect themselves in the root development. Therefore, it will be instructive before passing on to a consideration of the

4 Several species of plants were observed to blossom from 10 to 17 days later on north than on south slopes.
root-systems themselves to consider briefly the above-ground environment.

Enough will have been said about summer temperatures, if we add that the long days, mostly cloudless, are followed by cool nights, during which the temperature usually reaches 45°-58°F. During the winter the ground seldom freezes below 4 inches in depth, and, of course, on the exposed slopes the process of alternate freezing and thawing is most pronounced.

A continuous record of humidity has been kept for more than two complete growing seasons and it has been found that the air is often 5 per cent to 10 per cent drier on the exposed than on the sheltered slopes. It is not uncommon on the dry slopes and during late afternoons for the humidity to fall to 15–30 per cent, while during the night it may rise again to about 75 per cent or even 95 per cent.

The wind, prevailingly from the southwest, is of great importance to vegetation, because it increases the evaporating power of the air, and the greater saturation deficit increases transpiration. During the season of 1913 (April 16 to September 3) a total of 13,605 miles of wind passed over the southwest slope at a height of 0.5 meter, while only 56 per cent as many miles were recorded by the anemometer similarly placed on a northeast slope. In general, these conditions were duplicated in the season of 1914 with the ratio of 100:49 (April 18 to August 15).

However, these factors of temperature, humidity, and wind movement, as Livingston has shown, may be quite satisfactorily summed up by measuring the evaporating power of the air. A rather detailed report of evaporation rates as determined by Livingston’s standardized porous cup atmometers in prairie and other stations has already been made, in which it was shown that from May 5 to September 23, 1913, the average daily evaporation on the northeast prairie slopes was only 64 per cent of that on southwest exposures. Similar records for 1914 bear

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out this condition in general, with higher average daily evaporation on both slopes (23.9 cc. on northeast and 33.0 cc. on southwest) and a ratio on the two slopes of 72 : 100.

Fig. 5. One end of a trench used in excavating root systems. Many roots of prairie plants reach depths of over 10 feet.

When we consider that the daily evaporation in July and August often reaches a maximum of 40–55 cc., and at a time when the available soil water may be depleted to a depth of two feet, we can see the necessity for extensive root-systems in the sub-
stratum, as well as aerial structures for enduring drought. Another fact of importance must not be overlooked. Owing to the cool nights the greater bulk of these high water losses (82.5 per cent as determined for three days in July) occurs during the day, and thus very xerophytic atmospheric conditions are brought to bear upon the plant.

Summarizing briefly the factors of the habitat in which these studies were carried on, we find a region of moderate winter and low summer precipitation. The soils are composed of a fine silt-loam of high water-holding capacity, they are usually very deep, and the soil water extends down many feet beyond the greatest root depth. In early summer the superficial layers of soil soon lose all of their water available for plant growth, and as the season advances this condition occurs in the deeper soils, while the entire soil mass to a depth of 5 feet and beyond, gradually yields up most of its available water. Soil temperatures at 3 inches show a daily range of from 3°F. to 24°F., while at 1 foot the daily range is seldom over 1°F. The seasonal range (April—August) of the soil temperatures varies from 22°F. at 1 foot to 16°F. at 5 feet. Air temperatures show a mean daily range varying from about 25°F. in April and May, to 38°F. in July and August. The cool nights on the high plateau tend to counteract the low humidity of the day and to reduce the high daily rates of evaporation.

North and northeast slopes are less xerophytic than the south and southwest slopes. This is due in part to actually greater precipitation caused by blowing snow and in part to soil texture which is more open, has more humus, and a greater water-holding capacity. These factors are reflected in the greater amount of soil water and in lower soil temperatures. Likewise, these slopes are sheltered from the drying southwest winds, and from the perpendicular rays of the sun. This is reflected in slightly lower air temperatures and greater humidity, and especially in the lower evaporating power of the air.

7 Wells dug only into the soil often afford a good supply of water, although usually they are drilled into the porous layers of basalt. See also Landes, Henry, Underground Waters of Washington. Water Supply and Irrigation Paper, No. 111, 1905.
SCOPE AND METHODS OF THE STUDY OF ROOT-SYSTEMS

The object of this study was to determine the depth at which the most important prairie plants obtain their water supply; to get accurate data on the distribution and extent of the root-systems in the soil; and to examine enough plants of each species so that the conclusions might be thoroughly reliable. Finally, it was hoped to use these data in helping to solve the problems of succession and structure of prairie vegetation.

Owing to the tenacious structure of the soil and the great depth of most roots, it was found impracticable to wash out the root-systems. The method finally employed was to dig a trench 2 feet wide and 8 to 16 feet long to a depth of about 6 feet on the hillside where roots were to be examined. This offered an open face into which one might dig with a hand pick, and, after sufficient practice, and acquaintance with the soil texture, successfully excavate a root-system almost in its entirety. Of course the trenches were deepened as work progressed and the working level sometimes reached to a depth of 10 or 12 feet. (See fig. 5.)

Five of these larger pits were used and several smaller ones.

