1919

The Ecological Relations of Roots

John E. Weaver
University of Nebraska

THE ECOLOGICAL RELATIONS OF ROOTS

BY

JOHN E. WEAVER

Professor of Plant Ecology in the University of Nebraska

PUBLISHED BY THE CARNEGIE INSTITUTION OF WASHINGTON

WASHINGTON, 1919

CARNEGIE INSTITUTION OF WASHINGTON
PUBLICATION No. 286

PRESS OF GIBSON BROTHERS
WASHINGTON, D. C.

CONTENTS.

List of Illustrations v
Introduction 1

I. The Prairies.

Panicum virgatum 4
Andropogon furcatus 4
Andropogon scoparius ....
Andropogon nutans 5
Stipa spartea 6
Kœleria cristata 6
Elymus canadensis 6
Agropyrum repens 6
Distichlis spicata 6
Sporobolus longifolius 7
Aristida oligantha 8
Bulbilis dactyloides 8
Bouteloua gracilis 8
Liatris punctata 9
Liatris scariosa 9
Solidago rigida 9
Solidago canadensis 11
Silphium laciniatum 11
Amorpha canescens 11
Helianthus rigidus 11
Brauneria pallida 11
Petalostemon candidus 11
Vernonia baldwinii 12
Kuhnia glutinosa 12
Verbena stricta 12
Grindelia squarrosa 12
Glycyrrhiza lepidota 13
Astragalus crassicarpus 13
Psoralea tenuiflora 14
Psoralea argophylla 14
Baptisia bracteata 14
The Subclimax Prairie 15
Brauneria pallida 15
Lygodesmia juncea 16
Lespedeza capitata 16
Ceanothus ovatus 17
Amorpha canescens 17
Prairie Root Systems and Prairie Environment 18

II. The Chaparral Community.

Symphoricarpos vulgaris 25
Rhus glabra 26
Corylus americana 27
Vitis vulpina 27
Rosa arkansana 27
Shrub Root Systems and the Shrub Environment 28

III. The Prairies of the Pacific Northwest.

The Root Systems of the Grasses 31
Agropyrum spicatum 31
Festuca ovina ingrata 33
Poa sandbergii 33
Kœleria cristata 33
The Root Systems of other Prairie Species . 33
Lupinus ornatus 33
Lupinus leucophyllus 35
Astragalus arrectus 35
Balsamorhiza sagittata 35
Geranium viscosissimum 35
Wyethia amplexicaulis 35
Heuchera glabella 37
Leptotænia multifida 37
Helianthella douglasii 37
Hoorebekia racemosa 37
Lithospermum ruderale 37
Sieversia ciliata 37
Sidalcea oregana 37
Hieracium scouleri 38
Potentilla blaschkeana 38
Eriogonum heracleoides 38
Prairie Root Systems and Prairie Environment 38

IV. The Plains Association.

Bouteloua gracilis 46
Aristida purpurea 46
Muhlenbergia gracillima 47
Gutierrezia sarothræ 49
Psoralea tenuiflora 49
Artemisia frigida 50
Argemone platyceras 50
Yucca glauca 51
Agropyrum ~~glaucum~~ smithii 52
Carex pennsylvanica 52
Andropogon scoparius 52
Stipa comata 53
Lithospermum linearifolium 53
Lygodesmia juncea 53
Aragallus lambertii 55
Petalostemon purpureus 55
Petalostemon candidus 57
Eriogonum jamesii 57
Ratibida columnaris 59
Senecio aureus oblanceolatus 59
Asclepias verticillata pumila 59
Opuntia camanchica 61
Opuntia fragilis 62
Plains Root Systems and the Plains Environment 63

V. THE SANDHILLS SUBCLIMAX.

	PAGE
Redfieldia flexuosa	68
Calamovilfa longifolia	68
Andropogon hallii	70
Muhlenbergia pungens	70
Sporobolus cryptandrus	71
Eriogonum microthecum	71
Artemisia filifolia	73
Tradescantia virginiana	73
Heliotropium convolvulaceum	74
Petalostemon villosus	74
Gilia longiflora	75
Euphorbia petaloidea	76
Psoralea lanceolata	78
Ipomœa leptophylla	78
Sandhill Root Systems and the Sandhill Environment	79

VI. THE GRAVEL-SLIDE COMMUNITY.

Krynitzkia virgata	81
Paronychia jamesii	82
Aletes acaulis	83
Apocynum androsæmifolium	84
Smilacina stellata	85
Pachylophus cæspitosus	85
Thlaspi alpestre	86
Mentzelia multiflora	87
Eriogonum flavum	87
Gravel-Slide Root Systems and Gravel-Slide Environment	88

VII. THE HALF-GRAVEL-SLIDE COMMUNITY.

Elymus triticoides	92
Solidago oreophila	92
Rubus deliciosus	93
Besseya plantaginea	94
Geranium cæspitosum	95
Calamagrostis purpurascens	95
Kœleria cristata	95
Gilia aggregata	95
Potentilla arguta glandulosa	97
Frasera speciosa	97
Aster porteri	98
Half-Gravel-Slide Root Systems and the Half-Gravel-Slide Environment	98

VIII. THE FOREST COMMUNITY.

Pirola chlorantha	100
Thalictrum fendleri	100
Erigeron asper	101
Erigeron macranthus	101
Fragaria virginiana	102
Allium cernuum	103
Aralia nudicaulis	103
Opulaster opulifolius	103
Ribes lacustre	104
Rosa acicularis	104
Arctostaphylos uva-ursi	105
Senecio cernuus	105
Castilleia miniata	105
Heuchera parvifolia	105
Saxifraga bronchialis	106
Haplopappus parryi	107
Forest Root Systems and the Forest Environment.	108

IX. ECADS.

Smilacina stellata	110
Chamænerium angustifolium	110
Elymus triticoides	112
Bouteloua gracilis	112
Stipa comata	113
Yucca glauca	114
Allionia linearis	114
Abronia fragrans	115
Kœleria cristata	117
Chrysopsis villosa	117
Euphorbia montana	119
Root Modifications of Polydemics	121

X. SUMMARY.

Summary	122
Bibliography	128

LIST OF ILLUSTRATIONS.

PLATES.

PLATE A.
Quadrat-bisect showing root distribution of certain dominant and subdominant plains species: A, *Aristida purpurea;* B, *Bouteloua gracilis;* Ar, *Artemisia frigida;* P, *Psoralea tenuiflora;* C, *Chrysopsis villosa;* Y, *Yucca glauca.*

PLATE B.
Quadrat-bisect in the half-gravel-slide. The face of the trench was cut along the front of quadrat shown in Plate 25, A: S, *Solidago oreophila;* A, *Allium cernuum;* E, *Elymus triticoides*, fragments of which are shown in blue; C, *Calamagrostis purpurascens;* H, *Heuchera parvifolia;* B, *Besseya plantaginea.*

PLATE C.
Quadrat-bisect showing root systems of shrubs and herbs of the forest floor. This was made along the front edge of the quadrat shown in Plate 27, B: H, *Haplopappus parryi;* R, *Rosa acicularis;* Pi, *Pinus flexilis;* F, *Fragaria virginiana;* C, *Chamænerium angustifolium;* P, *Picea engelmanni.*

PLATE 1.
A. One end of a trench used in excavating root systems.
B. *Distichlis spicata*, showing the long rhizomes and shallow roots.

PLATE 2.
A. A prairie of eastern Nebraska in June, *Erigeron ramosus* and *Meriolix serrulata* in the foreground, and bushy *Psoralea tenuiflora* in background.
B. An area dominated by *Agrostis hiemalis*, with *Allium mutabile*, *Achillea millefolium*, and *Stipa spartea.*

PLATE 3.
A. *Andropogon furcatus.*
B. *Andropogon scoparius.*
C. *Andropogon nutans.*

PLATE 4.
A. *Panicum virgatum*, showing rhizomes, coarse roots, and complete single root.
B. *Stipa spartea.*

PLATE 5.
A. *Kœleria cristata.*
B. *Elymus canadensis.*

PLATE 6.
A. *Sporobolus longifolius.*
B. *Bouteloua gracilis*, excavated near the quadrat shown in text-figure 1.

PLATE 7.
A. *Silphium laciniatum*, roots partially excavated.
B. *Amorpha canescens*, showing the wide lateral spread.

PLATE 8.
A. *Kuhnia glutinosa*, roots partially excavated.

PLATE 8—continued.
B. *Glycyrrhiza lepidota;* *a′* is a continuation of *a.*

PLATE 9.
A. *Astragalus crassicarpus*, mature root system.
B. *Astragalus crassicarpus*, showing root of young plant.
C. *Baptisia bracteata.*

PLATE 10.
A. *Psoralea tenuiflora*, the tap root decayed.
B. *Psoralea argophylla*, showing entire root in center.

PLATE 11.
A. *Brauneria pallida.*
B. *Lygodesmia juncea*, in two sections.
C. *Lespedeza capitata.*

PLATE 12.
A. *Ceanothus ovatus*, root of a thirteen-year old plant; *a′* is a continuation of *a.*
B. *Amorpha canescens;* *a′* is a continuation of *a.*

PLATE 13.
A. *Symphoricarpos vulgaris*, showing fine network in surface soil.
B. Rhizomes and runners of *Symphoricarpos vulgaris;* the horizontal line is the ground line.

PLATE 14.
A. *Rhus glabra*, a portion of the root network with ascending rootlet *a.*
B. *Rhus glabra*, with ascending rootlets.

PLATE 15.
A. *Corylus americana*, the roots shown in two sections.
B. *Rosa arkansana*, the roots shown in two sections.
C. *Corylus americana*, rhizomes and roots

PLATE 16.
A. *Rosa arkansana*, showing method of propagation.
B. *Rhus glabra* invading subclimax prairie.

PLATE 17.
A. *Yucca glauca*, showing the multicipital stems and rhizome habit.
B. Prairie of southeastern Washington.
C. Meter quadrat in the prairie, showing *Balsamorhiza*, *Festuca*, *Lithospermum*, and *Hieracium.*

PLATE 18.
A. The plains association near Colorado Springs, showing *Aristida purpurea* bunches in *Bouteloua gracilis* turf.
B. *Psoralea tenuiflora*, in two sections.
C. *Yucca glauca.*

PLATE 19.
A. *Stipa comata.*
B. *Petalostemon candidus.*
C. *Eriogonum jamesii.*

PLATE 20.
A. Short-grass plains, showing *Bouteloua gracilis* and *Opuntia polyacantha.*
B. General view of the sandhill community.

PLATE 21.
A. A sandhill community, showing *Redfieldia, Petalostemon villosus, Psoralea lanceolata*, and *Chrysopsis villosa*, with a socies of *Eriogonum microthecum* at the left.
B. Roots and rhizomes of *Calamovilfa longifolia*.
PLATE 22.
A. *Andropogon hallii*.
B. *Muhlenbergia pungens*.
PLATE 23.
A. Consocies of *Aletes acaulis* on the gravel-slide, with *Krynitzkia virgata* in the foreground.
B. Quadrat on the gravel-slide, showing detail of surface.
PLATE 24.
A. *Aletes acaulis*.
B. Network of fine rootlets of *Aletes*.
C. *Smilacina stellata*.
D. *Thlaspi alpestre*.
PLATE 25.
A. Half-gravel-slide, showing *Elymus triticoides* and the large bare intervals.
PLATE 25—continued.
B. *Elymus triticoides*.
C. *Rubus deliciosus*.
PLATE 26.
A. *Kœleria cristata*.
B. *Calamagrostis purpurascens*.
C. *Potentilla arguta glandulosa*.
PLATE 27.
A. *Picea engelmanni* consociation, showing the forest floor.
B. Quadrat in the same spruce forest, showing *Haplopappus parryi, Fragaria virginiana, Thalictrum fendleri*, etc.
PLATE 28.
A. *Arctostaphylos uva-ursi*, showing a portion of the root system.
B. *Ribes lacustre*, seven years old.
PLATE 29.
A. Root systems of ecads of *Smilacina stellata; a*, gravel-slide; *b*, spruce forest.
B. *Bouteloua gracilis* from the sandhills.
C. *Abronia fragrans* from the plains.
PLATE 30.
A. *Opulaster opulifolius*, twelve years old.
B. *Chrysopsis villosa* from the sandhills.

TEXT-FIGURES.

PAGE
1. A meter quadrat in the *Bouteloua* community dominating a gravelly ridge at Belmont, near Lincoln; B, *Bouteloua gracilis;* A, *Andropogon furcatus;* S, *Sporobolus longifolius;* M, *Meriolix serrulata;* Am, *Amorpha canescens* 9
2. Root system of *Liatris punctata* 10
3. Root system of *Kuhnia glutinosa* 10
4. Graphs showing the average daily temperature (heavy line) and humidity (light line) in the prairie during 1916 22
5. Graphs showing the average daily evaporation rates in the prairie during 1916 (heavy line) and 1917 (light line) 22
6. Schematic bisect showing the root and stem relations of important prairie plants. This and figures 7 and 8 were drawn from photographs and data obtained by the excavation and examination of 325 root systems of these 18 species: H, *Hieracium scouleri;* K, *Kœleria cristata;* B, *Balsamorhiza sagittata;* F, *Festuca ovina ingrata;* G, *Geranium viscosissimum;* P, *Poa sandbergii;* Ho, *Hoorebekia racemosa;* Po, *Potentilla blaschkeana* 32
7. Schematic bisect: S, *Sieversia ciliata;* W, *Wyethia amplexicaulis;* Ll, *Lupinus leucophyllus;* Lo, *Lupinus ornatus;* P, *Poa sandbergii;* E, *Leptotœnia multifida;* A, *Agropyrum spicatum* 34
8. Schematic bisect: Hu, *Heuchera glabella;* A, *Astragalus arrectus;* S, *Sidalcea oregana;* H, *Helianthella douglasii;* Ag, *Agropyrum spicatum* 36
9. *Aristida purpurea* 47
10. *Artemisia frigida* 47
11. *Gutierrezia sarothræ*, showing wide lateral spread of roots in the surface soil 48
12. A small part of caudex of *Yucca glauca*, showing number and extent of horizontal roots, many exceeding 25 to 30 feet in length 48
13. *Argemone platyceras* 54
14. *Lithospermum linearifolium* 54
15. *Lygodesmia juncea* 56
16. *Aragallus lambertii* 56
17. *Petalostemon purpureus* 58
18. *Ratibida columnaris* 59
19. *Senecio aureus oblanceolatus* 60
20. Underground parts of *Asclepias verticillata pumila* 61
21. *Opuntia camanchica*, showing vertical anchorage roots 62
22. Top view of surface roots of *Opuntia camanchica*, showing the wide lateral spread 62
23. *Redfieldia flexuosa*, showing rhizomes and root distribution 69
24. *Eriogonum microthecum* 72
25. Root system of a ten-year-old *Artemisia filifolia* 74

PAGE
26. *Tradescantia virginiana* 74
27. Root system of *Petalostemon villosus* .. 75
28. *Gilia longiflora* 76
29. Underground parts of *Psoralea lanceolata*. showing root tubercles at a depth of eight feet 77
30. *Ipomœa leptophylla*. showing a portion of the very extensive root system 78
31. *Krynitzkia virgata*. The heavy slanting line indicates the actual ground-line 81
32. *Paronychia jamesii* 82
33. Surface view of a single root of *Paronychia jamesii* at a depth of 2 to 2.5 inches 83
34. *Apocynum androsæmifolium*, showing rhizomes and dense network of roots 84
35. *Pachylophus cæspitosus* 86
36. *Eriogonum flavum* 87
37. Quadrat-bisect showing root relations of gravel-slide plants. This was made along the front of quadrat shown in Plate 23, B: P, *Paronychia jamesii;* A, *Aletes acaulis;* K, *Krynitzkia virgata* 90
38. *Solidago oreophila*, showing wide-spreading lateral and deep central roots 93

PAGE
39. *Besseya plantaginea*, showing the wide-spreading root system 94
40. Root system of *Geranium cæspitosum*. 96
41. Root system of *Frasera speciosa* 97
42. *Pirola chlorantha* 100
43. *Thalictrum fendleri* 101
44. Rhizome and roots of *Erigeron asper* .. 102
45. *Fragaria virginiana* 102
46. *Allium cernuum* 102
47. Rhizomes and root system of *Aralia nudicaulis* 103
48. *Senecio cernuus* 106
49. *Heuchera parvifolia* 107
50. *Haplopappus parryi* 107
51. Root systems of ecads of *Chamænerium angustifolium: a*, gravel-slide; *b*, forest 111
52. Fragments of the roots of *Yucca glauca: a*, plains form; *b*, half-gravel-slide form 114
53. *Allionia linearis* from the plains 115
54. *Allionia linearis* from the sandhills ... 115
55. *Abronia fragrans* from the sandhills .. 116
56. *Chrysopsis villosa*, showing various stages of development in the plains soil 118
57. *Euphorbia montana* from the plains ... 120
58. *Euphorbia montana* from the half-gravel-slide 120

THE ECOLOGICAL RELATIONS OF ROOTS.

INTRODUCTION.

Although considerable progress has been made in the study of root systems of desert plants (Cannon, 1911, 1913; Markle, 1917), very little information is available concerning the roots of other native species. During 1914 the writer investigated the root systems of the prairie plants of southeastern Washington, where the annual precipitation is only 21.6 inches and occurs mostly in the period of rest. Since that time it has been planned to make a comparative study of the roots of prairie plants growing in a more humid region and where the precipitation occurs mostly during the season of plant growth. The opportunity for such study came during the fall of 1917 and work was carried on vigorously until the soil became frozen in December. The study was resumed early in the following spring. In June 1918 the field of investigation was extended to the Great Plains and sandhill region of Colorado, while later in the summer a large number of plants were excavated and examined in various habitats about Pike's Peak in the Rocky Mountains.

A knowledge of root distribution and root competition under different natural conditions is not only of much scientific value, but it also finds practical application in a better understanding of the value of plants as indicators for distinguishing lands of grazing value only from those with possibilities of crop production. It will result in a more intelligent solution of the ecological problems of grazing and will likewise be of great aid to the forester in selecting sites for afforestation. Moreover, a knowledge of root distribution will throw a flood of light upon many of the problems of plant succession. Indeed, the phenomena of ecesis, competition, and reaction can not be completely, if indeed correctly, interpreted without a knowledge of the extent, position, and relation of the root systems of the plants.

Shantz has given us an excellent example of the value of a knowledge of root distribution in his study of the natural vegetation of the Great Plains as an indicator of the capabilities of land for crop production (1911). Sampson (1914, 1917) has made a study of root systems of many range plants in considering their life history, forage value, and the natural revegetation of range lands; while foresters are just beginning to study the roots of plants as indicators of conditions of soil moisture on various sites (Korstian, 1917).

This paper contains descriptions of the character, depth, and distribution of the roots of about 140 species of plants. These include shrubs, grasses, and other herbs, a few of the latter being noxious weeds. It represents the results of the examination of approximately 1,150 individual plants in 8 different communities, as follows: prairies of eastern Nebraska, chaparral of southeastern Nebraska, prairies of southeastern Washington and adjacent Idaho, plains and sandhills of Colorado, the gravel-slide, the half-gravel-slide, and forest communities of the Rocky Mountains of Colorado.

The method employed in excavating root systems was to dig trenches 2 to 3 feet wide and 6 to 10 feet long to a depth of about 6 feet by the side of the plants to be examined. This offered an open face into which one might dig with a hand pick furnished with a cutting edge on one end, 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 a depth of 10 or even 16 feet (plate 1). A total of more than 100 such pits was used. To assure absolute certainty as to maximum depth, for extreme care must be used in excavating root termini, the soil underlying the deepest roots was usually undercut about 12 to 18 inches below the root-ends and carefully examined as it was removed. For the deepest-rooted species of herbs and shrubs it was found expedient to have a longer trench with two levels, one at about 7 to 9 feet and a second one about twice as deep. Thus the soil could be removed from the lower to the higher level as work proceeded. Indeed, in several cases where the roots extended to depths of 18 or 20 feet or more (for example *Rosa arkansana* or *Lygodesmia juncea*), the deeper soil was removed by means of a bucket attached to a rope. Considerable danger from caving was experienced, especially in the sandhill soils and also in the deeper loose loess soils as well. In fact, it was found inexpedient to remove the entire root system in a few cases. In each community the work extended over a field sufficiently large, sometimes several square miles in extent, so that any local differences in soil texture, etc., were eliminated.

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

During the course of these investigations the writer has become greatly indebted to the following persons for faithful assistance in the pursuance of this work. It is a pleasure to acknowledge here the indebtedness to my students, Messrs. F. C. Jean and Alvin Goke, for much help in the excavation of the plants, and to Miss Annie Mogensen and Mrs. F. C. Jean for their assistance in drawing many of the root systems. I wish also to acknowledge the helpful suggestions and encouragement given by Dr. F. E. Clements and Dr. R. J. Pool throughout the period of the work. To Professor T. J. Fitzpatrick I am also indebted for careful reading of the manuscript and proof.

I. THE PRAIRIES.[1]

The prairies of eastern Nebraska in which these studies were made are too well known to need discussion here (plate 2). A general floristic description has been given by Pound and Clements (1898, 1900), a more detailed one for a portion of southeastern Nebraska by Thornber (1901), and recently a more specific account of the local region under consideration by Weaver and Theil (1917). As the various species are considered, brief comment will be made upon their relative importance. Therefore, we may proceed to a consideration of the root habits of the individual species and then examine the environmental conditions under which the plants grow. Finally, the correlations between root habit and environment will be discussed. This sequence will be followed for each plant community.

Panicum virgatum.—Although showing a preference for loose sandy soils, panic grass grows abundantly in many situations throughout the prairies. Its size, abundance, and duration combine to make it an important component of the prairie vegetation, where it often holds the rank of a dominant species.

This grass has the longest root system of any species examined. The roots are very coarse, many having a diameter of 3 or 4 mm. They pursue a vertically downward course, spreading only a little near the surface, to a maximum depth of over 9 feet. Several plants reached depths of over 8.5 feet (plate 4, A). In the first 6 or 7 feet of soil the roots are very little branched, the laterals (usually less than 3 inches long) occurring only scatteringly. In the deeper soil numerous fine laterals occur, although the last 6 to 12 inches are often very poorly branched and the roots end abruptly. The main roots remain nearly uniform in diameter for most of their course or taper so slowly that at 5 or 6 feet they may still have a diameter of 2 mm. The type of soil considerably modifies not only the root penetration but also the manner of branching. The plants that were growing in a gravelly soil with a sandy subsoil underlaid with an impervious blue clay were found to penetrate only 7 feet to the clay, but the branching was much more pronounced. The cortex on younger roots is pearly white and very brittle; on older ones smooth, pinkish white, and of a papery consistency. Eight plants were examined.

Andropogon furcatus.—The two bluestems are dominants among prairie grasses. They form a large part of the prairie hay of Kansas and Nebraska. The taller and deeper but coarser-rooted *A. furcatus* is less resistant to drought than the shorter, finer-rooted *A. scoparius*, as is shown both by their local and general distribution. Throughout the prairies the former luxuriates in the draws and on lower lands, while the latter dominates higher areas. Westward the big bluestem soon drops out, while little bluestem not only forms a "dominant of widest distribution and most controlling influence in the bunch-grass association of the sandhills" (Pool, 1914: 224) and "enters into disturbed areas of the wiregrass association in Colorado" (Shantz, 1911: 52), but also occurs on rough hillsides where water penetrates readily, throughout much of the area included in Wyoming and Montana.

[1] The major portion of the work in this section was done by the writer in conjunction with Mr. Lyman H. Andrews, who voluntarily joined the colors in December 1917, and to whom joint credit is herewith acknowledged.

Ten Eyck (1904: 216) examined the roots of *A. furcatus* at Manhattan, nsas, and found that they "form a dense, tough sod, from 6 to 8 inches ck, and the subsoil is filled with a great mass of roots." "The roots were broken off at 4.5 feet from the surface, but from their size they must have extended at least 2 feet deeper into the compact clay subsoil."

Twelve plants were examined near Lincoln. The very abundant roots ow both vertically and obliquely downward, a few almost horizontally, and at once thoroughly occupy the soil and form a dense sod. The roots may extend obliquely away from the bunches to more than a foot before turning wnward. The larger roots vary from 0.5 to 3 mm. in diameter and may ch a depth of 6 feet and 10 inches. Most of the plants examined reached depths of over 6 feet ~~(plate 3, A)~~. In locations where ~~a~~ hard clay subsoil occurred the roots ~~were 2 to~~ 2.5 ~~feet shorter~~. All of the roots branch profusely, e main laterals being from 2 to 6 inches long. However, here again the iount of branching and the length of the laterals are closely correlated with the soil texture, always being less in hard soils. The roots taper so gradually that at 4 feet thay are nearly as large as at the surface. ~~The soil is thoroughly~~ cupied to a depth of 5 ~~feet~~. The ends of the roots are extremely well anched to the very tip. In color the roots are reddish-brown. They have a very loose papery cortex which is easily removed and reveals the tough, yellowish stele.

Andropogon scoparius.—This grass is figured by Shantz (1911: 56) as tending to a depth of about 5 feet and thoroughly occupying the sandy soil in the bunchgrass association of eastern Colorado. It is interesting to note that the deep-rooted *Panicum virgatum* also occurs here.

In these studies plants of this species were examined in two soil types. The st group was in porous, gravelly soil mixed with sand and underlaid with a rocky subsoil of decayed sandstone at a depth of 3 feet. The other group grew in clay-loam soil with a clay subsoil. In the former habitat none of the ots of the several plants examined reached depths greater than 28 inches, hile in the clay loam several plants had a maximum root depth of about 65 inches (plate 3, B). The roots are much finer than those of *A. furcatus*, being only 0.1 to 0.8 mm. in diameter. The lateral spread of the roots is very milar but somewhat more pronounced. Roots are so abundant as to form dense sod, completely filling the soil to a depth of from 12 inches in gravelly soil and to as much as 30 inches in clay loam. The surface is especially well occupied with dense masses of finely branched rootlets. All the roots branch profusely to the third or fourth order, many of the branches being over 30 ches long. The deeper soil (from 30 to 60 inches) is fairly well occupied. The roots are light-brown in color and have a very thick cortex which peels off easily, thus exposing the tough yellowish stele. The deeper roots are lighter in color, profusely branched, and very brittle.

Andropogon nutans.—Goldstem is a dominant in the subclimax prairie. Like the other andropogons and *Panicum virgatum*, it also matures late in summer. It is one of the deeper-rooted prairie grasses. Of the 5 plants xamined the maximum depth of root varied between 51 and 59 inches plate 3, C). These were growing in a clay-loam soil which extended to a depth of 3.5 feet and below which occurred pure sand. The roots vary from 2 mm. to less than 0.5 mm. in diameter. They are very abundant, spread terally but little, and completely occupy the soil, branching profusely to the cond and third order. Within a foot from the surface, however, most of the roots become less than 0.5 mm. in diameter, forming a dense network to a depth of about 3 feet. Even in the fourth foot the roots are quite numerous, many of them breaking up at this depth into clusters of small branches. The roots are slightly reddish in color. The branching is characteristic but difficult to describe.

Stipa spartea.—This perennial grass is one of the dominants in the prairies, being especially conspicuous during the month of June, when it gives tone to the estival aspect. Its root system is rather meager when compared with most of the other prairie grasses. Strong fibrous roots from 1 to 1.5 mm. in diameter descend rather vertically into the soil to a maximum depth of only 21 to 26 inches (plate 4, B). A few spread laterally in a diagonal direction to a distance as great as 10 or 12 inches. Numerous smaller roots fill the surface soil, while the larger ones send off many laterals to a depth of about 14 inches, where the main roots may break up into many fine branches. The hairy cortex causes the soil to cling to it very closely. This pulpy cortex has a grayish-white color and peels off very easily, leaving a very wiry, tough stele.

Kœleria cristata.—Whether on the prairies of Minnesota or Nebraska or in the Pacific Northwest, *Kœleria* is an important grass in the estival aspect. As in the case of *Stipa spartea*, which also makes a rapid growth and blossoms early, the vegetative and reproductive activity may be correlated with the shallow root system. In eastern Washington, where *Kœleria* is a common bunchgrass, it flowers in late June, soon dries up, and remains dormant until revived by the autumn rains. In this region the deepest root found was at 28 inches, and 15 inches was determined as the average depth (Weaver, 1915).

This plant has a very shallow but exceedingly well-developed root system. None of the roots of the 7 plants examined reached depths of over 21 inches, while the average root depth was about 15 inches (plate 5, A). A great abundance of fine rootlets spread out from the base of the plant and occupy the soil exclusively for a distance of 8 inches on each side of it. Indeed, some of the roots run almost horizontally and are less than 0.5 inch deep in the soil. The roots are yellowish-brown in color, usually less than 0.2 mm. in diameter, and branch and rebranch to form a dense mat.

Elymus canadensis.—This plant is an important prairie species of wide distribution. Like *Kœleria*, it is comparatively shallow-rooted, but has a widely spreading root system. Five plants in loess soil gave maximum root depths of 16, 17, 20, 21, and 22 inches respectively. Plate 5, B, shows the rather meager root development when compared with most of the other grasses. The obliquely running roots reach distances of 20 inches or more on either side of the base of the plant. Lateral rootlets are seldom over 2 inches long and may branch to the third or fourth order. The roots are white in color and from 0.1 to 0.5 mm. in diameter. They are very tough and wiry.

Agropyrum repens.—From the extensive rhizomes of this perennial, which are often 2 to 3 feet long, arise numerous fine, silvery-white roots. These send off rather poorly branched laterals as they descend somewhat vertically downward, some to a maximum depth of 8 feet. The first 30 inches of soil is abundantly filled with roots, while many penetrate to a distance of 4 to 7 feet. Many of the roots of the 10 plants examined pursued a peculiar zigzag course, a character which was more pronounced in the deeper roots.

Distichlis spicata.—This low, diœcious perennial of seacoasts and alkaline soils is still quite abundant on the "salt flats" about Lincoln, although it is being replaced by other species as the soil becomes less salty, due to better drainage resulting from the straightening of stream courses. It has considerable forage value throughout the West, where it occurs abundantly in low saline situations. About Lincoln most of the area occupied by salt grass is alluvial wash, the various soil strata often showing quite distinctly (plate 1, B). The plants examined were growing in pure stands. A chemical examination of the first 8 inches of soil (the samples being taken soon after a rain had wet the soil to just this depth) gave a salt content of 2.6 per cent. This is less than in the adjacent and successionally earlier *Atriplex* zone, which gave 3.1 per cent alkalinity. In both cases the greater part of the salt was sodium carbonate.[1]

In the succession it is replaced by *Agropyrum repens*, which in turn is followed by *Sporobolus longifolius*, *Panicum virgatum*, *Andropogon furcatus*, and other prairie plants. An interesting successional sequence was determined in a rich alluvial flood-plain, where the water-level occurred in gumbo soil at a depth of about 6 feet. Although only an occasional specimen of *Distichlis* was to be seen, the soil contained three distinct strata of the abundant and well-preserved rhizomes at depths of 13, 9, and 6 inches respectively. These indicated successive overflows and deposits. Above these the soil was filled with a dense network of the rhizomes of *Agropyrum repens*. However, only a few of these plants were still alive, the soil being almost completely occupied by alternate areas of *Sporobolus longifolius* and *Bulbilis dactyloides*.

Distichlis has better developed rhizomes than almost any other grass examined. They vary from 2 to 5 mm. in diameter, often being somewhat flattened parallel with the soil surface. One specimen was found to be 9 feet long. It supported 19 tufts of plants. The rhizomes are exceedingly tough, being covered with a hard, shell-like cortex. The terminal buds are long and sharp-pointed, as are also the leaf-scales at the regularly spaced nodes which are about 2 inches apart. The rhizome depth is quite uniform at from 4 to 6 inches. The rhizomes branch extensively, sending off laterals in all directions.

The roots are relatively shallow, but few occur in the first 4 inches of soil. They branch from the rhizomes in both vertical and horizontal directions, and while the lateral spread is not great, they occupy the soil thoroughly to a depth of about 18 inches. Relatively few reach a depth of over 2 feet. They are from 1 to 3 mm. in diameter and branch rather sparingly to the third order, these laterals being only 1 or 2 inches long. The deeper roots are even more sparingly furnished with laterals, which are only 1 to 3 mm. in length. The yellowish-white cortex of the older roots is thick and pulpy. When removed it reveals a pearly-white stele. Thirteen plants were examined.

Sporobolus longifolius.—This perennial, late-maturing grass is often an important component of prairie vegetation, especially in the earlier stages of development. Although it occurs in typical prairie, it is often more abundant on eroding banks along roadsides and in disturbed areas generally from dry hill-tops to alluvial flood-plains. The short, thick rootstocks spread in all directions and form bunches varying from 4 to 18 inches in diameter.

The rather coarse, fibrous roots penetrate the soil to an average maximum depth of only 24 inches. The greatest root depth of the 17 plants examined ranged from 17 to 40 inches. However, the roots are very dense and thoroughly occupy all of the soil, spreading laterally from the base of the plant in an almost horizontal direction to a distance of from 12 to 20 inches (plate 6, A). Thus an area of soil of 6 or 7 square feet may be thoroughly occupied to a depth of 18 inches by the roots of a single bunch. The roots vary from 1 to 2 mm. or less in diameter, many of them keeping the original diameter to a depth of 18 inches. They are pearl-white in color, very tough and wiry, and the cortex is densely covered with short hairs. When the cortex is removed it reveals the thick, white stele. All of the roots branch profusely,

[1] The writer is indebted to Professor C. J. Frankforter for these determinations.

but the laterals are only 0.5 to 2 inches long. These often branch again. The roots below the 18-inch level are relatively few and the soil is not well occupied. Roots were examined in 3 different soil types and found to be very similar in all.

Aristida oligantha.—This species is abundant on prairies, especially in drier soils. It frequently dominates areas where the soil is shallow, or plays the rôle of an interstitial among the taller grasses. The root systems of 10 plants of this annual grass were examined. They were growing in a clay-loam soil. The white, threadlike roots are less than 0.2 mm. in diameter and are found abundantly only in the first 10 inches of soil. While some of the longest reach depths of 40 inches, relatively few occur below 18 inches. They are so fine and brittle that it proved impossible to secure material for a photograph. Compared with other grasses the roots are much less abundant.

Bulbilis dactyloides.—Perhaps no grass of the western plains, except grama, is better known for its valuable characteristics as a pasture grass than the buffalo grass. In the region of this study it can not compete with the taller prairie plants. However, it is found in dense patches resulting from its method of propagating by stolons, on low-lying lands where water may stand for a time in "pockets" or where over-grazing has killed the taller grasses.

Ten Eyck (1904), working at Manhattan, Kansas, and in a soil of which the surface foot was a mellow, dark loam, underlaid with a rather compact, clayey subsoil, found "the roots are numerous but they do not penetrate deeply into the soil". Shantz (1911: 38), dealing with the hard soils of the Great Plains region of Colorado, where "the soil is only rarely wet down to a foot or more," states that "almost the entire root system of the short grasses (*Bulbilis dactyloides* and *Bouteloua oligostachya*) is limited to the first 18 inches of soil. They have a very extensive surface root system." Robbins (1917: 70) states that roots of buffalo grass sometimes go to a depth of 7 feet. This latter statement checks up more nearly with our findings.

A dozen root systems of this grass were examined in two different areas, both of which were in alluvial soil on bottom lands. The roots are very fine, the largest being less than 0.5 mm. in diameter. They scarcely spread at all laterally, but form a dense mat to a depth of 12 to 18 inches, branching mostly only to the second order. These hairlike laterals are usually not over 0.5 inch in length. Although these roots are very fine, they are quite tough and easy to follow. At 18 inches depth they become less numerous and are poorly branched, so that the deeper soils are sparsely occupied. However, many roots occurred at 4.5 feet, and numerous others continued vertically downward to a maximum depth of from 58 to 73 inches and in one of the trenches in gumbo soil to the ground-water level. The shallower roots are light-brown in color, while the deeper hairlike roots are nearly white.

Bouteloua gracilis.—Grama grass occurs often in fairly pure stands on the lighter soils of gravelly ridges and it is also frequently found dominating areas of alluvial soil on bottom lands. Figure 1 shows a typical area dominated by *Bouteloua* into which *Andropogon furcatus* is invading. The soil is a very porous coarse sandy to gravelly loam deposited by glacial action, with a water-holding capacity of about 40 per cent of its dry weight. This grama consocies, in which a number of root systems were examined, dominates a ridge at Belmont near Lincoln, which is entirely surrounded by tall prairie grasses rooted in clay loam. The transition from one soil type to the other is very abrupt and the ecotone is correspondingly sharp. Frequent determinations invariably showed a higher available water-content in the clay-loam soil.

The root system is extremely well developed, great masses of fine roots occupying every cubic centimeter of soil to a depth of 18 inches. A few roots reached a maximum depth of 46 inches, although below 2 feet the roots are very sparse (plate 6, B). The largest roots are only 0.5 mm. in diameter. The laterals are usually not over an inch long. These abundant threadlike laterals branch only poorly. The roots are brownish white in color and of a very firm texture. Other groups of plants examined in two locations on alluvial soils showed a somewhat poorer development of the root system, but the general distribution and depth were very similar to those growing in the gravelly soil. This root distribution stands quite in contrast to that found by Shantz in Colorado. This would seem to be a clear case of environmental conditions profoundly modifying root development.

Liatris punctata.—Of the numerous blazing-stars which add beauty to the prairies in autumn, *L. punctata* and *L. scariosa* are probably the most abundant. The xerophytic nature of the former and its extensive range far into the drier regions westward may be explained in part by its deep root system.

Seven individuals of this species were excavated. All had strong tap-roots. Those growing in clay with a sandy subsoil reached depths of 11 feet 5 inches and 15 feet 9 inches respectively, while three growing in clay-loam with a clay subsoil penetrated only to a depth of about 6 feet 8 inches. A diagram of one of the larger specimens (fig. 2), reconstructed from a photograph and from a drawing made to scale in the field, pictures the roots as occurring in one plane. On other specimens small laterals were very scarce to a depth of 9 feet, while at 12 feet the soil was filled with small, silvery white, sparsely branched rootlets. This scarcity of absorbing laterals was again noted in the clay-loam soil of the high prairie until a depth of about 6 feet was reached. Even here the branching was not so pronounced as on the specimens in the lighter soil. The older roots are woody and chocolate-brown in color.

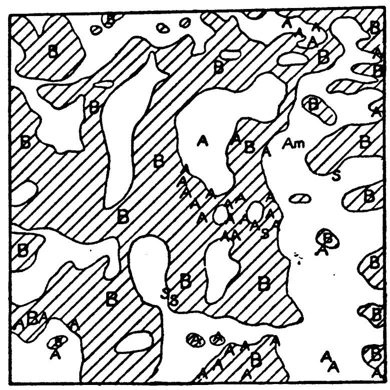


FIG. 1.—A meter quadrat in the *Bouteloua* community dominating a gravelly ridge at Belmont, near Lincoln.

B, *Bouteloua gracilis*.
A, *Andropogon furcatus*.
S, *Sporobolus longifolius*.
M, *Meriolix serrulata*.
Am, *Amorpha canescens*.

Liatris scariosa.—This plant, unlike *L. punctata* with its strong deep taproot, is characterized by a large woody corm, 3 to 5 inches in diameter, from which arise very numerous fibrous roots. These are only 1 to 2 mm. in diameter, but they are very finely branched and spread laterally, thus thoroughly occupying the first 2 feet of soil. The depth of penetration was not determined.

Solidago rigida.—This goldenrod is not only abundant in the less xerophytic prairies of Minnesota and Nebraska, but extends far westward into the drier grasslands. In Wyoming and Montana its presence, together with certain other species, invariably indicates rather permeable soils with at least a fair amount of available water.[1]

[1] During the summer of 1917 the writer, while working on grazing problems in the prairies of the Northwest, had an excellent opportunity to trace the westward extension of many species typical of the less xerophytic prairies of eastern Nebraska and Minnesota far into the Great Plains. Indeed, of the two associations of the prairie-plains climax of Clements (1916), the *Stipa-Agropyrum* prairie occupies much more territory in the Northwest than the *Bulbilis-Bouteloua* plains.

This plant has a root system which spreads immediately below the surface. Many of the numerous small roots pursue an oblique direction and spread from 12 to 18 inches on either side of the plant before they turn downward. Most of the roots are only about 1 mm. in diameter and poorly branched.

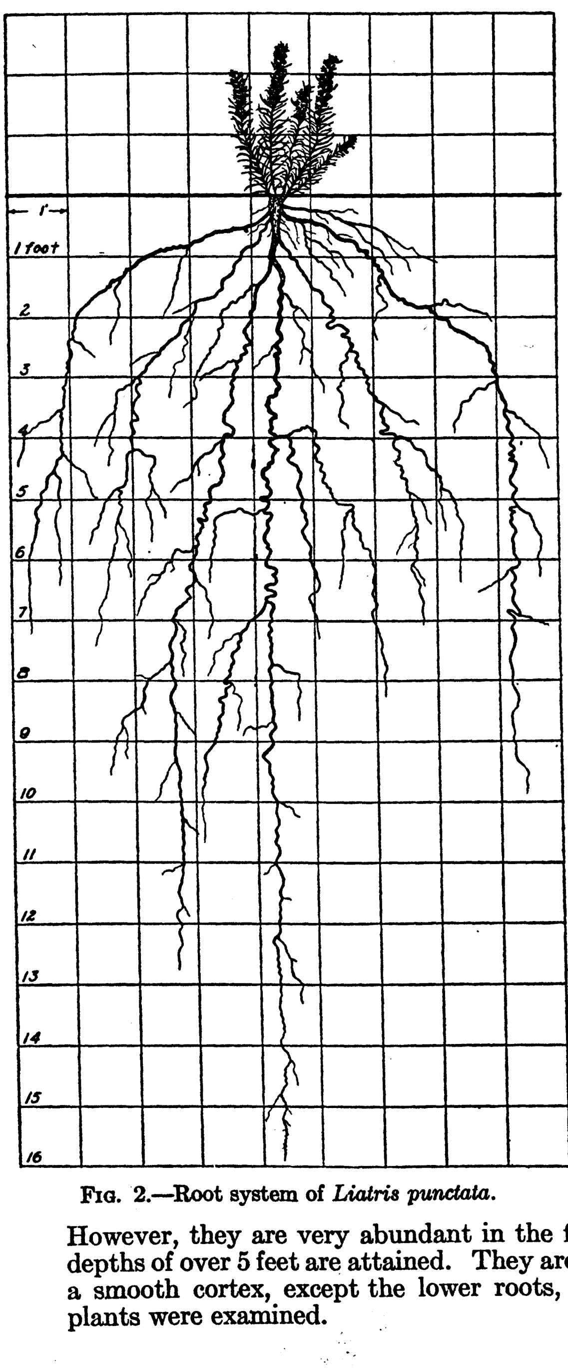


Fig. 2.—Root system of *Liatris punctata*.