Fig. 6. Lumps of soil taken at a depth of 5 feet on a northwest slope, showing the numerous large earth worm burrows. They are from 7 to 8 mm. in diameter and reach depths of more than 13 feet.
The soils on the sheltered slopes were much more open in texture at all depths, and roots were removed with much greater facility than on south slopes where it was often necessary to use a pickaxe to open the trench.

Root-systems were examined on the southwest slope, and on a northeast slope, both, respectively, near the stations where factor determinations were made; and also on a northwest slope near the station where deep soil moisture samples were taken as a check (see table 3). It should be made plain here that this last station was on a slope only slightly north of west but sheltered by a low westward extension of a ridge in such a manner as to combine more nearly northside substratum conditions with the aerial conditions, as regards exposure to wind and sun, approaching those of a south slope.

A biotic factor affecting soil texture and one which shows a marked effect upon root-systems is the earthworm, a species of *Lumbricus*. The soils of north and northeast slopes especially, were literally honeycombed with holes ranging from 7 to 8 mm. in diameter and reaching depths of over 13 feet. (See fig. 6.) In the soil of south slopes the work of earthworms is much less in evidence,—perhaps less than half as many holes occur here. Black soil was noted in these burrows at depths of 9–13 feet, perhaps in part worm-casts and in part surface soil washed down from above. Certainly these holes play a large part in the penetration of soil water, and it seems that the additional aeration they afford in these fine-textured soils might be of great importance.

All the roots examined were of mature perennial plants. The practice followed was to examine six or more roots of a given species and then to write a working description of the roots. These descriptions were kept at hand in the field and as new roots of the same species were studied any variation from the original description was carefully noted. It is believed in this way that thoroughly reliable results have been obtained for the species studied.

A few of the root-systems were photographed in place, but most of them were removed from the soil and afterward photo-
graphed, together with a meter stick, for purposes of comparing lengths. It was usually necessary to double the root one or more times in order to get it all on the ground glass at a distance close enough to show the details of structure. Root-systems of the following plants were studied.

**Fig. 7.** A root of *Lupinus ornatus* with a length of 163 inches.

**Fig. 8.** *Lupinus leucophyllus* has a much larger transpiring surface and a smaller absorbing surface than the preceding species. Note the large root tubercles.

*Lupinus ornatus* (*Fig. 7*)

Only two species of lupines occur widely distributed on the high prairies of eastern Washington. Of these *Lupinus ornatus* is the more xerophytic, while *Lupinus leucophyllus* rarely occurs
except on moist north or northeast hillsides or in the narrow intervening valleys. The aerial parts of the lupines begin renewed growth in April, and come into bloom in June. *L. ornatus* remains green only until late July or early August, while *L. leucophyllus* seldom dries out until after the frosts of September. The dense coat of appressed hairs on the former, on both leaves and stems, gives the plant a silvery gray appearance, and as the aerial parts reach a height of more than a foot, they add considerably to the leaden aspect caused by *Balsamorhiza* and *Hieracium*. As regards abundance, an average of 7 plants per square meter is not unusual, while *L. leucophyllus* seldom averages more than one per square meter.

Twenty-four root-systems were examined. Several reached a depth of over 10 feet. The diameter of the tap root is seldom over 0.5 inch. It may have few or no large branches, but is often well supplied with wide-spreading laterals. The whole root is well clothed with fine rootlets to the third order, and the last foot or eighteen inches is often a mat of small branches and root hairs. In fact, the root hairs are far more abundant than on any other plant studied. The roots pursue a very devious course, especially in more compact soils. For example, one plant reached a depth of only 5 feet and 5 inches but the main root ran along under the ground at a depth of only 12 inches and for a distance of 4 feet. It sent up a whole thicket of stems. Another root, with a circumference of 1.5 inches, which it maintained for 3 feet, was over 10 feet long, but reached a depth of only 5 feet and 5 inches. When the top parts of the main roots die, sprouts, seen as deep as 3 feet, grow up to the surface. The average depth of the roots for all the plants studied was 7 feet and 7.1 inches. Nodules were found to depths of 11 feet. Nine plants on a northeast slope gave an average depth of 6 feet; five on a southwest slope, 5 feet and 11 inches; and ten on a northwest slope 9 feet and 10.4 inches.

*Lupinus leucophyllus* (Fig. 8)

This lupine has a much larger transpiring surface and a much smaller absorbing surface than the preceding. Its tap root,
which is seldom over 0.5 inch in diameter, may be abundantly branched all the way to the tip with short laterals (about 3 inches long), but more frequently it throws off several laterals at various depths. These vary in direction of growth from nearly horizontal to nearly vertically downward. All are profusely branched to the third or fourth order, especially near the tip.

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Fig. 9. Astragalus (Phaca) arrectus. This root reached a depth of 60 inches.

The nodules are much larger than those on Lupinus ornatus, often 10–15 mm. in diameter. As in the preceding plant, the legume taste is characteristic. Fourteen plants were excavated on a northeast slope. The deepest reached only 5 feet and 5 inches. The average root depth was 4 feet and 9.6 inches.
Astragalus (Phaca) arrectus (Fig. 9)

Although a common prairie species, this plant is less abundant than _Lupinus ornatus_. Like most of its neighbors on the dry hillsides, it flowers early and dries up during the first week of July.

Six plants were examined on a southwest slope with an average root depth of 4 feet and 7.8 inches. The strongly developed tap root is seldom over 0.5 inch in diameter, usually pursues a course directly downward, and sends out many strong laterals at various depths. These laterals sometimes branch off even at 3 inches below the soil surface, and, like other laterals which may be thrown off all the way to the tip, often run in a rather horizontal direction before again turning downward. Like all the laterals, the tap root is usually profusely branched and the tip is also well provided with branchlets. One case was observed where the end of the tap root entered a worm hole at a depth of 47 inches and extended downward in the hole for 9 inches to its end, without branching, but it was densely covered with root hairs. _Astragalus_ roots have a light tan color. The shortest root-system reached a depth of 3 feet and 4 inches; the longest, 5 feet and 10 inches.

(To be continued.)
A STUDY OF THE ROOT-SYSTEMS OF PRAIRIE PLANTS OF SOUTHEASTERN WASHINGTON

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(Concluded)

II.

Agropyron spicatum (including var. inerme) (Fig. 10)

This is the most common bunchgrass in eastern Washington. It has its best development westward of the high upland prairies of extreme eastern Washington and along the rim-rock through the eastern part. The bunches are often 10 inches in diameter and reach a height of over 3 feet. As many as 300 to 350 individual stems may occur in a single bunch. The plant blossoms in June and dries out in early July, only to take on renewed growth after the autumn rains, and remain green all winter. Figure 10 shows Agropyron on the rim-rock with its roots penetrating the rock crevices to depths of 45, 46 and 48 inches. Ten plants were examined under these conditions. The roots of all followed the cleavage planes of the basalt on an average to a depth of 4 feet and 1.3 inches, but one extended along the deeper moist crevices to a depth of 5 feet.

In the well-developed highland prairies the bunch habit is partially abandoned and long rhizomes are produced. The clumps are always much smaller here, perhaps only a few centimeters wide, but there are usually as many as 5–6 per square meter. Twelve prairie Agropyrons were examined. This grass has coarser roots than any of the other three important native grasses. These coarse, fibrous roots have many short laterals. Some of these roots reach a depth of 4 feet and 9.5 inches, although on an average 4 feet and 2 inches was the greatest depth attained. Five plants on a southwest slope gave an average depth of 4 feet and 1.6 inches, while seven on a northwest slope reached an average depth of only 3 feet and 2.6 inches.
Festuca ovina ingrata (Fig. 11)

The blue bunchgrass ranks in importance with Agropyron spicatum on the well-developed high prairies west of the foothills of the Bitter-root Mountains between Spokane, Washington, and Lewiston, Idaho. Because of its abundance (often 10–13 bunches per square meter), the very appropriate name Palouse (Fr. Pelouse, a land clothed with a short, thick growth of herbage)
was early applied to the region. The slightly pale green plants are densely tufted into bunches from 1 to 4 inches in diameter, and, while the numerous setaceous leaf blades are mostly basal and about 12 inches high, the stems which bear flowers reach a height of 12 to 18 inches. The whole plant dries out considerably by the middle of July, but the autumn rains revive it, and it is green throughout the rest of the year.

*Festuca ovina* has a great mass of jet black roots which occupy the soil thoroughly from the surface to a depth of about 18 inches, below which depth relatively few roots extend. None of the roots are over one millimeter in diameter. They branch profusely to the third order mostly, and the laterals are usually less than an inch in length. This branching continues to the very tip, and there the laterals are usually longer. Twenty-two plants were examined. The longest root found was 3 feet and 3 inches, the average length 2 feet and 1.5 inches for the deepest roots, but the great bulk of roots were less than 18 inches long. All the plants examined were on a southwest slope.

*Poa sandbergii (Fig. 11)*

Sandberg’s Poa is one of the earliest plants to gain a foothold upon the thin rocky soil of the scab-lands, and along the rimrock. It grows in small tufts usually only from 0.5 to 1.5 inches wide, puts out new roots when the fall rains begin, grows throughout the winter and spring, and evades drought by flowering late in May or in early June, and remaining dormant the rest of the growing season. On the prairies it is an interstitial plant, often as many as 30–40 small tufts occurring in a single square meter on the dry south slopes.

*Poa* has smaller roots than *Festuca ovina ingrata*, they are more profusely branched, and the fine laterals which are short (usually less than 1 inch) are more numerous, smaller, and much more branched. The creamy-white roots spread laterally 3 to 5 inches and occupy thoroughly the first few inches of soil, relatively few extending below a depth of 8 inches, and none were found beyond 13 inches. The root branches are longer and more
numerous at the tip than are those of *Festuca*. *Poa* roots branch to the fourth order. Six plants were examined on the rim-rock with an average root depth of 7.2 inches. Eight prairie species of *Poa* growing on a southwest slope gave an average maximum depth of 9.7 inches.