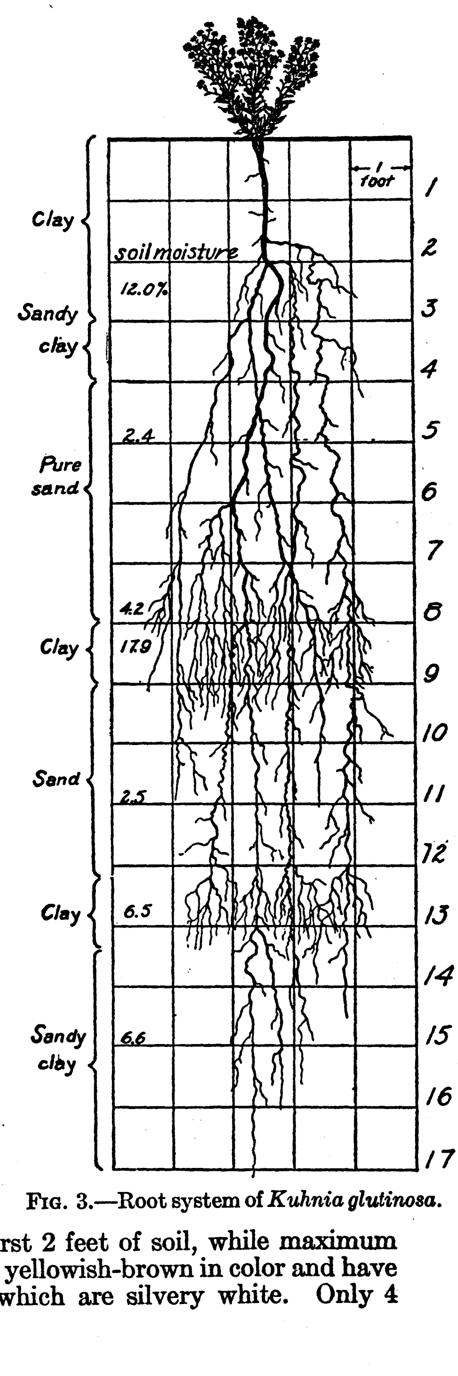


Fig. 3.—Root system of *Kuhnia glutinosa*.

However, they are very abundant in the first 2 feet of soil, while maximum depths of over 5 feet are attained. They are yellowish-brown in color and have a smooth cortex, except the lower roots, which are silvery white. Only 4 plants were examined.

Solidago canadensis.—This abundant prairie goldenrod propagates by means of strong woody rhizomes, a centimeter or less in diameter, which run horizontally about 2 inches below the soil surface. As in *S. rigida*, the roots are fibrous. They are about 1 to 2 mm. in diameter and pale yellow in color. They descend rather vertically into the soil. From these abundant roots numerous laterals are sent off, beginning just below the surface and continuing to a depth of from 9 to 10 feet. However, the main roots keep their identity throughout their course and are very poorly branched throughout the last foot. Thus the soil was well occupied with the roots of this species and few other roots were found in the *Solidago* area. Eleven plants were examined, most of which gave a maximum root depth of 10.5 feet, while one reached 11 feet.

Silphium laciniatum.—The wide distribution of this coarse perennial prairie plant is well known. It has a large, fleshy, deep tap-root. The root diameter just below the multicipital crown, which gives off numerous shoots, varied from 1 to 2 inches in the 5 plants examined. The tap-root descends vertically and tapers so rapidly that at 3 feet it may be only 0.5 inch in diameter (plate 7, A). It pursues this general vertical direction to a maximum depth of from 9 feet to 13 feet 8 inches, the last 2 or 3 feet of its course being somewhat tortuous. The whole root is a dark reddish-brown in color, the cortex of the first 18 inches being distinctly ridged and wrinkled. Scattered laterals, 2 mm. or less in diameter and from 6 to 18 inches long, are present on this upper portion of the root. There are relatively few large laterals. These frequently run off horizontally for a distance of 3 or 4 feet and then turn downward. The deeper roots are also fleshy and brittle and end rather abruptly; usually they are freely branched.

Amorpha canescens.—This half-shrub is a characteristic subdominant of the summer aspect on the prairies of eastern Nebraska. Late in June it begins to blossom and throughout July its leaden color gives tone to the landscape. This perennial legume has a very extensive, woody root system which reaches depths of 6.5 to 7.5 feet. While some of the plants examined branched into large lateral roots just below the enlarged knotty crown, others sent vertically downward a single tap-root. These extremely tough woody roots have a maximum diameter of more than a centimeter. Frequently, large laterals run off horizontally at a depth of only 4 to 6 inches below the soil surface to a distance of 2.5 to 3 feet before they begin their downward course (plate 7, B). Few laterals are given off until the roots reach a depth of from 2 to 3 feet; then the roots by dividing become much finer and branch quite profusely. The terminal branches are very fine, almost threadlike. The roots are cinnamon-brown in color; the cortex is smooth, except on older portions, where it is finely scaly. Five plants were examined.

Helianthus rigidus.—This sunflower, common on Nebraska prairies, propagates by strong rhizomes, from which arise abundant fibrous roots only 1 to 1.5 mm. in diameter. These reach a depth of about 50 inches.

Brauneria pallida.—Only 2 plants were examined. Both had strong, vertically descending tap-roots which reached depths of 51 and 66 inches respectively. These roots were 1 or 2 cm. in diameter. They were poorly supplied with branches, only 3 or 4 short, weak laterals occurring on each root. Even the tip is unbranched. They are woody, and are chocolate-brown in color.

Petalostemon candidus.—Both this plant and *Brauneria* are common and often very abundant prairie species. Like *Brauneria*, it has a strong, deep, rather poorly branched tap-root. Of the two specimens examined the smaller had a root 7 mm. in diameter and a total length of 42 inches. The larger was 10 mm. in diameter and 68 inches deep. The laterals that do occur may originate near the surface and are branched to the third or fourth order. One plant sent off two strong laterals at a depth of 12 inches. The deeper roots are very fine and quite well branched. All have a characteristic yellow color throughout.

Vernonia baldwinii.—This weed propagates by strong rhizomes, a centimeter or more in diameter, which occur about 4 inches below the soil surface. The roots, which are very abundant (20 or 30 arising from a single plant), are very different from any other roots examined. They are tough, smooth, yellowish-white, and unbranched throughout the first few feet of their course. While the stele is only about 1 mm. in diameter, the fleshy cortex is thick enough to give a total root diameter of from 3 to 9 mm. Many spread to a distance of 20 inches from the base of the plant before turning downward. Thus in a weedy pasture the surface soil is filled with the shiny, white, unbranched, rope-like roots. At about 3 feet in depth they begin to branch and the branches become more numerous in the deeper soils. Most of the finer branches and terminal rootlets, however, occur at 9 or 10 feet. Seven plants were examined, all of which penetrated to a depth of about 11 feet. The maximum depth recorded was 11 feet 6 inches.

Kuhnia glutinosa.—This prairie plant has deeper roots than most other species examined. The maximum depths of 4 plants were 16 feet 8 inches, 16 feet 6 inches, 16 feet 10 inches, and 17 feet 3 inches, respectively. A part of one of these is shown in plate 8, A, where only about a third of the root system is exposed. The root in figure 3 was reconstructed from the photograph of another root and a diagram made to scale in the field while excavating the plant. This diagram shows all of the larger roots, the extent of their lateral spread, degree of branching, etc. Although single water-content determinations without wilting coefficients are usually of little value, yet here the wetness and dryness of the various soil strata and the corresponding root branching were so marked as to warrant including duplicate determinations made on November 5, 1917, after several weeks of very dry weather. The clay layers at 8 and 12 feet respectively are more or less impervious, and collect and hold water readily. The tap-roots vary from 1.2 to 3.5 cm. in diameter. All the roots are nearly white in color.

Verbena stricta.—This weed, very common in old pastures, has a strong tap-root from 1 to 2 cm. in diameter, which reaches depths ranging from 3.5 to over 4 feet. Seven plants were examined. In all cases profuse branching occurred from the soil surface to the extreme root-tip. Because of the numerous strong laterals sent off from the tap at all levels, the latter decreases in size rapidly. These lateral branches lay hold of the soil to a distance of 18 inches on all sides of the plant. Small rootlets are abundant, the whole forming an extremely well-developed root system.

Grindelia squarrosa.—This weed has a strong tap-root abundantly supplied with well-developed laterals. The main root varies from 0.5 to 1 inch in diameter, but it gives off laterals so abundantly that this size is not long maintained. Maximum depths of 50, 52, 40, and 73 inches were recorded for the 4 plants examined. There are many very fine roots, 3 to 9 inches long, occupying the surface soil. The larger laterals begin to branch off in the first foot of soil, and run off obliquely from the main root to a distance of about 2 feet. Like the tap, these are supplied with abundant rootlets, the whole forming a very extensive absorbing surface. The roots have a light yellow color.

Shantz lists *Grindelia* as one of the plants commonly found in the short-grass association of Colorado. It usually indicates disturbed conditions and is especially abundant during wet years. It appears that its root system must be greatly modified under these conditions where the soil is only rarely wet below a foot or two. Indeed, it seems to thrive so well and under such varied conditions that it is a conspicuous weed throughout many of the Western States. It is likely that the great plasticity of its root system makes this wide distribution possible.

Glycyrrhiza lepidota.—This characteristic legume has much-branched rhizomes several feet long and a deep, fleshy tap-root. In the several specimens examined the tap-root varied from 0.5 to 2 inches in diameter. From the multicipital crown as many as 15 to 20 stems may arise. Just below the surface soil small laterals, a few millimeters to a centimeter in diameter, are often given off, in a more or less horizontal direction. These often turn down abruptly. At a depth of 1 to 3 feet the tap frequently breaks into many strong branches with a lateral spread of 2 or 3 feet from the base of the crown. They run off rather obliquely from the main root (plate 8, B) giving rise to numerous long branches. These tertiary roots are usually only 2 to 5 mm. in diameter and rebranch poorly, a lack of small, absorbing roots being quite characteristic. The deeper soils (8 to 10 feet) are thus well filled with small, vertically descending, poorly branched roots, 1 to 3 mm. in diameter. Like the older roots, these are of a light-brown color and fleshy but quite firm. They shrink rapidly upon exposure to the air. At 10 to 12 feet, where these rootlets entered the jointed clay-loess soil, they branched rather profusely. The roots of several plants were traced to depths of 11 or 12 feet. One of the larger ones was still 2 mm. in diameter at this depth and probably penetrated several feet deeper. The odor is very characteristic.

Astragalus crassicarpus.—During May 1918, a large trench was dug on a west hillside at Belmont, about 45 feet from a wet *Spartina cynosuroides* zone in the valley. The surface foot of good loam soil gave way to about 3 feet of exceedingly hard joint clay, in which roots (and especially those of grasses) frequently followed the joints and branched largely (locally) in one plane. The deeper soil became wetter and also somewhat sandy, but very gummy and sticky. The water table was reached at about 7 feet. From this trench *Astragalus*, two species of *Psoralea*, and *Baptisia* were excavated.

Astragalus crassicarpus forms extensive societies in the early spring. A group of 3 younger ground-plums was first examined; the plants were very similar in size, root diameter, branching, and depth. One (shown in plate 9, B) had a pronounced tap-root with a diameter of 1 cm. and ran almost vertically downward to a depth of 6 feet, giving off a number of horizontal branches, 1 to 2 mm. in diameter, near the surface, and extending laterally only a few inches before turning downward. Other smaller laterals from 0.5 mm. to those hairlike in diameter occurred sparingly and at intervals of about 1 cm. or less to a depth of 4 feet. Most of these branches were less than a centimeter in length. Below 4 feet, in the softer, wetter soil, the branches became more pronounced, being densely covered with root-hairs and often branching in two planes. However, none of these branches exceeded an inch in length. The tip of the tap (as well as the tips of the laterals, which reached depths only about half as great as the former) was no better branched than was the last 2 or 3 feet of the root. There is a very noticeable tendency for the roots to follow the crevices in the joints of the clay.

An older plant had a strong tap-root with a diameter of 1 cm. At a depth of 2 cm. it gave off a strong lateral 5 mm. in diameter and at about the same level 3 other branches of equal or slightly smaller diameter (plate 9, A). They ran off obliquely in 4 different directions, but none to a distance greater than 10 inches before they turned rather vertically downward; two more branches, each 4 mm. in diameter, were given off at depths of 6 and 8 inches respectively. All of these branches were very poorly supplied with laterals, as has already been noted for the younger plants. They taper uniformly, so that at a depth of 2 feet none had a diameter of more than 3 mm. The tap as well as several of the ultimate branches of the laterals reached a depth of 6.5 feet. The hairlike termini are sometimes unbranched, often for several inches, but are more often well-branched. Nodules 1 mm. or less in diameter occur at all depths, even near the root-tips. The roots are very brittle and hard to recover from the joint clay. They are yellowish brown in color except the older portions, which are dark brown.

Psoralea tenuiflora.—This very abundant legume forms societies over large areas of prairie during June. Indeed, for a period these tall, coarse herbs quite overtop the grasses. The one shown in plate 10, A, had a tap-root 3 cm. in diameter, which ran vertically downward. At a depth of 27 inches it appeared dead, but it was traced to a depth of 52 inches, where it was still 3 mm. in diameter. At a depth of from 1 to 2.5 feet many laterals occur. These are from 7 to 12 mm. or less in diameter and frequently run off obliquely (as shown in the figure) for distances of 8 to 18 inches before turning, often abruptly, vertically downward. Several of these laterals, including some of the smaller ones, reached depths of 5 or 6 feet. The lateral spread is such that at the tips many of these roots are at a horizontal distance of from 18 to more than 24 inches from the base of the plant.

Little absorption occurs in the first 2 feet of soil and this entirely from lateral roots. The laterals are very poorly furnished with fine branches, although at intervals of about a centimeter short branches occur not unlike those of *Astragalus*. The root extremities, while very fine, are poorly branched. In color the roots are reddish-brown, except the younger portions, which are tan-colored. They are rather soft and more or less herbaceous, and have a papery bark which is readily peeled off from the older ones.

Psoralea argophylla.—This legume, which is much less conspicuous than the preceding, forms estival societies over much of the prairie region. Plate 10, B, shows the dominant, little-branched tap-roots of several plants of this species. A single root will be described. This had a tap (with a diameter of 8 mm.) which tapered so rapidly that at 2 feet it was less than 1 mm. wide, and then pursued a vertically downward course to the water-level at a depth of 6 feet. No large branches were given off except at a depth of 2 feet, where a lateral occurred which was equal in diameter to the main root. This ran quite parallel with the tap and at a distance of 4 to 6 inches from it, both reaching approximately the same depth.

Except for the surface foot, exceedingly fine branches, not more than an inch in length and rarely rebranched, occurred at intervals of about 5 mm. throughout the entire course of the root. At 3 inches from the tip the roots each divided into 2 or 3 branches, all of which were branched to the first order only. The roots are dark brown to black in color.

Baptisia bracteata.—This showy legume, which forms vernal societies, has very characteristic roots, the older portions being greenish-yellow and the younger ones orange in color. From the base of the crown the roots spread out obliquely and run downward, but in such a manner that the most widely spreading were less than 18 to 24 inches horizontally away from the base of the crown at any depth (plate 9, C). The main roots are poorly branched and there are scarcely any absorbing laterals in the first 2 or 3 feet of soil. In the deeper soil they branch irregularly but not very repeatedly, many of the roots reaching the water-level at about 80 inches. It is probable that in drier soil they would penetrate deeper. The smaller roots near the tips (1 or 2 feet of the extremities) often form brownish, hairlike branches which may run 12 to 18 inches without giving off laterals or, on the other hand, may be profusely supplied with small branches. Not infrequently the root-ends break up into two or three pieces, all of which are supplied with laterals. In general the extremities are covered with fine, short branches which extended to the water-level.

THE SUBCLIMAX PRAIRIE.

During the last week in March of 1918, a number of root systems were studied near Peru, Nebraska, at a station about 60 miles southeast of Lincoln. The prairies in this region are very similar in floristic composition to those near Lincoln, as has been shown by the studies of Thornber (1901) and others. Root systems of a number of species were studied in a prairie area covering the exposed southeast slope of a loess hill. A number of list quadrats which were made during the preceding summer revealed the dominance of *Andropogon furcatus* and *A. scoparius*. Indeed, the striking feature of the vegetation is the luxuriant growth of these bluestems. *Andropogon furcatus* extends to the very crest of the ridge. Here the stems reach heights of 5.5 feet, while the roots penetrate the mellow loess soil to a maximum depth of 9 feet 3 inches. This root penetration exceeds by 2 feet the maximum depth recorded for any plant of this species in clay-loam soil.

As pointed out by Clements, this type of prairie, lying in a region of somewhat higher rainfall, is probably subclimax. The luxuriant growth of *Andropogon* upon the high ridges indicates conditions very favorable for chaparral growth and (as indicated later) thickets of *Corylus*, *Rhus*, and *Symphoricarpos* are very frequent in this grassland. It is not uncommon also to find seedlings of elm and oak near the edges of these thickets. Indeed, except for fires, grazing, or other disturbances, much of this grassland area would probably become chaparral and forest.

Other species examined near the hilltop were *Brauneria pallida* and *Lygodesmia juncea*. Near the foot of the slope, and where an abundance of clay makes the soil much harder and more compact, specimens of *Lespedeza capitata*, *Amorpha canescens*, and *Ceanothus ovatus* were excavated.

Brauneria pallida.—As is frequently the case in eastern Nebraska prairies, this perennial herb, while never abundant, occurs in such numbers as to be a conspicuous component of the prairie flora. Two plants were examined. The smaller had a tap-root 5 mm. in diameter and reached a depth of 5.5 feet; the larger, with a diameter of 11 mm., reached a depth of 8 feet. The strong tap pursues a vertically downward course, tapering very slowly. While the older parts (the first 2 to 5 feet) are more or less woody and chocolate-brown to almost black in color, the younger parts are lighter in color and herbaceous. Short laterals (about 9 cm. in length and mostly devoid of branches) occur 5 to 25 mm. apart. This branching may continue to the tip, which is about 0.3 mm. in diameter and is poorly branched. On the larger specimen two laterals occurred (plate 11, A). The larger of these ran off at a depth of 5 feet and at an angle of about 60° to a distance of 28 inches. It was almost destitute of branches. The roots are tough and easily followed. The coal-black streaks within the cortex and stele make their identification easy. Although extending somewhat deeper, these specimens correspond rather closely with those examined in the clay-loam soil at Lincoln.

Lygodesmia juncea.—This perennial stem-xerophyte is common in prairies throughout Nebraska and is often abundant on the crests of ridges or other dry situations. A trench about 8 feet long and 3.5 feet wide was dug on a slope just below a group of these plants and more than a dozen roots were examined. The tap-root, varying from 2 to 6 mm. in diameter, may give rise to several plants by means of short branches 2 to 8 inches below the surface (plate 11, B).

The roots descend in an almost vertically downward course and frequently in parallel groups only a few inches or indeed a few millimeters apart, to distances of 15 to 20 feet or more. At these depths the tips are frequently only 1 or 2 feet from a vertical line with the top. The roots are fleshy, very brittle, especially after a depth of 3 or 4 feet is reached; they are from light cream to dark brown in color and exude a white latex upon injury. The side of the trench was dotted with drops of latex, showing the abundance of the cut roots. This character aids greatly in recovering the broken ends of these brittle roots. Branching occurs not at all, except for tiny laterals less than 1 mm. in diameter and an inch in length, which come off very sparingly at almost right angles and at intervals of 6 to 12 inches. These tiny laterals are poorly or not at all branched, the secondary branches being only 1 to 2 mm. long. The tap narrows slowly and is frequently 2 mm. in diameter at a depth of 16 to 18 feet. Numerous roots occurred at 18 feet in depth and one was traced to a maximum distance of 20 feet 7 inches. Here it was still 2 mm. in diameter. Because of the danger of caving of the mellow loess soil, deeper excavation was abandoned. The loess was of very uniform texture throughout and well moistened to the depth examined.

Lespedeza capitata.—This tall, conspicuous legume is common throughout central and eastern Nebraska. It is very abundant on the lower slopes of the loess hill, where 6 or more plants were examined. The very characteristic light-yellow roots are much branched just below the surface, where numerous strong laterals, 5 to 7 mm. in diameter, run off in all directions, some almost horizontally at depths of only 3 to 6 inches. These large laterals branch very irregularly but profusely, giving rise to numerous finely branched roots which fill the surface soils to a distance of 2 or 3 feet on either side of the plant, when the main branches may turn abruptly almost vertically downward (plate 11, c). In addition to these shallower roots, which compete with many of the grasses for the water in the surface layers of soil, numerous other branches pursue a more or less vertically downward course from the outset and reach depths of 5 or 6 feet or more. These, with the vertical extremities of the horizontal laterals, which may also reach similar depths, furnish a very extensive absorbing area for the plant. The deeper roots taper rapidly, but all are furnished with short rebranched laterals. Even the root-ends are well-branched, but no matting was observed, as in the case of several of the other legumes. A maximum depth of 7 feet 10 inches was recorded.

Ceanothus ovatus.—This low shrub, with its many stems 1.5 to 3 feet high, is quite common on prairies, especially in the eastern part of Nebraska. It also occurs widely throughout the sandhills westward, and on the loess hill, where the following specimen was excavated, it is rather abundant.

The plant examined was 13 years old. It had 14 stems arising from the enlarged crown. The woody tap-root was 1.5 inches in diameter. At a depth of 8 inches it gave off a large lateral and 2 inches below another which was equal in diameter to the tap (2 cm.) at this depth. While the first lateral and the tap pursued a rather vertically downward course (being, like all of the roots, very much curved and twisted, so that at a depth of 11 feet the tap was only 15 inches from a vertical line with the top), the second lateral at a depth of 7 feet was 50 inches from this vertical line (plate 12, A). Also, numerous small, repeatedly branching laterals and a few larger ones (6 mm. in diameter) came off in the surface foot of soil and ran in rather horizontal directions for a distance of 3 to 5 feet. In addition to these surface absorbing roots, both short and long laterals were given off at intervals at all depths, the whole root branching and rebranching freely. While some of the roots branched coarsely and ended abruptly, others formed a most delicate mass of absorbing rootlets. As a whole, the root system is well-branched, but some of the roots at a depth of 10 or 11 feet (and where they were only 2 or 3 mm. in diameter) ran 2 or 3 feet without giving off any branches. Numerous roots occurred at a depth of 8 feet, several reached 12 feet, and the longest one was traced to a depth of 14.5 feet, where it was still 1 mm. in diameter and giving off frequent threadlike laterals. The older parts of the root are woody and extremely hard. Deeper down they lose their toughness and become very brittle, while the smaller roots are again fairly tough. All parts of the root are characterized by a reddish-brown color, all but the oldest being more or less streaked with white. They reveal a reddish color upon removal of the bark, this color also extending into parts of the wood.

Amorpha canescens.—A 7-year-old specimen, which is very representative of others examined, was excavated near the foot of the loess hill. It gave off 11 large woody roots, 8 to 14 mm. in diameter, from the knotty crown. These ran off at various angles from almost parallel with the hillside to almost vertically downward (plate 12, B) where the roots are somewhat grouped, owing to the fact that the background was only 5 feet wide. These have very few surface laterals, but those that do occur are well-branched. In the surface 2 to 4 feet of soil relatively little absorption takes place. *Andropogon scoparius* and other grasses frequently grow vigorously between these spreading *Amorpha* roots and doubtless suffer little competition for water. The roots taper uniformly and at a depth of 3 feet are often still 7 mm. in diameter. They frequently pursue a rather tortuous course and branch in a way more or less dichotomous. Rebranching gives rise to many small laterals only 1 to 4 mm. in diameter, which pursue a vertically downward course for many feet, giving off very few branches and tapering only slightly. Even the tips are usually poorly branched. The lateral spread of the roots is remarkable. One lateral reached a depth of 12 feet 10 inches and a horizontal distance of 4 feet from the base of the crown. Another was also 4 feet from a vertical line with the crown at a depth of 12 feet 2 inches and about 5 feet from the end of the first lateral. Similar conditions obtained on the other sides of the plant, so that a very large area of soil was penetrated by the roots of a single plant.

Small nodules only 1 mm. in diameter occur as deep as 10 or 12 feet. On the higher slope one plant was noted that showed much-branched root-tips and nodules at a depth of 16.5 feet. The roots are smooth and chocolate-brown in color, all being rather tough and the older parts distinctly woody. Here again it should be noted that the plants growing in the mellow loess reached depths 4 or 5 feet greater than those examined in the clay-loam soil at Belmont.

PRAIRIE ROOT SYSTEMS AND THE PRAIRIE ENVIRONMENT.

The most obvious conclusion from a consideration of these data is the fact that prairie species are provided with well-developed, deep-seated, and extensive root systems. Upon the basis of root depth the 33 species examined may be divided into three groups:

1. Shallow-rooted plants are those that seldom extend below the first 2 feet of soil. These consist wholly of grasses, such as *Kœleria cristata, Stipa spartea, Elymus canadensis, Distichlis spicata, Sporobolus longifolius,* and *Aristida oligantha.*

2. Plants with roots extending well below the second foot of soil but seldom deeper than 5 feet may be grouped as intermediate in root depth. Here belong *Andropogon scoparius, A. nutans, Bouteloua gracilis, Bulbilis dactyloides, Verbena stricta, Helianthus rigidus, Solidago rigida,* and *Petalostemon candidus.* Here also may be placed *Grindelia squarrosa,* a plant which sometimes extends beyond this depth.

3. Of the plants studied, 55 per cent have roots which extend beyond a depth of 5 feet; indeed, most of them to depths of from 7 to 9 feet and a few to a maximum depth of from 13 to 20 feet or more. These may be classed as deep-rooted species. Here belong *Panicum virgatum, Andropogon furcatus, Agropyrum repens, Solidago canadensis, Liatris punctata, Silphium laciniatum, Amorpha canescens, Astragalus crassicarpus, Psoralea tenuiflora, P. argophylla, Lygodesmia juncea, Ceanothus ovatus, Baptisia bracteata, Lespedeza capitata, Glycyrrhiza lepidota, Brauneria pallida, Vernonia baldwinii,* and *Kuhnia glutinosa.*

To understand the causes for such remarkable root development it will be necessary for us to study the prairie environment. The prairies of eastern Nebraska receive more moisture than most of the great grassland area. The mean annual precipitation for Lincoln, together with its seasonal distribution (which is of greater ecological significance), is shown in table 1.

It may be seen that most of the precipitation falls during the growing season and less than one-tenth of it during the three winter months. About half of the rainfall of May, June, and July is from rains of an inch or more in 24 hours. Such a seasonal distribution of moisture is very favorable for the growth of grasses. Not infrequently, however, storms occur with a rainfall exceeding 2 inches and occasionally 4 or 5 inches in a period of 24 hours. Such storms invariably result in a high run-off and they account largely for the observed deficiencies of moisture for crops in seasons where the recorded rainfall would indicate an abundant supply. Drought periods of 30 or more consecutive days between March 1 and September 30, in which precipitation to the amount of 0.25 inch does not occur, are not infrequent. Indeed, 16 or 17 such periods have occurred at Lincoln during the past 22 years. The average annual snowfall is about 24 inches. "As a rule snow covers the ground but a few days at a time after each snow storm, and the ground is covered with snow less than half of the time even during the months of the heaviest snowfall" (Loveland, 1912). Much of the snow is swept by high winds into depressions, and thus contributes often but little to the supply of soil moisture of the land upon which it falls. Hence it may be seen that precipitation is only a general indicator of conditions for plant growth. Obviously its influence upon the distribution and seasonal activities of plants is exerted through its power to replenish soil moisture.

TABLE. 1.—*Mean monthly and annual precipitation at Lincoln, Nebraska, in inches.*

Months.	Precipitation.	Months.	Precipitation.
Jan........	0.67	July........	4.01
Feb........	0.96	Aug........	3.72
Mar........	1.26	Sept........	2.91
Apr........	2.51	Oct........	1.94
May........	4.39	Nov........	0.94
June........	4.43	Dec........	0.85
		Annual...	28.59

The fertile, dark-colored prairie soil of the region is of the type commonly called loess, much of which, however, is confounded with glacial drift. "The loess covers the hills and valleys alike to a depth of from 20 to 100 feet, being much thicker than this in places and much thinner in others. Throughout the first 100 miles westward from the Missouri it is underlain by Kansan till" (Alway, 1916). "The uniformity in the physical properties, recognized as characterizing the material of the loess, should tend to produce, under uniform climatic conditions, soils uniform in chemical properties." The water-holding capacity of the surface foot of soil is about 60 to 70 per cent of its dry weight, while the moisture equivalent and wilting coefficient are 25 per cent and 13.5 per cent respectively.[1]

Studies of the water-content of upland prairie soils have been carried on for more than two seasons. Table 2 gives the results of water-content determinations during the growing season of 1916. The minus sign indicates water non-available for plant growth.

A glance at these results shows that at four different periods no water was available for growth at a depth of 4 inches, while during late August the same condition obtained for the 4 to 12 inch layer. Unfortunately, deeper soil samples were not obtained, but during the following seasons samples were taken at irregular intervals to a depth of 5 feet. These data are shown in table 3.

[1] The writer is indebted to Dr. L. J. Briggs, of the Bureau of Plant Industry of the U. S. Department of Agriculture, for determinations of moisture equivalents and wilting coefficients.

TABLE 2.

In tables showing water-content it will be understood that the figure columns represent percentages.

Date.	Depth of samples.		Date.	Depth of samples.	
	0 to 4 inches. Wilting coefficient 12.	4 to 12 inches. Wilting coefficient 12.7.		0 to 4 inches. Wilting coefficient 12.	4 to 12 inches. Wilting coefficient 12.7.
May 21....	19.5	17.3	July 31....	− 0.8	0.1
June 5....	− 2.5	4.8	Aug. 7....	9.5	8.8
June 10....	− 3.5	3.8	Aug. 15....	20.0	13.8
June 17....	3.5	9.1	Aug. 22....	− 2.2	−2.7
June 26....	16.5	9.5	Aug. 28....	− 1.7	3.8
July 1....	1.3	5.5	Sept. 4....	13.1	8.8
July 8....	− 2.4	2.0	Sept. 12....	13.5	5.3
July 17....	9.5	2.8	Sept. 19....	2.0	1.8
July 24....	− 1.2	0.3			

TABLE 3.—*Available water-content of the prairie soil during 1917.*

The minus sign indicates water non-available for plant growth.

Date.	Depth of sample, 0 to 6 inches. Wilting coefficient, 13.4.	Depth of sample, 6 to 12 inches. Wilting coefficient, 13.4.	Depth of sample, 1 to 2 feet. Wilting coefficient, 15.4.	Depth of sample, 2 to 3 feet. Wilting coefficient, 14.5.	Depth of sample, 3 to 4 feet. Wilting coefficient, 16.1.	Depth of sample, 4 to 5 feet. Wilting coefficient, 16.1.
Apr. 3...........	4.3	4.3	−2.6	−1.6	−2.9	−0.4
May 6...........	−2.9	6.7	2.2	−1.4	....	....
June 19...........	4.9	9.8	8.1	8.4	6.1	4.3
July 9...........	−1.9	2.0	....	....	....	....
July 16...........	−1.7	0.7	2.1	1.7	....	....
July 23...........	−3.1	−1.7	....	....	....	....
July 30...........	−5.3	−2.3	−4.0	....	....	....
Aug. 6...........	1.6	−1.3	....	....	....	....
Aug. 13...........	7.0	0.5	....	....	....	....
Aug. 28...........	2.1	1.7	−2.1	−1.3	−4.5	−1.9
July 24 (1916)......	....	....	−0.9	2.3	....	....
Jan. 5 (1918)......	3.3	1.9	−0.9	−0.7	0.6	2.1
Mar. 26 (1918)......	7.2	7.4	1.4	−3.9	−4.2	−2.8

On May 6 and again throughout the whole of July, no water was available in the first 6 inches of soil. During late July and the first week of August soil moisture was depleted to a point below the wilting coefficient for a depth of 12 inches. On April 3 and again on August 28 no water was available at a depth of 1 to 5 feet. These results are rather surprising, but an examination of the rainfall record shows that during 1916 the precipitation was 5.5 inches below normal, while during 1917 it fell to 6.5 inches below. The dryness of the soil during 1916–17 was shown by an abnormal amount of winter-killing of trees and shrubs. During July the rainfall was only 0.56 inch instead of the normal 4 inches. The determinations on July 24 (1916) at 2 and 3 feet respectively show that the soil was very dry. It is interesting to note in this connection that similar results were obtained in the prairies of southeastern Washington, where during 1914 the water-content to a depth of 4 feet was reduced to the non-available point (Weaver, 1915: 233–235).

The available water-content in the loess soils supporting the subclimax prairie vegetation was not only higher but much more constant. These data are shown in tables 4 and 5. Here also are included determinations from an adjacent thicket of *Corylus americana*. A comparison of these results is made on page 30.

TABLE 4.—*Available water-content in prairie and shrub communities near Peru, Nebraska, during April to September 1917 and May 1918.*[1]

The minus sign indicates water non-available for plant growth.

Depth, 0 to 6 inches. Wilting coefficients: Prairie 11.7; scrub 13.8.			Depth, 6 to 12 inches. Wilting coefficients: Prairie 10.9; scrub 12.3.			Depth, 1 to 2 feet. Wilting coefficients: Prairie 10.4; scrub 12.5.			Depth, 2 to 3 feet. Wilting coefficients: Prairie 9.9; scrub 11.3.		
Date.	Prairie.	Scrub.	Date.	Prairie.	Scrub.	Date.	Prairie.	Scrub.	Date.	Prairie.	Scrub.
1917			1917			1917			1917		
Apr. 5	13.4	21.4	Apr. 5	12.2	18.0	Apr. 5	8.5	12.1	Apr. 5	5.0	8.0
May 15	13.0	14.7	May 15	12.0	14.1	May 15	10.5	11.7	May 15	8.1	......
June 30	13.9	20.8	June 30	11.8	17.1	June 30	12.3	13.1	June 30	12.6	12.9
July 9	6.5	3.9	July 9	7.3	7.4	July 9	....	......	July 9	....	......
July 14	9.5	11.5	July 14	7.4	5.2	July 14	....	......	July 14	....	......
July 24	0.1	4.5	July 24	2.5	3.4	July 24	3.1	3.0	July 24	5.1	5.5
July 28	−1.4	−1.7	July 28	0.4	−0.4	July 28	2.1	1.2	July 28	4.5	4.4
Aug. 6	4.0	6.6	Aug. 6	−0.5	2.6	Aug. 6	−1.0	0.7	Aug. 6	1.9	2.4
Aug. 11	8.4	12.6	Aug. 11	1.5	5.7	Aug. 11	....	......	Aug. 11	....	......
Aug. 18	2.3	7.6	Aug. 18	1.9	1.5	Aug. 18	....	......	Aug. 18	....	......
Aug. 25	1.3	6.4	Aug. 25	0.2	1.8	Aug. 25	0.6	−0.1	Aug. 25	0.9	1.2
Sept. 8	6.2	10.2	Sept. 8	−0.8	2.4	Sept. 8	0.8	−0.4	Sept. 8	1.6	−1.0
Sept. 22	−1.2	−1.6	Sept. 22	−1.7	0.5	Sept. 22	−1.0	−0.7	Sept. 22	0.1	0.5
1918			1918			1918			1918		
May 16	13.8	16.3	May 16	15.0	18.3	May 16	12.5	16.5	May 16	12.7	16.5

[1] The writer is indebted to Prof. F. C. Jean for the major portion of the data in these tables.

The greater water-content of these mellow loess soils compared with those of the prairie near Lincoln gives us a clue to the much more luxuriant growth of certain prairie and shrub species. There is also a great difference in depth of root-penetration, plants like *Andropogon furcatus* and *Brauneria pallida* being much deeper-rooted in loess soil.

However, vegetation is not only an expression of present conditions, but also to a greater extent a record of conditions that have obtained during a period of years, and the record is not likely to be altered greatly in a year or two in which conditions may depart from the normal. The preceding pages show that many prairie plants absorb moisture well beyond a depth of 5 feet, while soil-moisture extends many feet beyond the greatest root depth. In excavating root systems, during September to December 1917, the soil below 5 feet was found almost invariably to be quite moist. Some of the root systems were excavated on bench-lands in the Salt Creek basin, where the alluvial soils are somewhat different from those described. Such differences were noted in discussing these species.

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 subjected, especially as concerns their water relations, must reflect themselves in the root development. Therefore, it will be instructive to consider briefly the above-ground environment.

TABLE 5.—*Total water-content of soil during 1917.*

Date.	3 to 4 feet.		4 to 5 feet.	
	Prairie.	Scrub.	Prairie.	Scrub.
1917				*p. ct.*
Apr. 5.	15.9	16.6	13.0	16.1
June 30.	20.5	24.7	21.4	24.9
Aug. 6.	15.5	15.4	16.9	16.7
Sept. 22.	12.2	12.1	11.9	13.0
1918				
May 16.	13.1	15.0	15.4	15.1

TABLE 6.

Month.	Temp.	Month.	Temp.
	°F.		°F.
Jan....	22.6	Aug....	75.0
Feb....	24.3	Sept....	66.6
Mar....	37.4	Oct....	54.6
Apr....	51.5	Nov....	40.4
May...	61.7	Dec....	28.5
June...	71.2		
July....	76.4	Aver..	50.8

The mean monthly temperature at Lincoln, Nebraska, for a period of more than 30 years is shown in table 6.

The season without killing frosts usually extends from the first day of May into the first week of October, but frosts have occurred as late as the last week of May and as early as the second week of September. Figure 4 shows the average daily temperatures obtained during the growing season of 1916, as recorded by a hygrothermograph placed in an appropriate shelter in the prairie at a height of 17 cm. The weekly means were obtained by drawing a horizontal line through the weekly record sheet in such a manner that the total area above this line included by the graph was equal to the total area below the line.

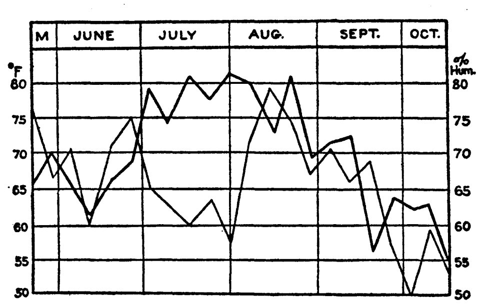


FIG. 4.—Graphs showing the average daily temperature (heavy line) and humidity (light line) in the prairie during 1916.

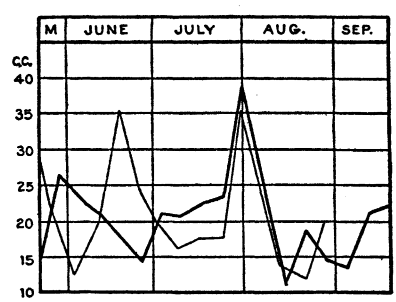


FIG. 5.—Graphs showing the average daily evaporation rates in the prairie during 1916 (heavy line) and 1917 (light line).

The areas were determined by the aid of a planimeter. In this interpretation both temperature (or humidity) and the time factor are taken into consideration. This figure also gives a record of the mean weekly humidity of the air during this same period. Not infrequently during the long summer afternoons the humidity falls to 20 per cent or less, while the temperature may reach 95° to 100° F.

During the growing season the prevailing winds are from the south or southeast. A standard anemometer placed in the prairie on a gentle southwest slope and at a height of 0.5 meter recorded 4,905 miles of wind from July 13 to September 19, 1916, an average of 72 miles per day. A similar instrument placed at the same height above the soil surface, but on a hill top in the same prairie area, showed an average daily wind movement of 122 miles per day.

The factors of high temperature, low humidity, and wind movement combine to increase the evaporating power of the air. Livingston's porous-cup atmometers, fitted with non-absorbing mountings, were operated in the usual manner in duplicate and at a height of about 17 cm. above the soil surface during 1916 and 1917. The combined evaporation records from two prairie stations, reduced to the readings of the standard cup, are shown in figure 5. During the last week in July 1916, when the mean daily temperature was 81.4° F. and the mean relative humidity 57.4 per cent, the daily evaporation was 38 c.c. During this period no soil moisture was available in the first foot of soil. The average daily evaporation throughout this whole summer was 21.6 c.c. Atmometers exposed at a height of 0.5 meter during the last 10 days in July gave losses over 50 per cent greater than similar instruments placed at the usual height of 17 to 23 cm. In the prairies near Peru, Nebraska, the average daily evaporation from May 15 to September 22, 1917, was 20.9 per cent.

Summarizing briefly, we find that prairie plants of this region grow under semi-arid climatic conditions in which the supply of water is the chief limiting factor of plant growth. During certain portions of the growing season extremely xerophytic conditions are brought to bear upon the vegetation. It has been shown that the water-content of the soil is reduced to the non-available point to a depth of 4 or 5 feet at least during certain years and often at times when the evaporating power of the air is very high (38 c.c. daily).

In response to these environmental conditions many species have developed surprisingly extensive root systems. In fact, all of the dicotyledons examined, as well as many of the grasses, extend their root systems to depths of from 3 to 7 feet or more. For just as the evaporating power of the air and the nature of the transpiring organs determine the water-loss of plants, likewise the soil water and the nature of the root systems determine the supply. These findings of great root depths, which are correlated with deep soil moisture, bear out Cannon's suggestion of the probability that the longest or 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.

The roots of prairie plants are grouped into more or less definite absorbing layers, many of the deeper-rooted species having few or no absorbing roots in the first few feet of soil. This layering of the roots reduces competition and permits the growth of a larger number of species. Any of the shallow-rooted grasses extract water from the soil layers quite above those from which *Andropogon furcatus* or *Solidago rigida* draw their supply, while still deeper soil strata furnish moisture for such deep-seated species as *Panicum virgatum*, *Silphium laciniatum*, and *Kuhnia glutinosa*. It should be pointed out here that prairie plants very seldom show the widely spreading and superficial laterals so characteristic of many plains species. The cause seems to lie in the greater water-content of the deeper soil in the prairie.