Fig. 11. Three important prairie grasses. *Koeleria cristata* (to the left), *Festuca ovina ingrata* (center), and *Poa sandbergii*. All are relatively shallow rooted.

*Koeleria cristata*. (Fig. 11)

This is a very common bunchgrass on the prairies of eastern Washington, not infrequently occurring as abundantly as 6 clumps per square meter. However, the bunches are smaller in diameter (0.5 to 2 inches, usually) than those of *Festuca ovina ingrata*, and also of less height (1–2.5 feet) than *Agropyron spicatum*. *Koeleria* flowers in late June or early July and like *Poa* remains dormant until revived by the autumn rains.
The roots, which are a dirty-gray in color, resemble those of *Agropyron* but taper down faster, and have finer laterals which branch mostly to the third order. These laterals, like those of the shallow rooted *Poa*, are more numerous than in *Agropyron*. Six plants were examined. The deepest root found was at 28 inches, and 15 inches was determined as the average maximum depth.

*Balsamorhiza sagittata* (Fig. 12)

The balsam root is, with the exception of *Agropyron spicatum* and *Festuca ovina ingrata*, the most characteristic plant of the high prairies of eastern Washington. Its abundance, size, and duration all unite to make it a very important ecological species. It is not unusual to find a dozen of these plants in an area of 4 square meters. Only on the steeper northeast slopes and wet valleys is it absent. A medium sized mature plant occupies an area of 4-5 square feet, may have as many as 50-80 of the large sagittate leaves, and a total leaf surface of 30 square feet. From the short, thick, multicipital stem (I have counted 39 individual shoots on a stem 9 inches in diameter) the new leaves appear in April. By the first of May the plant is often in full bloom and is the most conspicuous member of the vernal aspect which lasts until about June 1st. After this the whole aerial part dries up, but the dead leaves are conspicuous throughout the year.

Twenty-five root-systems were excavated and examined. *Balsamorhiza* has a tap root sometimes reaching a diameter of 4 inches and an extreme depth of 8 feet and 10 inches. The laterals seldom come off in the first 6 inches of soil, but below this numerous strong laterals occur, sometimes 1 inch or more in diameter, and these often run rather horizontally for 2 or 3 feet before they turn downward. They may ultimately reach depths of 5 feet or more. The lateral branching is profuse, and in all directions the soil is laid hold upon. Sometimes the tap splits up into nearly equal parts at a depth of a few feet. The tip of the tap root is often dead, and, if alive, never much branched. Small branch orders near the tip are not abundant. The older
part of the root especially is covered with a deeply furrowed bark. These furrows in old roots are sometimes 0.5 inch deep. The taste is characteristic, and a balsam-like substance exudes from the old roots when injured. Five feet and 6.1 inches was determined as the average root depth. Nine plants on a south-west slope gave an average depth of 5 feet and 1.5 inches; fourteen on a northwest slope, 5 feet and 9.8 inches, and two on a north-east slope, 5 feet.

Fig. 12. Two roots of Balsamorhiza sagittata partially uncovered and photographed in place. Note the deeply furrowed bark and extensive system of laterals.

Geranium viscosissimum (Geranium incisum) (Fig. 13)

Just as Balsamorhiza is characteristic of dry slopes, so Geranium is found most abundantly on moist northeast hillsides and in the valleys. It seldom occurs abundantly on exposed hillsides. Geranium is a large plant reaching a height of from 20 to 30
inches, with a wide spreading top which often covers an area of 4 to 5 square feet. It begins blossoming in late May or early June, and its large red flowers (sometimes as many as 80 to 100 in bloom at one time on a single plant) are conspicuous in the estival aspect especially of moist situations. By the second week in July blossoming ceases, but the plant often remains green till late into the summer, if not all fall.

*Geranium* has a well-developed tap root which may reach three inches in diameter. It is often more or less decayed and may split up into two or more parts, thus giving rise to new plants. The tap sends off many laterals both large and small at all levels, all of which may branch profusely to the fifth order. The larger laterals usually run off in a horizontal direction, sometimes for nearly 3 feet before turning downward. The end of the tap root is either unbranched or branched but little, and is often dead. The bark is reddish and scaly on the older parts. Hard soil seems to be a marked limiting factor to root growth, and under this condition especially the usual very irregular course of descent is greatly emphasized. Twenty-four root-systems were examined. The greatest root depth, 9 feet and 6 inches, was reached on a northwest slope, and an average depth of 5 feet and 3.4 inches was determined. Thirteen plants on a northeast slope gave an average root depth of 4 feet and 8.1 inches, while eleven on a northwest slope reached an average depth of 6 feet and 0.2 inch.

*Wyethia amplexicaulis* (Fig. 14)

The black sunflower, at home in the moist meadows, also often occurs on rather dry hillsides. Like *Balsamorhiza*, it is large and abundant and of considerable duration, being conspicuous even after drying out, but, unlike it, its distribution on the high prairies is local and patchy. When we recall that a single plant may have from 14 to 31 leaves, each from 3 to 5 inches in greatest diameter and from 13 to 17 inches in length, the enormous transpiring surface may be realized. This shiny, resinous, dark green plant blossoms during the last week of May or the first week of June and rapidly dries up in early July. The
numerous large yellow flowers 2.5–3 inches in diameter make these societies very conspicuous.