Root variations of prairie plants may be due to a number of factors, among which the water-content of the soil and its penetrability probably stand first in importance, at least in non-alkaline soils. Although the problem of the causes of root variation is one which must be solved under control conditions where one factor can be varied at a time, considerable evidence has been found in the field that both soil moisture and soil texture profoundly influence root distribution.

The effect of compact soils upon root penetration is shown not only by the tortuous courses pursued by roots and the distortions of the roots themselves, but also by their modified branching. Several species, including grasses, were found to penetrate from 2 to 3 feet deeper in deep loam soil than in the same type of soil when it was underlaid with a hard clay subsoil. In soils with a subsoil of alternating layers of sand and clay a striking distribution of lateral roots was observed. These often occurred abundantly near the bottom of the sandy layers and in the clay strata where the latter acting as a rather impervious layer had retained much soil moisture.

It is interesting to note that species of the same genus may have an entirely different type of root system. *Liatris punctata* has a deep tap-root, while the multitudinous roots arising from the corm of *L. scariosa* are fibrous. Likewise, the roots of *Andropogon scoparius* are as different from those of *A. furcatus* as are the roots of *Kœleria cristata* from those of *Stipa spartea*. Indeed, the roots studied are remarkable for their individuality. The roots of each species, because of peculiarities of form, branching habit, position in the soil, texture, color, odor, or taste, can be easily distinguished, and these distinguishing characters have often proved useful in ecological work. In some cases it has been possible to reconstruct successional changes from the record left in the soil by partially preserved roots and rhizomes.

II. THE CHAPARRAL COMMUNITY.

Between the great Ohio-Missouri deciduous forest complex on the east and the prairies to the westward, there extends a chaparra community. Indeed, this is more or less continuous from Canadl to Texas. In this shrub community, tongues of which extend far into the subclimax prairie, species of *Symphoricarpos*, *Rhus*, *Corylus*, and *Rosa* play the rôle of dominants. Indeed, all but the latter form thickets of greater or less extent in the moister places throughout much of the prairie community or occur as more or less isolated clumps or individuals held in check only by the severe root competition of the prairie species (plate 16, B). They rapidly spring into dominance, suppress the grasses, and form centers for further outward invasion, when soil-moisture conditions are even slightly increased above the normal. This may be due in the first instance to the loosening of the soil by burrowing animals, the building of a fence, or other disturbance of the sod.

In order to understand more clearly the nature of the competition between scrub and grassland, as well as to determine more exactly environmental conditions indicated by these phyads, a number of root systems were examined along the loess hills of the Missouri River near Peru, Nebraska.

Symphoricarpos vulgaris.—This species, together with its western ecological equivalent, *S. occidentalis*, is a very conspicuous and important shrub of the chaparral community. Growing in clumps to a height of only 2 to 4 feet, its shade is frequently so dense as to exclude even the very tolerant *Poa pratensis*. In a well-established shrub area the latter almost invariably occurs between the individual clumps.

A long trench was dug at the edge of such a thicket and the roots of numerous plants were examined. The larger roots arise mostly from near the base of the erect shoots, but numerous smaller ones occur, especially all along the underground stems (plate 13, A). The maximum depth to which the roots penetrate in the loess soil is only 65 inches. Although the trench was sunk to a depth of about 8 feet and a part of the soil underlying the thicket at this depth was removed, no roots of *Symphoricarpos* were found below the 65-inch level. Indeed, except for a few plants of *Rhus*, competition for light above ground was so intense that no other plants were present and the deeper soil was free from roots of any kind. But lack of linear extent is amply recompensed by a wonderfully well-developed absorbing surface. Perhaps the roots of no other plant examined, with the exception of certain surface-feeding grasses, occupy the soil more thoroughly than does the delicate network of the root branches of this shrub.

The larger roots vary from 3 to 7 mm. in diameter. While they may come off vertically, usually they pursue an oblique direction for some distance (1 to 3 feet) before turning downward (plate 13, A). These reddish-brown, tough, woody roots taper uniformly, frequently giving off large branches and a network of finer ones, beginning just beneath the surface of the soil. Indeed, the roots are profusely and minutely branched and rebranched throughout, the ultimate branches being almost microscopic in size. The laterals vary in length from those only an inch long to others extending a distance of 2 or more feet, sometimes almost at right angles. The last foot or 18 inches of the root is usually threadlike but extremely well branched. Above the level of 65 inches the soil is well filled by great numbers of these fine root-endings.

Rhus glabra.—A trench 10 feet long was dug just within a thicket of sumac which, according to ring counts, had been in possession of the area for at least 12 years. Practically all herbaceous species had disappeared except *Poa pratensis*. A brief examination showed the soil to be filled with a network of rhizomes from which numerous roots ascended more or less vertically and ended at the surface of the soil in a brush-like mass of branches. Further study revealed the really wonderful complexity of these underground parts as well as the great absorbing area of this xero-mesophytic shrub (plate 14, A, B). Roots were examined in three different situations. Although they differ in details, the following is a typical example:

A tap-root 3 cm. in diameter and 12 or 13 years old pursued a downward course at an angle of about 40° from the vertical to a depth of 22 inches. Here it turned off at an angle of 30° from the horizontal and ran a distance of 2 feet, at which length (48 inches) it was only 1.5 cm. in diameter and 37 inches deep. Here it forked into two equal branches, one (*a*) running almost horizontally to a distance of 68 inches and at a depth of 3 feet, while the other (*b*) turned off at an angle of 40° from the first and, after running rather obliquely downward for a distance of 15 inches, gave off two horizontal laterals 3 and 6 mm. in diameter respectively, while the main root turned vertically upward. It ran in this direction for a distance of 8 inches, when it divided into 3 equal branches. Two of these were each 6 mm. in diameter and tapered gradually till they reached the surface, 26 inches above, and at a horizontal distance of 26 inches beyond the vertical root from which they branched. They ended about 2 feet apart in an extremely well-branched and rebranched network of fine rootlets. These root termini were 70 inches in a horizontal line from the beginning of the tap.

The third branch from the upright portion of the root turned off horizontally and ran a distance of 8 inches, when it again turned at right angles and ran horizontally in another direction (away from the main tap) 16 inches, finally turning downward at right angles and descending to a depth of 80 inches. The tip, which ended in a much-branched network of almost hair-like terminals, was located at a horizontal distance of 68 inches from the beginning of the tap. The two 3 and 6 mm. laterals of root (*b*) ran off horizontally, but in a direction opposite from the others, finally ascending to the surface several feet from the other roots. Branch (*a*), which was partly cut off in digging the trench, also sent off numerous roots to the surface as well as some into the deeper soil. The surface soil is filled with rootlets with such a network of absorbing terminals that competition with the grasses for soil moisture must be very severe. Nor is the main absorbing area confined to the surface. Well-branched laterals, both large and small, arise at all depths, and even the deeper soil is rather thoroughly occupied. The well-branched root system, together with the large area it occupies, must afford abundant moisture, even in fairly dry soil.

While all of the main roots examined in two separate thickets showed the oblique to horizontal course with a depth never exceeding 80 inches, one root of a *Rhus* plant growing in the *Symphoricarpos* thicket was 0.5 inch in diameter and pursued a vertically downward course to a depth of over 90 inches. The roots are characterized by a thick cortex which exudes a white latex when injured, and upon removal reveals the small, woody, glistening white stele. The younger roots vary in color from brown to nearly black.

Corylus americana.—This shrub does not get so far into the prairies from the bordering eastern forests where it forms a layer as do the preceding, and in this respect shows its less xerophytic habit. But in many situations, from Minnesota to Kansas, thickets of *Corylus* come into direct competition with prairie vegetation.

Corylus spreads by means of large woody underground parts, as shown in plate 15, c. These run at a distance of only 4 to 6 inches under the surface and give rise at intervals to numerous erect shoots from 2 to 7 feet high and also to multitudinous roots, some of which are more than 1.5 cm. in diameter. Some of the smaller roots run vertically toward the surface and branch profusely into very fine ultimate branchlets, for *Corylus*, like the preceding shrubs, is a strong competitor of the grasses for moisture in the surface soil. Indeed, the surface foot or two of soil is well filled with absorbing rootlets, the longer roots being only fairly well supplied with laterals to a depth of 10 or 11 feet. These larger roots, as shown in plate 15, A, either pursue a rather vertically downward course, or extend obliquely for a distance of 1 or 2 feet or more and then turn downward. Roots were traced to depths of 10, 10.5, and 11.5 feet respectively. They are dark brown in color, very woody, with a very thin cortex, and frequently branch rather dichotomously, although the branches are seldom equal in size. The branches are often very coarse and sometimes run in parallel groups several inches without giving rise to absorbing rootlets. The main root-ends are not very well supplied with fine branches. Thus it may be seen that while *Corylus* penetrates to greater depths than *Rhus* or *Symphoricarpos*, its absorbing system is hardly developed to such a high degree.

Vitis vulpina.—At a depth of over 10 feet in the *Rhus* thicket a root of *Vitis* was encountered. It was 18 mm. in diameter and ran horizontally across the trench. It gave off numerous branches, some of which reached depths of 12 feet. Its branching is not unlike that of the larger roots of the hazel. In the *Corylus* thicket, roots of grape were traced to depths of 13 feet 3 inches and 13 feet 6 inches respectively. The diameter of roots near the surface was about 1 cm.; at 10 feet it was 2 and 3 mm. respectively. Another underground part ran horizontally at a depth of 2 feet for a distance of more than 6 to 8 feet. Such an enormous absorbing area as is possessed by *Vitis* gives us the clue to its ability to have a leaf area not unlike that of many trees and yet be able to live often in apparently rather dry situations.

Rosa arkansana.—This shrub is widely distributed throughout the scrub and prairie areas. Although usually held in check in the dense grassland sod, except where local disturbances have favored its development, in the subclimax grassland it frequently forms dense brush over the less-exposed slopes. In the sandhills westward it again assumes an important rôle, areas several acres in extent frequently being controlled by this species.

As shown in plate 16, A, this plant propagates by rhizomes. This parent plant had given rise to 5 distinct clumps of stems, the youngest of which was 5 years old and more than 5 feet from the oldest. Fragments of other horizontal parts, which had not yet developed shoots, may be seen. It may also be noticed that the plant next to the parent is the only one that has developed a tap-root of its own. Indeed, the other roots arising from the horizontal portion ran obliquely upward, rather horizontally or, at most, only very obliquely downward, and none reached any considerable depth when compared with the taps from the older plants. The tap-root from the second plant reached a depth of 15 feet 2 inches; the main tap pursued a nearly vertically downward course to a depth of 21 feet 2 inches.

It should be noted here that these roses grew about midway up a southeast slope. Here the loess soil was intermediate between that described for *Lygodesmia* near the crest and for *Amorpha* near the foot of the hill. Beyond a depth of 10 feet the soil was quite compact.

Plate 15, B, illustrates well the paucity of large branches. The lateral spread of any branch measured horizontally from the base of the crown did not exceed 4 feet. Although many fine branchlets occurred along the course of these main roots and extended off laterally for distances of 6 to 18 inches, still other portions were quite free from branches. The breaking up of the larger roots near their extremities into numerous long, slender, often more or less parallel rootlets is well shown on the root in the figure, which ends at a depth of about 6 feet.

The older woody roots can easily be identified by scraping off the outer black part of the thin cortex, which then reveals a bright red color, while similar treatment of the younger roots shows their orange color.

SHRUB ROOT SYSTEMS AND THE SHRUB ENVIRONMENT.

From the preceding descriptions it may be seen that the members of the chaparral community of the tension zone are all supplied with splendid absorbing systems, which are somewhat variable as to depth, but all of which are deep-seated. In addition, all have excellent methods of vegetative propagation.

The rôle played by these shrubs in modifying prairie conditions to such an extent that the habitat becomes rather favorable to the growth of the more xerophytic trees, such as bur oak, should not be overlooked. All are well adapted, either by means of above-ground or underground stems or root offshoots, to slowly but successfully invade the prairie sod. For example, the whole loess hill, where these shrubs were excavated, would probably be covered by a chaparral complex except for repeated fires which are more detrimental to shrubs than to grasses and most other prairie species. The proof of this statement lies not only in the presence even over much of the more exposed hillside of a potential scrub mictium, but also in the fact that *Rhus*, *Symphoricarpos*, and other shrubs dominate over other portions of the same ridge where soil conditions are identical but where fires have not been permitted to run.

Synphoricarpos extends its area by migrating by above-ground stems as well as by those below the surface. This mechanism of invasion is well illustrated in plate 13, B. While the above-ground stems furnish the more rapid method of migration, they frequently fail to become rooted in the prairie sod. They then become greatly attenuated and soon die. The under-ground stems are more certain of establishment.

Once established, this shrub rapidly reacts upon the habitat by increasing the water-content both of air and soil, and also by modifying the texture and composition of the latter. The presence of the shrubs decreases wind movement and their shade reduces not only the light but the temperature as well. This reacts favorably upon the humidity and also decreases the evaporation from the soil surface. The reduction of the evaporating power of the air within a *Symphoricarpos* area at a height of 17 cm. as compared with that 2 meters beyond in the prairie is well illustrated by the following data, giving the average daily evaporation in a clump of *Symphoricarpos* and in the adjacent grassland, both near the crest of a loess hill:

Date.	Prairie.	Scrub.
	c. c.	c. c.
July 1 to 7, 1918........	33.1	25.6
July 29 to Aug. 5, 1918..	46.0	33.8
Aug. 26 to Sept. 4, 1918.	18.0	14.6

Not only is the evaporating power of the air lowered by the presence of the scrub, but among its stems drifts of snow find lodgement and upon melting add considerably to the moisture content of the soil. The run-off is greatly reduced as a result of the rich mulch of fallen leaves and large quantities of wind-transported plant débris lodged among its stems. Only a few years are required, owing to the more favorable conditions for the formation of humus under the shrubs, to fill the former prairie soil with a rich humus mulch not unlike that of the woodland. Thus by cumulative favorable reactions the scrub is frequently able to extend its area of dominance and also to prepare a fine nursery for the seedlings of trees, thus initiating a new stage in the normal succession. Repeated determinations of water-content to a depth of 3 feet show that the thicket soil is moister than that of the prairie.

The reactions of *Rhus* upon the habitat are similar to those described for *Symphoricarpos*. Being a taller shrub, its effect upon the bordering grassland is more pronounced. It invades the prairie by means of rhizomes. These have been traced at a depth of only 4 to 8 inches to a maximum distance of over 20 feet from the edge of a thicket, their course being marked by the presence of erect shoots.

The evaporating power of the air is greatly reduced under *Rhus* as compared with that in the prairie, as is shown by the following experiment: From May until September, 1916, non-absorbing atmometers placed just 6 meters within the sumac thicket gave evaporation losses averaging about 10 c.c. per day as compared with average daily losses of 22 c.c. from similar instruments 24 meters outside the thicket in the prairie. Likewise, the water-content of the soil at the scrub station as compared with that of the grassland was found to average about 6 per cent higher throughout the season to a depth of 10 inches. The deeper layers of soil to 5 feet were invariably much moister in the sumac community.

The profound effect of a growth of hazel upon modifying prairie conditions is well illustrated by a series of evaporation and soil-moisture readings obtained on a flat hilltop in the edge of a hazel thicket and a few meters beyond in the prairie. The evaporating power of the air measured during the growing season of 1916 and 1917 was about 50 per cent less in the *Corylus* thicket. On the other hand, the water-content of the soil, as in the case of the other shrub communities, was found to be somewhat higher.

During 1917 another series of evaporation readings and soil-moisture determinations was made at Peru in the loess soil. The atmometers gave an average daily loss of 20.9 c.c. in a prairie on a southeast slope, while in a *Corylus* thicket on a northwest slope the loss was only 14.4 c.c. daily. This ratio was maintained almost throughout the summer and at no time were the losses in the shrub as great as those in the prairie. That the water-content of the soil in the shrub was usually much higher than that in the prairie may readily be seen by an examination of tables 4 and 5 on pages 21 and 22.

III. THE PRAIRIES OF THE PACIFIC NORTHWEST.

The prairies of southeastern Washington and adjacent Idaho, where the following studies were carried on, represent an extreme westward extension of the great grassland formation lying east of the Rocky Mountains. *Agropyrum spicatum, Festuca ovina ingrata, Kœleria cristata,* and *Poa sandbergii* are dominants. *Stipa* is entirely absent, as are also the late-blooming grasses, such as *Andropogon, Bouteloua,* and others of the eastern prairie. The absence of these late-maturing grasses may be accounted for by the peculiar distribution of the precipitation. Only about one-fourth of the annual 21 inches of moisture falls during the growing season. Except for the extremely retentive silt-loam soil, the region would be almost a desert. This is an extremely important fact to keep in mind while considering root systems. The important rôle played in the eastern prairies by *Andropogon scoparius* is here taken by *Agropyrum spicatum,* its ecological representative. Like *Andropogon,* it presents the bunch habit in drier soils, but becomes a sod-former with well-developed rhizomes under more favorable moisture conditions. Eastward, these prairies adjoin the main area of grassland lying east of the Rocky Mountains. At Missoula, Montana, for example, the *Agropyrum-Festuca* community of Washington and Idaho (Weaver, 1917) meets and intermingles with such eastern prairie species as *Stipa comata, Aster multiflorus,* etc., while *Agropyrum spicatum, Kœleria cristata, Solidago missouriensis, Achillea millefolium,* and others occur throughout both regions.

The writer has presented elsewhere (1917) a detailed description of the extent, successional relations, and floristic composition of these western prairies. A glance at plate 17, B and C, may give some impression as to their general character. Hence we will proceed at once to a discussion of root distribution.

THE ROOT SYSTEMS OF THE GRASSES.

Over 60 individuals of the four dominant grasses were excavated and examined. Three, *Kœleria cristata, Poa sandbergii,* and *Festuca ovina ingrata,* are shallow-rooted, the bulk of the absorbing system lying above the 18-inch level, while *Agropyrum spicatum* penetrates to a maximum depth of 4 feet 10 inches.

Agropyrum spicatum.—This is the dominant 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. The plant blossoms in June and dries out in early July, only to take on renewed growth after the autumn rains and to remain green all winter.

This grass has coarser roots than any of the other three important native grasses. These coarse, fibrous roots have many short laterals. Some of the

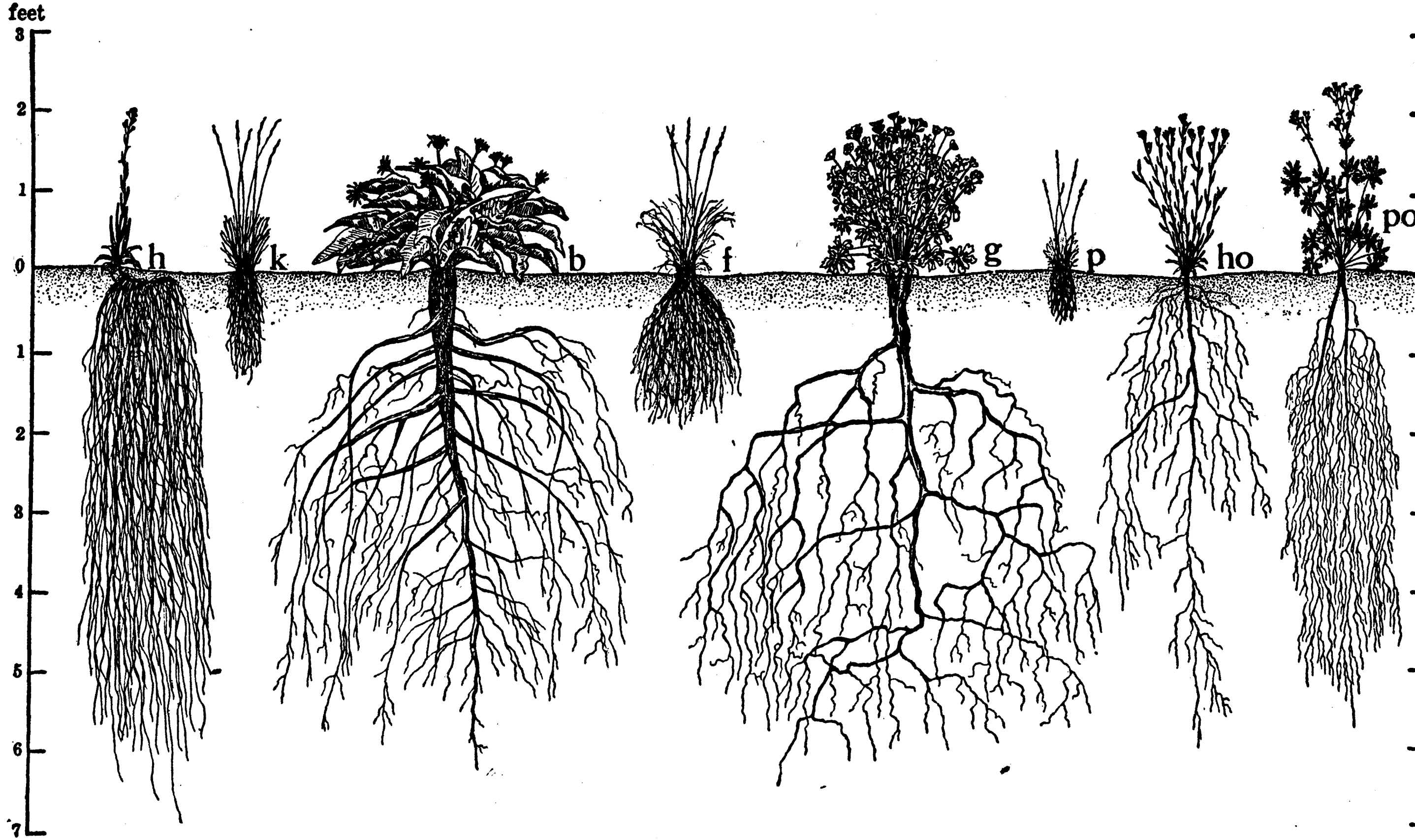


FIG. 6.—Schematic bisect showing the root and stem relations of important prairie plants. This and figures 7 and 8 were drawn from photographs and data obtained by the excavation and examination of 325 root systems of these 18 species: *h, Hieracium scouleri; k, Kœleria cristata; b, Balsamorhiza sagittata; f, Festuca ovina ingrata; g, Geranium viscosissimum; p, Poa sandbergii; ho, Hoorebekia racemosa; po, Potentilla blaschkeana.*

roots reach a depth of 4 feet 10 inches, although on an average 4 feet 2 inches was the greatest depth attained.

Festuca ovina ingrata.—The blue bunchgrass ranks in importance with *Agropyrum* on the well-developed high prairies west of the foothills of the Bitterroot Mountains between Spokane, Washington, and Lewiston, Idaho. Because of its abundance the very appropriate name Palouse (Fr. *pelouse*, a land clothed with a short, thick growth of herbage) was early applied to this region. 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 1 mm. 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. The longest root found was 3 feet 3 inches, and the average length was 2 feet for the deepest roots, but the great bulk of these roots were less than 18 inches long.

Poa sandbergii.—This species 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.

Poa has smaller roots than *Festuca;* they are more profusely branched, and the fine, short laterals 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 was found beyond 13 inches. The root branches are longer and more numerous at the tip than are those of *Festuca.* The average maximum depth was found to be 10 inches.

Kœleria cristata.—This is also a dominant bunchgrass on the prairies of eastern Washington. It flowers in late June or early July, and like *Poa* remains dormant until revived by the autumn rains. The roots resemble those of *Agropyrum,* but taper 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 *Agropyrum.* The deepest root found was at 28 inches, and 15 inches was determined as the average maximum depth. The shallow root habit of the three last species as compared with the deeper-root habit of *Agropyrum* and certain dicotyledonous plants is shown graphically in figures 6 and 7.

THE ROOT SYSTEMS OF OTHER PRAIRIE SPECIES.

Since the root systems of 21 of the most important non-grassy prairie species have been described in detail in a former publication (1915), it will be necessary here only to present a summary statement, so that it may be possible to compare their root systems directly with the plants of the eastern prairies and later with those of the plains. Such a comparison will help us to more clearly evaluate the response to the conditions under which the several plant communities grow.

Lupinus ornatus.—This plant and *L. leucophyllus* are the two species of lupines most widely distributed on the high prairies of eastern Washington. Both form extensive summer societies, the former on the drier slopes and ridges, the latter on moist hillsides and in the valleys. Several of the 24 root

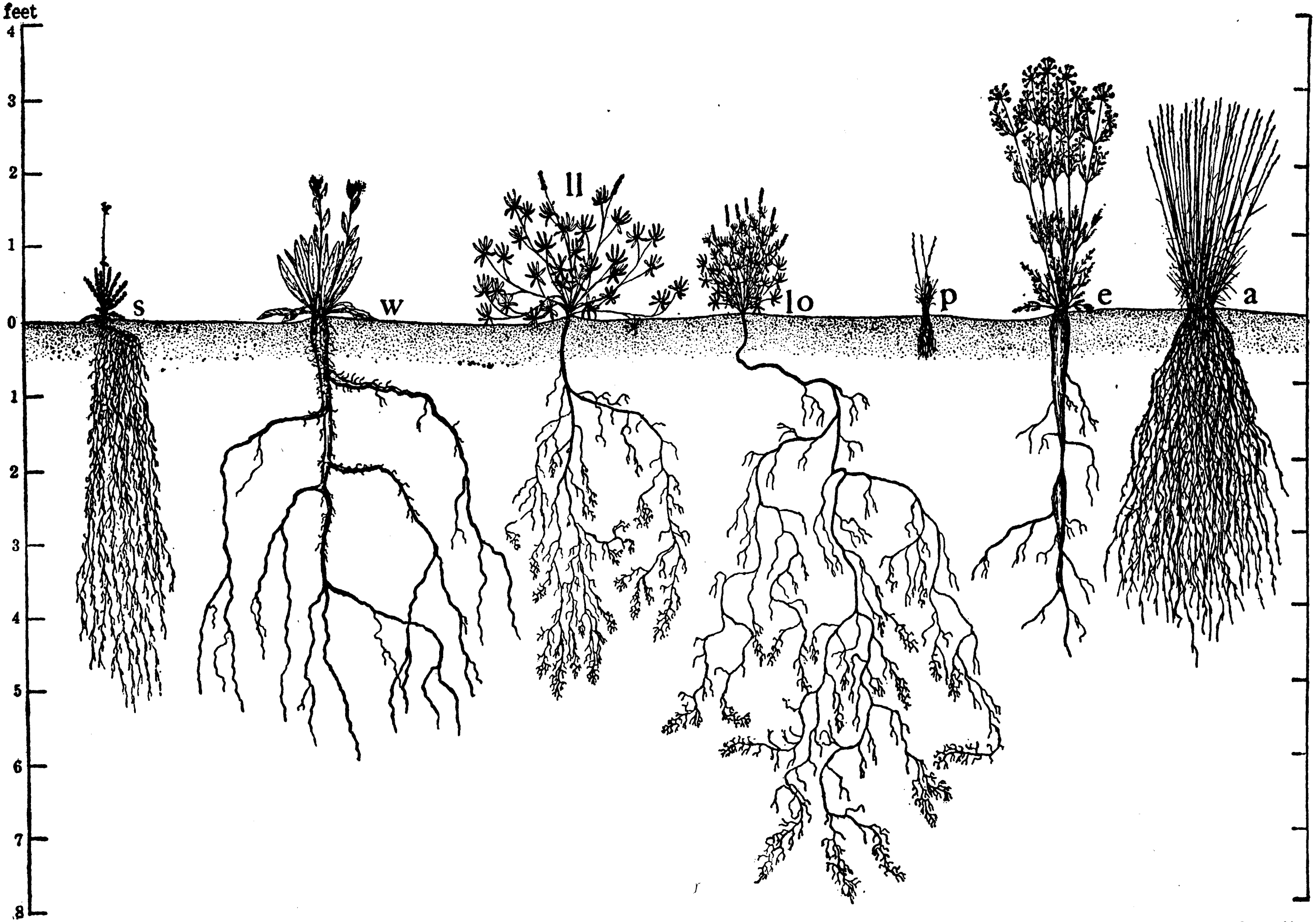


Fig. 7.—Schematic bisect: *s, Sieversia ciliata; w, Wyethia amplexicaulis; ll, Lupinus leucophyllus; lo, Lupinus ornatus; p, Poa sandbergii; e, Leptotænia multifida; a, Agropyrum spicatum.*

systems examined reached depths of over 10 feet; because of the devious course they pursue, the tap is frequently much longer. Indeed, one was found to have a length of nearly 13 feet. The abundant laterals, their wide spread, and the clusters of terminal branches, together with the root nodules, are shown in figure 7.

Lupinus leucophyllus.—This lupine has a much larger transpiring surface but a much smaller absorbing surface than *L. ornatus*, which it resembles in having a well-developed tap-root, usually with several laterals, all of which are branched to the third and fourth order. However, the root system is much less extensive than that of *L. ornatus*; its average depth is only about 5 feet (fig. 7).

Astragalus arrectus.—This legume forms marked estival societies, the plants drying up during the first week in July. It has a strongly developed tap-root, which usually pursues a course directly downward and sends out many strong laterals at various depths. These laterals are fairly widespreading and profusely branched to the tip. They reach depths of 4 or 5 feet (fig. 8).

Balsamorhiza sagittata.—The balsam-root is a dominant in the high prairies of eastern Washington. Its abundance, size, and duration all unite to make it a very important species ecologically. From the short, thick, multicipital stem the new leaves appear in April. By the first of May the plant is often in full bloom, forming societies which are very conspicuous, even after the whole aerial part has dried up. 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 10 inches. The laterals seldom come off in the first 6 inches of soil, but numerous strong laterals occur below this, 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 is never much branched. The older part of the root especially is covered with a bark furrowed sometimes 0.5 inch deep. The average root depth was found to be 5.5 feet (fig. 6).

Geranium viscosissimum.—This subdominant forms extensive societies in the estival aspect. It has a well-developed tap-root which may reach 3 inches in diameter. 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. 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. While one plant penetrated to 9.5 feet, the average depth was found to be 5.5 feet (fig. 6).

Wyethia amplexicaulis.—This large, rather coarse plant is at home on moist hillsides and especially in valleys, where it forms extensive estival societies. It has a fleshy tap-root, which sometimes measures 9 inches in circumference and may reach a depth of 6 feet 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. Often at a depth of 1 to 3 feet the whole tap breaks up into 2 to 5 nearly equal

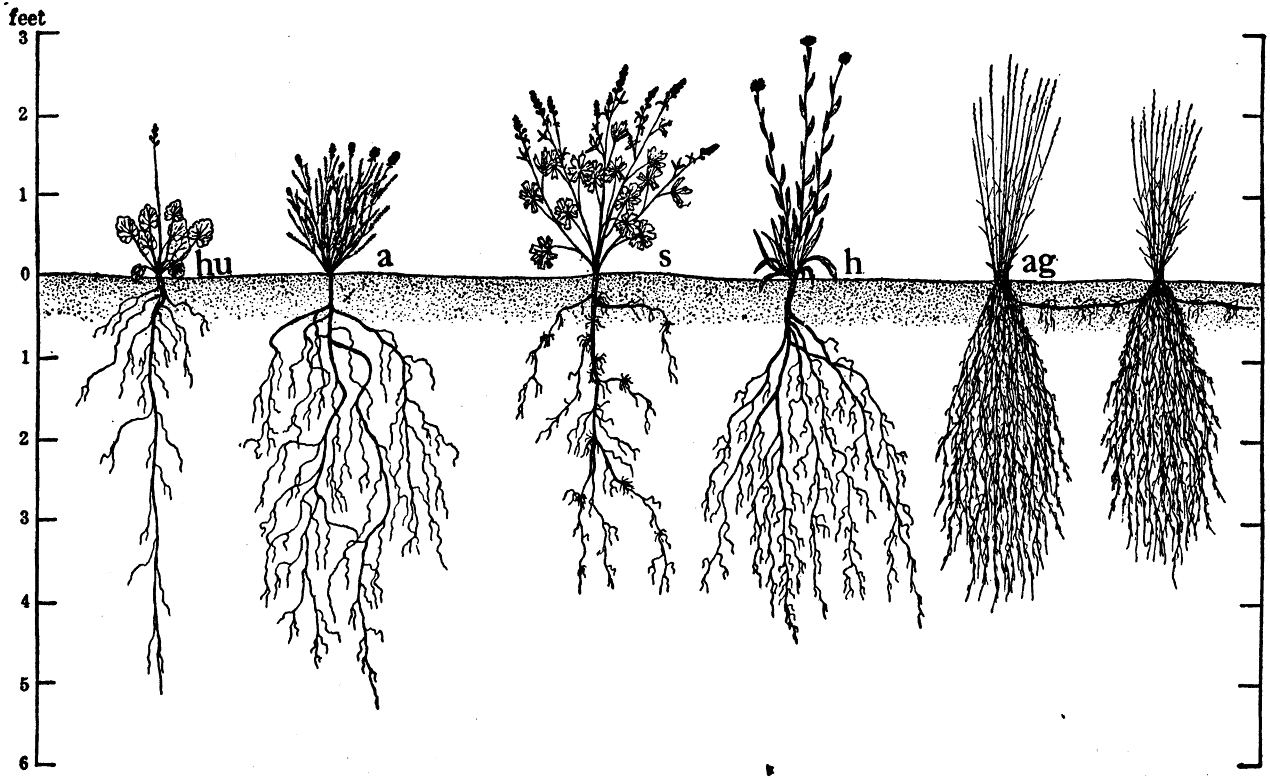


FIG. 8.—Schematic bisect: *hu*, *Heuchera glabella;* *a*, *Astragalus arrectus;* *s*, *Sidalcea oregana;* *h*, *Helianthella douglasii;* *ag*, *Agropyrum spicatum.*

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 mm. 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 dry out and shrink rapidly upon removal from the soil. The 18 plants examined had an average root depth of 5 feet (fig. 7).

Heuchera glabella.—This saxifrage has a strong tap-root supplied, especially in the first foot of soil, with rather numerous but poorly branched laterals. It reaches depths of about 5 feet (fig. 8).

Leptotænia multifida.—*Leptotænia* is a subdominant which forms conspicuous societies in the vernal aspect. It has a large fleshy tap-root, sometimes 7 inches in circumference, which may reach a depth of over 5 feet. The fusiform roots may narrow down gradually or rather abruptly, even to a diameter of 1 or 2 mm., and then again enlarge to a size equaling 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. The average depth of penetration is 5 feet (fig. 7).

Helianthella douglasii—This species, like the following, forms societies in the autumnal aspect. It has a tap-root with a diameter seldom more than 2 cm. It throws out many large 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. Of the 20 plants examined the deepest penetrated only to 5.5 feet, while the average depth was found to be 4.5 feet (fig. 8).

Hoorebekia racemosa.—The strong tap-root of this plant sometimes reaches a depth of 10 or 11 feet, but usually ends near the 5.5 foot level. 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 the tip. The main root is usually not more than 0.5 inch in diameter (fig. 6).

Lithospermum ruderale.—The tap-root of this species varies from 3 to 10 inches in circumference and gives promise of a deeper root system than is actually attained. Only one plant reached a depth of over 6 feet, while the average depth of the 5 specimens examined was 4 feet 10 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.

Sieversia ciliata.—This species forms societies in the estival aspect. Few roots of *Sieversia* penetrate beyond depths of 5 feet 6 inches. It sends out as many as 20 to 30 roots from a single inch of its thick rootstock. None of these roots is over 3 to 4 mm. 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 11 plants examined gave an average root depth of 4 feet 9 inches (fig. 7).

Sidalcea oregana.—This mallow is confined to north hillsides and low ground. It has a tap-root which gives off strong laterals, beginning in the first foot of soil. The tap penetrates to depths of only 3 or 4 feet. The roots are characterized by the origin of short laterals in groups of 3 to 8 (fig. 8).

Hieracium scouleri.—This hawkweed is one of the few species of the western prairies which forms autumnal societies. For the 26 root systems examined an average depth of 5.5 feet was determined. It sends out numerous roots, as many as 50 from a single inch of its rhizome. The rhizome is 8 to 12 inches long. None of these roots are over 3 mm. in diameter. They pursue a nearly vertically downward course and throw off practically no laterals, except where they enter earthworm holes. Here strong laterals, equaling the main root in diameter, are developed 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 tip of the main root may branch very profusely, or very little if in hard soil. The longest root reached a depth of 7 feet 9 inches, although 5 feet 4 inches was found to be the average depth (fig. 6).

Potentilla blaschkeana.—The tufted stems of this subdominant are borne on a short, thick crown from which 2 to 5 main roots originate. These average about 7 mm. in diameter. They taper off gradually till at about 2 feet in depth they are often only 2 mm. 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 perhaps 2 feet before entering the soil again. In these holes they give off many threadlike branches which follow down the same hole, branching profusely and often not reentering the soil. The roots are dark brown in color. They are unbranched or very poorly branched at the tip. Thirty root systems were examined. The longest roots penetrated to a depth of 7.5 feet, while the average root depth was found to be about 5 feet (fig. 6).

Eriogonum heracleoides.—This mat-former, at home on dry ridges, has a strong, woody tap-root often an inch in diameter. It sometimes breaks up just below the soil surface into several more or less equal parts. The roots penetrate to a depth of 6 to 8 feet or more. They spread widely and are well branched.

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 10 inches, and *Berberis repens* to a depth of over 10 feet.

PRAIRIE ROOT SYSTEMS AND PRAIRIE ENVIRONMENT.

From these data it may readily be seen that most of the prairie plants are deep-rooted. With the exception of *Kœleria cristata, Poa sandbergii,* and *Festuca ovina* (which are confined largely to the surface 18 inches of soil) all of the species examined reached depths of from 4 to 6 feet, while some penetrated even deeper. However, when compared with the species of the eastern prairie, these plants are not as deeply rooted. It may be recalled (p. 18) that about 55 per cent of the roots in the latter community penetrated well beyond 5 feet and many of them beyond 10 or 12 feet. Here, however, with a few exceptions, the plants usually terminate their root systems at depths of about 5 or 6 feet, while only one or two species have roots penetrating to 10 feet. A proper interpretation of this difference can be made only by a careful study of the habitat.

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 of 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 the same time the general northern boundary of the exposed part of the great lava sheet and its accompanying prairie formation. 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, 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 low annual precipitation. Even on its high eastern border, where these studies were carried on, it is only 21 inches. Table 7 shows in inches the mean monthly and annual precipitation at Pullman, Washington.

TABLE 7.

Month.	Precipitation.	Month.	Precipitation.
	inches.		*inches.*
Jan......	2.55	Aug......	0.68
Feb......	2.18	Sept......	1.29
Mar......	2.02	Oct......	1.70
Apr......	1.50	Nov......	3.41
May.....	1.84	Dec......	2.66
June.....	1.20		
July......	0.57	Total..	21.60

It may be seen at a glance that about three-fourths of the precipitation occurs during the resting period. The light showers of July and August seldom have much influence on the water-content of the soil. The soils of this region may be compared to a gigantic reservoir replenished mostly during the resting season and 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 southeastern Washington are so gentle that there is practically no run-off, and the silt-loam soils have a wonderfully retentive power.

The prairie soil has originated from the decomposed underlying basalt. It consists of a friable, dark-brown silt loam which has a water-holding capacity of 50 or 60 per cent of its dry weight. By the action of water and especially of the prevailing southwest wind, the prairie topography has been molded into rounded hills which reach a height of 100 to 360 feet and resemble sand-dunes. The soil is usually many

TABLE 8.

Date.	SW. slope. Wilting coefficient 11.	NE. slope. Wilting coefficent 12.2.	Date.	SW. slope. Wilting coefficient 11.	NE. slope. Wilting coefficient 12.2.
1913.			1913.		
Apr. 25....	10.0	21.0	Aug. 15....	−4.2	0.0
May 2....	12.0	22.2	Aug. 22....	−2.6	−1.3
May 8....	9.0	20.5	Aug. 28....	−3.0	−1.0
May 14....	13.3	25.6	Sept. 5....	−2.2	−2.0
May 20....	13.0	25.0	Sept. 10....	−3.4	−1.8
May 27....	5.2	18.0	Sept. 17....	−3.9	−1.0
June 2....	2.0	16.6	Sept. 25....	−2.2	0.7
June 10....	4.8	21.2	1914.		
June 15....	5.0	17.4	May 22....	4.0	13.0
June 25....	8.6	26.0	June 2....	0.1	7.5
July 2....	4.6	19.0	June 26....	−1.3	1.3
July 8....	4.0	15.2	July 4....	−0.2	1.8
July 16....	−0.5	9.4	July 8....	−1.2	1.1
July 21....	−0.5	6.4	July 19....	−4.5	0.0
July 28....	−2.6	4.4	July 27....	−5.0	−2.0
Aug. 4....	−1.4	0.2	Aug. 3....	−4.0	−2.0
Aug. 9....	−3.0	0.0	Aug. 10....	−4.0	−2.8

TABLE 9.

SOUTHWEST SLOPE.

Date.	Wilting coefficients at stated depths.					
	11.5 at 0 to 6 inches.	11.0 at 6 to 12 inches.	14.2 at 2 feet.	13.5 at 3 feet.	13.5 at 4 feet.	14.0 at 5 feet.
Dec. 13, 1913...	....	11.5	−1.2	−0.3	0.5	0.5
Apr. 18, 1914...	14.5	13.5	8.1	9.7	8.2	5.5
June 3, 1914...	−1.0	1.4	3.4	7.3	8.1	8.0
July 6, 1914...	−2.5	0.0	−0.7	1.0	5.1	6.8
Aug. 15, 1914...	−4.5	−1.6	1.9	0.6	2.1	2.6

NORTHEAST SLOPE.

Date.	Wilting coefficients at stated depths.					
	12.2 at 0 to 6 inches.	12.2 at 6 to 12 inches.	13.4 at 2 feet.	13.6 at 3 feet.	14.2 at 4 feet.	14.0 at 5 feet.
Dec. 6, 1913...	....	15.8	11.2	−0.8	0.6	5.0
Apr. 18, 1914...	22.8	20.0	15.6	13.4	9.9	9.5
June 3, 1914...	6.6	8.5	13.1	16.5	13.6	9.8
July 6, 1914...	3.3	1.0	6.8	12.1	10.8	3.9
Aug. 15, 1914...	−3.0	−1.7	−0.6	0.0	2.3	3.0

feet deep. The wind has drifted much surface soil and humus material from the exposed south and southwest slopes and deposited it upon the steeper north and northeast leeward slopes.