The fleshy tap root sometimes measures 9 inches in circumference and may reach a depth of 6 feet and 5 inches. It usually has several strong laterals which come off from 8 inches to 3 feet in depth, and may run out in a somewhat horizontal direction for 3 or 4 feet from the main root. Sometimes, however, only a single lateral occurs. Often at a depth of 1–3 feet the whole tap breaks up into 2–5 nearly equal parts which pursue a downward course, or later extend out as laterals. Primary laterals are not much branched. The whole root from crown to near the tip is covered with scattered small laterals usually not over 2 milli-
meters in diameter. These are poorly branched, not often giving off roots of the fourth order. The tip of the main root likewise is little branched. The roots are black externally, grayish inside, have a characteristic odor, and dry out and shrink rapidly upon removal from the soil. Eighteen plants on a northeast slope were examined. They had an average root depth of 5 feet and 0.4 inch.

*Heuchera glabella*

This plant, so characteristic of the rim-rock crevices especially on the more moist exposures, also occurs rather frequently (often 2 or 3 per square meter) on moist slopes in the prairie. The tufted radical leaves mostly remain green all winter. It belongs to the estival aspect. An examination of seven plants gave an average root depth of 5 feet and 1.4 inches. One root reached a depth of 5 feet and 11 inches. The strong tap is triangular in section near the top and often retains this shape to a depth of 2 feet. The laterals, which are quite numerous, usually come off in the first foot of soil. The root-system as a whole is poorly branched, even the root tips are poorly supplied with branches.

*Leptotaenia multifida*

This large, much branched, umbelliferous plant occurs quite commonly on both dry and moist hillsides. The great ternately decompound, pinnatifid leaves, together with the main stems which stand up well above other prairie vegetation, are very conspicuous even when the plants are not abundant, and especially so in June, when after flowering, the leaves turn yellow before drying up.

Fourteen root-systems were examined, mainly incidentally while excavating other roots. These large fleshy roots are sometimes 7 inches in circumference and may reach a depth of 5 feet and 7 inches. The fusiform roots may narrow down gradually or rather abruptly, even to a diameter of one or two millimeters and then again enlarge at a greater depth to a size equalling the original. This is sometimes repeated several times, thus giving
the root as a whole a beaded appearance. In general the roots are very poorly branched. Ten plants on a northwest slope gave an average depth of 3 feet and 11.3 inches, while five on a northeast slope reached an average depth of 4 feet and 6.7 inches, thus giving a total average root depth of 4 feet and 0.7 inch.

*Helianthella douglasii (Fig. 15)*

This and the following composite are both important and abundant prairie species. They occur typically on dry hillsides, often as many as 2–8 per square meter. While *Helianthella* adds much to the estival prairie aspect, with its large yellow flowers, its blooming period is well past when *Hoorebekia racemosa* comes into bloom in late July. The latter is one of the few species giving tone to a poorly defined autumnal aspect.

*Helianthella* has a tap root with a diameter seldom more than 0.8 inch. It throws out many big laterals just beneath the surface, most of which come off within the first 18 inches of soil, although there are some lower, and a cone may be formed all the way to the tip. The laterals usually pursue rather a vertically downward course, and are profusely branched. *Helianthella* branches more at the tip than does *Hoorebekia*, and it also throws out more laterals than that species. The roots are reddish-brown in color, those of *Hoorebekia* are white. They have a strong, characteristic odor, and an oily taste slightly resembling carrots. By these characters it is easy to distinguish *Helianthella* roots from others. Twenty plants were examined. An average depth of 4 feet and 4.5 inches was found; the deepest-rooted plant exceeding this by only 12.5 inches. Six plants on a southwest slope gave an average root depth of 4 feet and 4 inches; five on a northeast slope 4 feet and 8.6 inches; and ten on a northwest slope 4 feet and 7.1 inches.

*Hoorebekia (Aplopappus) racemosa (Fig. 16)*

Thirty-four plants were examined. The deepest roots reached 7 feet and 7 inches, and 11 feet respectively, but the average depth was 5 feet and 5 inches. *Hoorebekia* has a strong tap root
which tapers gradually to the end. The larger laterals (if any) are often thrown off within the first 18 inches of soil. These are branched to the third order, and may run off in a rather horizontal direction. The tap grows directly downward and is sparingly branched all the way to and at the tip. The main root is not usually more than 0.5 inch in diameter. It changes in color from light yellowish near the surface to nearly white below three feet. It has a sharp bitter taste and lacks the odor so characteristic of Helianthella roots. Twelve roots on a northeast slope averaged 5 feet and 3.4 inches in depth; twelve on a southwest slope 5 feet and 4 inches; and ten on a northwest slope 5 feet and 8.2 inches.

*Lithospermum ruderale*

These plants occur as isolated individuals, but their large size, densely tufted leaves, and numerous if not showy flowers, make them conspicuous objects in the bunchgrass association of the rim-rock as well as in the prairie.