It may be seen in tables 8 and 9 that the soil in the spring shows a maximum water-content, the autumn and winter precipitation having replenished the water lost during the long period of summer drought. Table 8 gives the available water-content of the prairie soil to a depth of 10 inches during 1913 and 1914. Table 9 shows the available water-content of prairie soils to a depth of 5 feet during 1913–14. The minus sign indicates water non-available for plant growth.

TABLE 10.

Depth.	May 22.		July 6.		Aug. 15.	
	NW.	S.	NW.	S.	NW.	S.
0 to 6 inches.....	23.4	12.5	15.2	11.1	11.6	6.7
6 to 12 inches....	25.7	17.9	13.7	11.4	12.1	10.2
At 2 feet........	27.0	19.9	18.9	12.6	11.8	10.2
At 3 feet........	30.2	20.2	23.7	13.2	14.4	10.6
At 4 feet........	27.2	22.0	24.9	17.3	18.0	10.5
At 5 feet........	24.3	22.4	21.3	19.6	19.5	12.3

The greater water-content on northerly exposed slopes is the result of several causes. More precipitation actually occurs here as far as effective moisture is concerned, much of the 46 inches of normal snowfall being blown over to the sheltered north hillsides. The soil on north slopes is deeper, has more humus, and a greater water-holding capacity. It has been seen that this reflects itself both in plant distribution and root development. An examination of table 9 shows not only a gradual depletion of soil moisture as the season progresses, but also that to a depth of 2 or 3 feet little or no moisture is available in late summer.

This seasonal march of soil-moisture, together with its greater scarcity on south slopes, is further illustrated in table 10, which shows the water-content of soil samples taken from another set of stations during 1914.

To evade the drought conditions thus imposed upon them, a few plants, notably the shallow-rooted grasses, complete their period of growth and produce seed early in the season, and then lie dormant until revived by the autumn rains. Most prairie species, however, extend their roots far down into the deeper moist soil. As the moisture supply decreases with the progress of summer, the evaporating power of the air becomes more and more intensive. This is shown in table 11.

Thus, high evaporation and low available soil moisture combine to make conditions rather unfavorable for plant growth, especially in late summer and in exposed situations. As has already been mentioned, late-maturing species are not at all abundant. No late-maturing grasses are components of the prairie flora. Flowering begins later and growth continues much longer on north hillsides.

Soil temperatures on the two exposures differ notably. These data are shown in table 12, which gives the soil temperature at 1 to 5 feet on April 18 and August 15, 1914, on a northeast and southwest slope respectively.

TABLE 11.—*Average daily evaporation in cubic centimeters on a northeast and a southwest slope respectively.*

Date.	SW. slope.	NE. slope.	Date.	SW. slope.	NE. slope.
1913.			1913.		
May 10..	12.0	10.5	Sept. 3..	33.0	21.7
May 15..	9.8	6.5	Sept. 7..	32.1	21.6
May 26..	13.1	10.2	Sept. 13..	33.6	23.8
June 3..	15.2	10.2	Sept. 20..	46.0	20.0
June 10..	13.0	8.6	Sept. 23..	21.0	17.0
June 15..	14.2	7.8	1914.		
June 25..	7.8	5.4	May 15..	20.1	19.0
July 3..	11.0	6.7	May 21..	19.0	15.1
July 8..	21.0	13.5	May 30..	17.8	15.6
July 13..	27.2	14.0	June 7..	20.0	11.2
July 18..	31.0	21.8	June 15..	16.1	12.5
July 25..	30.8	20.3	June 22..	32.1	19.0
July 29..	41.5	26.4	June 29..	19.0	12.8
Aug. 4..	33.0	23.8	July 6..	27.2	22.5
Aug. 10..	39.5	24.5	July 13..	44.0	30.5
Aug. 16..	26.5	15.8	July 20..	44.8	26.0
Aug. 20..	38.0	27.2	July 27..	49.0	32.0
Aug. 25..	44.3	30.0	Aug. 3..	51.5	42.6
Aug. 31..	43.8	27.5	Aug. 10..	57.8	39.1
			Aug. 15..	64.0	50.1

TABLE 12.

Depth.	April 18.		August 15.	
	NE.	SW.	NE.	SW.
1 foot....	45.7°F.	50.3°F.	65.0°F.	73.0°F.
2 feet....	45.1	50.0	61.7	70.0
3 feet....	45.0	48.2	58.0	66.2
4 feet....	45.0	47.0	57.2	64.4
5 feet....	45.0	46.4	54.5	62.6

The daily midsummer range at a depth of 3 inches on the northeast and southwest slopes was 12° F. and 26° F. respectively. It is probable that these differences in temperature have considerable effect at least on the rate of root development (Cannon, 1918).

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 and they are usually very deep. 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 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 to 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. On the part of the plants the most obvious response to these severe environmental conditions is the development of extensive root systems. For just as the evaporating power of the air and the nature of the transpiring organs determine the water-loss of plants, likewise the soil-water and the nature of the root systems determine the supply.

TABLE 13.—*Average root depths (in inches) of plants on different slopes.*

	SW. slope.	NE. slope.	NW. slope.
Lupinus ornatus	72.1	71.0	128.4
Lithospermum ruderale	....	48.7	74.5
Potentilla blaschkeana	....	59.2	64.3
Geranium viscosissimum	....	56.1	72.2
Hoorebekia racemosa	64.0	63.4	68.2
Hieracium scouleri	62.8	63.4	66.8
Helianthella douglasii	52.0	55.6	55.1
Balsamorhiza sagittata	61.5	....	69.8
Leptotænia multifida	....	54.7	47.3
Agropyrum spicatum	....	49.6	38.6

It is instructive to note that according to the types of root systems as set forth by Cannon, all the roots here described, with the possible exception of *Leptotænia multifida,* fall under the generalized class. This was true also for all but a few of the eastern prairie species. 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 are 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 inherited tendencies, table 13 is instructive.

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. The greater root depth of most species on the northwest slope at a station which combined a porous moist soil with rather extreme xerophytic above-ground conditions is at once evident. In all habitats studied the writer has found that hard soil profoundly affects the amount of branching, laterals practically always being more numerous in a less compact substratum. This may be closely connected with water-content and aeration—the looser soils, of course, if of the same type, having the greater water-holding capacity. A discussion of the effects of various habitats on the root development of polydemics will be found on page 110.

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 compact 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. Cannon and Free (1917) have found that roots of various plants respond quite differently to variations in the composition of the atmosphere. This difference appears to be related to the character of the natural habitat of the species in question. Their results indicate that plants growing in well-drained soil are much more sensitive to the composition of the soil atmosphere than those from poorly drained and poorly aerated habitats.

Contrasting grassland species of the east and west, we reach the following conclusions: Prairie plants of eastern Nebraska growing in the clay-loam or loess soil under an annual precipitation of 28 to 30 inches, most of which occurs during the growing season, and with an average daily summer evaporation of 21 c.c., have root systems very similar in distribution but somewhat greater in depth than prairie species of southeastern Washington growing in the silt-loam of disintegrated basalt under an annual precipitation of 21 inches, most of which falls during the resting season, and with an average daily summer evaporation of 30 c.c.

In both of these semiarid regions it has been shown that the water-content of the soil is reduced to the non-available point to a depth of 3 or 4 feet, at least during certain years. It has also been shown that in both of these prairie communities all of the dicotyledonous plants, as well as many of the grasses, extend their root systems to depths of from 3 to 7 feet or more.

The absence of very shallow, widely spreading laterals is characteristic of plants of both prairie communities, perhaps being more pronounced in the Palouse region. This is in distinct contrast to the root habit of many plains species, to which we shall now turn our attention.

IV. THE PLAINS ASSOCIATION.

This great grassland community extends from northwestern Texas and northern New Mexico to northern Colorado and Nebraska and from the Rocky Mountains eastward to central Texas and Kansas, where it meets the prairie. While soil moisture seems to be the limiting factor in the extension of the prairies westward, this is so intimately connected with the amount and distribution of the precipitation and with the soil type that great tongues of true prairie extend far into the Great Plains. This is especially true northward, while over much of the broad ecotone plains and prairie vegetation alternate. The plains community differs from the prairie chiefly in the dominance of short grasses, especially *Bouteloua gracilis* and *Bulbilis dactyloides*, and in the smaller number and reduced importance of the societies.

An excellent description of various plains communities, together with their successional relations and indicator values, especially for Colorado, has been given by Shantz (1911). Plate 18, A, affords a glimpse of the plains vegetation near Colorado Springs, Colorado, where the roots described below were excavated. Here about 80 to 85 per cent of the soil surface was covered with vegetation.

Bouteloua gracilis.—This well-known and important grass is a dominant over the plains from western Nebraska to the Rocky Mountains and from Texas far into Canada. From the standpoint of grazing it ranks among the highest of all the grasses, being equaled only by *Bulbilis dactyloides*.

The soil is well filled with fine rootlets to a depth of 30 inches, while in the next 6 inches they are still fairly abundant, some of the longer ones penetrating to a maximum depth of 48 inches. The surface roots spread very widely in the shallow soil to 1.5 feet or more and are exceedingly well branched.

Aristida purpurea.—Much of the plains association is characterized by the bunches of this very widely distributed dominant, wherever overgrazing or other disturbance has given it a foothold in competition with *Bouteloua gracilis*. From the bases of the individual clumps strong fibrous roots arise, from 0.5 to 1 mm. in diameter. These rather coarse roots either descend vertically or run off obliquely at an angle of from 20 to more than 45 degrees with the surface of the soil to a distance of 5 to 8 inches before turning downward. The surface of the soil below the clump is completely filled with these cord-like roots, but they do not branch profusely until they have penetrated 4 or 5 inches into the soil. Below this depth for 3 or 4 feet the roots become smaller, giving off both large and small laterals, many of the latter being only 1 to 10 mm. in length. The ground is rather well occupied to a depth of 3 feet, at which depth many of the roots terminate in rather well-branched tips, while others penetrate to a depth of 4 feet or slightly beyond. A maximum depth of 4 feet 3 inches was recorded for several of these tiny, hairlike termini. Branching is especially well developed in joints between the lumps of hard soil. The older roots are ashy-gray in color, and are provided with a rather papery cortex, which upon removal reveals the tough, light-yellow stele. The deeper roots are threadlike and are very fragile and usually well branched, although they sometimes run for several inches without giving off any laterals (fig. 9). Fissures occur in the soil, extending to a depth of 2 or 3 feet. These have evidently been open cracks and the soil on the sides of them is much darker in color, having been washed down from the surface. It is in these crevices, where the moisture-content is somewhat higher, that grasses and other plants branch and rebranch so profusely.

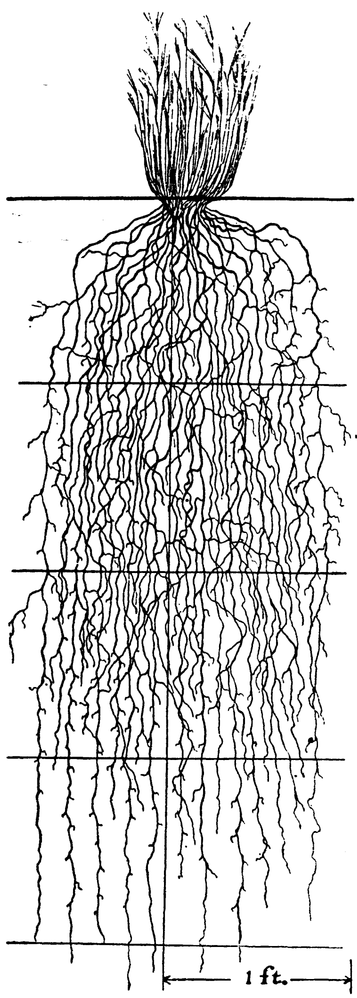


FIG. 9.—*Aristida purpurea.*

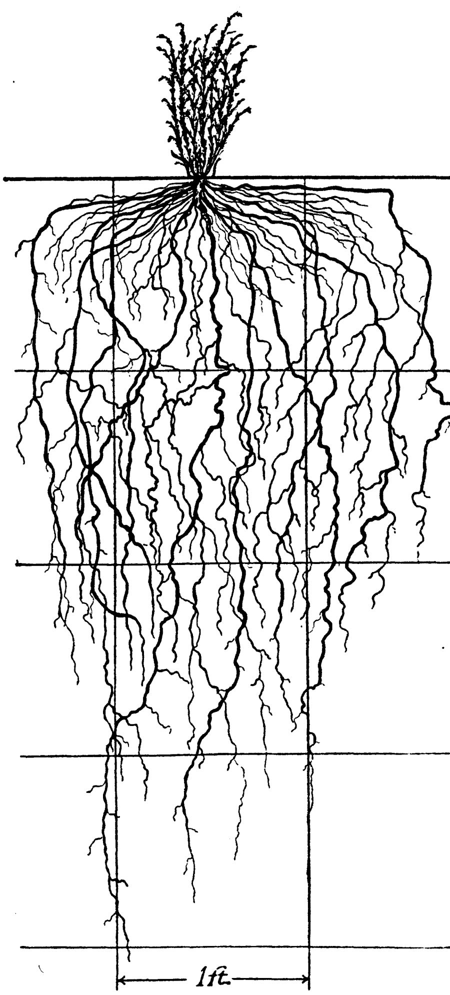


FIG. 10.—*Artemisia frigida.*

Muhlenbergia gracillima.—This grass is also a dominant of the short-grass plains; it is less widely spread and less abundant than *Bouteloua gracilis*, though in some places it ranks close to the latter. Superficially, it appears like *Bulbilis dactyloides*, because of its mat-like growth in small areas and the short, curled leaves. Frequently the center of the mat is dead and only the peripheral portions produce flowers.

A trench over 4 feet long was dug with one face cutting through a pure stand of this grass to a depth of about 5 feet. Great clusters of roots, only about 0.5 mm. or less in diameter, ran off in all directions from the very sur-

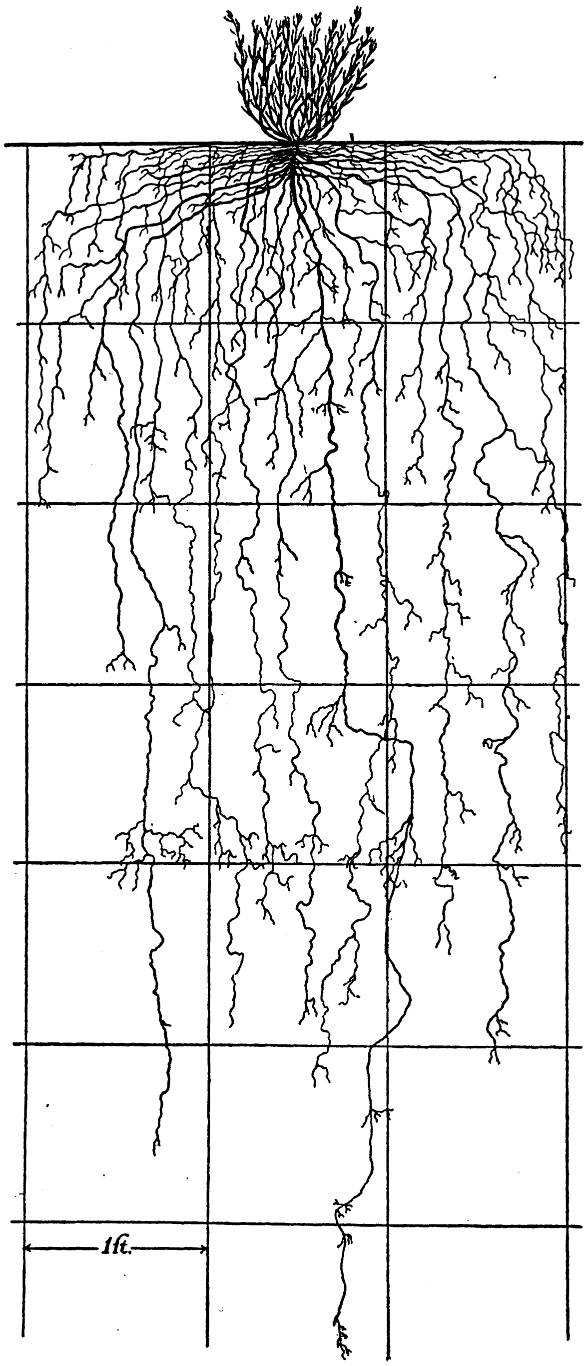


FIG. 11.—*Gutierrezia sarothræ* showing wide lateral spread of roots in the surface soil.

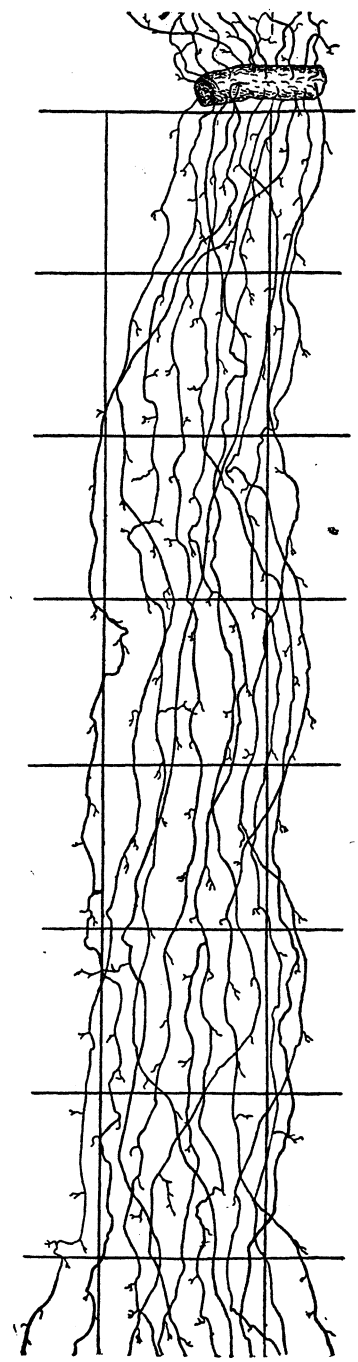


FIG. 12.—A small part of caudex of *Yucca glauca*, showing number and extent of horizontal roots, many exceeding 25 to 30 feet in length.

face to the average working depth, and are abundantly supplied with short, much rebranched laterals. Many of these spread very widely laterally, branching and rebranching into both long and short termini, so that the surface 27 inches of soil is completely filled with a dense network of absorbing rootlets. Every cubic centimeter of the soil to a depth of 2 feet is occupied by a network of this absorbing system. At a depth of 27 inches most of the rootlets end in very much branched termini, but a few penetrate to greater distances. By undercutting the face of the trench and working upward from a depth of 5 feet, several of these threadlike rootlets were encountered at a depth of 55 inches. The roots are tan in color.

Gutierrezia sarothræ.—This half-shrub occurs throughout the plains region, although it is usually more abundant in areas of less thoroughly disintegrated soil or in overgrazed areas. In such situations it forms extensive societies. The plants examined were quite abundant and from 6 to 9 inches high. Numerous stems arise from a strong tap-root from 5 to 8 mm. in diameter. The tap immediately gives rise to 5 to 9 large laterals, 2 or 3 mm. in diameter, and as a result, at a depth of 2 to 6 inches the tap is no larger than one of these laterals. The main root descends more or less vertically and at a foot in depth is seldom over 1 mm. in diameter. It is much curved and kinked, but these twists are usually small, so that at a maximum depth of 6 or 6.5 feet the tip of the root is not more than a foot or 18 inches horizontally from the base of the stem. Just at the surface, to a depth of 12 to 18 inches, very numerous threadlike laterals, 0.5 mm. or less in diameter, run off horizontally in all directions for a distance of 3 to 24 inches, the plant thus being well supplied with surface feeders. The large laterals frequently pursue a course nearly parallel with the surface of the soil at a depth of 2 to 5 inches, or run somewhat obliquely to distances of 12 to 20 inches before turning rather abruptly and vertically downward. Like the tap, they are profusely branched and rebranched with short, threadlike laterals, but after a depth of 18 inches is reached the branching becomes much poorer. These deeper roots may run a distance of a foot or more without giving off any laterals, or again short laterals only 2 or 3 inches long may occur in groups. The tips of these deeper roots are only fairly well branched. Some were found which gave off a whole network of branches matted in the cracks. While the larger roots are brown, tough, and rather woody, the deeper ones are nearly white and rather brittle. Several roots were traced to a depth of over 5 feet, while a few reached a maximum depth of 6 to 6.5 feet (fig. 11).

Psoralea tenuiflora.—This is one of the important legumes throughout the plains. Under favorable conditions of soil moisture it forms extensive societies. A number of individuals of this species were examined. They all had strong tap-roots varying in diameter with the age of the plant. One large root, which unfortunately was dead, had a diameter of 2 cm. At a depth of 1.5 feet it gave off numerous large lateral branches, the branching system being not unlike that of the more robust form of the prairies. A younger specimen, with a tap-root 7 mm. in diameter, pursued an almost vertically downward course to a depth of 42 inches. At a depth of 2 feet a small lateral ran off rather horizontally to a distance of 20 inches. No other branching occurred except near the tip, where 5 large branches and several smaller ones originated. Except for a very few rootlets, 5 to 10 mm. long and distributed very irregularly along the course of the tap, no other branching occurred.

A large plant, with a tap 8 mm. in diameter, reached a depth of 8 feet. Like the former, it pursued an almost vertically downward course. It was unbranched to a depth of 28 inches, where it gave off a horizontal lateral only

1.5 mm. in diameter and 27 inches long. A similar lateral about the same size arose 6 inches deeper in the soil. At 5 feet the tap, now only 1.5 mm. in diameter, forked dichotomously. At 6 feet the two branches entered a layer of moist sand through which they ran for 26 inches to a total depth of 8 feet, but they gave off very few branches. Rootlets of other plants of this species were quite numerous in these deeper soils. Finally, a plant was excavated and photographed (plate 18, B) which reached a depth of 12 feet 2 inches. The roots are brown to reddish-brown in color.

Artemisia frigida.—Mountain sage is a competitor of the plains grasses, especially northward, for the rather meager water-supply. Near the mountains, in rocky or gravelly situations, it frequently forms extensive societies.

From the base of the clustered woody stems a tap-root arises; it is from 5 to about 10 mm. in diameter and descends rather vertically to a distance of from 4 to over 6 feet. The tap, however, becomes rapidly attenuated, so that at a depth of 6 inches it is scarcely 1 to 2 mm. in diameter and indeed no larger than the numerous strong, rather horizontal laterals which arise from the tap or the base of the woody stem at just below the ground surface. These larger laterals, frequently as many as 5 to 9 on a single plant, run off obliquely in the shallow soil, sometimes almost horizontally and from a depth of only 1 to 2 inches to a distance of 8 to 12 inches or more before turning rather abruptly downward. The woody bases of the stem, as well as the first 6 to 10 inches of tap-root, give rise to very abundant rootlets, 1 mm. or less in diameter, which thoroughly fill the surface soil, branching and rebranching into threadlike termini and furnishing *Artemisia*, as is the case with so many plains plants, with a splendid surface absorbing system.

Like the tap-root, the larger laterals upon turning downward become greatly attenuated, the diameter remaining uniformly a millimeter or less for several feet. When near the ends they often become hairlike but are not well branched. The deeper roots, while branching from time to time and pursuing a rather tortuous course through the soil, are characterized by the absence of numerous laterals. A large number of plants were examined and most of the major branches extended with the tap to depths of from 3 to 6 feet. The deepest root examined entered at a depth of 5 feet into the soft soil filling an ancient burrow, in which it continued, giving rise from time to time to long, threadlike, unbranched laterals. It reached a depth of 7 feet 9 inches. The roots are chestnut-brown in color and all but the larger ones are very brittle, being removed with extreme difficulty from the hard, lumpy soil (fig. 10).

Argemone platyceras.—This wild poppy, conspicuous because of its large size and showy white flowers, is found as a frequent component of plains vegetation throughout much of the association. As a rule, it is more abundant in disturbed areas, often becoming ruderal.

The plant examined had a strong tap-root. It was partially decayed, portions of it being dead and easily dug out. At the end of the first foot, however, it branched dichotomously. These branches diverged not more than 6 to 8 inches and took a downward course, continuing to branch dichotomously at irregular intervals for the first 8 feet, the whole trend being downward (fig. 13). At no point in the first 8 feet of soil did the branches spread more than 1.5 feet from the vertical. At about 8 feet a layer of moist sand was encountered and here some of the branches turned outward almost horizontally, extending 18 to 24 inches, where they ended. Other branches continued downward through moist sand to a maximum depth of over 12 feet, the last 10 to 12 inches of their length passing into a very moist sandy clay. From about 4 feet downward these branches gave off occasional laterals about 2 to 4 mm. in diameter, which extended from a few inches to a foot or more. These laterals tended to take a more or less horizontal direction.

The color of the root is dark brown. It was very thick and fleshy and extremely brittle, so much so that near the terminus great difficulty was found in following it. Throughout its length, whenever broken, a clear to milky fluid exuded in limited quantities. The surface of the root was extremely rough and pitted; its diameter was often irregular. Throughout the whole course two or more branches had a tendency to twist about each other. This was marked in branches occurring not more than 2 feet from the surface, again at intermediate depths, and still again at not less than 6 inches from the extreme depth.

Yucca glauca.—The soap-weed is a widely distributed species, being especially abundant on dry, sandy, rocky slopes and forming extensive societies throughout many areas in the plains association. Its size, duration, and often its abundance combine to make it an important species. From the standpoint of the stockman it is often a bad weed.

A number of specimens were examined. An excavation was made about two large plants growing 2 feet apart. They each sent down a strong caudex 3 inches in diameter, but neither of them reached a depth greater than 18 inches. At this depth they branched and ran off laterally in a direction either parallel with or ascending toward the surface. The two plants were connected by a large underground rootstock (plate 17, A), while another (over 2 inches in diameter) ran off at nearly right angles from the connecting rootstock and reached the surface 3 feet beyond. It had given rise to several small plantlets. From the multicipital stem as many as 25 to more than 50 rosettes of leaves arose. Many of these were dead. One crown measured 21 by 26 inches in diameter, this being only a medium-sized plant. It reached a height of 30 inches. The multicipital branching extended to a depth of 5 to 7 inches and profound contractions were in evidence.

Beginning at the very surface, the stems are supplied profusely with roots. These vary from 2 to 4 mm. in diameter and run off horizontally to great distances, the lateral spread being remarkable. A number of these horizontal roots were traced to a distance of 32 feet (fig. 12). They occupied the soil chiefly at a depth of 6 to 18 inches, and, because of a somewhat tortuous course, terminated at a horizontal distance of 27 feet from the caudex from which they arose. These roots are reddish in color, of nearly uniform diameter for long distances, and very sparingly branched. Only at intervals do short, usually unbranched, secondary laterals occur. The cortex is thick and fleshy and serves for water storage; upon the death of the older roots it shreds off and reveals the tough wiry stele. The abundance of these roots is surprising. In a single square foot of vertical trench face, at a depth of 18 inches, 54 roots were counted. They extend outward in all directions from the rhizome, as was proven by digging a series of small trenches at distances of 18 to 20 feet on all sides of isolated specimens. Invariably *Yucca* roots were found. Such a trench, dug halfway between two isolated *Yucca* plants 66 feet apart, revealed the presence of laterals. Thus it may be seen that these large plants absorb water and soil solutes over a very extensive area in direct competition with the grasses.

A trench 6 feet long and 7 feet deep revealed very few *Yucca* roots below 2 feet. However, some do occur and penetrate to maximum depths of about 7 feet. Like the shallower laterals, the deeper ones are poorly branched, even the tips having few branches and ending abruptly. The ends are not more than 0.25 to 0.2 mm. in diameter. At a depth of 4 or 5 feet, a few roots were found running horizontally, simulating those of the shallower soils.

Another plant had a caudex 3 inches in diameter which reached a depth of 23 inches. Here it was still 2 inches thick. It branched into two equal laterals. These were much flattened and distorted, one being less than an inch thick but 2 inches wide. These branched and rebranched, as shown in plate 18, c, all ending within a horizontal distance of 16 inches from the base of the plant. Each was abruptly tipped with a bud. These deeper branches were not so well provided with roots as was the upper part of the stem.

Agropyrum glaucum.—Wheat grass, if at all abundant, is an indicator of favorable deep soil-moisture conditions. However, in thin stands and as dwarfed individuals it occurs in rather dry places. The plants here described were growing in low ground near a ravine.

The tufts of these coarse plants are connected by stout, tough rhizomes about 2 mm. in diameter and from a few inches to more than 18 inches in length. From the base of these clumps and from the rhizomes, which lie at a depth of about 1 inch, arise numerous short horizontal roots. These are profusely branched and rebranched to the third and fourth orders, the ultimate branches being almost microscopic in size, and thus furnishing a splendid surface absorbing system.

An abundance of coarse, tough roots, from 1.5 to 2 mm. in diameter, penetrated in a more or less vertical direction and others at an oblique angle to a maximum depth of over 7 feet. These coarse roots are covered with a brown papery cortex, rather readily removed from the large wire-like nearly white stele. These roots are profusely branched with laterals from a few millimeters to 2 or 3 inches long, many of these branches running off more or less horizontally. At a depth of about 4 feet many of these roots become only 0.2 mm. in diameter, but the branches (which are somewhat shorter) are no less abundant to the very tip. The roots have such an abundance of root hairs that the whole surface appears to be covered with wool. Thus *Agropyrum* is supplied with an absorbing system which thoroughly permeates all portions of the soil to a depth of 6 feet.

Carex pennsylvanica.—This sedge has a wide range throughout the grassland formation. Because of its early growth and flowering habit, it forms conspicuous societies in the prevernal aspect, often before the taller grasses resume growth.

The roots of a number of plants of this species were examined. The tufts are connected by coarse rhizomes, 2 to 10 inches long, at a depth of 1 to 3 inches. The much-branched fibrous roots have a lateral spread from the base of a tuft of only 2 to 3 inches. They originate from the rhizomes as well as from the base of the clumps. While many of the roots, after sending off abundant laterals which branch to the third and fourth order, end at a depth of 12 to 14 inches in exceedingly well-branched tips; others penetrate deeper. A few roots were traced to their delicate endings at a depth of 3 feet, while others occurred below the second foot. The chief absorbing area lies within the first and second feet of soil.

Andropogon scoparius.—The little bluestem occurs throughout the grassland formation wherever enough water is present to support its growth. In the drier plains association it is often confined to slopes with a rough topography and greater water penetration or to sandy soil. It dominates the shortgrasses under the latter soil condition and forms an extensive bunchgrass consocies. Under the still more favorable moisture-supply of the prairies it abandons the bunch habit and becomes a sod-former. The lateral spread of the roots is about 1 foot on each side of the plant and within 4 inches of the surface. The roots are very abundant up to the very surface, thus affording a distinctly shallow absorbing system. Many of the laterals run out to a distance of 12 to 14 inches and at a depth of only 1 to 4 inches, while below and inside of these at all angles to the vertical they are very abundant. The maximum depth for several roots was 6 feet. They are very abundant to a depth of 3.5 feet. The surface absorbing roots were especially well branched.

Stipa comata.—This grass often appears to be a dominant in the plains association where overgrazing has not thrown the advantage in favor of the short grasses. Although its aerial part is not extensive, it has a much deeper and better developed root system than the corresponding species of the prairies, *S. spartea.* A trench 6 feet long and 5.5 feet deep was dug in a nearly pure *Stipa* community. From the base of the clumps arise exceedingly numerous fibrous roots, 1 mm. or less in diameter. While many of these descend vertically, others run off at various oblique angles, some of them having a lateral spread of more than 18 inches from the base of the plant, while at a distance of 14 inches horizontally they reach a depth of 6 inches (plate 19, A). Beginning at the very surface of the soil, the main roots are clothed with relatively short but well-branched laterals, 2 to 20 mm. long. Thus the first 28 inches of soil are thoroughly occupied by the main roots, which are only a few millimeters apart, the interstices being completely occupied by horizontal branches. Even to a depth of 32 inches the soil is fairly well filled with much kinked and rebranched threadlike rootlets, while not a few reach a maximum depth of over 5 feet. Thus *Stipa comata* is provided with a much finer, more branched, more widely spreading, and deeper root system than is *Stipa spartea* of the prairies.

Lithospermum linearifolium.—This is a common and rather conspicuous plant of the grassland formation. Eastward it forms vernal societies. The plant examined had a crown of 10 stems arising from the top of the tap-root, which was 13 mm. in diameter. The tap proceeded straight downward 2.5 inches, where it divided into two equal branches, each about 7 mm. in diameter. These branches then took a downward course, their diameter decreasing very rapidly, so that at a distance of 22 inches from the surface they were not more than 1.5 mm. wide. This diameter remained almost uniform for several feet. They continued their downward course almost vertically, one part branching again at a distance of 3.5 feet and the other at a depth of 5 feet. These branches of the second order also took a downward course, being not more than 0.8 mm. in diameter. Lower down, one of these branches again branched and penetrated to the maximum depth of 10 feet, ending in hairlike termini. The root was very dark, almost black in color, and had a papery cortex which could be removed very easily, revealing a white hard and very brittle stele. Throughout the lower 5.5 feet the roots were fairly well supplied with short, attenuated branches 0.5 to 3 cm. long. Above this point shorter branches were few in number. Very little absorption took place in the first 4 feet of soil (fig. 14).

Lygodesmia juncea.—Although this plant is of frequent occurrence, especially in drier situations, it plays a rôle of no great importance in the grassland. It is interesting because of its xeroid-shoot habit. Two plants were examined. Each had a tap-root about 7 mm. in diameter, which took an almost vertically downward course, in one plant penetrating to a depth of 5 feet 8 inches. At 10 to 12 inches from the surface strong laterals were given off, which (after taking a horizontal course from 8 to 22 inches) turned downward not unlike the tap-root. Practically no small branches were given off and only very seldom, as shown in figure 15, did any branching at all occur. The roots throughout, both tap and laterals, pursued a very zigzag and tortu-

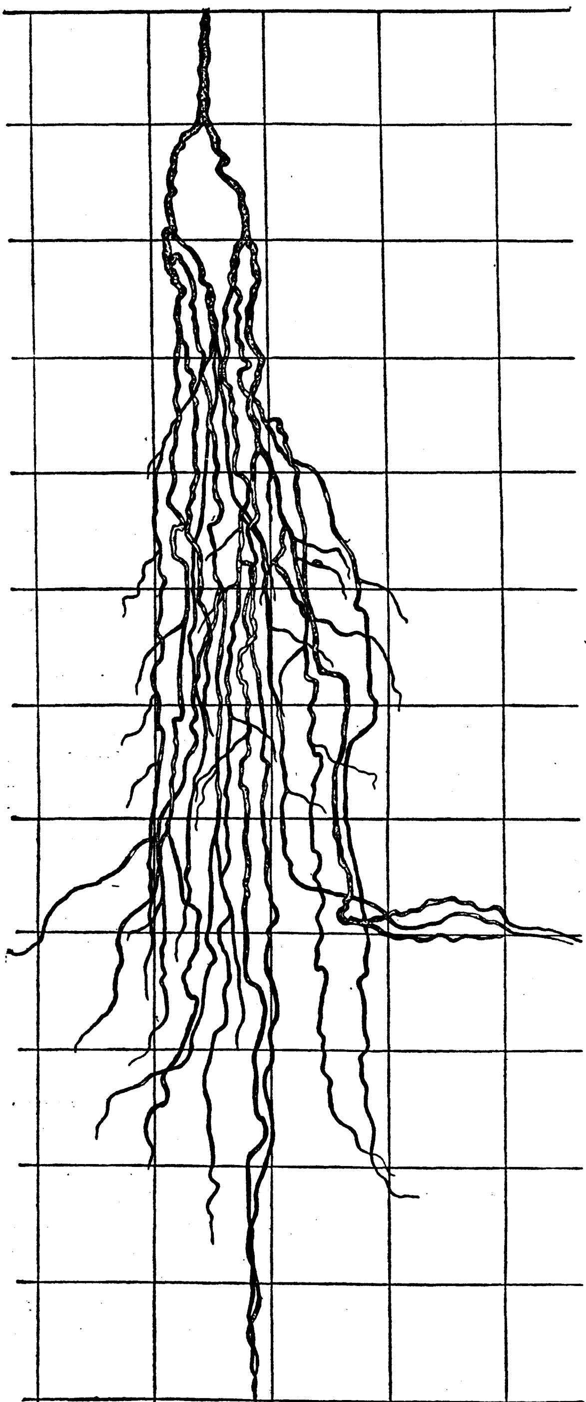


FIG. 13.—*Argemone platyceras.*

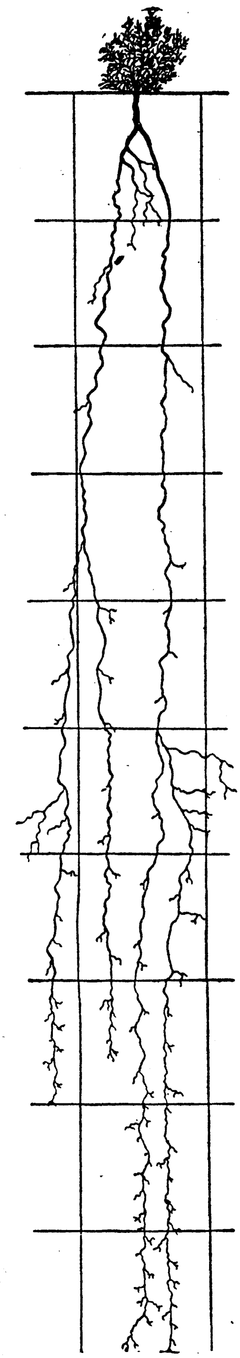


FIG. 14.—*Lithospermum linearifolium.*

ous course. The roots were dark brown with a very fleshy cortex, extremely brittle, and when broken exuded a milky latex. At the top the diameter was about 5 mm. As the root proceeded downward the diameter fluctuated from 4 to 7 mm., but gradually grew smaller to the tips, which were about 1 mm. in diameter and ended abruptly. These roots are very different from the much longer but almost unbranched roots of the same species growing in loess soil (p. 16).

Aragallus lambertii.—This loco unfortunately is a widely distributed legume throughout the plains grassland, forming one of the most important of the vernal societies. As is characteristic of most legumes, *Aragallus* has a strong tap-root. At the top this was 9 mm. in diameter and with a long gradual taper it penetrated the soil with a tortuous course almost vertically downward to a maximum depth of 8 feet. For the first 4 inches of its course there were scarcely any branches except 3 or 4 small hairlike laterals, which penetrated horizontally for a distance of 2 or 3 inches. Below this point and to a depth of 30 inches the tap was marked by rather profuse, small laterals, ranging from hairlike to 0.7 mm. in diameter. These penetrated the earth in a more or less horizontal direction for a distance of 2 to 8 inches; they were themselves branched to the second or third order. Below 30 inches the tap was very sparingly branched throughout its course, these branches being of the same character but much smaller than those already described. The tap ended by dividing into 3 or 4 ultimate rootlets, 3 or 4 inches long. The root was tough, rather woody, light brown in color. Three plants were excavated and examined (fig. 16).

Petalostemon purpureus.—This and the following subdominant have a wide distribution throughout the grassland formation. Their presence in the plains association is indicative of at least fairly good soil-moisture conditions. They reach their best development in the prairies, where they form typical societies.

More than a dozen plants were examined. They have tap-roots varying from 3 or 4 mm. to 1 cm. in diameter. The general root system of all was very similar. At a depth of 1 to 4 inches they invariably throw off 3 to 7 large laterals in a rather horizontal direction. These run off in the shallow soil almost parallel with the surface and often not more than an inch below it, to a distance of 8 to 18 inches before turning rather abruptly downward. Usually 3 or 4 of these laterals are more pronounced than the others, some of them being as large as 6 mm. in diameter. Like the tap-root, they taper very rapidly and throughout their horizontal course give off both large and small sublaterals. These are frequently minutely branched and compete with the grasses for the water in the surface soil. Upon turning downward, these laterals, now usually not more than 1 to 2 mm. in diameter, pursue a course in general vertically downward, though more or less curved backward and forward. The tap-root descends vertically or runs off 6 to 12 inches from this direction like the laterals, and tapers so rapidly that at a depth of 1 foot it is seldom more than 1 or 2 mm. in diameter. Below this level, all the roots are more or less threadlike, branching profusely, especially with small rebranched feeders varying in length from a few millimeters to several inches. The depth of the lateral branches usually does not exceed 4 or 5 feet, although some were traced to a depth of more than 6 feet. The maximum depth of a tap-root 6 mm. in diameter was 5.5 feet, while another 9 mm. in diameter reached a depth of 6.5 feet. Unlike the white prairie-clover, this plant is well adapted to absorb the moisture in the surface soil, but like the former the roots occur quite abundantly to a depth of 5 or 6 feet, through a cross-section of 3 or

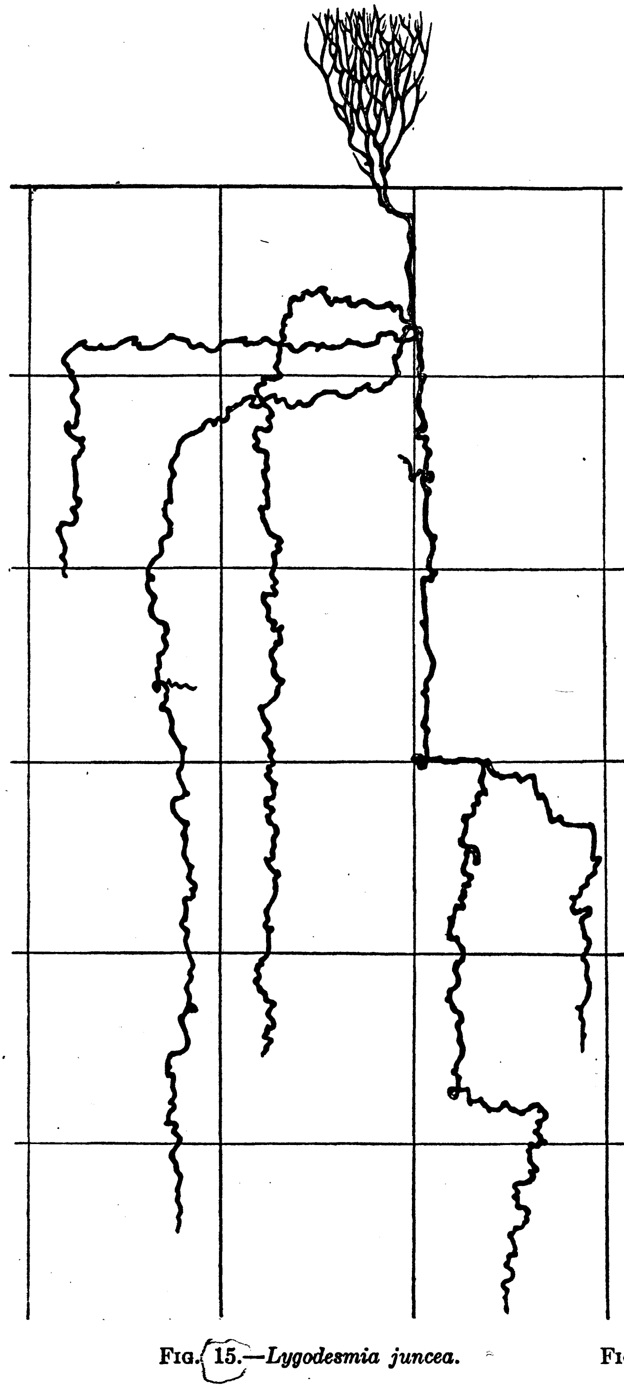


FIG. 15.—*Lygodesmia juncea.*

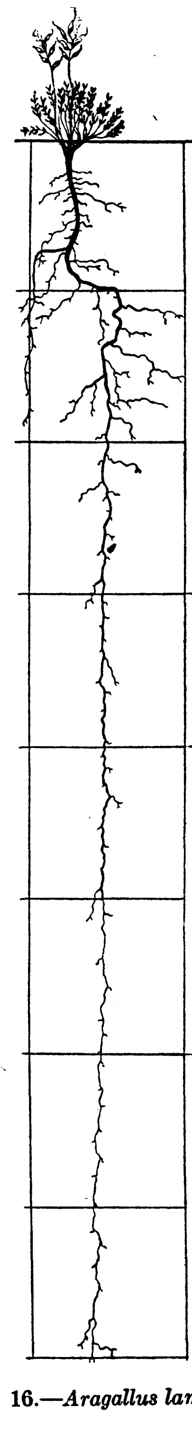


FIG. 16.—*Aragallus lambertii.*

4 feet square under the plant. They are orange-brown in color, the deep roots especially being easily followed and distinguished from their competitors by this character (fig. 17).