Five root-systems were examined. The large tap roots, from 3 to 10 inches in circumference, give promise of deeper root-systems than are actually attained. Only one plant reached a depth of 6 feet and 3 inches, and the average depth was only 4 feet and 10.3 inches. Large laterals were sent off from the main root at various depths from 1 to 2 feet. These ran horizontally several feet before turning downward. One main root curved and twisted a great deal finally ending 3 feet northwest of the place where it started. The tip of the largest root examined had decayed. These roots have a very thick cortex, which separates easily from the stele. The outer part of the cortex is bright reddish especially on the parts below 1 foot. The old root bark is shreddy and gray, but firm. A peculiar taste and odor characterize these roots. Two plants on a northwest slope each reached a depth 16 inches greater than any examined on north or south slopes.
Sieversia ciliata

The soft hairy, tufted, radical leaves of *Sieversia* often remain green throughout the winter. The simple erect stems reach a height of 12–18 inches and bear their blossoms in late May or early June, while in late July or the first of August the aerial

![Image](image_url)

Fig. 15. Root-system of *Helianthella douglasii*. It may be noted that the tap root was decayed.

Fig. 16. *Hoorebeka racemosa*. This specimen had no large laterals.

plant parts largely dry up. This is a common, abundant, and cosmopolitan prairie species.

Few roots of *Sieversia* penetrate beyond depths of 5 feet and 6 inches. It sends out as many as 20–30 roots from a single inch of its thick rootstock. None of these roots are over 3–4 millimeters in diameter. They pursue a vertically downward
course and branch profusely all the way to the tip, sending off laterals seldom over 3 inches long but branched to the fifth order. The roots are jet black. Eleven plants were examined on a northeast slope and an average root depth of 4 feet and 8.6 inches was determined.

_Sidalcea oregana_

This mallow is confined to north hillsides and low ground. While much less abundant than _Geranium viscosissimum_, it is similar in habit in exposing a great number of large leaves. This plant may reach a height of over 3 feet. It blossoms later than _Geranium_ but like it retains green foliage until frost.

Only two root-systems were examined. In both numerous strong laterals were thrown off within 4 inches of the surface. At 24 inches the tap broke up into three nearly equal parts, the largest and longest part reaching a depth of only 3 feet and 1 inch. The other plant reached a depth of 4 feet and 1 inch. _Sidalcea_ roots cannot easily be confused with others for they send off small laterals in groups ranging from 3 to 8 in a group. This is most pronounced in the older parts of the roots. Often where a big lateral comes off one or more little ones originate with it. These groups of small laterals are usually less than 2 inches in length.

_Hieracium scouleri_ (Fig. 17)

The Hawkweed, with its densely hairy clusters of basal leaves, and its similarly leaden colored cauline leaves and stems reaches a height of about two feet. The rather small yellow flowers appear late in June and blossoming continues until August, even after the basal leaves have dried and turned brown. It is an important prairie species.

Twenty-six root-systems were examined. They gave an average depth of 5 feet and 4.3 inches. _Hieracium_ sends out numerous roots,—as many as 50 from a single inch of its which in turn is from 8–12 inches long. None of these roots are over 3 millimeters in diameter. They pursue a nearly
vertically downward course and throw off practically no laterals, except when they enter earthworm holes. Here, strong laterals equaling the main root in diameter, are thrown off and run parallel with it in the hole a foot or two or further. All give rise to abundant root hairs and it is seldom that these roots again enter the soil. The main root may branch very profusely or very little (in hard soil) at the tip. These light-cream-colored roots are very brittle but are easy to follow because of their latex. The acrid taste also is very characteristic and this character was sometimes used to distinguish *Hieracium* roots, especially near the tip where the latex is less abundant. The longest root reached a depth of 7 feet and 9 inches. Fifteen plants on a northeast slope gave an average depth of 5 feet and 2.8 inches; five on a southwest slope 5 feet and 3.4 inches; and six on a northwest slope 5 feet and 8.8 inches.

*Potentilla blaschkeana*

This very common prairie plant occurs in all situations, but shows a decided preference for the more moist conditions. A few new leaves may appear in the fall, but the plant starts renewed growth early in April. It blossoms in late May and dries out during July or August, depending upon the environmental conditions.

The tufted stems are borne on a short, thick crown from which several (2–5) main roots originate. These average about 7 millimeters in diameter. They taper off gradually till at about two feet in depth they are often only 2 millimeters in diameter. Here they usually branch dichotomously, and again branching break up into numerous small roots—mere hairs—which have a strong tendency to grow in earthworm holes. These they follow for two feet, perhaps, before entering the soil again. In these holes they give off many threadlike branches which follow down the same hole branching profusely, and often never re-entering the soil. The roots are dark brown in color. They are unbranched or very poorly branched at the tip. Thirty root-systems were examined. Three of the longest roots pene-
trated to depths of 6 feet and 9 inches; 7 feet and 5 inches; and 7 feet and 5 inches respectively. The average depth was found to be 5 feet and 1.8 inches. Twelve plants on a northeast slope gave an average root depth of 4 feet and 11.2 inches, while 17 on a northwest slope reached an average depth of 5 feet and 4.3 inches.

Fig. 17

Fig. 17. This shows the numerous roots sent out from the plant of Hieracium scouleri. The total length of only one root is shown.

Fig. 18. Eriogonum heracleoides from the rim-rock. A single branch of the large mat is shown just above the meter stick. Note the adventitious roots. Only a small part of the complete root-system is shown in the figure.

**Eriogonum heracleoides (Fig. 18)**

This plant seldom occurs except on the very driest ridges of high basaltic prairies, but is a very important ecological species upon the rim-rock and in the bunchgrass association. The great mats often cover an area of 2–3.5 square feet and the prostrate branches with their adventitious roots serve both to
anchor the plant in place and lay hold upon the moisture of the superficial soil layers. It is a notable fact that the Eriogonums (including *E. compositum* and *E. niveum*) blossom and appear to thrive when most other plants of the rim-rock have long since dried out. This is explained in part by their extensive root-systems, of which the one shown in the figure will be described. A few others were excavated as checks.

The strong, woody, tap root 1 inch in diameter broke up at a depth of 6 inches into seven nearly equal laterals; only about one-fourth of the old tap root is shown in the figure. One of these laterals extended a distance of 13 feet and 6 inches as measured in a direct line from the plant, but had an actual length of 14 feet and 3.6 inches. It tapered off gradually, throwing off both large and small laterals which branched to the fifth order. Upon leaving the main tap it ran along in very shallow soil for 7 feet and 6 inches before turning down in the rock crevices, where it followed a very devious route dipping up and down more than a foot, and branching profusely to the tip.

Some examinations were also made of the roots of *Rosa nutkana*, and *Symphoricarpos racemosus*, both very common in nearly all prairie situations. They were found extending to depths of from 6 to over 8 feet. *Iris missouriensis* roots penetrated the soils of dry hillsides to 3 feet and 10 inches, and *Berberis repens* to a depth of over 10 feet. The orange-yellow roots of the latter, arising from the great system of horizontal stems on the rim-rock (where it often forms societies), resemble *Eriogonum heracleoides* in their abundant laterals and in the devious route they pursue in following the basaltic crevices.

Likewise, two species of *Lomatium*, *L. grayi* and *L. macrocarpum*, both abundant on thin soils, were examined. The long, fleshy, poorly branched taps are usually flattened, folded, and twisted as they crowd into the narrow crevices of the rock to depths of 3 to 5 feet or more. On the other hand, *Polygonum majus*, growing with *Poa* on thin stony soil, has a shallow but well-developed root-system. The tap, seldom over 6.5 inches long (and usually less), sends off laterals profusely. In spite of the
small leaf surface of this knot-grass, it has always been a puzzle to the writer how the plant could keep alive and even thrive and blossom abundantly from July to October upon the parched soils of the rim-rock.

DISCUSSION AND CONCLUSIONS

The most obvious result of a consideration of these data is the fact that the response of the plant to these severe environmental conditions is met by well-developed and extensive root-systems. For just as the evaporating power of the air and the nature of the transpiring organs determine the water-requirements of plants, likewise the soil water and the nature of root-systems determine the water supply. It is interesting to note, however, that while the condition of light summer rainfall is quite unfavorable for shallow-rooted grasses, still three of the most important prairie grasses are shallow-rooted. Of these *Poa sandbergii* is the first to appear on the thin soils of the rim-rock and scab-land, where the underlying rock is little broken. In the prairie it is an important interstitial plant. It is only in the deep soils of the prairies that the shallow-rooted *Koeleria cristata* and *Festuca ovina ingrata* play their important rôle. The water-retaining capacity of the soils certainly favors these shallow-rooted species. On the other hand, the deep-rooted *Agropyron spicatum* early assumes importance as a crevice plant where sufficient cleaving of the rock has occurred. Indeed, from then on it becomes dominant in the bunchgrass association, where the soils of only a few inches depth overlie more or less decomposed basalt. In the prairie it is one of the facies, but under the new substratum conditions it partly abandons the bunch habit and may become more or less of a sod former. However, a discussion of the relation of root-systems to succession had best be considered at another time.

While the purpose of this study was not to arrive at a classification of root-systems, it is instructive to note that according to the types of root-systems as set forth by Cannon, all the roots

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here described (with the possible exception of *Leptotaenia multifida*) fall under the generalized class. By a generalized root-system is meant one that has both the tap and the laterals well developed. They penetrate deeply and reach out widely. In contrast, the specialized root-system has either the tap root as the chief feature, or the laterals are placed near the surface, and especially well developed, as in cacti. The generalized type of root is much more plastic and consequently reacts to a wider range of conditions than does the specialized type.

In considering the question of the susceptibility of roots to modification through variation in the soil texture or its water content, as against the conservative inheritance tendencies, table 6 is instructive.