Petalostemon candidus.—A group of more than 8 stems, all in blossom, arose from a woody tap-root 17 mm. in diameter. At a depth of 3 inches this tap split into three strong parts, 5, 6, and 8 mm. in diameter, respectively. A larger branch ran obliquely for a distance of 3 inches and divided into two equal parts, each 3 mm. in diameter. One of these descended rather vertically, but with long, loose loops, 2 to 4 inches in width, turning back and forth as was characteristic of other roots examined. The second fork ran off obliquely about 4 inches further before turning downward. At a depth of 12 to 18 inches both branches divided and rebranched again and again, so that at the 18-inch level none of the roots were more than 1.5 mm. in diameter. Below the second foot the roots ran for long distances, following much curved and tortuous courses but with little change in diameter. The branches that were given off at frequent intervals were very long and not much branched. Finally, in the soil from the third to the fifth foot the branches became more numerous and almost microscopic, the root-tips being well supplied with laterals only a few millimeters in length.

The other two main branches were very similar to those described, and spread in such a manner that a cross-section of the absorbing area under the plant would not include more than 4 square feet. Several of the hairlike ultimate rootlets reached a depth of over 5 feet; the deepest one examined, that of the vertically descending tap, reached a maximum depth of over 5.5 feet. After examining about a dozen species of each color, it was found that the purple prairie-clover had many more superficial branches, which lie nearer the surface. The roots are yellower in color, the older ones being almost black. The branches are fewer, seldom more than 3, and run downward at a much sharper angle. The types described are very characteristic. Thus it may be seen that the white prairie-clover, *Petalostemon candidus*, in comparison with the purple prairie-clover, *Petalostemon purpureus*, is not supplied with absorbing roots in the surface 18 inches of soil, but gets the bulk of its water and nutrients below this depth. The chief difficulty encountered in excavating these plants was that of following the minute, dark-colored termini in the third to the sixth foot of soil (plate 19, B).

Eriogonum jamesii.—This species is widely distributed over the plains, where it forms summer societies. The thick woody root, 3 cm. in diameter, gave rise to a large number of prostrate stems which formed a mat about 8 inches square. Within the first 6 inches of soil, 10 or 12 laterals, the largest of which was 5 mm. in diameter, ran off horizontally for a distance varying from a few inches to 2 or 3 feet before turning downward. The tap tapered gradually, so that at a depth of about 3 feet it was still 5 mm. in diameter. To this depth it also gave off 2 other strong laterals and numerous smaller ones, as in the surface 6 inches of soil. The former pursued a sinuous course, such as is characteristic of *Eriogonum* roots, to a depth of several feet. At a depth of about 3 feet, 2 other laterals arose which were only slightly smaller than the tap. With the tap and rarely more than 12 to 18 inches from it, these pursued an irregularly downward course, often turning backward and forward horizontally or almost so, through a distance of 6 to 8 inches or more. In the main, however, these roots as well as the tap had a vertically descending direction. They were very poorly branched, rarely giving off small unbranched wirelike laterals. The roots were traced to a depth of 7 feet 3 inches, where they were still 2 or 3 mm. in diameter, respectively, and they undoubtedly

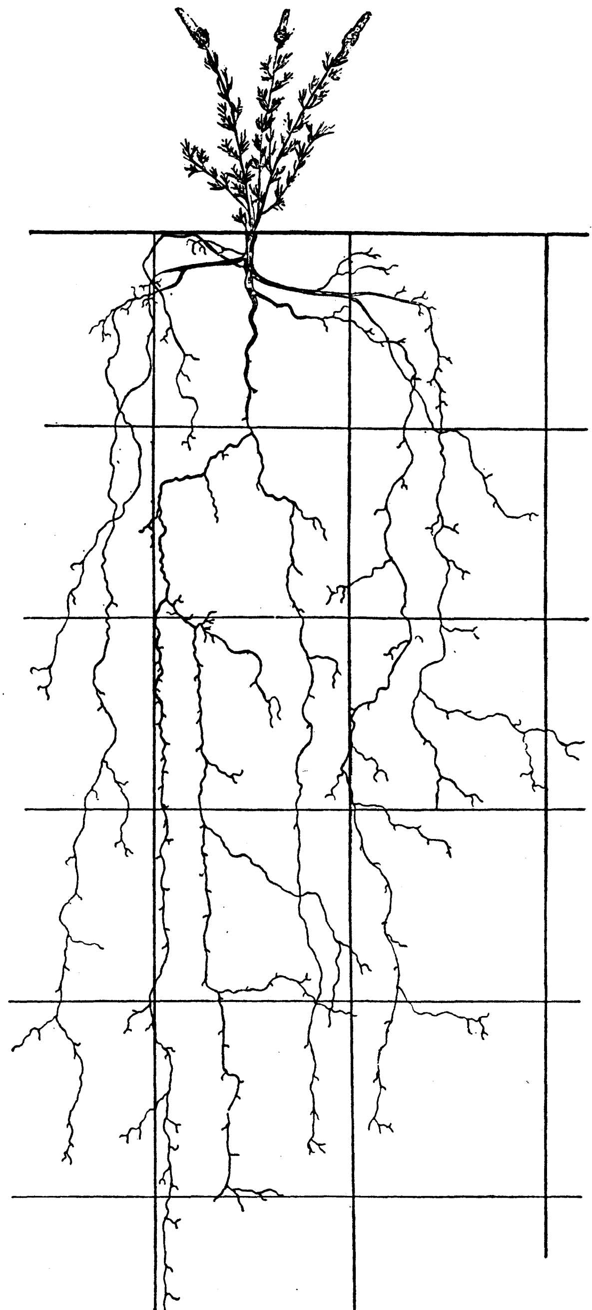


FIG. 17.—*Petalostemon purpureus.*

penetrated several feet further. In color the root is reddish brown and covered with a scaly, shreddy cortex, the older parts being quite woody (plate 19, c).

Ratibida columnaris.—This species is widely distributed throughout the grassland formation, where it forms summer societies dominating large areas. It has a strong tap-root, 8 to 10 mm. in diameter. For the first 5 inches it tapers very rapidly until at the end of that distance it is not more than 3 mm. in diameter. From that point it passes vertically downward with a zigzag, irregular course, very crooked and crinkled, tapering slightly (at 12 inches being 1.5 mm. in diameter) to a maximum depth of 2 feet. The first 4 or 5 inches is marked by an extraordinary number of more or less horizontal branches which vary in diameter from 0.2 to 0.5 mm.; these extend out through the surface soil to a distance of 6 to 12 inches and are themselves profusely branched with small hairlike rootlets from 0.5 to 2 cm. long. The number of these primary horizontal branches is very large; one count showed approximately 13, while another showed about 40. Below 4 or 5 inches the root is seldom branched, what branches there are being hairlike and from 1 to 3 cm. long. Near the end, however, the tap usually branches into two or three small, short ramifying parts. The root is dark brown in color, rather tough and unyielding. Four plants were examined (fig. 18).

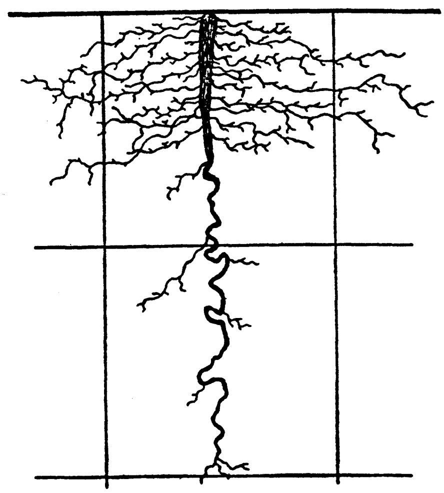


FIG. 18.—*Ratibida columnaris.*

Senecio aureus oblanceolatus.—*Senecio* is a very common and often abundant plains species, frequently forming vernal societies in the grassland. The specimens examined were small plants 6 to 10 inches high. The multiple roots are so finely divided as to be almost fibrous. The number originating from the crown varies from 15 or less to 30 or more. Some of these roots take a downward course from the crown, but many of them pass out at a slight angle from the surface to a distance of 4 to 12 inches. The point from which they start varies from a few millimeters to 2 inches below the surface of the ground, and the point at which they turn downward varies from 2 to 8 inches. These roots then penetrate to a maximum depth of over 3 feet. The diameter of these roots at the starting point varies from 0.2 to 1 mm. Throughout the surface soil they are branched and rebranched to the third and fourth orders, and each group of branches varies from 1 mm. to 3 inches in length. Below 6 inches these main roots, after starting downward, taper until they are not more than 0.2 mm. in diameter. They are more or less branched, the branches being almost hairlike in diameter and 3 to 10 mm. long. In color, the roots vary from a very light brown to a pure white. They are extremely brittle and easily broken. Five plants were examined (fig. 19).

Asclepias verticillata pumila.—This dwarf milkweed is generally distributed throughout the hard lands of the plains. It forms extensive midsummer clans. The stems vary from 3 to 5 inches in height and are connected by an extensive underground system which varies in diameter from 1 to 2 mm. These connecting stems extend from 2 to 5 inches in depth and range in distance between the plants from 1 to 15 inches or more. At the points from which the aboveground stems take their origin, one or two roots were found which penetrated the soil, usually vertically but occasionally obliquely downward, following a tortuous course. These vertical roots at the outset may range from 0.5 to 2 mm. in diameter and gradually taper downward to their extremity, which is more or less branched and hairlike. The maximum penetration found was 46

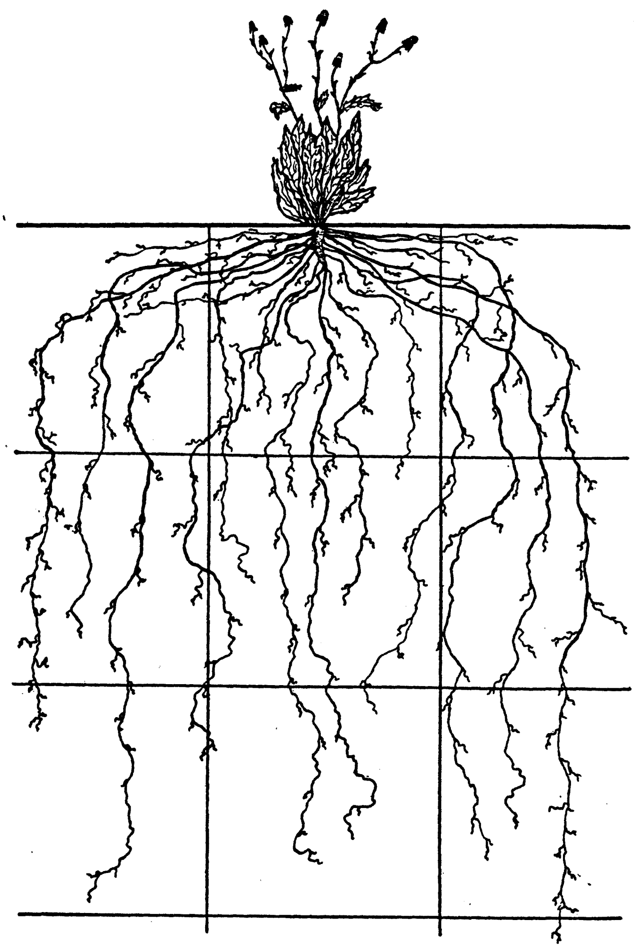


FIG. 19.—*Senecio aureus oblanceolatus.*

inches. All parts of the root system, beginning about 2 inches below the soil and extending to a depth of about 10 inches, are thickly supplied with small laterals, usually about 0.3 mm. in diameter and from 0.5 to 3 inches in length. These small laterals often come off in groups of 2 or 3. They are themselves branched, ending in very minute capillary termini, thus affording a very excellent system for surface absorption. The roots are white in color, herbaceous, and for roots of this character fairly tough. When cut, small amounts of latex exude. Six plants were examined (fig. 20).

Opuntia camanchica.—This *Opuntia* enjoys a very wide distribution in the plains grassland. Its water requirement seems to be somewhat less than that of *Bouteloua*. It is favored in its competition with the grasses by grazing, and its development in great abundance is frequently indicative of overgrazing.

A single, carefully selected plant of average size was examined. As is characteristic of the cacti in general, the root system consists of two distinct parts—a few vertically descending anchorage and deep absorptive roots, and

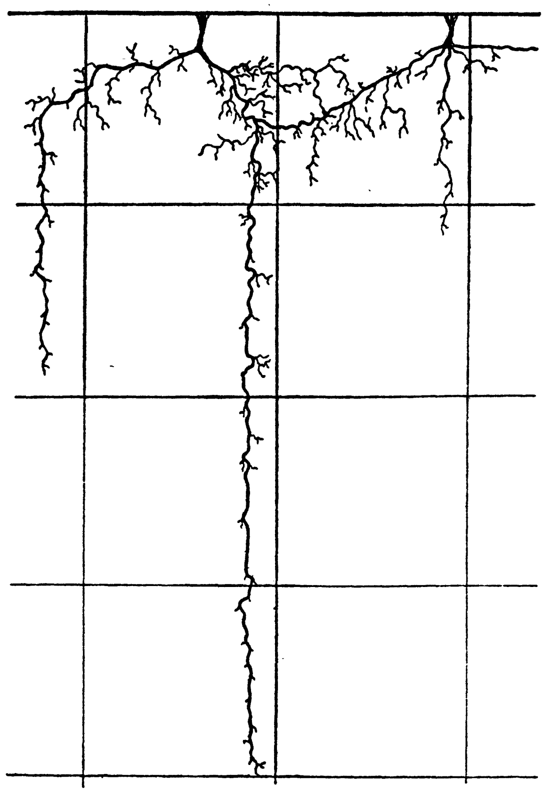


FIG. 20.—Underground parts of *Asclepias verticillata pumila*.

a much more extensive and shallow surface absorbing system. An examination of figure 22 shows 23 roots which run off in the surface soil, usually at a depth of about an inch and seldom deeper than 3 inches, to distances varying from 6 inches to 6 feet. The two largest roots were 5 mm. in diameter and tapered very slowly in spite of the repeated branching. They were branched repeatedly from their origin at the base of the plant to their extremity with both large and small branches, which ramified in all directions and thus furnished an enormous absorbing surface. The ultimate root endings, whether of the shorter or larger branches, consisted of much-branched and very delicate brushlike termini, to which the soil clung with great tenacity. The smaller branches, except for their lesser extent, are similar to those already described.

The deep anchorage and absorbing system of this plant consisted of 4 main roots, which at the outset were 2.5 to 3 mm. in diameter. These extended almost vertically downward, following a more or less irregular course through the hard soil, branching as shown in figure 21 and reaching a maximum depth of 35 inches. While the shallower roots were brownish in color and very tough, these deeper roots were glistening white and much more fragile (cf. Preston, 1900).

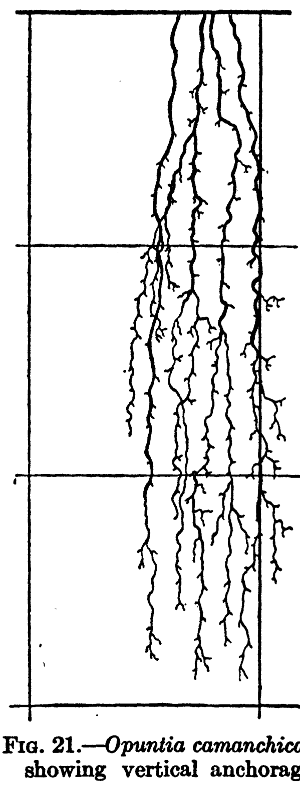


FIG. 21.—*Opuntia camanchica*, showing vertical anchorage roots.

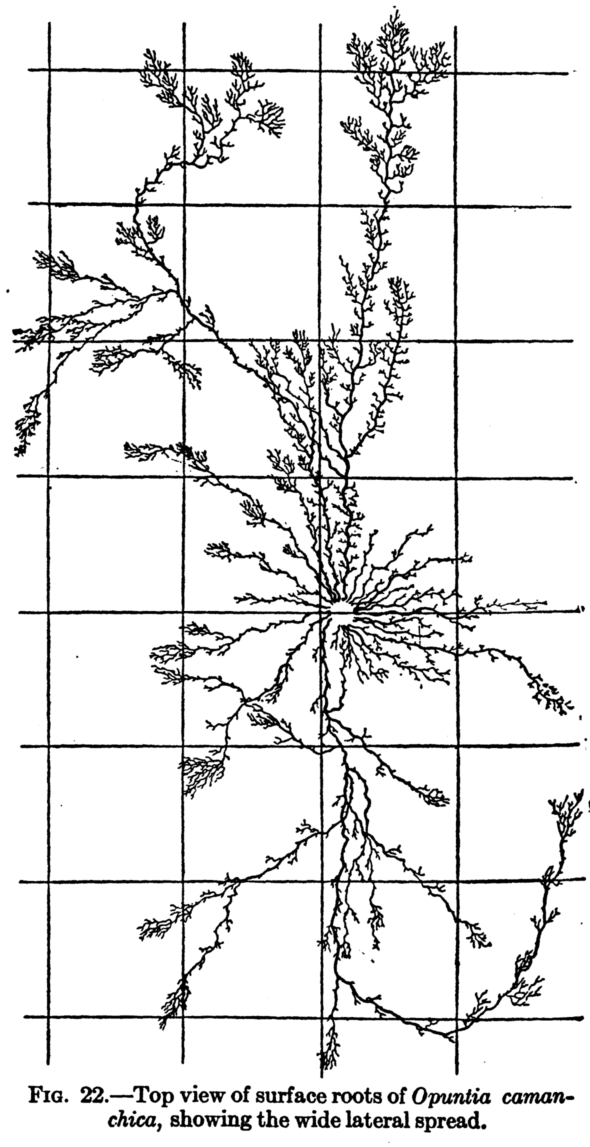


FIG. 22.—Top view of surface roots of *Opuntia camanchica*, showing the wide lateral spread.

Opuntia fragilis.—This cactus has a distinctively shallow root system. On all sides roots extended out from the base of the plant, ranging from 1 to 2 mm. in diameter, some having a lateral spread of 16 inches. There were about 20 on the plant examined. Most of these took a course parallel with the surface of the soil and lay within 3 inches of the surface, but a few took a slightly more downward course, penetrating to a depth of not more than 8 inches. The first 3 or 4 inches of the root were sparingly branched, the few branches being mostly mere tufts of rootlets not more than 3 or 4 mm. in length. Throughout the rest of their course these divergent roots were abundantly supplied with a system of laterals 0.2 to 0.3 mm. in diameter and 1 to 12 cm. long. These laterals were branched and rebranched to form extensive tufts interspersed throughout the soil, the whole forming a most excellent system for surface absorption. Another plant gave a root depth of 15 inches.

PLAINS ROOT SYSTEMS AND THE PLAINS ENVIRONMENT.

An examination of the foregoing data impresses one with the great depth to which the roots of most plains plants penetrate. There are only 3 species of shallow-rooted plants that seldom extend below the first 2 feet of soil (*Kœleria cristata*, *Opuntia fragilis*, and *Ratibida columnaris*). Perhaps *Opuntia camanchica* should also be placed here, though its vertically descending roots reach depths of 3 feet. This group constitutes only 11 per cent of the 28 plains species examined, while in the prairies 6 grasses or 18 per cent of the 33 species excavated had shallow roots. In the second group, made up of plants with roots extending well below the second foot of soil but seldom deeper than 5 feet, are found 32 per cent of the plains species as against 27 per cent among prairie plants. The third group of deep-rooted plants, which extend to depths greater than 5 feet, contains 57 per cent of the plains plants and 55 per cent of prairie species.

On the other hand, certain prairie plants, such as species of *Rosa*, *Lygodesmia*, *Liatris*, and *Kuhnia*, reached depths of 17 to 22 feet. This was quite beyond the greatest depth (about 13 feet) attained by any plains plant. It may be that the soil is never moist to greater depths on the plains. Moreover, most of the plains species are characterized, in addition to their great depth, by a fine system of surface absorbing and wide-spreading laterals. However, we must again resort to an examination of the habitat factors in order to properly interpret the root development.

The region in which these plants grow has an annual precipitation of only about 15 inches, an amount quite typical for much of the Great Plains area. Fortunately, the major portion falls during the growing season. There is as a rule considerable rainfall during the months from May to September, but often the rainy season covers only June, July, and August. The mean monthly and annual precipitation in inches for Colorado Springs, together with its seasonal distribution, is shown in table 14.

Such a seasonal distribution of moisture is very favorable for the growth of grasses. Because of the great compactness of the soil, brought about in part by the binding influence of the short-grass cover, the run-off is very high. Shantz has shown that at Akron, Colorado, the run-off varies from 15 to 43 per cent, the greater run-off naturally occurring during heavier rains. This combination of a meager amount of precipitation with a relatively low degree of penetration would lead one to think the soil must be quite dry. Weekly soil-moisture determinations at various depths for the summer of 1918 are shown in table 15, which gives the available water-content during the summer of 1918. The minus sign indicates that no moisture was available for plant growth.

TABLE 14.

Time.	Amount.	Time.	Amount.
Jan.	0.20	Aug.	2.20
Feb.	0.32	Sept.	1.17
Mar.	0.75	Oct.	0.67
Apr.	1.55	Nov.	0.35
May.	2.43	Dec.	0.25
June.	1.88		
July.	2.81	Annual.	14.58

An examination of these data shows that, aside from variations in the surface foot, the soil to a depth of 7 feet was rather uniformly dry. How much more deeply the rain may penetrate during a series of wet years was not determined. Certainly, available moisture must occur at least locally to depths reached by living roots of *Psoralea*, *Argemone*, and other species which penetrate to 10 or 12 feet. Only a long series of soil-moisture determinations, coupled with a dynamic study of root growth through at least one wet and one dry cycle, can answer this question of moisture penetration and its correlation with root development.

TABLE 15.

Date.	Depth 0 to 6 inches. Wilting coefficient 7.9.	Depth 6 to 12 inches. Wilting coefficient 8.4.	Depth 1 to 2 feet. Wilting coefficient 4.9.	Depth 2 to 3 feet. Wilting coefficient 5.1.	Depth 3 to 4 feet. Wilting coefficient 6.5.	Depth 4 to 5 feet. Wilting coefficient 6.8.	Depth 5 to 6 feet. Wilting coefficient 8.7.	Depth 6 to 7 feet. Wilting coefficient 7.0.
June 7	0.6	−0.5	1.8	0.3	−0.8			
June 14	−1.0	−0.5	3.5	3.9	2.0	0.7	−0.4	0.3
June 26	−0.5	−1.0	3.2					
July 1	−3.5	−3.3	1.2					
July 8	−2.8	−2.4	−0.6					
July 15	5.0	0.8	1.1	2.5	1.1	1.6	1.9	4.4
July 29	−2.0	0.0	1.8					
Aug. 5	−4.7	−3.2	0.4					
Aug. 12	−4.0	−4.0	−0.4	−1.0	−0.8	−0.6	0.5	1.8
Aug. 19	−3.4	−3.0						

In the short-grass community at Akron, Shantz found that for a period of several years little or no water was available for plant growth below a depth of 18 to 24 inches. Even a rainfall of 2.4 inches in a day had no effect upon the soil moisture below 18 inches. He states that "almost the entire root system of short grasses is limited to the surface 18 inches," while "deep-rooted plants are not found here for the reason that at greater depths the soil contains no water available for their use" (1911: 38). The results obtained by the writer in an area of short-grass land locally known as "adobe" do not correspond with these findings. Careful examination was made of the root systems of *Bouteloua gracilis* and *Muhlenbergia gracillima* in pure short-grass land about 25 miles southeast of Colorado Springs (plate 20, A). Here *Bouteloua gracilis* was dominant with *Opuntia polyacantha*, while *Muhlenbergia gracillima* was very abundant in matlike areas. *Schedonnar dus paniculatus*, *Senecio aureus oblanceolatus*, *Erigeron pumilus*, *Gutierrezia sarothræ*, and *Munroa squarrosa* were present, but were not at all abundant. In fact, only 15 to 25 per cent of the soil was covered with vegetation. Roots of *Bouteloua gracilis* were found to be very abundant to a depth of 40 inches, while several roots were traced to a depth of 51 inches. *Muhlenbergia gracillima* roots were very abundant to 50inches, and some reached a depth of 56 inches.

These findings are so different from those of Shantz that further work seems necessary for a thorough understanding of plains root systems. This also seems to be true for the roots of sandhill species (p. 68). Comparisons of the root habits of these plants with those of other communities are based upon the data made available by these studies, and may need revision when other regions are worked. The great variations of many root systems under different edaphic environments is clearly shown in the section on polydemics (p. 110). However, it is certain that plains plants grow in a soil of low water-content and of very hard texture. The soil in the area where these studies were made consisted of a light-colored loam intermixed with some sand. It is spaded with extreme difficulty and a hand-pick removes it so slowly that in digging the trenches a large pick was kept in constant use. Therefore, roots were unearthed only with great labor. For example, a single specimen of *Argemone platyceras* occupied the attention of two persons for 1.5 days, while it required the services of a third to do the sketching as the roots were uncovered. At depths varying from 6 to 10 feet a layer of sand occurred. This was in good tilth condition and usually moist enough to hold when pressed firmly into a lump.

The well-developed system of wide-spreading laterals, so characteristic of species of *Bouteloua*, *Gutierrezia*, *Artemisia*, and many others, is undoubtedly a response to the moisture in the surface soil resulting from summer showers. Such roots would be of small advantage to prairie plants in the Pacific Northwest. In the prairies of Nebraska they are probably not developed so extensively because of the greater available water in the deeper soils. This matter is further discussed on pages 79 and 88.

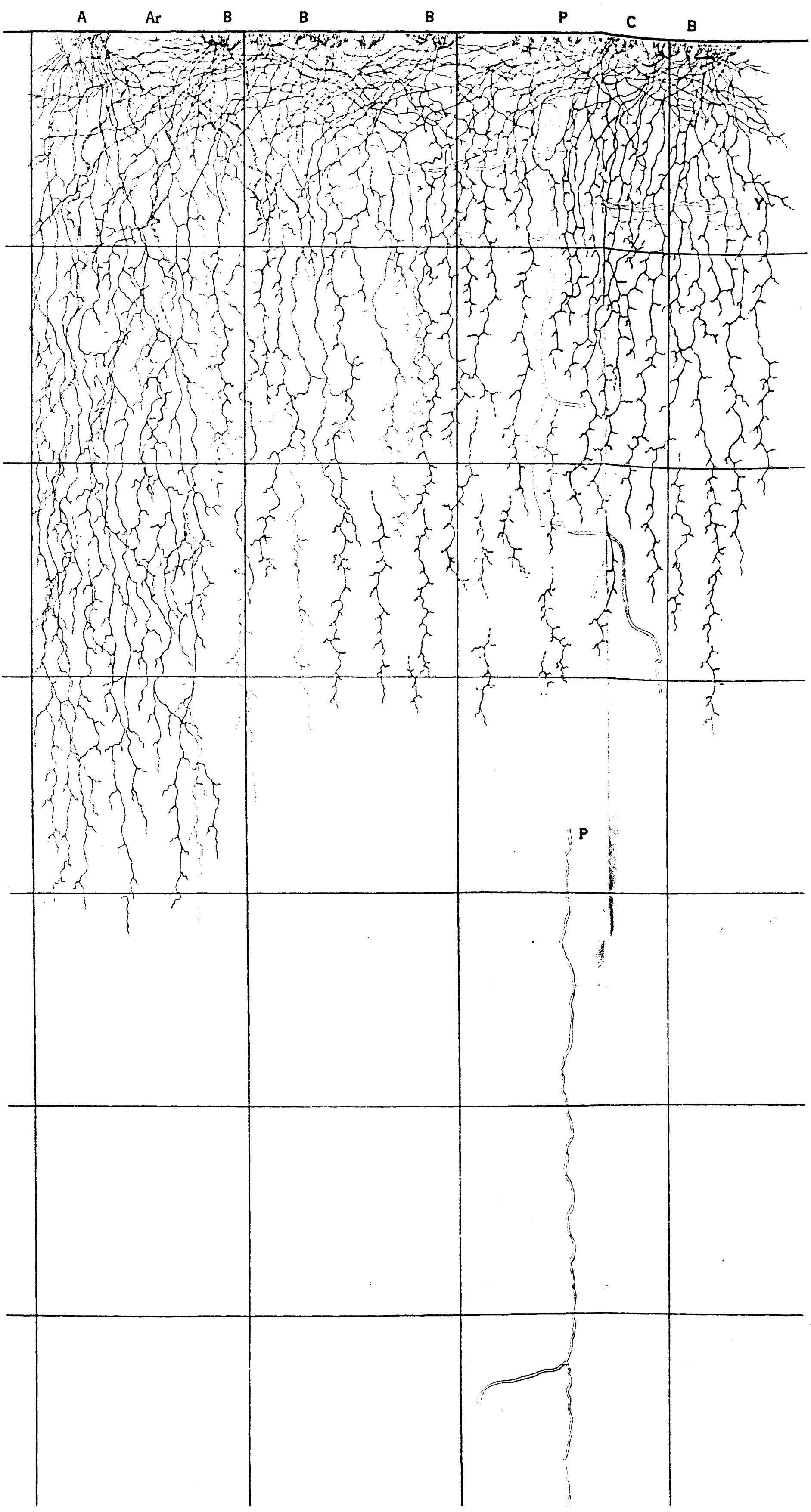
A continuous record of the soil temperature was obtained at a depth of 4 inches among these roots from June 5 until August 5. At this time the bulb of the soil thermograph was lowered to 8 inches. The most interesting fact disclosed was the extreme variation in temperature during the 24-hour period. This ranged from 60° or 70° to 90° or 95° F. or even more. During August, at a depth of 8 inches in the soil, the daily fluctuation was usually about 10° F. within the range of 70° to 85°. The daily fluctuation of air temperature among the plants was usually about 35° to 40° F., the air reaching a maximum of 90° or 95° F. in the shade in the afternoon and falling to 50° or 60° F. in the morning. Table 16 gives the mean monthly temperatures for Colorado Springs.

TABLE 16.

Time.	Temp.	Time.	Temp.
Jan.....	28.0° F.	Aug.....	66.9° F.
Feb.....	29.8	Sept.....	59.3
Mar.....	37.0	Oct.....	48.4
Apr.....	44.8	Nov.....	37.5
May....	54.1	Dec.....	30.6
June....	63.4		
July....	67.9	Aver...	47.3

The humidity is relatively low. During clear days, excepting early in the morning, it is usually less than 50 per cent and it not infrequently drops to 10 or 15 per cent and sometimes lower. Even at night, when the air is coldest, it seldom exceeds 80 or 90 per cent, and dew rarely forms. There is usually steady wind movement on the plains. Records from a standard anemometer placed just above the plants at a height of 0.5 meter show an average daily wind velocity of 120 miles during the growing season of 1918. Likewise daily water-losses from non-absorbing atmometers placed at a height of 10 cm. above the soil surface are relatively high. From the data given in table 17, which shows the average daily evaporation on the plains, it may be seen that the plains habitat is xerophytic as regards both air and soil environment.

In order to visualize clearly the actual root position and the conditions of competition, the accompanying bisect (plate A) was made. Similar bisects are also given for other plant communities. The method used is the same in all cases. A representative meter-quadrat was selected which showed both dominant and subdominant species. After charting and photographing, a trench was dug in front of the quadrat, care being taken to have the wall corresponding with a side



Quadrat-bisect showing the root distribution of certain dominant and subdominant plains species: A, *Aristida purpurea;* B, *Bouteloua gracilis;* Ar, *Artemisia frigida;* P, *Psoralea tenuiflora;* C, *Chrysopsis villosa;* Y, *Yucca glauca.*

of the quadrat cut smooth and perpendicular. Then by the use of a hand-pick the soil was carefully removed from the roots in the trench wall along the edge of the quadrat to a horizontal distance of 4 inches. While this was under way the roots were carefully measured and

TABLE 17.

Time.	Evaporation.	Time.	Evaporation.
	c.c.		c.c.
June 7–10	52.2	July 15–22	32.3
June 10–17	69.4	July 22–29	44.3
June 17–24	35.3	July 29 to Aug. 5	64.5
June 24 to July 1	66.1	Aug. 5–12	49.5
July 1–8	45.2	Aug. 12–19	41.0
July 8–15	26.5		

drawn in position to scale. This gives a picture of the exact root distribution in a block of soil a meter long, 4 inches wide, and 7 feet deep, in this particular case. Dotted lines indicate the exit or entry of roots from or into this soil area respectively. This plains bisect shows the complete occupancy of the soil by roots and the intense competition for moisture and soil solutes that must result.

V. THE SANDHILLS SUBCLIMAX.

In order to compare root development more extensively under different environmental conditions, work was continued in a sandhill area of Colorado adjoining the plains community and located about 40 miles southeast of Colorado Springs. Since general climatic conditions are almost identical with those described for the plains, any differences in root development may be attributed to edaphic causes. An excellent description of the sandhill communities, considered in the light of their successional relation, has been given by Pool (1914). Shantz (1911) also gives a thorough treatment of Colorado sandhill vegetation from the standpoint of its indicator significance in regard to crop production. The general character of the sandhills and their characteristic vegetation is shown in plates 20, B, and 21, A.

Redfieldia flexuosa.—This grass is at home in the sandhills. Indeed, it is the most abundant and controlling species of blowout pioneers. While it may be mixed with other pioneers, it is often the only plant present in such situations. The usually sparse and rather small clumps are connected by means of very long, coarse, tough rhizomes, which sometimes reach a diameter of 4 to 5 mm. but are usually smaller; they are frequently many feet in length and may be traced for a distance of 20 to 40 feet on the surface where the sand has been blown away from them. Because of the shifting sand, the depth at which they occur is variable. Living rhizomes with vertically descending branches were found at a depth of 38 inches and they are rather abundant between this depth and the surface, some running horizontally, others obliquely and sometimes almost vertically.

From the nodes of these tough rhizomes, which are from less than an inch to 6 inches apart, whorls of roots arise in addition to sharp-pointed buds. These consist of 2 to 10 roots, but are usually 3 to 5. The roots vary greatly in length, diameter, and direction of growth, depending upon the age and position of the rhizome. Those near the tip of the sharp-pointed, much elongated rhizome may be less than 1 inch in length, very fleshy, 2 to 4 mm. in diameter, and practically destitute of branches. Others a foot or two from the tip are 12 to 20 inches long and are covered with a fine absorbing system of short rootlets, except for the 4 to 6 inches of the growing end. The older roots, which are well branched to the very tips with much divided laterals 1 to 3 inches long, reach a maximum depth of 56 inches. They are often 2 to 4 mm. in diameter. They not only run rather vertically downward, but also diverge at all angles, even to the horizontal. Long, well-branched roots were traced to distances of over 3 feet from the base of the plant at depths of 4 to 8 inches. The laterals from these frequently ascend vertically upward and end in well-branched termini only 2 to 3 inches below the surface. Thus the length, position, and abundance of this rather coarse root system, together with the rhizomes, equip *Redfieldia flexuosa* in an effective manner for life in the shifting but moist soil of the sand-dune (fig. 23).

Calamovilfa longifolia.—The sand-reed is also an efficient sand-binder. It is frequently found associated with *Redfieldia flexuosa, Psoralea lanceolata,* and other pioneers in the shifting sands of the blowout, but normally occurs with *Andropogon hallii* and others somewhat later in the succession.

It forms a veritable mat of roots and rhizomes to a depth of 34 inches. A wide trench 6 feet long and over 5 feet deep was dug on a small dune which was well captured by a dense and nearly pure growth of this sand-binder. This plant has a great abundance of tough, wiry, and very much-branched rhizomes, 2 to 4 mm. in diameter, which form an underground network connecting the apparently isolated plants. These rhizomes are thickly covered with long scales and tipped with buds about an inch in length with very sharp, hard points. This branched network of rhizomes may be formed in the soil at al

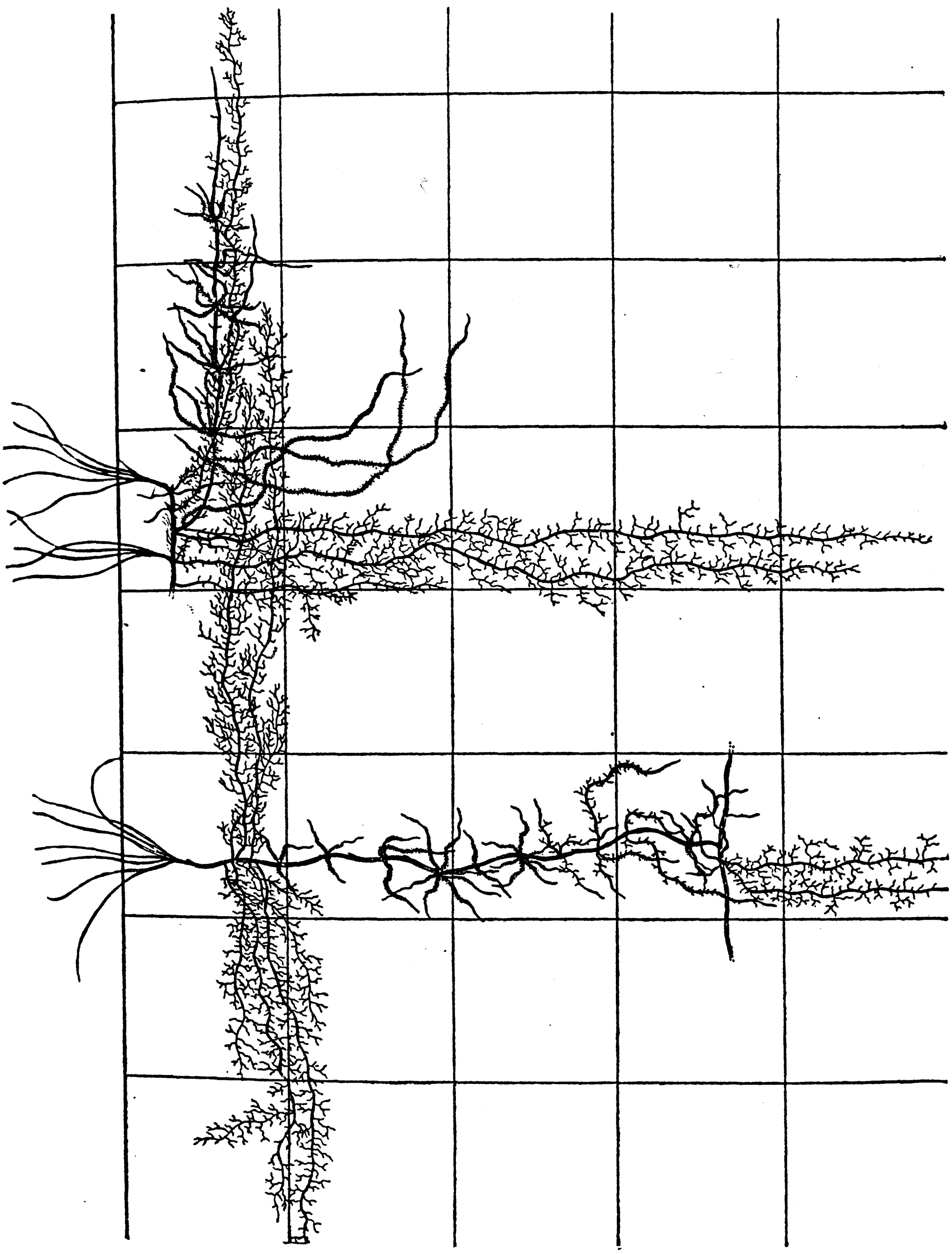


FIG. 23.—*Redfieldia flexuosa*, showing rhizomes and root distribution.

depths from the surface to 3 feet, the deeper ones undoubtedly having been buried by wind-blown sand. From these rhizomes originate multitudes of tough, wiry roots, 1 to 2 mm. or less in diameter, which penetrate the soil in all directions from vertically downward to horizontally. These roots taper gradually and many of them reach a maximum depth of 55 to 60 inches.

From a depth of an inch to their very tips they are abundantly supplied with laterals which extend out more or less at right angles to a distance of 1 or 2 inches or even more. These laterals are well provided with finer branches to the third and fourth order. Since these roots arise not only from the surface but also from the deeper rhizomes and penetrate to 3 or 4 feet in all directions, they form a confused tangle. Where the grasses are at all thick, as shown in plate 21, B, the roots completely fill the soil and bind it so thoroughly that a vertical face of a trench 6 feet long and nearly as deep held tenaciously without caving, even after it was somewhat undercut at the base.

Andropogon hallii.—This tall, coarse grass forms loose, open bunches with only a few large stems. It is a dominant along with *A. scoparius* in the bunch-grass subclimax of the sandhill region. Successionally it occurs somewhat later than the preceding sandhill grasses. It was excavated on a partially captured sand-dune (plate 22, A). It is a very coarse, glaucous grass connected by an elaborate system of rhizomes 3 to 4 mm. in diameter and lying at a depth of 2 to 6 inches. From the rhizomes many roots take their origin, some of which spread laterally, others penetrate almost vertically downward, while still others take an oblique course downward. The diameter of these varies from 1 to 2 mm. The roots running off laterally take a course almost parallel with the soil surface or in some instances curve downward and then up again to a point near the surface. These laterals lie at a depth of 2 to 16 inches and the maximum spread found was 3 feet. Of the roots taking a vertical course the maximum depth found was 27 inches; most of them, however, penetrated to a distance of about 22 inches or less. The oblique roots were of about the same length, but since they pass off at an angle the depth depends upon the degree of divergence from the vertical. All roots throughout their course were copiously branched with mostly short branches ranging from 0.5 to 3 inches in length; as many as 8 of these branches were counted on a single inch of the root. These small branches were themselves abundantly supplied with minute rootlets 1 to 5 mm. in length. Occasionally the main roots gave off a branch 4 to 8 inches long, but these were very rare and when they did occur were themselves branched in the same manner as the main roots. Altogether, this plant has an excellent soil-binding and absorbing system throughout the soil area of each bunch. Eight or nine plants were examined.

Muhlenbergia pungens.—This grass is characterized by tufted stems and glaucous, narrow, rigid leaves. The culms, which arise from rootstocks, are grouped in small tufts or cushions that lie close to the sand. It is a regular component of blowout communities and is not infrequently dominant.

This important sandhill grass was examined on the rim and grassy top of a blowout where it was growing very abundantly. Clusters of roots arise from the short rootstocks, which are 2 to 6 inches long and 1 to 3 mm. in diameter. These vary in number according to the length of the rootstock, from only 4 or 5 to 25 or more (plate 22, B); the largest are only 1 mm. in diameter. While some of the wirelike tough roots penetrate rather vertically downward to a maximum depth of 33 inches, others run off obliquely at various angles, even to almost parallel with the soil surface. The lateral spread varies from 10 to 25 inches on either side of the plant. Because of the dryness of the surface inch of sand, the glistening white roots are rather destitute of branches, but below this level all of the roots are densely covered with multitudes of very fine absorbing laterals. Indeed, a single inch of an average root was found to have approximately 75 of these hairlike absorbing laterals. While many of them are only a few millimeters long, others reach a length of 6 to 10 inches. All are profusely and minutely branched, the larger ones to the third and fourth order. Thus this wonderfully efficient root system is able to penetrate all portions of the sandy substratum and to extract the available water, while at the same time it forms a very effective means of preventing sand from blowing.

Sporobolus cryptandrus.—In aerial habit this grass is not unlike *Calamovilfa*. It ranks as a dominant among sandhill grasses. Three clumps of it were examined in two separate trenches on a half-captured blowout. As a whole, it is characterized by an extremely fine fibrous root system, the main divisions of which arise from a short stocky rhizome 2 to 4 inches in length. On a single rhizome 1.5 inches long, 40 of these main roots were counted. As they leave the rhizome they pass off in all directions, some vertically, some obliquely, and a great many of them almost parallel with the surface, but gradually growing deeper as they pursue their course, so that at a maximum distance of 18 to 20 inches many were found at 6 to 8 inches below the surface. The maximum vertical depth of penetration found was 22 inches. From the point where the major divisions of the roots leave the rhizomes, they are covered with a dense growth of root-hairs which hold the sand firmly and give the roots the appearance of being much greater in diameter than they really are. They are actually threadlike, usually less than 0.5 mm. in diameter and very tough. These roots are slightly, if at all, branched for a distance of 2 or 3 inches from the rhizome, but from that point on to the very extremity they are well supplied with branches from an inch or less to 8 or 10 inches long. These branches pass out in all directions from the main root and are themselves exceedingly finely branched and rebranched to the third and fourth order, so that the soil for a depth of from 10 to 13 inches is well filled with this fine, delicate absorbing system.

Eriogonum microthecum.—As shown in plate 21, A, this *Eriogonum* frequently controls local areas on sandy slopes and occurs rather widely throughout the sandy plains area. The plant has a multicipital stem, which at a depth of 4 to 8 inches merges into a strong tap-root 0.5 to 1 inch in diameter. At a depth of 2 or 3 inches the tap-root begins to branch, and for a depth of 2.5 to 3 feet sends off an extraordinary absorbing system (fig. 24). Some of these branches arise singly, but it is common to find 2 to 4 springing from approximately the same point. In diameter they vary from 1 to 5 mm. The general tendency of the branches is to pursue an almost horizontal course from a distance of a few inches to 2 feet and then turn almost vertically downward, penetrating the sand to a depth of 18 inches to 3 feet. A few of these branches, however, instead of taking this course, pursued an almost horizontal course to their very tips, which were sometimes 3 feet from the tap. These laterals for the first few inches of their course as they left the tap-root were very sparsely branched, the distance depending upon the size of the root. Beyond that point the branches gradually became more numerous and as one approached the extremities the number was so great as almost to form a conspicuous network in the light sand. As the main laterals and their larger branches approached their lower extremities, the little rootlets were so numerous as to form fairly brushy tips. Below 3 feet the branches of the tap were much fewer in number and much larger in size. As a rule they seem to occur in

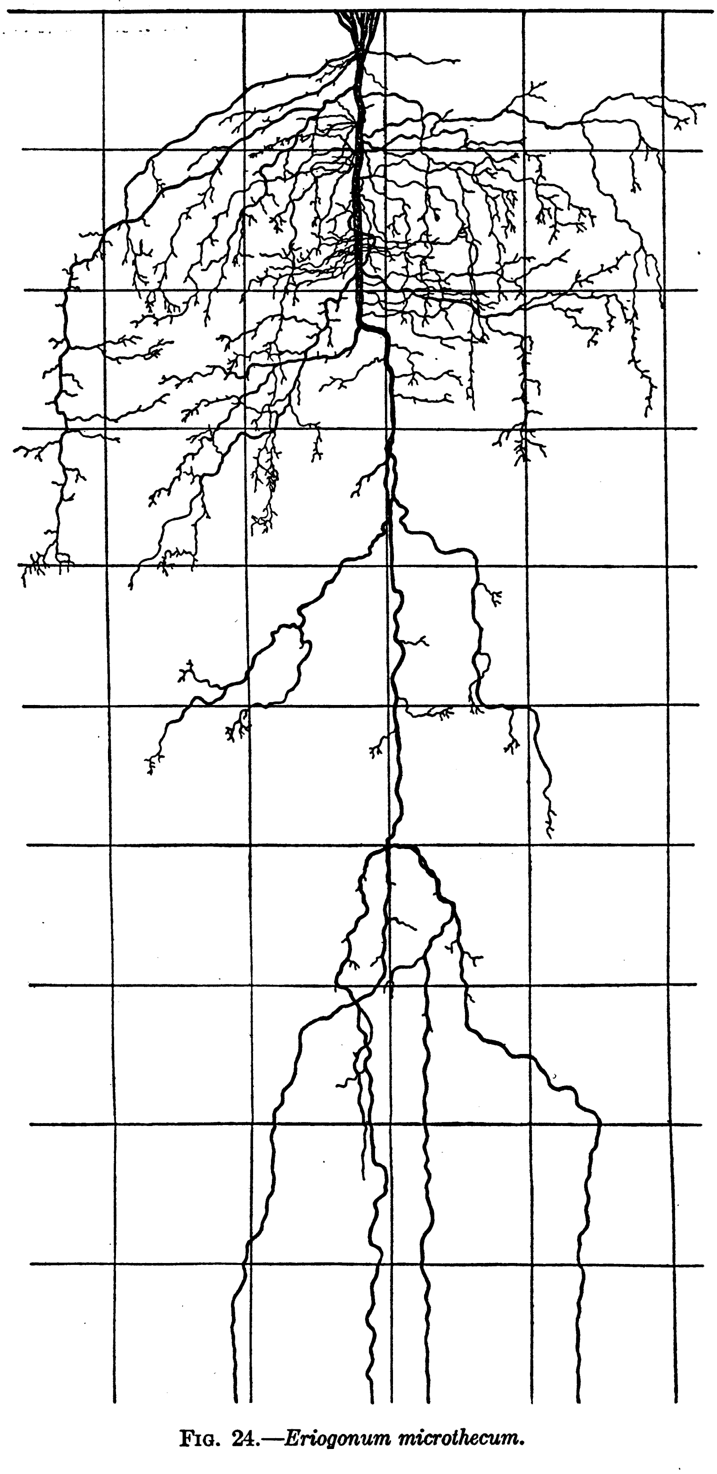


FIG. 24.—*Eriogonum microthecum.*

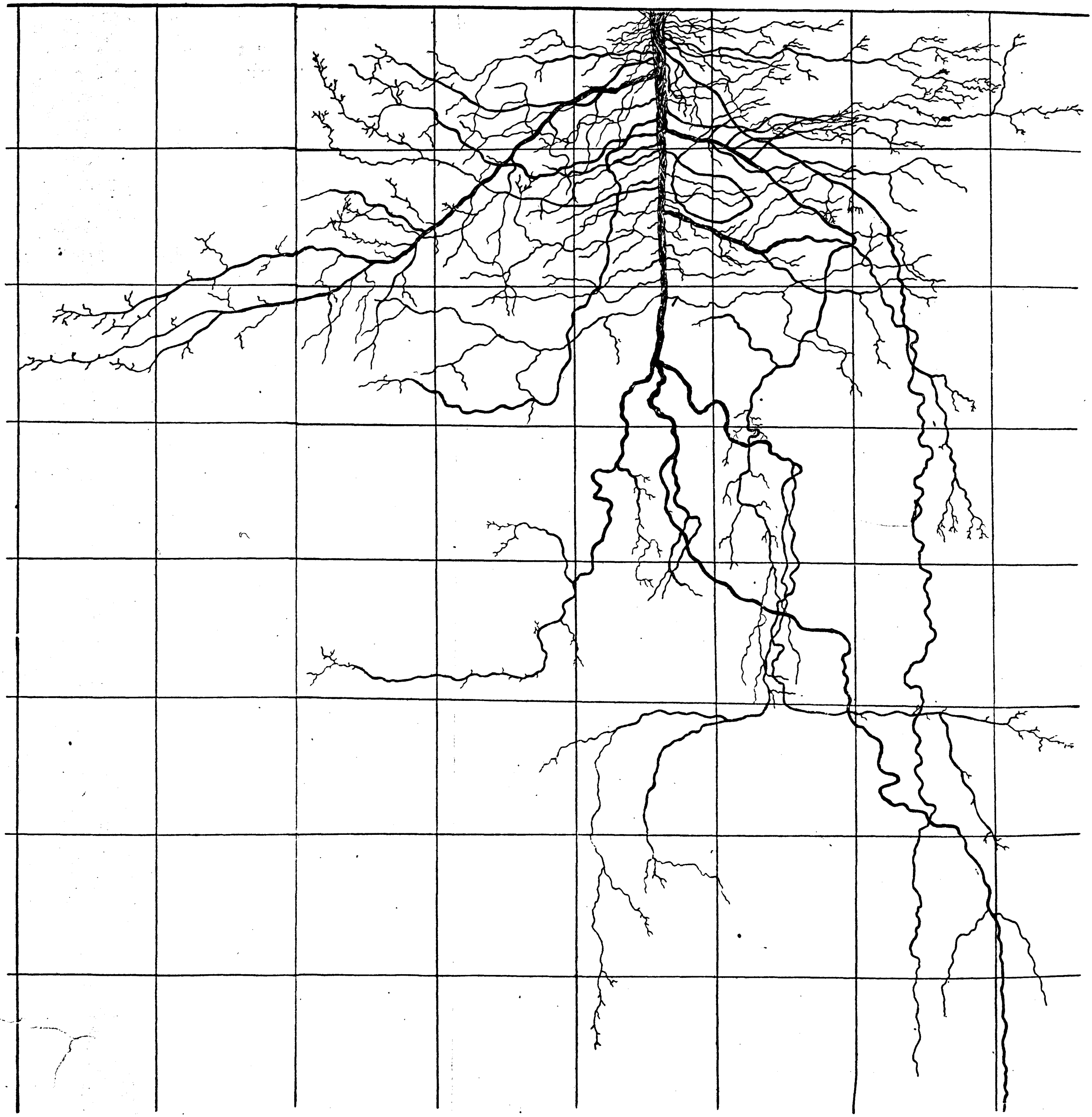


Fig. 25.—Root system of a ten-year-old *Artemisia filifolia.*

groups, ranging from 2 to 5 mm. in diameter. The larger branches, after diverging somewhat from the main tap, took a downward course similar to that of the main root. At 6 feet the tap divided up into a group of 3 or 4 roots of almost the same size, which after diverging took the usual downward course and at a depth of 10 feet were 2 to 3 mm. in diameter. At this depth repeated caving of the sand made further digging so dangerous that the work was abandoned.

Artemisia filifolia.—In the sandhill mixed association, aside from the two grass dominants, *Calamovilfa* and *Andropogon hallii*, the sand-sage is the most conspicuous plant. This is due both to its shrubby habit and its great abundance. It is indicative of a light type of soil with considerable moisture penetration. It drops out in the more compact hard lands of the plains.

Three plants were examined. They were growing on a stabilized area near the sand-dune. The largest had a tap-root 1.5 inches in diameter, from which arose a large number of stems to a height of 2 feet, forming a bush about 18 inches in diameter. The strong, vertically descending, woody tap-root tapered gradually and uniformly to a depth of 32 inches, at which point it broke up into 3 laterals, the largest 0.5 inch in diameter and the other two but slightly smaller. Some of these were traced to a depth of 9 feet, where they were still 4 mm. in diameter (fig. 25). In the surface 30 inches of soil the tap gave off 6 large laterals, from 6 to 13 mm. in diameter, and a very large number of smaller ones, some of them but 0.5 mm. thick. These branches formed a rather distinct surface absorbing system, and showed a strong tendency to run out in a direction parallel with the surface. In fact, some of them terminated in soil which was shallower than the depth at which they originated. These with their branches and the numerous rootlets from the somewhat oblique larger roots formed a dense network confined to the first 30 inches of soil. This was characteristic of all the plants examined and was not unlike the root habit of *Eriogonum*. Some of these larger branches ran off laterally to distances of 2 to 5 feet before turning downward. Although they branched somewhat freely at intervals in the fourth to seventh foot of soil, they often pursued their tortuous courses for long distances, sending off hardly any laterals.

The relative abundance of the shallower roots as contrasted with the deeper ones, together with their lateral spread and the extent of their branching, is well shown in figure 25. Unfortunately, because of the loose texture of the soil, it was unsafe to trace them to greater depths. The roots are dark brown in color, the older portions having a rough, fissured bark. The younger ones, and especially those in the deeper soil, were exceedingly brittle. The plant here described was 10 years old. The lower branches and divisions of the tap were very sparsely branched, the few rootlets being of the same character as those nearer the surface. From the description and figure it will be seen that while this species has a strong tap-root, it also has a highly developed absorbing and binding system characteristic of the general group of sandhill plants.

Tradescantia virginiana.—This spiderwort is rather common in the sandhills. The plants were examined on a partially captured blowout. They had a rather fleshy root system. As many as 18 of these fleshy roots, varying from 1 to 2 mm. in diameter, were found arising from the base of a single stem (fig. 26); some passed down almost vertically to a maximum depth of 19 inches; others started down more or less vertically, then with a gradual curve outward ended from 6 to 8 inches from the vertical; others passed more or less obliquely downward from the stem. The greater part of these fleshy roots, however, formed a surface absorbing system which spread out in all directions from the base of the stem, running more or less parallel with the soil surface at a depth of 2 to 5 inches and to a maximum distance of 30 inches.

All the roots, whether superficial or deeper, were practically free from branches for a distance of 4 to 6 inches. From that point on they began to branch, the branches increasing in number toward the tips. These branches varied from a few millimeters to 3 or 4 cm. in length, and at intervals on these

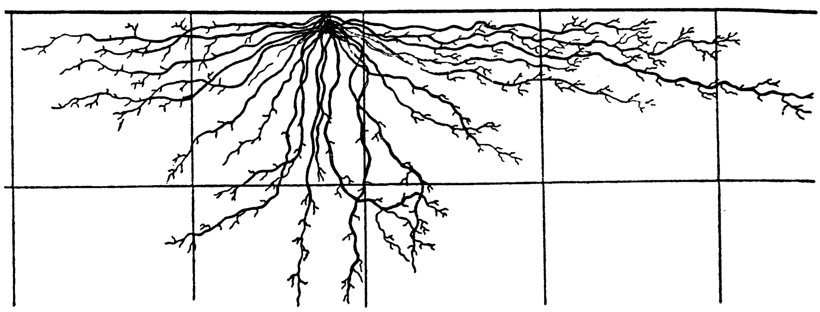


FIG. 26.—*Tradescantia virginiana.*

were found short hairlike branches 2 to 5 mm. in length. While the root system of this plant was fairly well branched, the branches were in the main not nearly so numerous as those of most of the other sandhill perennials. The roots were light brown to white in color, fleshy and brittle. Six plants were examined.

Heliotropium convolvulaceum.—This annual frequently forms small families or colonies on the rims of blowouts and on half-captured sandy slopes. The plants were examined on August 1. They were quite mature and in full bloom. None was over 7 inches high. They are characterized by a small tap-root, seldom over 2 or 3 mm. in diameter, which maintains its dominance in spite of the abundant laterals and reaches depths of 18 to 25 inches. Throughout its rather vertically downward course, after passing through the surface inch of dry sand, it continually gives off laterals, both short and long, to the very tip. While many of these exceedingly fine branches do not exceed a few centimeters in length, others with a diameter of 0.3 to 0.5 mm. extend for a distance of 6 to 20 inches, often in a rather horizontal direction with the soil surface. As a whole they are poorly supplied with smaller rootlets. Sometimes these run out obliquely for a distance and then turn downward. A single root may have 4 to 6 of these long laterals. They branch at intervals into long threadlike branches, which are themselves only moderately well supplied with absorbing rootlets. However, the lack of abundant branches, such as occur in many grasses and dicotyledons, is offset by the delicacy of the root system, all parts of which are efficient absorbers. These herbaceous roots are rather tough; they are light tan in color.

Petalostemon villosus.—This low, finely branched plant with its dense cover of silvery leaflets stands out as a prominent object in the sandhill flora, where it regularly plays the role of a pioneer in the blowouts. Sometimes it occupies such situations to the complete exclusion of other species. Of the half-dozen mature plants examined, all had strong tap-roots, about 1 cm. in diameter, a much-branched root system, and a root penetration of 4 or 5 feet. Figure 27 is illustrative of these. An examination of this figure reveals the numerous surface laterals with their large nodules 1 mm. wide and 2 to 3 mm. long, their wide lateral spread, sometimes to a distance of 2.5 feet, as well as the abundant system of well-branched absorbing laterals. Laterals of various sizes, and often with a spread of more than a foot, come off at all depths to near the tip. Characteristically these run off somewhat horizontally and then turn down rather abruptly. All of the termini are furnished with a profuse network of finely branched rootlets. In color the roots vary from light yellow and deep orange to brick-red. In diameter the tap was variable, lower portions often being of larger size than other parts above.

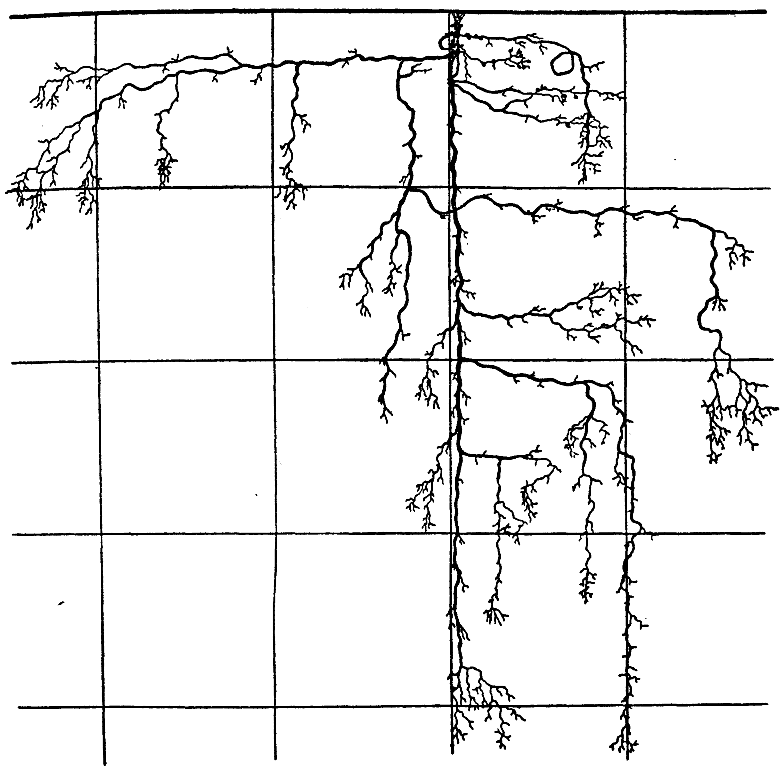


FIG. 27.—Root system of *Petalostemon villosus*.

Gilia longiflora.—Three plants of this annual, growing on a well-covered sandhill, were examined, all were mature and in full bloom; their underground system started with a strong tap-root, varying in size from 7 to 12 mm. in diameter. The tap penetrates almost vertically downward, tapering very rapidly until, at a point 6 inches below the surface, it is usually not more than 3 mm. in diameter. From this depth it tapers more gradually, pursuing a kinky and tortuous course downward through the sandy soil to a maximum depth of 40 to 50 inches (fig. 28). The most marked characteristic of these tap-roots is the remarkable number of both large and small laterals thrown off within the first 2 to 10 inches of soil. From 8 to 14 of these are often found, varying in diameter from 1 to 3 mm., not including numerous smaller ones. These larger laterals usually pursue a course almost parallel with the surface for a distance of 5 to 22 inches, and then almost invariably turn abruptly downward, reaching depths of 10 to 35 inches. Throughout their course they branch freely into both large and small rootlets, the larger branches spreading widely and then turning downward after the fashion of the main laterals. Throughout the course of the laterals and their larger branches, a striking

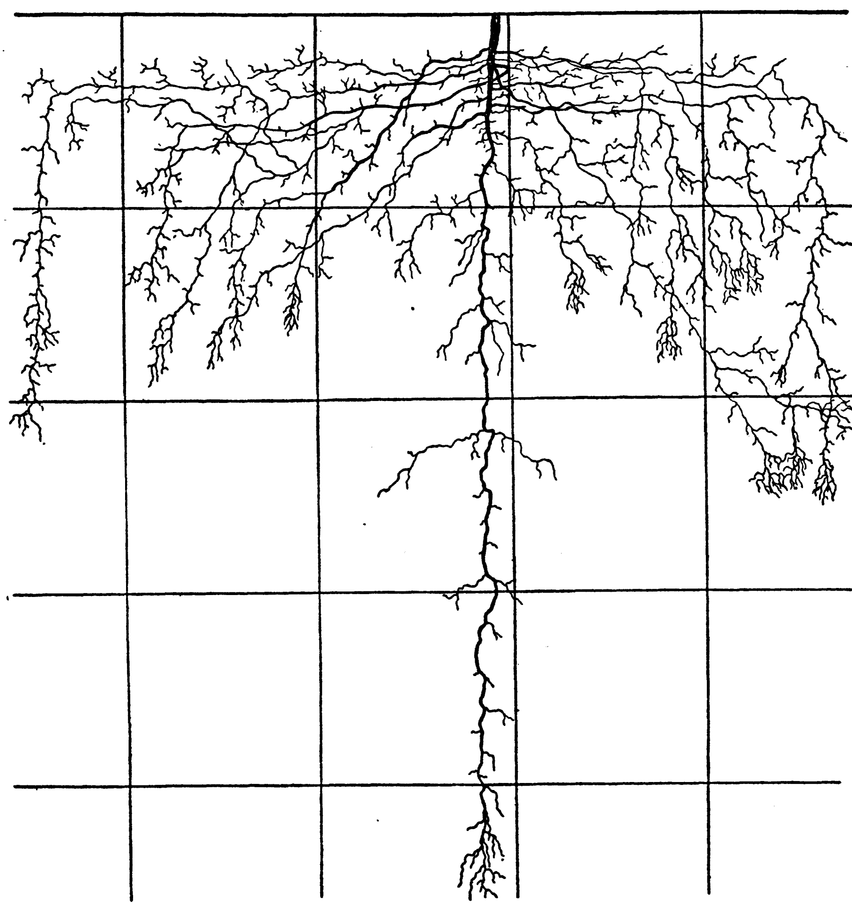


FIG. 28.—*Gilia longiflora.*

system of fine absorbing rootlets, branched to the second and third order, is found. Below the point where the tap throws off the larger laterals, it is much more poorly branched, the branches being relatively much smaller and shorter, but well supplied with fine rootlets, as are the laterals above. From the figure and description it will be seen that although this is an annual, the absorptive system is characteristic of that of most of the species found in the sandhills. The roots are glistening white and quite tough for herbaceous plants.

Euphorbia petaloidea.—*Euphorbia* is a sandhill pioneer which forms both families and colonies. The root system begins with a strong, smooth taproot, varying in diameter according to the age and size of the plant, the

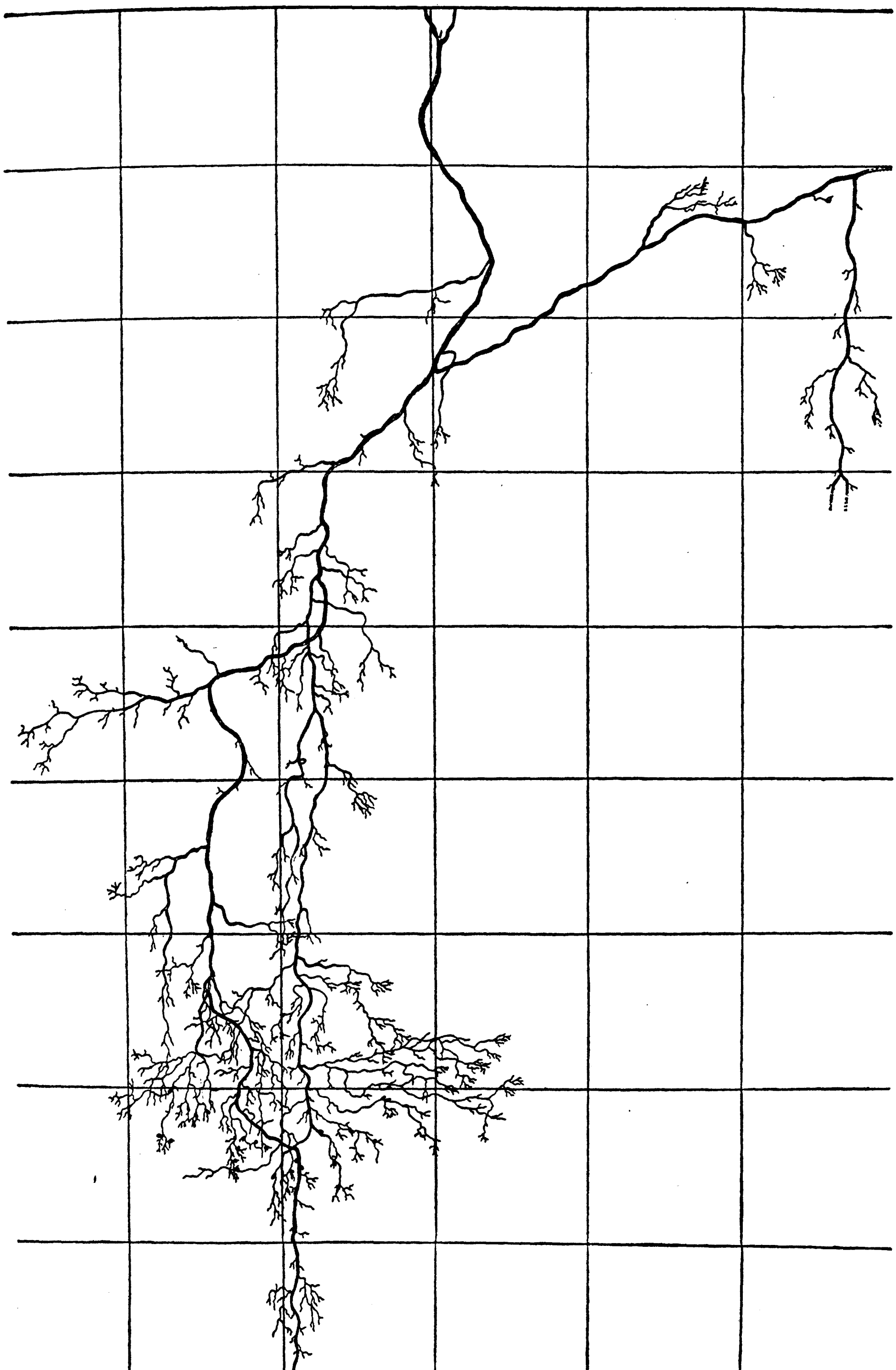


FIG. 29.—Underground parts of *Psoralea lanceolata*, showing root tubercles at a depth of 8 feet.

largest examined being 4 mm. in diameter. This tap penetrates almost vertically downward. Beginning at a depth of 2 to 3 inches, it sends off multitudes of fine fibrous roots which are much branched and penetrate the soil on all sides to a distance from a centimeter or less to 3 or 4 inches. In addition to these finer roots, the tap sends off longer laterals which traverse the soil in all directions, some taking a course almost parallel with the surface, while others pass off more obliquely. These vary in length, some being 10 to 12 inches long. The laterals are much branched and rebranched, and together with the finer rootlets form an effective absorbing system. Usually at a depth of 5 to 8 inches the tap divides up into such a system of large laterals as to almost if not quite lose its identity. These lower laterals vary from 0.5 to 1 mm. in diameter and diverge more or less obliquely downward, some penetrating to a depth of 26 inches or more. The deeper penetrating divisions of the tap branch rather freely and end in much divided termini. On the whole, however, these lower branches are more sparsely supplied with absorbing rootlets than those nearer the surface. The roots are of a light brown to white color, are rather fragile, and hard to trace. Six plants of varying sizes were examined.

Psoralea lanceolata.—This legume sometimes replaces *Redfieldia flexuosa* as the pioneer in the shifting soils of blowouts, but normally it belongs later in the succession. Its underground parts eminently fit it to succeed in a habitat where the ground-line is constantly lowered by wind erosion or built up by the same agency.

The individual plants, which may be a few inches or several feet apart, are connected by a more or less horizontal system of rhizomes, which varies in depth from 2 or 3 inches to more than 2 feet. These connecting parts vary from a few millimeters to more than a centimeter in diameter and may run horizontally for distances of 10 to 30 feet or more. At irregular intervals along their course occur erect portions, often a centimeter in diameter and frequently forked at the top. These give rise to the individual plants, while at other intervals, and not always below the erect stems, strong, rather vertically descending roots occur, many of which reach a depth of 8 or 9 feet (fig. 29). The surface 2 or 3 feet of the root system is poorly supplied with absorbing rootlets. In fact, only a few of the major branches have their origin in this layer of soil and the ultimate rootlets of these extend much deeper. The main system of branches begins in the fourth foot of soil and extends to the 8 or 9-foot level. This consists of both large and small wide-spreading and well-branched rootlets, the laterals often running out to a distance of 2 feet or more from the base of the tap. Large root nodules, 1 to 3 mm. in diameter, were observed at a depth of 8 feet. One large tap-root was traced to a depth of over 9 feet, where it still maintained a diameter of 4 mm. It was not followed further, because of the danger of caving the sandy-walled trench. The roots were dark brown in color and rather tough.

Ipomœa leptophylla.—The bush morning-glory is a common plant in the sandhills, where the large hemispherical tops, conspicuous because of their profuse purple blossoms, cover many square feet. Two plants which were growing together were examined. The top measured 7 feet in diameter and was 30 inches high. The multicipital stem arose from strong tap-roots 2.5 inches in diameter. At a depth of 9 inches the taps became greatly enlarged, reaching a diameter of 6 to 8 inches, which they maintained to a distance of about a foot, when they tapered off gradually, so that at a depth of 4 feet they were but an inch or two in diameter. Below this point the tap lost its dominance, breaking up into large numbers of deeply penetrating and widely spreading branches, as shown in figure 30.

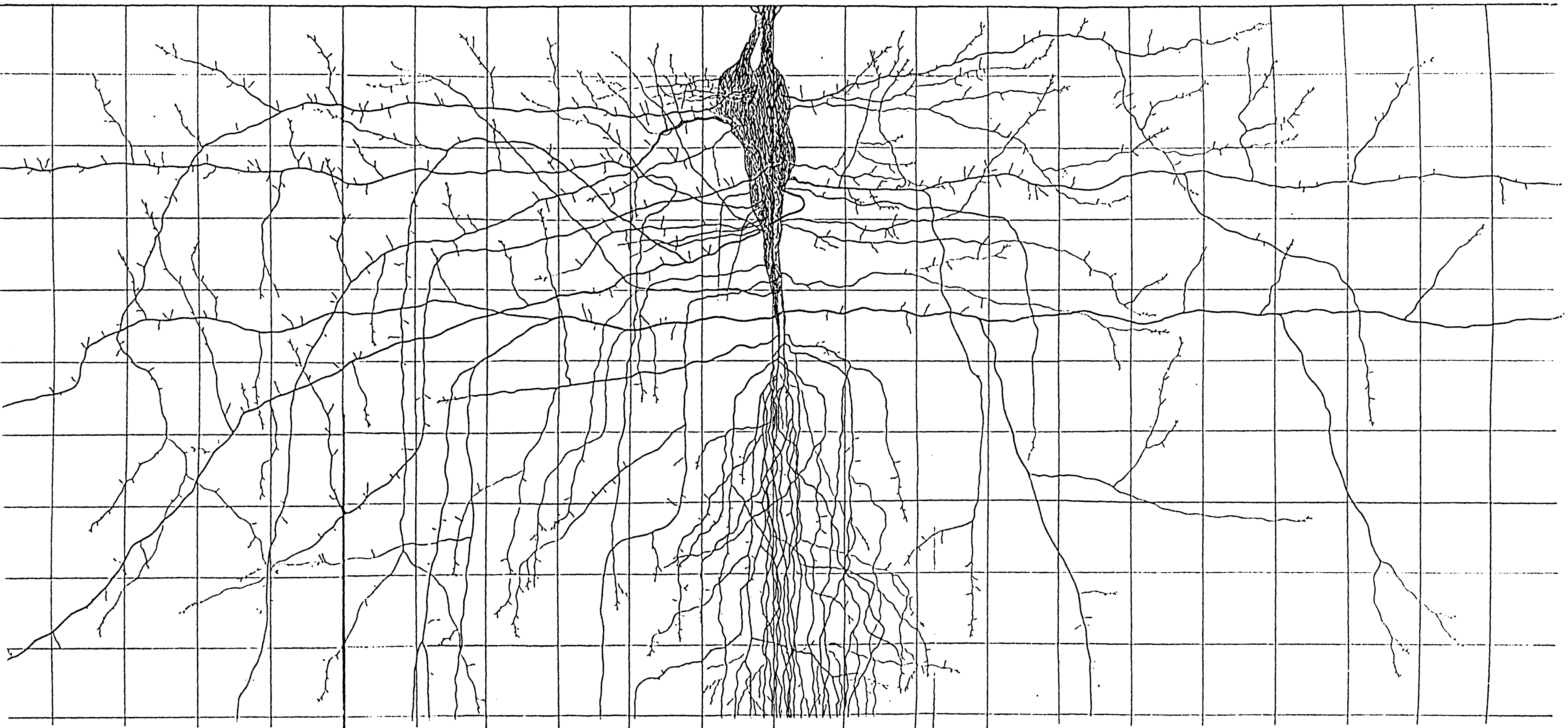


FIG. 30.—*Ipomœa leptophylla*, showing a portion of the very extensive root system.

In the first foot of soil scarcely any laterals originated, but below this point both large and small branches came off in great abundance. These varied in diameter from less than 1 mm. to half an inch. While a very few ran somewhat vertically or obliquely downward, the general course of most of them was quite parallel with the soil surface. The lateral spread was enormous, the roots running off to distances of 15 to 25 feet or more. One of the larger forks of a root, 0.5 inch in diameter, was traced to a distance of 14 feet and at a depth varying from 25 to 30 inches from the base of the plant, when it branched into two equal parts, 4 mm. in diameter. These wide-spreading laterals sent off abundant branches, many of which passed off at right angles, either vertically downward or vertically upward, for distances of many feet. Indeed, the surface foot of soil as well as the 10 feet below it were literally filled with the glistening white, brittle branches of this remarkable root system. The ultimate branches, however, while occurring in great numbers, were not profusely divided. The great network of roots originating at a depth of 5 feet is well shown in figure 30, but because of the caving of the sandy soil it was impossible to follow them to a greater depth. However, judging from their diameters of 2 to 4 mm. at this level and the nature of the other roots examined, it is highly probable that they penetrated many feet deeper. The enlarged portion of the tap-root not only furnishes an enormous reservoir for food, but also a storehouse of water upon which the plant may draw during a period of drought.

SANDHILL ROOT SYSTEMS AND THE SANDHILL ENVIRONMENT.

Eight of the 19 sandhill species examined[1] have roots which are entirely or nearly confined to the first 2 feet of soil. Of the others, all but one have their main root development in the first 2 or 3 feet of soil. Even the very deep-rooted *Eriogonum microthecum* and *Artemisia filifolia* show a striking profusion of long, wide-spreading laterals in this soil layer. Indeed, it will be shown later that *Stipa comata*, *Bouteloua gracilis*, and *Chrysopsis villosa*, all rather deep-rooted plains species, become rather shallow-rooted under sandhill conditions. Among the grasses the rhizome habit is extremely well-developed, while long, rather horizontal, shallow laterals are characteristic of most of the plants examined. In this soft substratum such a root habit can not be attributed to the mechanical difficulty of penetration, but seems closely related to the water-supply.

Rainfall is at once absorbed and there is practically no run-off, even in the heaviest showers. As soon as the storm passes, evaporation dries out the surface sand with great rapidity, but to a slight depth only. This surface layer of dry sand forms an excellent mulch, which has a wonderfully retarding effect upon further evaporation. At a depth of but a few inches below the surface the sand is always moist and may usually be molded into lumps by pressure of the hand. The vegetative cover is usually rather sparse and consequently water-losses by transpiration should be much less than on the plains. Unfortunately few data on soil-moisture in sandhill soils are available.

[1] Only 14 are here described; the others will be found under the section on ecads (p. 110).

Bates (1910) gives us the following table of water-contents for soils taken in the sandhills at Halsey, Nebraska:

TABLE 17.—*Amount of moisture in the soil, per cent of dry weight.*

Station.	At 1 foot.			At 2 feet.			At 3 feet.			At 6 feet.		
	May.	July.	Sept.	May.	July.	Sept.	May.	July.	Sept.	May.	July.	Sept.
South slope	4.1	1.9	3.1	4.8	1.6	3.1	4.3	1.8	3.2	3.9	2.8	3.3
Bottom	5.1	2.9	4.7	4.8	2.1	4.2	5.4	3.3	4.2	6.5	7.4	8.6
North slope	5.1	3.0	4.7	5.3	3.3	5.0	5.9	5.1	6.7	5.9	7.3	7.4
Ridge	3.3	4.0	3.6	4.4	3.8	3.9	5.2	3.7	3.7	5.4	4.2	4.9

From these data it may be seen that the soil was rather uniformly moist to a depth of 6 feet. We must keep in mind, however, that these data were taken under a rainfall of about 23 inches and during the wet phase of the climatic cycle.

A single set of duplicate determinations, taken in the area studied on July 30, showed the water-content to be rather uniform to a depth of 3 feet (about 4 per cent), 3 per cent of which was available for plant growth. While further determinations were not made, in all of the numerous trenches dug the sand was perceptibly drier at greater depths. It seems certain that under the normal light rainfall the surface soils from 4 to 36 inches would contain the most moisture, while the deeper soils would become wet only during the years of abnormal precipitation. The latter may account for the deep root habit of *Psoralea lanceolata* and others. The deeper soils, once wetted, would dry out very slowly, because of the relatively small number of plants drawing their water-supply from them. Soil nutrients may be a limiting factor, but this seems improbable in view of the luxuriant growth and complete occupancy of the soil by plants when sufficient water is supplied.

VI. THE GRAVEL-SLIDE COMMUNITY.

A fine series of diverse habitats for investigation are found in the mountains adjoining the plains. During August a detailed investigation was made of the roots of plants at an altitude of about 8,000 feet in the Pike's Peak region of the Rocky Mountains. Here the soil is composed of disintegrated granite, the degree of disintegration and decomposition determining largely the type of plant community occupying any particular area. The successional sequence and species belonging to each community of the sere may be found in publications by Clements (1904, 1905). The first herbaceous plants to occupy the new soils formed by the crumbling granite on the steep mountain slopes are members of the gravel-slide community (plate 23). The semibare areas thus populated are so extensive and the life conditions so unique that a rather detailed study was made of the most important species.