**TABLE 6**

*Average root depths of plants on different slopes*

<table>
<thead>
<tr>
<th>Plant</th>
<th>S. W. SLOPE</th>
<th>N. E. SLOPE</th>
<th>N. W. SLOPE</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lupinus ornatus</em></td>
<td>72.1</td>
<td>71.0</td>
<td>128.4</td>
</tr>
<tr>
<td><em>Lithospermum ruderale</em></td>
<td>48.7</td>
<td>74.5</td>
<td></td>
</tr>
<tr>
<td><em>Potentilla blashkeana</em></td>
<td>59.2</td>
<td>64.3</td>
<td></td>
</tr>
<tr>
<td><em>Geranium viscosissimum</em></td>
<td>56.1</td>
<td>72.2</td>
<td></td>
</tr>
<tr>
<td><em>Hoorebekia racemosa</em></td>
<td>64.0</td>
<td>63.4</td>
<td>68.2</td>
</tr>
<tr>
<td><em>Hieracium scouleri</em></td>
<td>62.8</td>
<td>63.4</td>
<td>66.8</td>
</tr>
<tr>
<td><em>Helianthella douglasi</em></td>
<td>52.0</td>
<td>55.6</td>
<td>55.1</td>
</tr>
<tr>
<td><em>Balsamorhiza sagittata</em></td>
<td>61.5</td>
<td></td>
<td>69.8</td>
</tr>
<tr>
<td><em>Leptotaenia multifida</em></td>
<td></td>
<td>54.7</td>
<td>47.3</td>
</tr>
<tr>
<td><em>Agropyron spicatum</em></td>
<td></td>
<td>49.6</td>
<td>38.6</td>
</tr>
</tbody>
</table>

It appears that the root lengths on northeast and southwest slopes are about the same and that the marked environmental differences play little part in determining root depth. However, the writer is of the opinion that the hard soil on dry southwest slopes is a limiting factor to root growth. When we note the greater root development on the northwest slope, which, as has already been pointed out, combines a porous moist soil with rather extreme xerophytic above-ground conditions, this conclusion would seem to be warranted, although the evidence of *Leptotaenia* and *Agropyron* is to the contrary. But more data,
both experimental and from field observations, are needed in this and other regions before this question can be answered. The illogical neglect of most ecologists in not working in this interesting field is to be deplored. However, we must not overlook the fact that the real solution of the problem of adaptation to environment will be solved only when the extent and character of both absorbing and transpiring parts of plants are studied and correlated. The writer has under way an investigation of the ecological anatomy of the leaves of the plants mentioned in this paper, together with the extent of the transpiring surface.

Cannon (loc.cit.) points out that for desert plants having generalized root-systems it is probable that the penetration of the roots, the character of the soil permitting, is equal to the penetration of rains; also that "the generalized roots are often extremely variable, ranging from a pronounced tap root to a marked development of laterals, dependent upon soil characters and water relations." No such marked changes as these were discovered, although since the variation in the branching habit is a matter of degree rather than kind, it would be difficult to express the differences in exact terms if indeed these differences had been noticeable. However, the roots of several species showed a marked increase in their output of branches upon leaving the compact soil and entering earthworm burrows. In practically all cases the root tips under such conditions were alive and at least well covered with root hairs, while in the more compacted soils of dry slopes especially, the root tips were often dead and decayed. The cause of these differences is yet to be determined. The differences may be due to the mechanical resistance offered by the soils, or to changed conditions of aeration, or perhaps to both factors acting together.

These findings of great root depths, correlated with deep soil moisture, bear out Cannon's suggestion of the probability that the longest or the most deeply penetrating roots are found, not in deserts, but where there is considerable rainfall, and where the penetration of rain is considerable and the water table relatively deep. It may be noted here, by way of comparison, that Andropogon scoparius at Manhattan, Kansas, penetrates the soil to
6 or 8 feet,\textsuperscript{9} while Ten Eyck has shown that at the same station \textit{Andropogon furcatus} reaches depths of 4.5–6.5 feet.\textsuperscript{10} Likewise, Shantz\textsuperscript{11} in his extensive studies on the Great Plains, has shown that the Prairie grass formation (characterized by the deep-rooted \textit{Andropogon scoparius}, \textit{A. halli}, \textit{Psoralea tenuiflora}, \textit{Redfieldia flexuosa} and others) is limited in its western extension by insufficient (deep) water supply, and is replaced by the shallow-rooted short grass formation.

The roots studied are remarkable for their individuality. The roots of each species, because of peculiarities of form, of branching habit, of position in the soil, of texture, color, odor or taste, can easily be distinguished, and these distinguishing characters have often proved useful in ecological work.

A knowledge of the distribution and extent of root-systems helps us to more correctly interpret the present structure of vegetation as well as to analyze the causes which have led up to and are constantly active in modifying these conditions.

In concluding, I wish to acknowledge my deep indebtedness to my onetime student, Mr. Walter L. C. Muenchener, whose keen interest in the work made him my almost constant companion in the course of this study.

\textsuperscript{9} Georgeson, C. C. and Payne, J. E., Bul. 75 Kans. Agric. Col., 1897.
\textsuperscript{11} Shantz, H. L., Natural Vegetation as an Indicator of the Capabilities of Land for Crop Production in The Great Plains Area. Bul. 201 Bureau of Plant Industry, 1911.