Krynitzkia virgata.—This striking plant has an erect, spike-like stem seldom reaching a height greater than 8 to 12 inches in this habitat. It is a principal species of the gravel-slide community. It has a tap-root 4 to 9 mm. in diam-

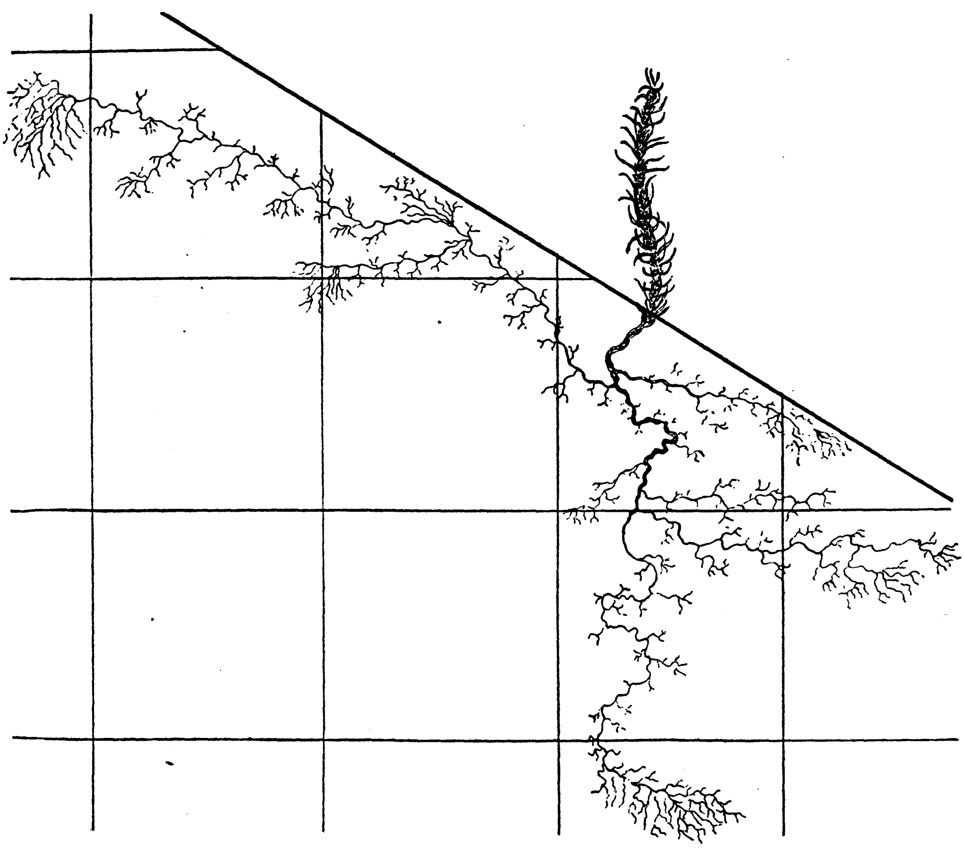


FIG. 31.—*Krynitzkia virgata.* The heavy slanting line indicates the actual ground-line.

eter, which reaches depths varying from 20 to 30 inches (fig. 31). Except for the first 3 to 5 inches, where the plant tops have slipped down the gravel slide, the root pursues a rather vertically downward course, the tip being only a few inches horizontally away from the base of the plant, in spite of the backward and forward meanderings of the root through bends of 3 or 4 inches in diameter. The tap is often flattened and kinked where it forces its way through the crevices of the semi-decomposed rock. The number of larger branches is few, usually not exceeding 2 or 3. One plant gave off only one large branch, about 2 mm. in diameter, at a depth of 3 inches. As is characteristic of numerous other plants examined, this lateral branched freely and ran off in a direction nearly parallel with the surface for about 15 to 20 inches, ending in a network of well-branched rootlets. On another plant a lateral ran off more than 36 inches from the base of the stem, branching again and again. Other smaller branches arise from the tap in great abundance. These are only a few centimeters long, but well-branched and densely covered with root hairs. The older cortex is black and of a papery texture, peeling off readily.

Paronychia jamesii.—This small, cespitose perennial forms a consocies of the community. It has a tap-root about 5 mm. in diameter. Like all other plants on the gravel-slide, the top has been pushed down the slope several

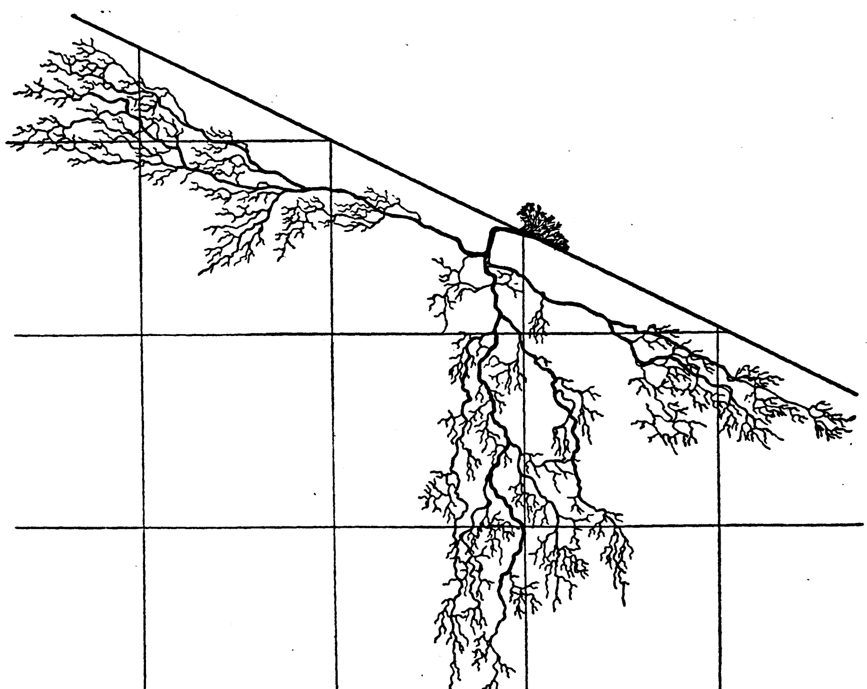


FIG. 32.—*Paronychia jamesii.*

inches. The tap breaks up into several larger laterals, usually 3 to 5, and a great number of smaller ones. Some of the laterals run off in a horizontal direction to a distance of 30 inches or more, at about 2 to 4 inches in depth, branching repeatedly, as shown in figures 32 and 33, and being abundantly supplied with minute, absorbing rootlets. Others run off obliquely, while still others parallel more or less the attenuated tap-root, and like the tap are abundantly supplied with both long and short rootlets, the whole forming a wonderfully efficient absorbing system. Compared with the transpiring surface, the root system is very well developed. The surface view in the figure shows the roots at a depth of 2 to 2.5 inches. The dotted lines show where they turn downward. No roots were found to penetrate to a greater depth than 30 inches.

Aletes acaulis.—This low umbelliferous plant, which is only 6 to 8 inches high in fruit, is the dominant of the gravel-slide, often being more abundant and conspicuous than all other plants combined (plate 23, A, B). From the large tap-root arises a large number of stems, each multicipital in character; 47 individual stems were counted on a single medium-sized plant. Such a group forms a formidable obstacle to the rock fragments moved by gravity, the latter pushing the top of the plant 6 to 10 inches downward from the top of the well-anchored tap-root. Both the main stems and the branches show marked wrinkles from profound contractions. At the base of the shoots of this perennial, great clusters of dead and decaying gray leaf-bases remain attached to the plant.

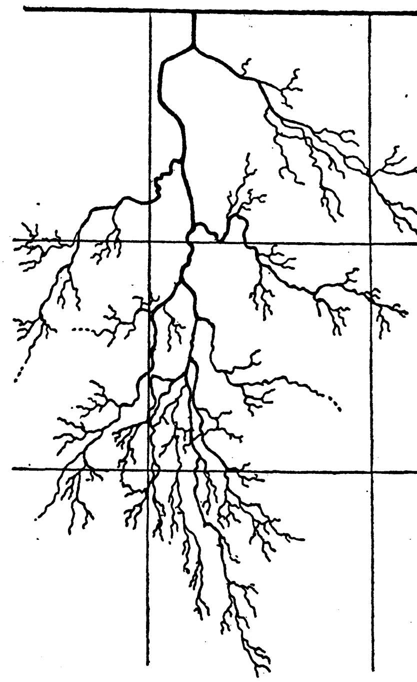


FIG. 33.—Surface view of a single root of *Paronychia jamesii* at a depth of 2 to 2.5 inches.

The tap-root is often 4 cm. or more in diameter. It is dark brown in color and quite spongy in texture, as was noted for several species in this habitat, the fleshy roots probably serving for water storage. One plant with a tap 4 cm. in diameter, from which originated 7 distinct stem-clusters, gave rise in the first 3 inches of soil to numerous laterals ranging from 1 cm. to only a few millimeters in diameter (plate 24, A, B). One of these laterals, 3 mm. in diameter, ran off at a depth of about 4 inches and in a direction parallel with the soil surface to a distance of 4 feet, giving off numerous branches, both large and small, each of which, after branching profusely, ended in a network of tiny, much-branched laterals. Another surface lateral, 8 mm. in diameter, ran up the slope at an average depth of 5 inches to a distance of 4.5 feet. At a depth of 6 inches the tap broke up into 3 parts—7, 8, and 10 mm. in diameter respectively. These were very much curved and twisted. They followed the crevices of the rocks and none reached a depth greater than 30 inches, but spread laterally to a distance of 3 or 4 feet or more from the base of the plant. All of the laterals branched profusely and terminated in the moist rock crevices in networks of tiny rootlets. The surface 2 to 5 inches of soil is especially filled with these absorbing laterals, but they are abundant throughout the soil to the tips of the deepest roots. Plate 24, B, shows a fragment of these branches. In fact, the soil is literally filled with these absorbing rootlets to a point several feet on each side of the plant. A single plant thus lays hold of the surface soil to a depth of 18 inches or more within a radius of 4 or 5 feet from its base.

Apocynum androsæmifolium.—Large areas, especially of the steeper gravel slides, are frequently covered by extensive communities in which this species is dominant, often forming families (fig. 34). The vertical portions arising from the horizontal rootstock are 2 to 5 mm. in diameter. From these origi-

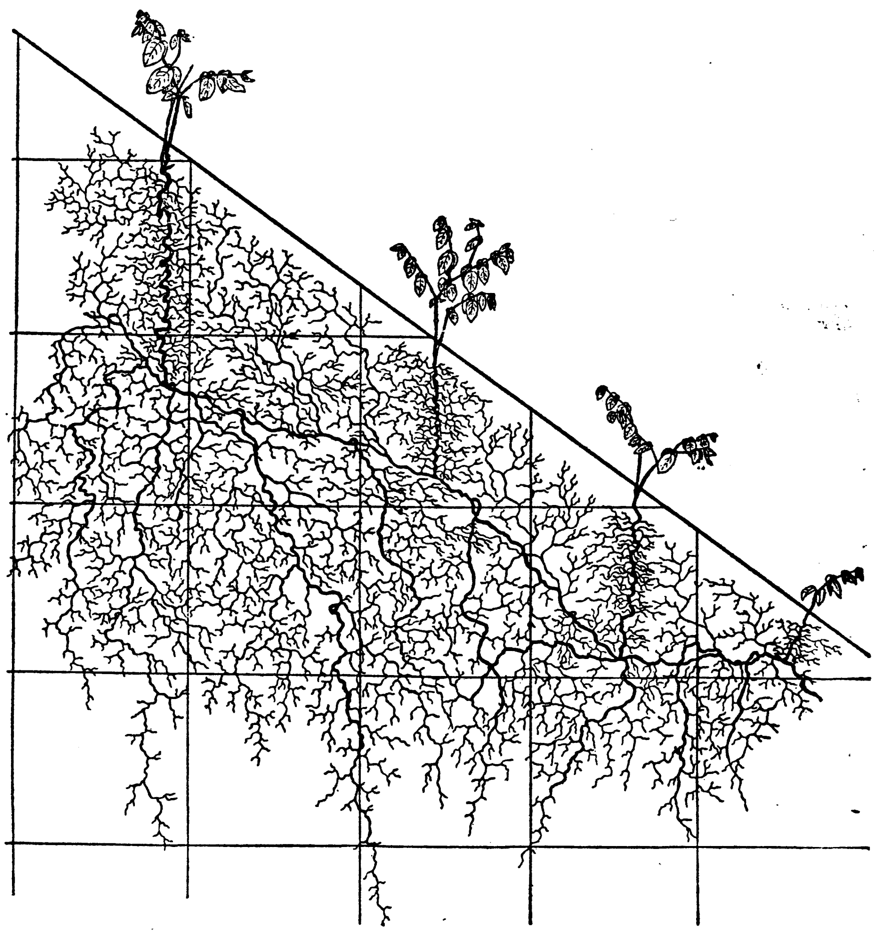


Fig. 34.—*Apocynum androsæmifolium*, showing rhizomes and dense network of roots.

nate groups of 2 to 5 erect stems. The rootstocks lie at a depth varying from 6 inches to 2 feet, but usually at about 8 to 16 inches. These run for distances of 6 to 10 feet or more, giving rise at irregular intervals to erect portions which bear new plants. Sometimes these connected plants are only a few inches apart, while at other times the interval between them may be 3 or 4 feet.

The vertically ascending parts seldom have large branches, but are well clothed with abundant laterals 1 mm. or less in diameter. These branches divide and subdivide into many branch orders, forming brushlike mats which run off in all directions to a distance of 6 or 8 inches or more. However, the most profound branching arises from the horizontal rootstocks. Like the former, these are not large in diameter, but are branched so profusely, extending vertically upward as well as downward and laterally, that they completely occupy the soil from a depth of 2 inches to a maximum depth of 4 feet. Many of these deeper roots originate from strong laterals 1 to 2 mm. in diameter, which branch off and run in various directions from the rootstocks. Figure 34 illustrates the profound absorbing surface characteristic of these gravel-slide plants. In color, the larger roots are dark brown, while the finer ones vary from tan to almost white.

Smilacina stellata.—Families of this plant often occur on steep gravel-slides, or they are the dominants of a gravel-slide colony. Stout stems, from 3 to 7 mm. in diameter, arise at intervals of an inch to more than a foot from the stout horizontal rhizomes. The latter are about the same diameter as the stem and lie usually at a depth of about 4 to 6 inches, although they are sometimes shallower where the gravel has rolled away and often much deeper where the gravel has covered them (plate 24, c). Some were found at a depth of 30 inches. The rhizomes are much branched, frequently at right angles, a single rhizome system often connecting a whole family of plants through a distance of 7 or 8 feet or more. These rhizomes furnish not only an excellent means for propagation, but also serve as storage organs for these herbaceous perennials.

The plants frequently grow in such dense clumps that the soil at a depth of 4 to 6 inches is quite filled with dense masses of these rhizomes. Although the vertical stems do not give rise to rootlets, the rhizomes are uniformly covered on all sides with rootlets about 0.5 to 1.0 mm. in diameter. These run off in all directions, including the vertical to a distance of 3 to 6 inches. Although they are entirely unbranched, they are completely and uniformly covered with a dense coat of root-hairs. Thus the plant is well provided for absorbing the moisture in the shallower soil. In addition to these shorter rootlets, groups of 2 to 5 larger branch roots arise at frequent intervals at the base of the vertical stems or where these stems have been, a place now marked by a seal-like scar. These vary from 2 to 4 mm. in diameter and throughout their course are densely covered with root-hairs. They penetrate the soil to a maximum depth of 44 inches. Through the first 6 to 12 inches of their course they are unbranched or at least poorly branched, but from this point they branch profusely to the third or fourth order, the branches spreading widely and the ultimate rootlets being rather coarse, often 0.2 to 0.5 mm. in diameter. Since these branches run obliquely and even horizontally as well as vertically downward, they furnish with the shorter roots already described an excellent absorbing system. Altogether the finer rootlets are very coarse and poorly branched when compared with *Aletes*, *Thlaspi*, and certain other gravel-slide plants. The entire underground parts vary from tan to white in color.

Pachylophus cæspitosus.—This is a common plant on bare gravel-slides where it forms pioneer consocies. The social habit is due to the method of vegetative propagation (fig. 35). The plants are frequently connected by rhizomes from which arise roots 2 to 5 mm. in diameter, none of which were found to reach a depth greater than 45 inches. Frequently at 4 to 8 inches deep, they turn off abruptly up or down the slope and run parallel with the surface for long distances. Large branches arise from these roots and do much of the absorbing for the plant. Of numerous specimens examined, the one illustrated in figure 35 is typical.

Both large and small rootlets may arise from the rhizomes. The main laterals are well supplied with rootlets and the soil is quite filled with them to a depth of 6 to 36 inches. As compared with *Aletes* and *Apocynum*, the rootlets are coarse and rather poorly branched. They vary from tan to nearly white in color. The tap, as in many gravel-slide plants, is rather fleshy.

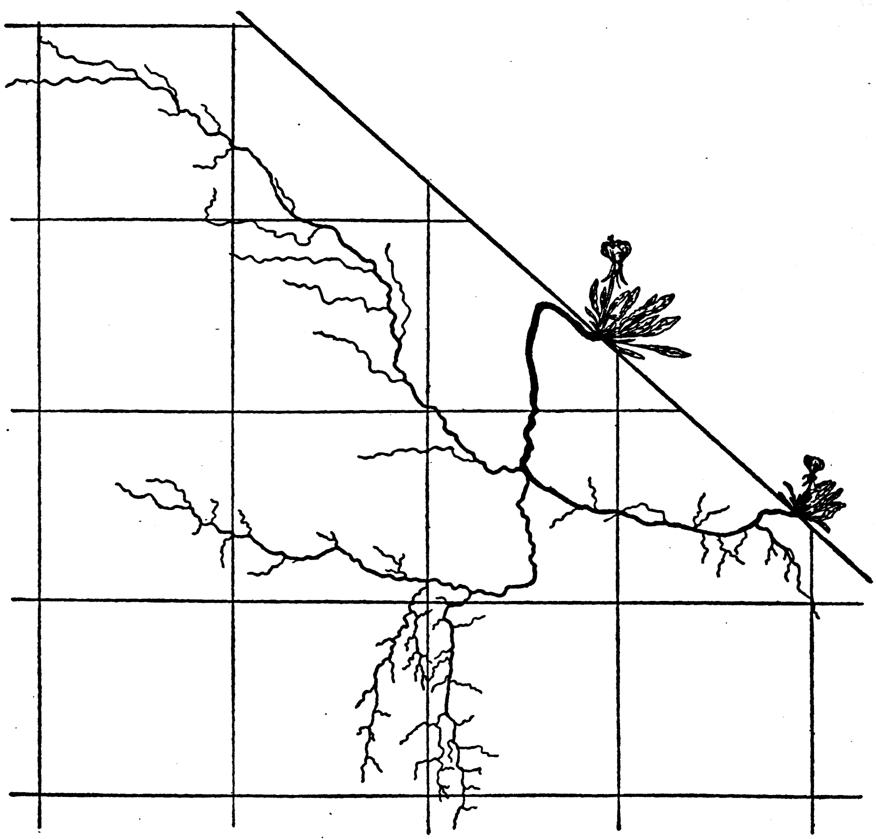


FIG. 35.—*Pachylophus cæspitosus.*

Thlaspi alpestre.—This penny-cress is abundant but rather inconspicuous, being only 5 to 8 cm. high. Its tap-root is usually not over 2 mm. in diameter, and penetrates the dry surface gravel to a depth of 1.5 to 2 inches before it gives off branches. Beginning at this depth, tiny laterals, ranging from almost microscopic in size to 1 mm. in diameter, develop in abundance (plate 24, D). The larger laterals are relatively few, usually not more than 2 to 5, but the smaller ones, many about the size of a fine silk thread or smaller, occur in great abundance. Often they run parallel with the surface throughout the soil, branching repeatedly in such a manner as to form a delicate mass of rootlets, the ultimate termini being minute. The lateral extent is usually not greater than 4 to 7 inches and the depth of the plant seldom exceeds 15 inches. To really appreciate the delicacy of the profusely branched fragile root system, it is necessary for one to carefully pick away the coarse rock particles.

Mentzelia multiflora.—Size, duration, and abundance combine to make this species a dominant on many gravel-slides. The plants are usually about 10 to 14 inches high when in full bloom. The roots start with a tap 12 mm. or less in diameter, which, after penetrating to a depth of 2 to 5 inches, sends off strong laterals as large as 3 or 4 mm. in diameter. These are distinctly shallow, run almost parallel with the surface, and are repeatedly branched, the fine rootlets ending in hairlike extremities. Although they seldom run more than 18 inches from the base of the tap, they are frequently much longer because of their curved and twisted course. The tap-root takes an almost vertically downward course, except where it follows for a time the crevices in the rocky soil, and penetrates to a maximum depth of about 22 inches. Although the tap is not so profusely branched as are the shallower laterals, the branches of both are very similar. The smaller branches of both the laterals and the tap are profusely covered with a fine growth of root-hairs. Although this plant, when compared with most others, has an exceedingly well-developed absorbing system, it does not compare favorably with the wonderfully extensive and excellently developed root system of *Aletes*. However, both are well adapted to get the water falling during the frequent mountain showers and thrive under conditions where most plants could not grow. The roots are almost white in color and very spongy in texture.

Eriogonum flavum.—This plant is a subdominant in the gravel-slide community, its masses of yellow flowers making it very conspicuous in the autumnal aspect. The specimen had a strong woody tap-root 2 cm. in diameter which tapered within a length of 6 inches to only 3 mm. in diameter. Here it gave off 2 laterals each 2 mm. in width. These ran off laterally for about 2 feet at a depth of 3 to 7 inches. An enormous number of smaller profusely branched laterals arose, forming a dense absorbing network about

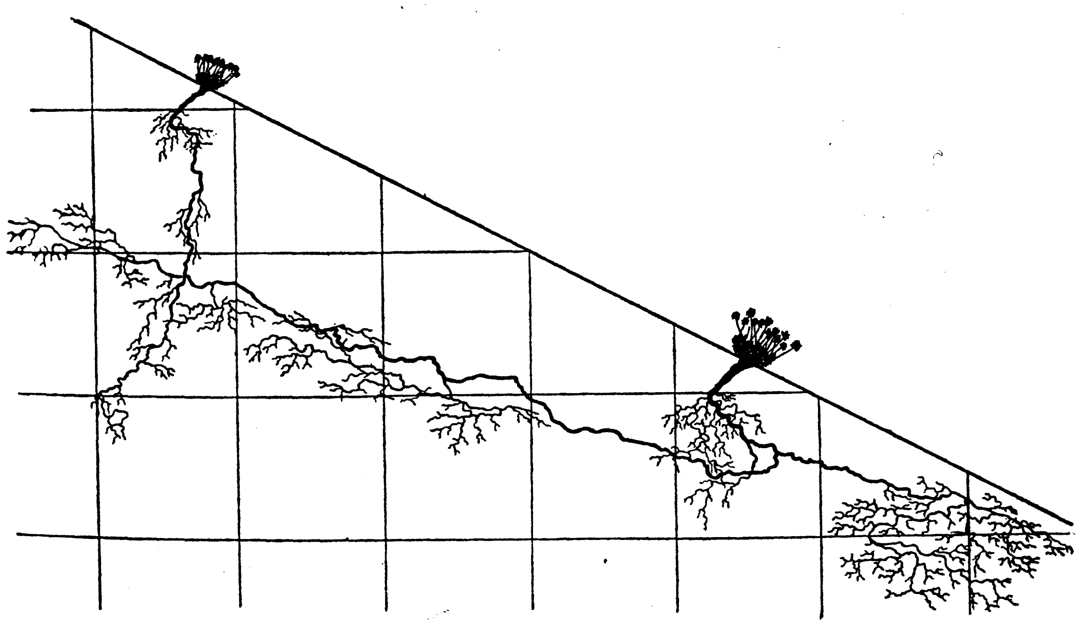


FIG. 36.—*Eriogonum flavum.*

the plant for a radius of more than 18 inches. These were extraordinarily well-branched and rebranched and were very dense. At 5 inches in depth another large lateral occurred, and the root broke into 2 nearly equal parts at 6 inches in depth. One of these ran off into the bank and slightly upward to a distance of 2 feet from the base of the crown, but it was really much longer. It ended 3 inches below the soil surface. This lateral, scarcely more than 1 mm. in average diameter, gave off both short and long branches in a profuse manner, all being repeatedly branched into minute termini and densely covered with root-hairs. They also dipped upward to within 2 inches of the surface and downward to 8 or more inches, but were most abundant at 4 or 5 inches in depth. The other root at the fork ran out into the slope for over 5 feet at an average depth of 16 inches. The roots often run long distances without much branching, but the last 2 or 3.5 feet form a great network of branches. The roots are reddish in color and relatively tough. None of those examined were deeper than 2 feet (fig. 36).

In another specimen the root system began to divide almost from the crown, some of the main parts, however, being much larger than the others, varying from 2 to 13 mm. All the rootlets, whether large or small, were marked by a diffuse dichotomous branching. Most of the branches were superficial, extending to a depth of 1 to 12 inches. These branches were themselves branched many times, and the termini of the branches of all sorts were persistently marked by capillary roots, ramifying and forming a conspicuous network in the soil. The course of most of these laterals was parallel with the surface. The maximum spread of the main absorbing branches was found to be 4.5 feet. A very few of the larger branches take a more marked downward course, branching very much the same as the horizontal laterals, but the branches are not so numerous nor so long. The maximum depth recorded was 39 inches and the tip of the root had wandered 43 inches from the vertical.

GRAVEL-SLIDE ROOT SYSTEMS AND GRAVEL-SLIDE ENVIRONMENT.

All of the plants of this community are similar in possessing roots adapted to secure moisture and nutrients from the surface soil. They are characterized by a shallow, widely spreading root system confined largely to the first 18 inches of the soil and in fact usually best developed in the surface foot. The lack of depth is compensated by a remarkably wide lateral extent combined with a profound system of branching. An explanation of these adaptations is readily found in a study of the soil and the distribution of the rainfall.

The gravel-slide soils consist of a superficial layer of coarse angular rock fragments varying in size from over an inch to a few millimeters in diameter. Except during rains this surface layer is very dry. The slope is so steep that there is often a constant movement of the rock particles down the mountain-side, the course of these moving pebbles being marked by depressions looking not unlike the tracks of harrow teeth. Most of the plant tops have slipped down the slope from 2 to 8 or more inches. This surface layer is very efficient in preventing run-off, as well as in forming a dry mulch and thus protecting the underlying soil from high evaporation. A concrete illustration of the effectiveness of this layer is shown in the following experiment. Two metal cylinders, 8 inches high and 5.5 inches in diameter, closed at one end, were filled with wet soil and one of them was covered with a layer of these coarse gravel particles to a depth of an inch. After an equal exposure to evaporation for a period of 30 hours, it was found that the one container had lost 202 grams of water, which was more than 8 times as much (24 grams) as evaporated from the soil covered with the gravel mulch. In nature, finer particles occupy the interstices between larger ones, and hence the gravel mulch must be much more efficient.

Below this surface gravel are about 4 inches or more of fairly well decomposed rock, a mixture of coarse gravel and sand. On older

TABLE 18.—*Water-content of the soil of the gravel-slide and half-gravel-slide during 1918.*

Date.	Depth 0 to 6 inches.		Depth 6 to 12 inches.		Depth 12 to 18 inches.	
	Gravel-slide.	Half-gravel-slide.	Gravel-slide.	Half-gravel-slide.	Gravel-slide.	Half-gravel-slide.
June 8	4.7	3.0	5.1	3.3	4.2	2.8
June 11	....	3.8	....	2.7	....	2.9
June 24	5.2	9.2	4.3	4.4	5.0	3.2
July 1	3.1	5.5	4.0	4.7	8.5	4.2
July 8	3.3	3.5	4.2	2.4	3.2	2.2
July 15	4.0	9.5	4.5	7.5	3.5	4.0
July 22	6.0	10.1	3.9	5.7	4.1	4.3
July 29	4.2	6.5	4.1	3.9	3.2	3.2
Aug. 5	4.9	3.1	3.2	2.1	2.7	2.1
Aug. 12	4.5	8.9	3.0	4.4	2.6	4.3
Aug. 19	5.1	6.6	4.3	3.8	4.6	3.4

slides this layer extends much deeper. Below this the soil changes from a dark brown to a more reddish color and consists of fairly well decomposed granite, which becomes less broken up as one goes deeper. At 2 to 4 feet in depth it changes into almost solid rock. The roots show a marked tendency to follow the cleavage planes of the rock. Below 4 to 6 inches the soil is remarkably compact, and it is necessary to remove it with a pick, this sometimes being accomplished with considerable difficulty.

An examination of the weekly soil-moisture determinations in table 18 shows that while the water-content is at no time high, it is rather uniformly distributed throughout the first 18 inches of soil. Owing to the extreme irregularity in degree of fragmentation of the rock particles and to the heterogeneous nature of these soils, moisture-equivalent determinations are not given. The amount of non-available water in the gravel-slide soils was found to vary from 1.9 to 7.8 per cent; in the half-gravel-slide from 2.0 to 8.6 per cent; and in the soils of the forest floor from 2.7 to 10.5 per cent (page 109).

The rather high evaporating power of the air as measured by non-absorbing atmometers is given in table 19.

TABLE 19.—*Average daily evaporation on the gravel-slide and half-gravel-slide during 1918.*

Date.	Gravel-slide.	Half-gravel-slide.	Date.	Gravel-slide.	Half-gravel-slide.
	c.c.	*c.c.*		*c.c.*	*c.c.*
June 6–10	26.6	20.2	July 15–22	19.8	15.5
June 10–17	51.6	40.1	July 22–29	31.5	21.4
June 17–24	25.8	22.8	July 29 to Aug. 5	49.4	31.1
June 24 to July 1	48.2	30.0	Aug. 5–12	22.9	17.0
July 1–8	35.8	25.0	Aug. 12–19	24.2	16.9
July 8–15	17.6	13.2	Aug. 19–23	54.2	32.0

One factor greatly accelerating evaporation is the marked wind movement. From June 6 to August 23 the average daily wind velocity at a height of 0.5 m. was 103 miles. Notwithstanding the high evaporation losses, nearly all of which occur during the day, the upper layer of the soil containing the roots is kept moist by frequent rains. Seven-

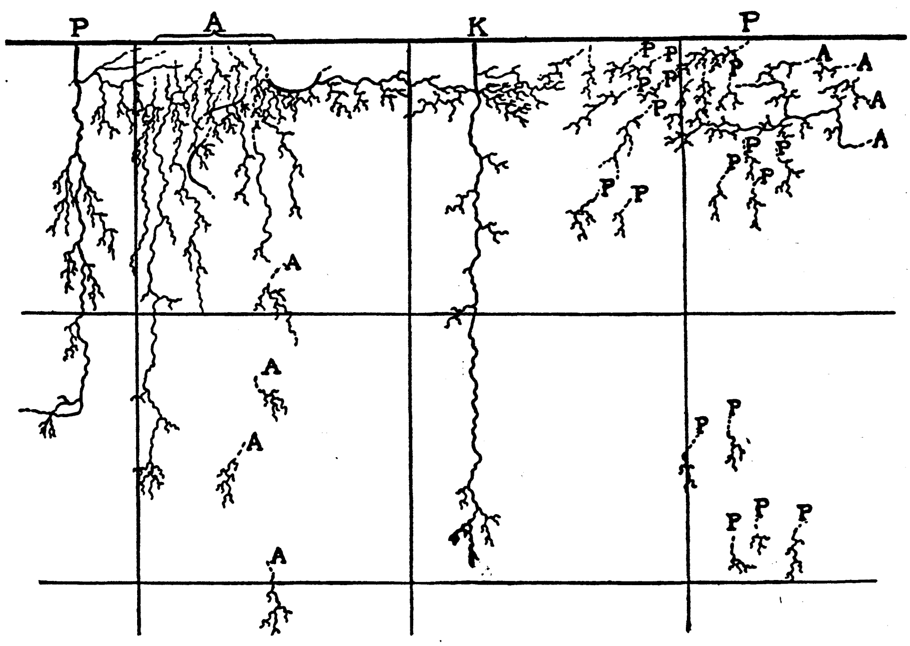


FIG. 37.—Quadrat-bisect showing root relations of gravel-slide plants. This was made along the front of the quadrat shown in plate 23, B. *P, Paronychia jamesii; A, Aletes acaulis; K, Krynitzkia virgata.*

teen showers, varying in intensity from 0.1 to 1.85 inches, occurred from June 21 to August 28, 1918, while the total rainfall during the period was over 10 inches. As already pointed out, none of this water runs off except during the heaviest rains, while the loose gravel inhibits high evaporation losses. Moreover, the plants are so sparsely spaced that only relatively small amounts of water are removed by transpiration. Perhaps 95 per cent of the rocky soil surface is bare except for *Parmelia saxatilis* and a few other crustose lichens (plate 23). This habitat is somewhat similar to that of the sandhills in respect to the dry surface mulch and the supply of moisture in the upper layer. The root habit is clearly a response to the environment. Undoubtedly the large number of roots which have such a strong tendency to run up the slope serve in part for anchorage. The distribution of soil nutrients may also have some share in this. The bisect in figure 37 shows that root competition on the gravel-slide is far from severe.

VII. THE HALF-GRAVEL-SLIDE COMMUNITY.

The half-gravel-slide community represents a distinct successional advance over that of the gravel-slide, both in the diversity of species and the density of plant population, as well as in the correspondingly more favorable habitat (plate 25, A). It is an intermediate stage between the gravel-slide and the forest. Here the root systems of the most important grasses, herbs, and shrubs were studied.

Elymus triticoides.—This grass is perhaps the most abundant and important species of the half-gravel-slide community. Because of its excellent root development and consequent ability to compete successfully with other species, it not infrequently controls large areas, sometimes almost to the exclusion of other plants.

Elymus was excavated at the half-gravel-slide station in coarse, rocky soil (plate 25, A, B). The soil of the upper 18 to 22 inches was light brown to gray in color. The roots were densely matted. The larger were 1.5 to 2 mm. in diameter, being much branched into fine rootlets supplemented by countless finer well-branched and matted ones. In fact, the soil to a depth of 15 or 18 inches was completely filled with a dense network of roots. The larger ones penetrated to a maximum depth of 46 inches. The mass of roots at the surface had a lateral spread of about 18 inches on either side of the bunch. Many of the larger roots descended at an angle of about 30 degrees from the vertical to a depth of 15 or 20 inches, when they turned directly downward to a depth of 40 to 45 inches. All of these deeply penetrating roots were, like the others, extremely well branched to the third and fourth order and ramified throughout the crevices of the gravel. Some of these larger roots, after reaching a depth of 13 inches, took a course up the steep slope, following at this depth a line approximately parallel with the surface of the soil. They were well branched, the branches coming up to a distance of only 5 or 6 inches from the surface of the ground. The lower part of the root system was white in color and extremely fragile.

Solidago oreophila.—The autumn landscape is frequently given tone by the masses of yellow flowers of this important half-gravel-slide species. This plant consists of clusters of stems connected by short rhizomes, thus forming a clump. From the base of the rhizomes arise great numbers of fibrous roots about 1 mm. in diameter; as many as 50 to 75 may originate from a single inch of the rhizome. Numerous roots run off parallel with the soil surface, or nearly so, to a distance of 20 to 30 inches from the base of the plant, sending off rather numerous branched and rebranched threadlike laterals from a few centimeters to a few inches long and finally terminating in a much-branched, brush-like ending. Many of the shallower roots also run off obliquely, so that at a distance of a foot from the plant they may reach to a depth of 8 to 10 inches or even more. However, these are not so numerous as the superficial ones. These shallower roots frequently turn down near their tips to a depth of 6 to 15 inches.

The vertically descending roots send off laterals rather sparingly to a distance of 12 or 18 inches, beyond which depth they become more and more profusely branched, finally terminating in great clusters of hairlike, minutely branched ends. In the more decomposed soils the deepest roots may penetrate to a distance of 30 to 38 inches, while in the more rocky substratum they are much shallower. This deeper group of roots usually spreads laterally to only 6 or 8 inches on either side of the base of the plant. The roots are light tan in color and show considerable tensile strength (fig. 38).

Rubus deliciosus.—This plant is one of the most important of the shrubs of the half-gravel-slide. With *Opulaster* and certain others it forms the transition stage to forest.

Three specimens were examined which were so similar that only one will be described. This plant arose from a tap-root 15 mm. in diameter. It had 3 main branches, two of which reached a height of 20 inches. At a depth of 3 inches the tap-root gave off 2 laterals, 2 and 3 mm. in diameter respectively. The smaller of these ran off almost horizontally to a distance of 20 inches, giving off great numbers of much-branched laterals, the termini being almost

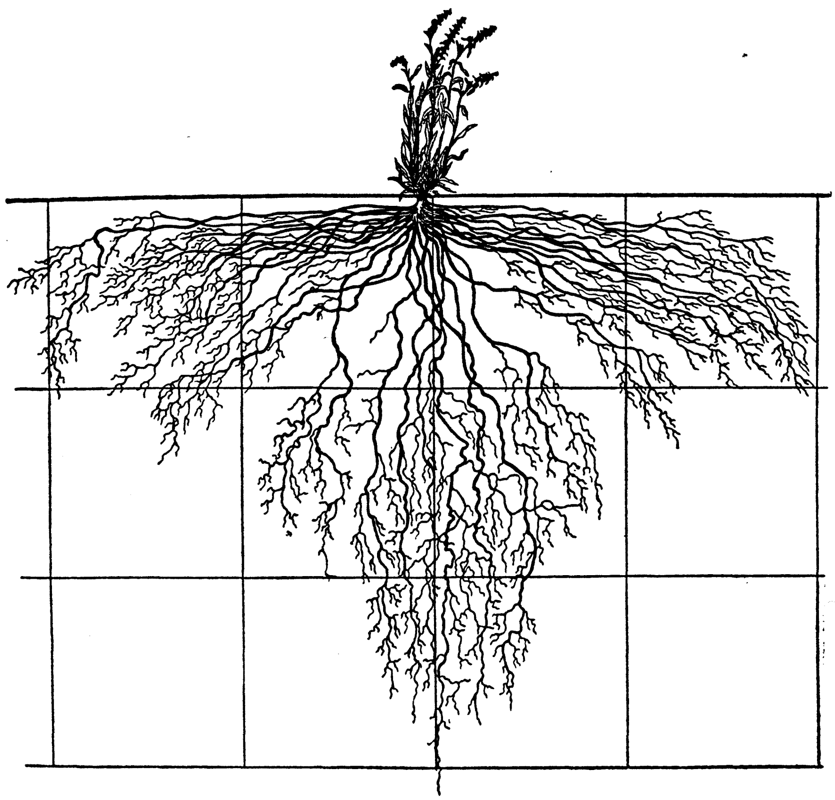


FIG. 38.—*Solidago oreophila*, showing wide-spreading lateral and deep central roots.

hairlike and reaching a depth of over 20 inches (plate 25, c). The larger lateral ran off in the opposite direction to a distance of more than 2 feet, branching repeatedly and ending in clusters of rootlets only 4 inches below the soil surface. On the first 5 inches of the tap several other smaller rootlets occurred, while at 6 inches depth the root divided into 2 equal parts about 6 mm. in diameter. One of these soon rebranched, while all ran off more or less horizontally or obliquely, some to a distance of approximately 3 feet from the base of the plant. The maximum depth did not exceed 36 inches. These roots branched repeatedly into both large and small laterals, those running horizontally being characterized by a multitude of shorter, minutely branched, often vertically descending rootlets. Thus the plant is provided with an effective absorbing system, which ramifies widely and fills the soil from a depth of from 4 to 36 inches. The whole root system is characteristic of the half-gravel-slide root habit.

Besseya plantaginea.—This plant frequently grows in clusters of 3 or more, the individuals of which are connected by short rhizomes about 5 mm. or less in diameter and 2 or 3 inches long. The base of the plant and these rhizomes are densely covered with fleshy roots about 2 mm. in diameter. As many as 30 to 40 of these roots occur on a single inch of the rhizome. Many of them pursue a vertically downward course and end at a maximum depth of from 25 to 30 inches (fig. 39). Others run out rather parallel with the surface of the soil and at a depth of 2 or more inches to a distance of over a foot, when they turn abruptly downward, reaching a depth of 16 or 18 inches. Still others

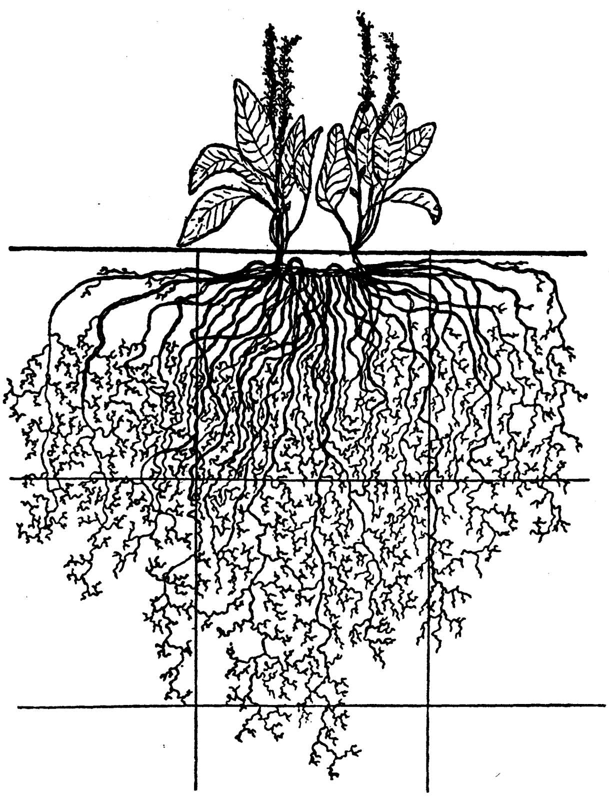


FIG. 39.—*Besseya plantaginea*, showing the widely spreading root system.

fill in the angle between the horizontal and vertical roots, running off obliquely and then turning downward. Very few branches occur on the first 4 to 6 inches of the root. But beyond this point the roots (which are now a millimeter or less in diameter) branch freely, sending off laterals to a distance of 5 or 6 inches, the last 12 to 18 inches being so well branched and rebranched as to form a fine absorbing network. Thus the soil within a radius of at least a foot from the plant and at a depth of from 20 to 30 inches (except the surface 2 inches) is rather completely filled with absorbing rootlets of this fleshy perennial. As its root system shows, *Besseya* is an excellent illustration of a transitional form between the gravel-slide type and that of ordinary soil. The roots are dark tan in color and are fairly tough and resistant. Five plants were examined.

Geranium cæspitosum.—This plant is often rather abundant on the half-gravel-slide, where its size and duration give it considerable importance. Several plants were examined, which in general were similar (fig. 40). The largest had a tap-root an inch in diameter, which at a depth of 3 inches gave off a strong lateral more than 1 cm. in diameter. This ran off horizontally, following a curved course to a distance of 42 inches, and ended only 18 inches below the surface. At a depth of 6 inches the root broke up into 3 parts, all of which grew more or less horizontally, none of the branches reaching depths of more than 37 inches. Most of these laterals approached the surface, the profuse branches often ending within the second to the fourth inch of gravelly soil and forming a fine system for surface absorption. Another lateral ran off at a depth of about 15 inches to a distance of 52 inches from the base of the plant. *Geranium* also has the same root habit of forming large mats of fine rootlets, not only at the ends of the larger branches but also at the extremities of the numerous smaller ones. The roots are reddish-brown in color, rather brittle, and are uncovered with considerable difficulty. The older roots and the crown are frequently more or less decayed.

Calamagrostis purpurascens.—This plant holds an important place in the composition of the half-gravel-slide community. Like *Elymus triticoides*, its root system is so well developed that it can compete successfully with most other species (plate 26, B). Two clumps, each about 8 inches in diameter, were examined. These were old plants with the flower-stalks 15 inches high and in full bloom. From the base of the clumps almost countless numbers of rather tough fibrous roots arose, the largest scarcely more than a millimeter in diameter, while many were much smaller. Among them were many new roots only a few centimeters long. These ran out in all directions like the radii in a half sphere. The soil was well filled with those that extended vertically and slightly obliquely to a depth of 18 or 20 inches, few of the longer roots reaching depths of 32 inches, while the lateral extent of those running vertically just beneath the surface was at least 2 feet on either side of the plant. Many of the deepest and widest-spreading laterals maintain about half their original diameter for a distance of 12 to 14 inches. From the very base of the plant to the extreme tips the supply of fine rootlets is remarkable. They branch and rebranch again and again into conspicuous mats of almost microscopic rootlets which penetrate every crevice of the gravelly soil. Few if any of the grasses examined had such great masses of delicate clusters of absorbing rootlets. Such a grass is excellently adapted to live in the half-gravel-slide, as more thorough occupancy of the soil can scarcely be imagined. In color the roots are brown to light tan. They were removed from the gravelly soil with no great difficulty.

Kœleria cristata.—This grass, which is a characteristic dominant of the half-gravel-slide, is distinguished by an extremely fibrous root system. The main roots at their outset vary from 0.2 to 0.3 mm. in diameter. At a depth of 1 to 4 inches many of these run off parallel with the surface to a maximum distance of 12 inches. These are branched and rebranched to the third and fourth order, the ultimate termini being almost microscopic in size (plate 26, A).

Gilia aggregata.—The long pink or red racemes of this abundant biennial are very conspicuous on the half-gravel-slide, where the plant is quite abun-

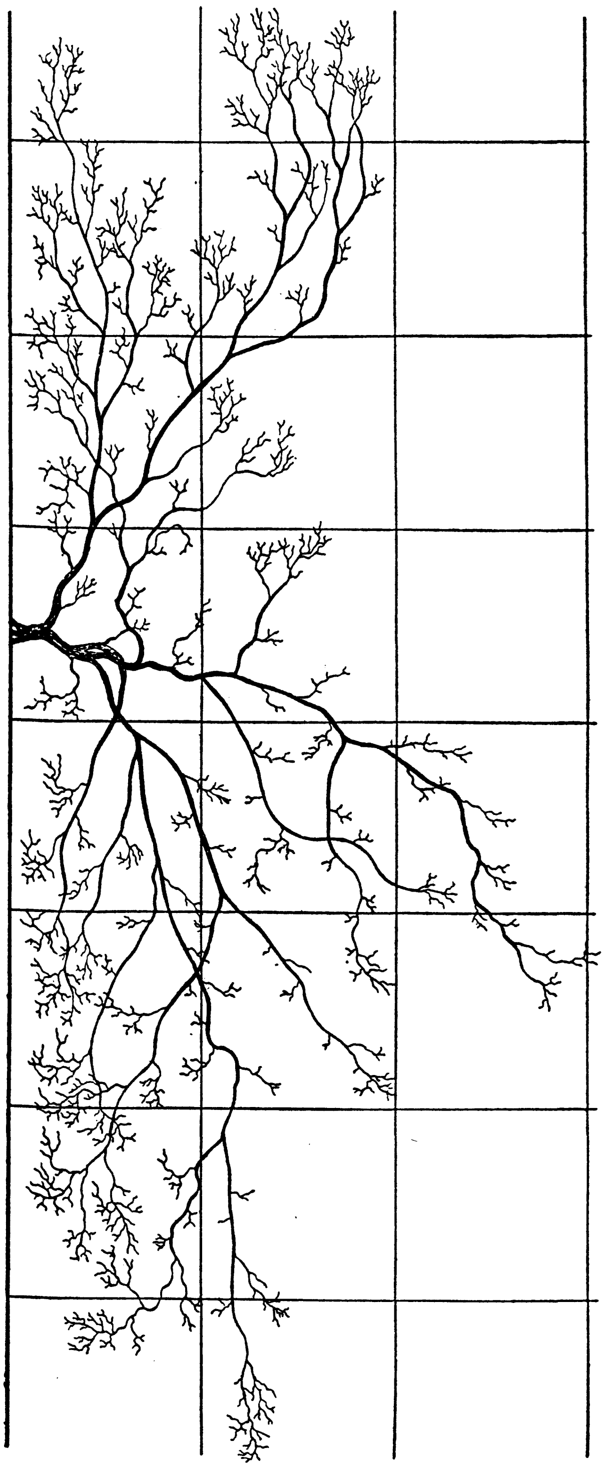


FIG. 40.—Root system of *Geranium cæspitosum.*

dant. Of the 6 plants examined all had a large tap-root from 4 to 8 mm. in diameter. The tap sends off numerous branches near the surface and tapers so rapidly that at a depth of 10 inches it seldom exceeds 1 or 2 mm. in diameter. The laterals are mostly wide-spreading, frequently nearly horizontal in position, and much forked and rebranched into very abundant fine termini. They reach distances of over a foot from the base of the plant. Like most plants of this habitat the root system is not deep. No *Gilia* roots were found below the 28-inch level, but the moist surface soil is well filled with great quantities of fine absorbing rootlets, especially to the depth of 18 inches.

Potentilla arguta glandulosa.—This species frequently forms families on the half-gravel-slide. A large clump of these plants was examined. The complexity of the rootstocks is such that they are hard to describe. The individual clumps are connected throughout long distances by much-branched underground parts, which often run horizontally or sometimes obliquely at depths varying from 3 to more than 18 inches. These underground connecting parts may reach a diameter of a centimeter, but are usually much smaller. They are very much branched and give rise to the clusters of stems at intervals of 3 inches to more than a foot. At a depth of 2 to 5 inches the roots often throw off a large number of small, short, but exceedingly well-branched surface absorbing laterals. The larger roots are usually only 2 to 6 mm. in diameter and run off in all directions, some to a maximum depth of 4.5 feet, while the surface of the soil is filled with the extremely well-branched brush-like termini of the laterals. These clusters are from 6 to 10 inches in length. The deeper soils are also completely occupied by the irregularly branched and rebranched root network, often to a depth of 4 feet (plate 26, c).

Frasera speciosa.—This striking plant starts with a strong, rather fleshy, glistening white tap-root, which is 1.5 to over 2 cm. in diameter. It penetrates

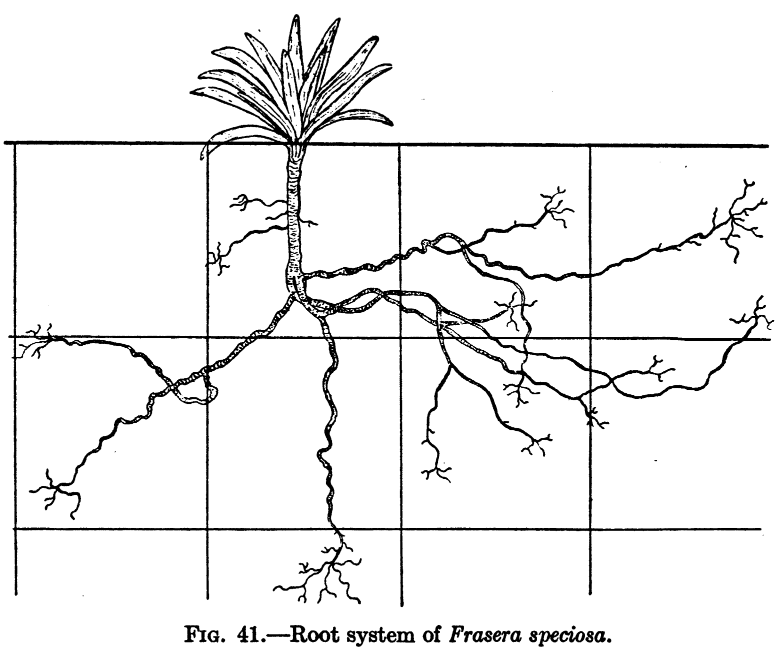


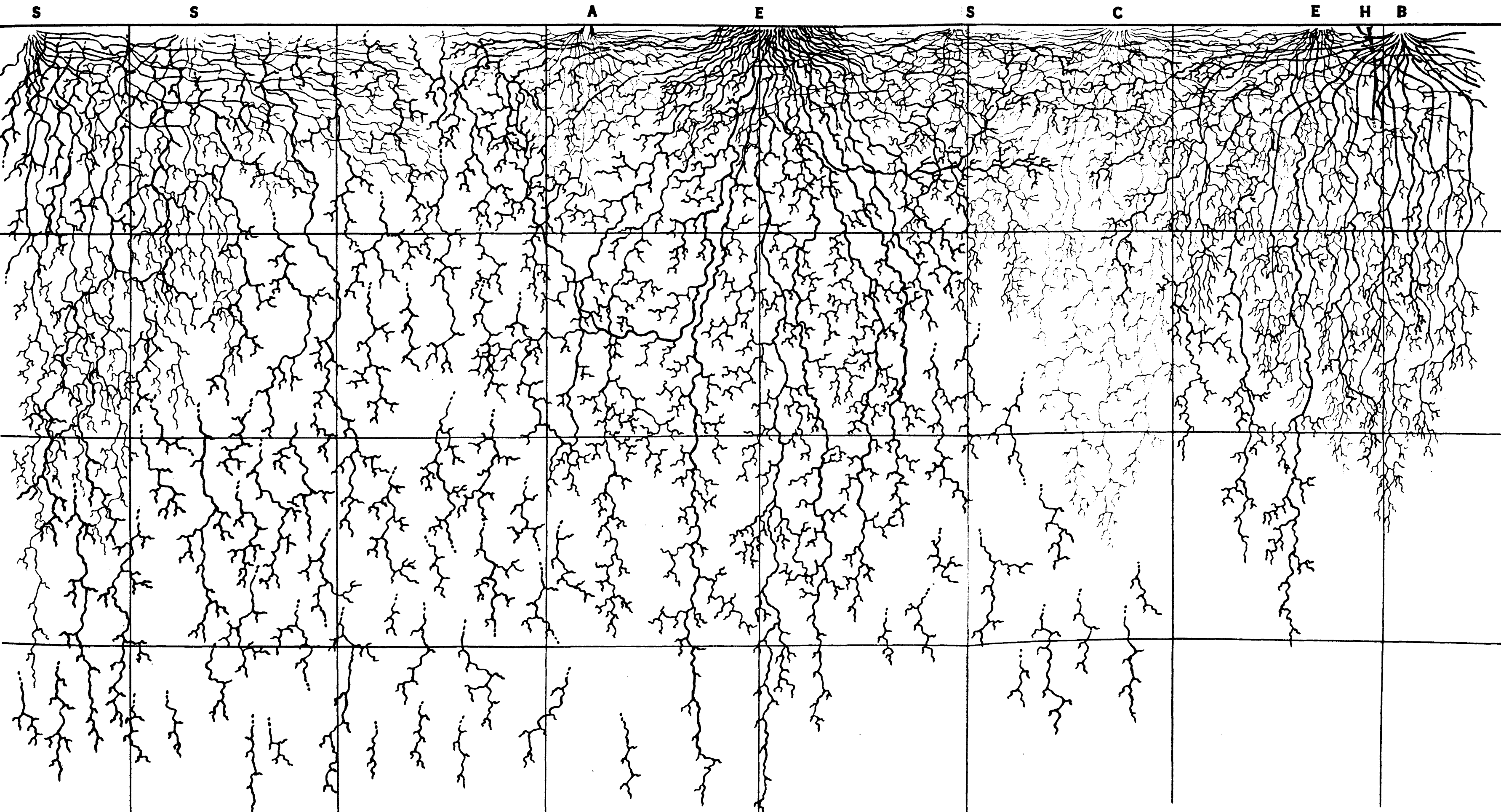
FIG. 41.—Root system of *Frasera speciosa*.

vertically downward to a depth of 9 inches, where it divides into 4 branches of almost equal diameter. This main tap, throughout its length and even to a short distance on the branches, was strongly marked by wrinkles, indicating a considerable degree of contraction. Indeed, throughout the entire root system, not excluding the smaller branches, characteristic wrinkles and constrictions occurred. At the point of origin the branches were about 7 or 8 mm. in diameter. They traversed the soil in diverse directions, for the most part running more or less parallel with the surface, but giving off some vertically or obliquely descending branches. The former sometimes ran off laterally to a distance of 2 or 3 feet and at a depth of from 6 to 18 inches below the surface of the soil. As the ultimate laterals approached their extremities they were characterized by a marked, abrupt branching habit, which resulted in a tuft of from 6 to 10 or more rather coarse, poorly branched termini varying from 2 to 5 cm. in length (fig. 41). The diameter of the laterals at the point where they develop these tufts is often 2 mm. or more. Arising from these more or less horizontal laterals, vertically descending roots were found to penetrate a maximum depth of 24 to 30 inches. Like the tap, the branches of all orders were more or less fleshy and very brittle, affording a decided capacity for food storage. Several plants of different ages were examined. In general the above description answers for all.

Aster porteri.—This plant, which grows abundantly on the half-gravel-slide, has the stem clusters connected by short rhizomes and possesses the root system characteristic for plants of this habitat. From the base of the stems arise a multitude of fibrous roots, the largest seldom being over 2 mm. in diameter. Great numbers descend vertically or somewhat obliquely, some to a maximum depth of 30 inches. Many others run off rather horizontally or obliquely to a distance of 6 to 12 inches on either side of the plant before turning downward. All are profusely branched and rebranched into a fine absorbing network, so that every cubic inch of the soil for nearly a foot on each side of the plant and to a depth of over 2 feet is forced to yield up its available water and solutes to the excellent absorbing system.

HALF-GRAVEL-SLIDE ROOT SYSTEMS AND THE HALF-GRAVEL-SLIDE ENVIRONMENT.

While the plants of the half-gravel-slide habitat still retain the superficial and wide-spreading root habit of their predecessors of the gravel-slide, this is supplemented by a much deeper portion which extracts water and nutrients below the 18-inch level, as well as very largely from the second and third foot of soil. The surface-spreading roots may be explained by the frequent mountain showers which supply water rather continuously to the shallow soils, while the deeper-seated ones reflect the better deep-soil conditions, but especially the more intense competition for water of this denser population. The thick surface layer of loose rock fragments of the gravel-slide has here become more disintegrated and closely packed, and soon gives way to soil. Hence water evaporates more freely. This, with the competition of the taller half-gravel-slide plants, accounts for the disappearance of gravel-slide species. The former shade those of lesser height, but especially compete with them for water, undoubtedly relying upon their deeper penetrating roots during periods of drought.



Quadrat-bisect in the half-gravel slide. The face of the trench was cut along the front of the quadrat shown in Plate 26 A: S, *Solidago oreophila;* A, *Allium cernuum;* E, *Elymus triticoides,* fragments of which are represented in blue; C, *Calamagrostis purpurascens;* H, *Heuchera parvifolia;* B, *Besseya plantaginea.*

The soils of the half-gravel-slide are much more favorable for plant growth. Although from one-third to one-half of the surface may still be unoccupied, enough plants are present to prevent almost wholly the slipping of the soil, even the thin surface layer of pebbles being moved between plant clumps only during heavy showers. The first 8 to 10 inches of soil has a rich brown color, due to the presence of considerable humus formed by the decayed vegetation. It has many more fine particles and fewer large, coarse ones than the corresponding layer on the gravel-slide. Although there is considerable variation, the rock is decayed to a greater depth, due undoubtedly in part to the excretions of plant roots and the resultant porosity of the soil, and to greater water penetration following the death and decay of the roots. The soil underlying the surface layer already described, while still consisting largely of the decayed granite, is looser in texture and has fewer large particles and much more sand intermixed with it, thus affording a more congenial home for roots. In the gravel-slide only local areas of soil about the sparsely spaced plants are filled with roots, especially in the surface layer. In the half-gravel-slide, on account of the greater number of plants and especially grasses, all of the soil is well filled with roots to a depth of at least 18 to 20 inches or more, while many roots penetrate to a depth of 3 feet.

The amount and distribution of the precipitation is practically identical with that of the gravel-slide and the actual available water-content is about the same also (table 18). This results from the greater water-holding capacity of the soil, due to the presence of more humus coupled with more perfect rock decomposition, and occurs in spite of the increased absorbing and transpiring surface offered by the plant population. The evaporating power of the air as shown in table 19 is considerably less than that of the gravel-slide, owing to the greater transpiration and shade and the reduced wind movement resulting from the denser community. Notwithstanding the fact that one-third to one-half of the soil surface may still be unoccupied, root competition is rather severe. This is well illustrated in the bisect shown in plate B, though this was made in a rather open portion of the community. It should be borne in mind that the roots seen represent only those actually occurring in a rectangle of soil 7 feet long and 4 inches wide. Undoubtedly competition is one of the large factors in determining root distribution. This must be taken into account with the soil conditions in reaching a logical explanation of the root habits of the plants of this habitat.

VIII. THE FOREST COMMUNITY.

A forest community finally occupies the half-gravel-slide. It is represented by *Pinus ponderosa* or *Pseudotsuga mucronata*, both of which are frequently preceded by a chaparral stage. Along the streams and moister slopes, Douglas fir meets the Engelmann spruce, *Picea engelmanni*, with which it often forms a mictium. A rather large number of herbs and undershrubs characteristic of the more mesophytic type of forest were examained (plate 27, A, B).

Pirola chlorantha.—This evergreen herb is very abundant and forms extensive clans on the floor of the spruce forest. The clusters of leaves arise at intervals from a few inches to more than a foot from the glistening white underground stems. These vary from 1 to 3 mm. in diameter, branch freely, and form a connecting system for the individual plants. They lie at a depth varying from 0.5 inch to about 5 inches. Just before the rootstock approaches the surface to send up a cluster of leaves, it invariably branches, the branch continuing to the next plant, etc. The root system is very meager and consists of brownish roots arising at irregular intervals, usually about 1 inch apart on the horizontal rootstock, although it is not unusual to find several inches of the rootstock practically free from rootlets. These roots penetrate the moist duff and rich humus soil to a depth of only 6 to 10 inches; while many of them are only 1 to 1.5 inches long, others form brush-like clusters 3 to 5 inches in length (fig. 42).

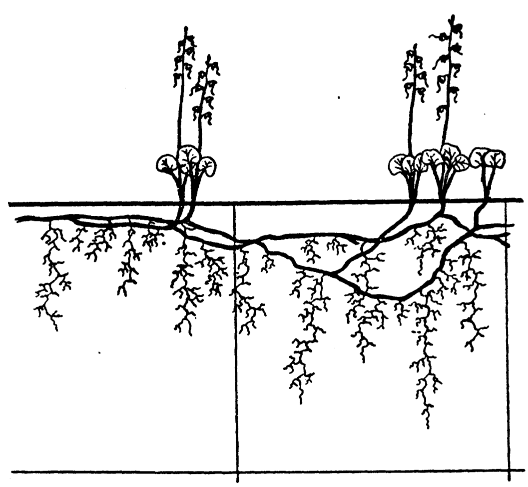


FIG. 42.—*Pirola chlorantha.*

Thalictrum fendleri.—This polydemic ranges in habitat from the half gravel-slide, into which it has worked its way from the bordering woodland to dense spruce forest. In the Douglas fir forest it forms extensive societies. The plants here described were examined in a spruce forest. The slender tops of these plants arise from a meager system of rhizomes almost black in color, from 0.5 to 2 mm. in diameter, and seldom over 6 to 8 inches long. The root system springs from the rhizome near the base of the erect stems, sometimes as many as 30 or more fibrous roots originating from the base of single plant. For the most part the roots extend in a direction almost parallel with the surface of the soil. The depth at which they lie varies from 2 to 8 inches and the maximum lateral extent is 14 inches. Relatively a very few of the roots take a more vertical or slightly oblique downward course, but none reach a depth below 18 inches. The main roots are a millimeter or less in diameter. Throughout the course of the roots an elaborate system of branching occurs. The branches ramify to the third and fourth order, and vary in length from a few millimeters to 3 or 4 inches. Near their extremities the main roots are so well branched and divided that the tip consists of a brush-like mat of fine rootlets (fig. 43).

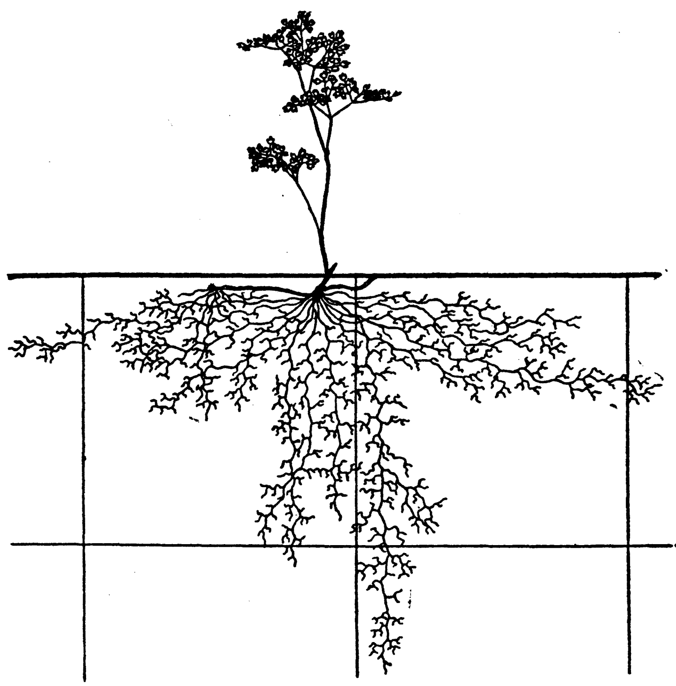


FIG. 43.—*Thalictrum fendleri.*

Erigeron asper.—This plant forms fine societies in the dense shade of the spruce-fir forest. The individual clumps are connected by means of branched surface rhizomes, seldom over and often less than 2 mm. in diameter, which usually do not lie at a depth beyond 2 inches. From the base of the plant in particular, as well as along the rhizome, a well-developed system of rather fibrous roots arises. The largest of these do not exceed a millimeter in diameter and are usually much smaller. While some of these penetrate to maximum depths of 26 to 30 inches, the first 18 inches of soil and especially the first 6 inches are thoroughly filled with the hairlike and profusely branched rootlets. Frequently these branches, which arise in great abundance all along the main roots, run off obliquely and even almost horizontally to distances of 5 to 10 inches from the base of the plant (fig. 44).

Erigeron macranthus.—This plant, which is not infrequent in openings in the forest, propagates by means of rather coarse rhizomes often about 5 mm. in diameter and several inches in length. From the base of the plant and from the rhizomes arise great clusters of fibrous roots from 3 to 4 mm. to only 0.5 mm. in diameter. While many of these run rather vertically downward, so that some of the longer ones reach depths of 40 inches, others spread laterally to a distance of 14 to 18 inches and reach depths of only 4 to 12 inches. Thus the soil for a distance of more than a foot on either side of the plant and to a depth of 2 or 3 feet is well supplied with these fibrous roots. The branching of the root is almost identical with that of *Erigeron asper* (fig. 44), with which this species seems to intergrade.

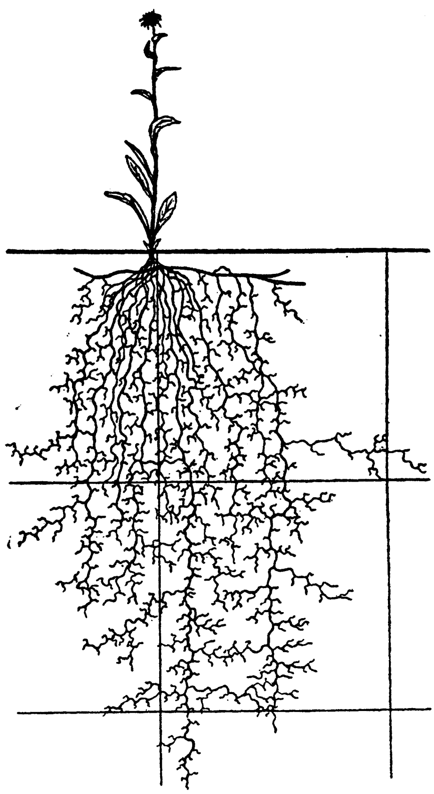


FIG. 44.—Rhizome and roots of *Erigeron asper*.

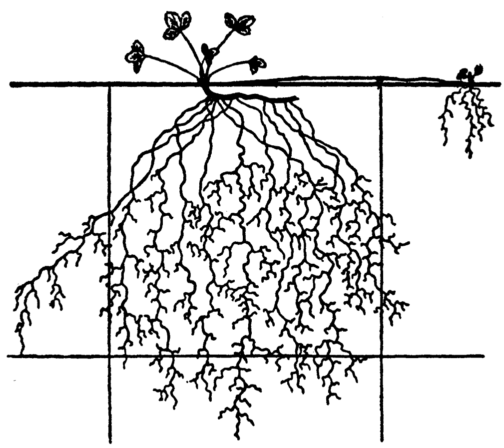


FIG. 45.—*Fragaria virginiana*.

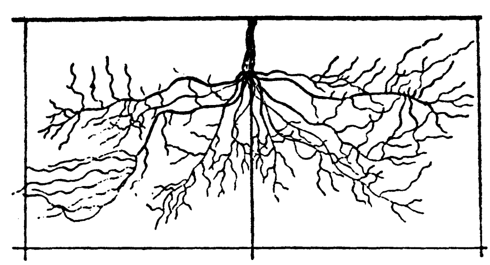


FIG. 46.—*Allium cernuum*.

Fragaria virginiana.—*Fragaria* forms societies rather extensively on the forest floor, even in the dense shade of spruce seedlings. In addition to the long, slender stolons, it is furnished with rhizomes only 3 to 5 mm. in diameter but often several inches long. From these arise the dark-colored fibrous roots a millimeter or less in diameter. There are usually 6 to 10 of these on an inch of the rhizome. Many of them pursue an oblique course to a lateral distance of 4 to 10 inches from the base of the plant, where they reach a depth of 4 to 12 inches. Others penetrate more vertically downward to a maximum depth of 12 to 14 inches. While the first inch of the roots below the superficial rhizomes is rather destitute of branches, below this depth, especially in the last 6 to 8 inches, the roots are supplied with an abundance of fine rebranched termini ranging in length from 1 to 5 cm. (fig. 45).

Allium cernuum.—This plant is very characteristic of half-gravel-slides, but also occurs rather abundantly in the open portions of the fir forest. The plant was examined in the forest habitat. The bulb, which is usually 12 to 15 mm. in diameter, occurs at a depth of about 2 inches. From its base arises a cluster of 10 to 20, or sometimes more, fibrous roots a millimeter or less in diameter. These spread widely in the surface 6 or 8 inches of soil. Laterals were traced to a horizontal distance of 8 to 12 inches from the base of the bulb, where they ended at a depth of 4 to 8 inches. No roots were found at a greater depth than 10 inches. These glistening white fibrous roots branch freely into laterals from a few centimeters to 4 or 5 inches in length, but these secondary roots are themselves scarcely at all branched (fig. 46).

Aralia nudicaulis.—This plant is often abundant on the lower slopes of the fir and spruce forests, where it sometimes forms extensive communities. The individuals are connected by a much-branched system of rhizomes, which vary in diameter from 3 to 4 mm. to more than a centimeter. Frequently they lie just below the soil surface, but they are quite abundant at all levels and run in all directions and at all angles in the first 18 to 24 inches of soil.

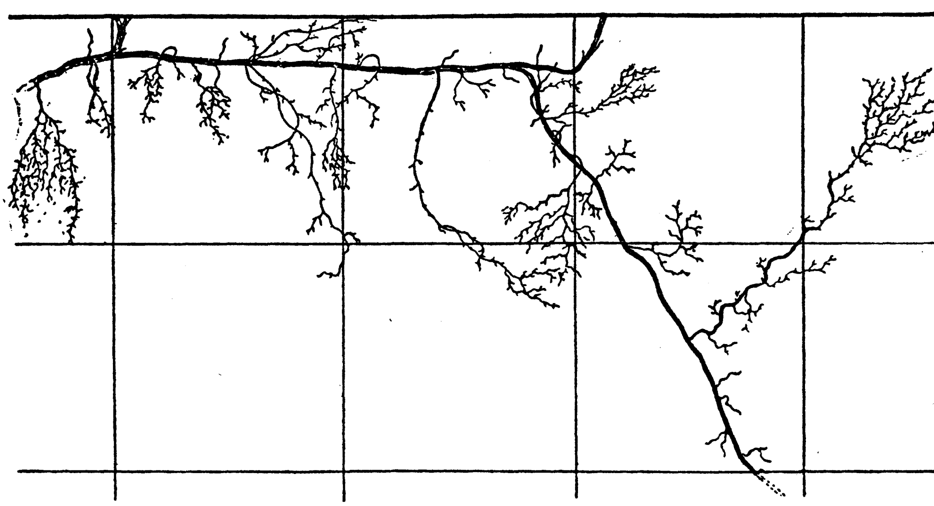


FIG. 47.—Rhizomes and root system of *Aralia nudicaulis.*

As shown in figure 47, there arise from the nodes of the rhizomes rootlets with clusters of well-branched termini, the whole usually not over 2 to 5 cm. long. Often, however, rather well-branched roots 18 to 20 inches in length occur. The direction in which these run depends somewhat upon the depth of the rhizome. If the root arises from a rhizome near the surface it takes a vertical or oblique course downward; at intermediate depths the roots frequently run off horizontally, while from the deepest rhizomes it is not unusual to find them ascending in an oblique direction toward the surface. As a whole, the root system is rather poorly developed, probably due to the dense shade in which the plant grows.

Opulaster opulifolius.—This shrub forms a very characteristic undergrowth in pine woods as well as in the open fir forest. Indeed, it reaches its best development in the better light of the chaparral community and dies out almost completely in forests with a closed canopy. Its rôle in succession is not unlike that of *Corylus* (page 30). Two plants, 5 and 12 years old respectively and about 3 feet high, were examined in the Douglas fir forest. From the base of the clump prostrate stems about a centimeter or less in diameter run horizontally just beneath the surface, or at least at a depth of only a few inches, to distances of 2 or 3 feet, where they give rise to new plants. The roots of this plant are often large and woody, sometimes a centimeter or more in diameter, but usually smaller. They have a lateral spread of 5 to 8 feet, but seldom penetrate the soil to a greater depth than 3 feet (plate 30, A). From the base of the clump 6 to 12 of these roots arise. They run out laterally in all directions, tapering gradually and branching freely and often dichotomously, the ultimate branches being very minute and forming a great network of absorbing brushes. From the main roots and their branches, as well as from the rhizomes, great clusters of exceedingly well-branched laterals (from a few centimeters to several inches in length) lay hold upon the moist soil of the forest floor. In fact, the majority of the roots are confined to the surface 8 inches, while only one or two branches were found to reach the maximum depth of 32 inches.

Ribes lacustre.—This plant is characteristic of rather dense moist woodland. Four specimens, 6 or 7 years old and 1.5 to 2 feet high, were examined. They spread through distances of 1 to 2 feet or more by means of rhizomes or prostrate stems. From the base of the clump a tap-root 10 to 15 mm. in diameter arises. Instead of descending vertically, this almost invariably runs off in the surface soil, dividing rapidly into many major branches. While many of these are only 2 to 4 mm. in diameter, they taper so slowly that at a horizontal distance of 3 to 4 feet from the plant they may still be 1 to 2 mm. wide. These long, tough surface laterals pursue their winding way through a length of 6 to 8 feet, frequently reaching distances of from 5 to 7 feet from the plant. They are usually unbranched or only poorly branched, save for isolated brushes of small laterals, until within 12 to 18 inches from their tip. Here they divide up into long, slender laterals all well-branched near their extremities, but not at all to the same degree as *Opulaster*. While many of these branches end in moist duff, others penetrate downward to a depth of 8 to 12 inches. The major portion of the root system is confined to the surface soil, but a few branches were found at a depth of 2 to over 3 feet (plate 28, B).

Rosa acicularis.—The rose frequently occurs in the spruce-fir forest, where it is a relict of earlier stages in the succession. While under the lower light intensity of the forest it is merely a low shrub, outside the forest it frequently forms dense chaparral several feet in height. The plants are connected by an extensive system of rhizomes which lie at a depth of 2 to 10 inches and vary in diameter from 2 to 6 mm. These rhizomes run in all directions, branching freely and at irregular intervals, giving rise to the stems which seldom reach a height in the forest of more than 1.5 to 2.5 feet. The root system originating from these rhizomes consists of both long and short roots. The shorter ones vary in length from 1 to 12 inches. Almost from their point of origin they are profusely branched and rebranched so as to form a brush-like mat. These groups of thickly branched roots penetrate the surface soil in all directions, forming a very efficient absorbing system. The longer roots vary in diameter from 1 to 4 mm. at their point of origin and penetrate the soil downward in a wandering course to a maximum depth of 2 to 5 feet. Throughout their course, these longer roots are fairly well supplied with both short and long branches, the shorter ones varying in length from 0.5 to 3 inches. The longer ones, which are almost threadlike in appearance, may wander off in all directions, even obliquely upward to a distance often of 2 feet or more. These branches are rebranched much after the fashion of the main roots already described. As the main roots and these larger branches approach their extremities, they are divided several times so as to form fairly well-branched termini.

Arctostaphylos uva-ursi.—This ericad, which is the typical undershrub of the pine forest, also occurs rather abundantly in the more open portions of the Douglas fir forest, where it forms great mats covering areas of many square meters. Its xerophytic qualities are shown by its frequent appearance in the half-gravel-slide community. A very elaborate and well-developed root system arises from the woody prostrate stems, which vary from a few millimeters to 3 cm. in diameter. While some of the roots reach a maximum depth of from 40 to 46 inches, the major portion of the absorbing system lies in the first 18 inches of soil. From the base of the prostrate stems as well as from numerous shallow horizontal roots arise great numbers of rootlets only 1 to 2 mm. in diameter and from 4 to 8 inches long, but so abundantly supplied with masses of branched and rebranched laterals that they fill the surface soil with a network of roots. In addition to these, larger branches, sometimes even a centimeter in diameter, run off at all angles from the horizontal to vertically downward, pursuing tortuous courses and branching and rebranching freely. They attain a length of 3 or 4 feet and end at depths varying from a few inches to more than 3 feet. The branches from these as well as the ends of the main roots themselves form great mats of well-developed rootlets in the crevices of the gravelly soil. Plate 28, A, shows something of the extent and abundance of these branches.

Senecio cernuus.—This herb is abundant in the fir forest. The root system consists of a group of from 8 to 20 white, somewhat fleshy roots. At their point of origin they vary from less than 0.5 mm. to 2 or 3 mm. in diameter. Relatively few of these penetrate the soil in a vertical or slightly oblique direction to a maximum distance of 12 to 15 inches. By far the greater part of these roots take a course practically parallel with the surface at a depth of from 1 to 3 inches—in fact, many of them run just below the surface accumulation of duff and semi-decayed leaves; others may take a slightly more downward course and end at a depth of from 4 to 8 inches below the surface. The maximum spread of these horizontal roots may vary from a few inches to 18 or 25 inches. Throughout their course the main roots are fairly well supplied with laterals varying in length from a centimeter or less to 6 or 8 inches. These in turn may be branched again to the second and third order, so as to form a very efficient surface system well adapted to absorb the shallow water-content resulting from the frequent mountain showers. Eight plants were examined (fig. 48).

Castilleia miniata.—This plant is a common component not only of grassy half-gravel-slides, but it also occurs rather abundantly in the fir forest. Relative to the size of the plant it has a very meager root system. This consists of 5 to 20 main branches, varying in size from 1 to 3 mm. These all show a strong tendency to spread out laterally and run off in the surface soil, usually at a depth not greater than 5 to 6 inches to distances of 12 to 18 inches or less. No roots were found penetrating deeper than 8 inches. While these rather coarse, yellow, brittle roots are fairly well branched, they are only poorly supplied with fine absorbing laterals as compared with other plants examined in this community.

Heuchera parvifolia.—This plant is fairly abundant in the Douglas fir forest. It has a strong tap-root, sometimes as large as 15 mm. in diameter. However, this tapers so rapidly that within a distance of 6 to 8 inches it is usually not more than 1 to 2 mm. wide (fig. 49). Of the 10 plants examined only 3 had roots penetrating deeper than 6 inches. In these cases the tap penetrated rather vertically downward, having no large branches but being covered below a depth of 4 inches with multitudes of fine laterals only a centimeter or two in length. Near the tips they branch profusely and reach depths of 15, 18, and 20 inches, respectively. Even in these plants the 2 or 3

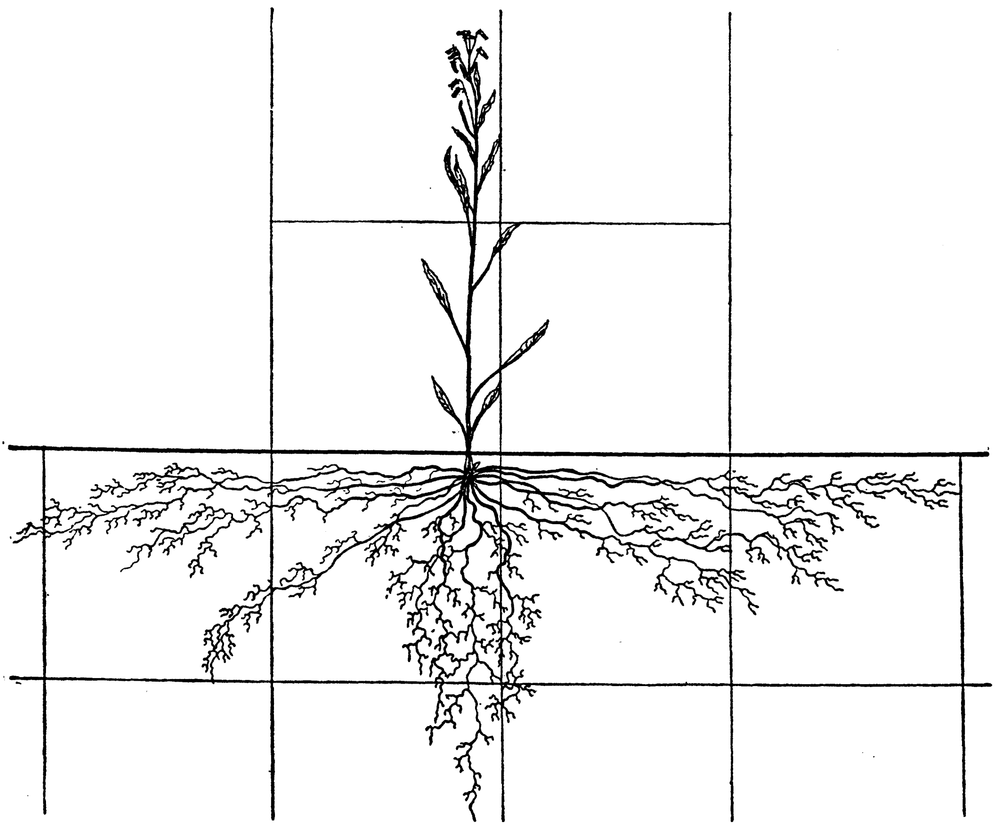


FIG. 48.—*Senecio cernuus.*

strong laterals, 4 to 7 mm. in diameter, originated just below the crown and, tapering rapidly like the tap-root, ran off horizontally at a depth of about 2 inches to a distance of 18 to 24 inches from the base of the plant. Unlike the tap, these large laterals were well branched with rather widely spreading rootlets, which gave off multitudes of tertiary branches, all of which ended in a great network of absorbing rootlets. Many fine, much-branched rootlets, only a few inches long, also originated from the crown of the plant where it was buried in the moist duff. The root systems of those described were the same as the others examined, except that the tap-roots of the latter group took a course up the slope and assumed the rôle of laterals already described.

Saxifraga bronchialis.—This plant forms large mats, often several feet in extent, which cover the moist soil on the forest floor or even occur on moist rock surfaces. It is especially well developed in the Douglas fir community. From the main root prostrate stems from 1 inch to over 1 foot in length extend out in all directions in the surface soil. These send up erect branches 5 inches long, the shorter ones being near the growing tip. As the soil accumulates about the bases of these erect stems, the lower leaves die and only an inch or less of the living tip is exposed. These branches with their dead leaves and accumulated débris occur in such density that they afford a congenial substratum for the abundant rootlets which arise from the horizontal portion especially, as well as from the erect part of the stems. These delicate roots, however, which vary from 1 to 14 inches in length, run off in a horizontal direction in the moist soil just below the mat and seldom reach a depth greater than 3 to 4 inches. They divide into fine, hairlike, well-branched termini and occur in exceedingly great numbers. The main root or roots, depending upon the size of the mat, are tough and somewhat woody, black in color, and from 2 to 3 mm. in diameter. They also run off horizontally and usually up the slope, branching profusely and often dichotomously. They spread out somewhat fan-shaped and reach a distance of from 3 feet to over 5 feet from the base of the plant. Although they were found to penetrate not deeper than 4 to 5 inches, their wide spread and the great numbers and extreme division of their branches enable them to extract sufficient water from the surface soil. Indeed, the termini of many of these branches consists of such a mat of delicate, almost microscopic, ultimate branches that it is quite impossible to depict them adequately either with the pen or the camera.

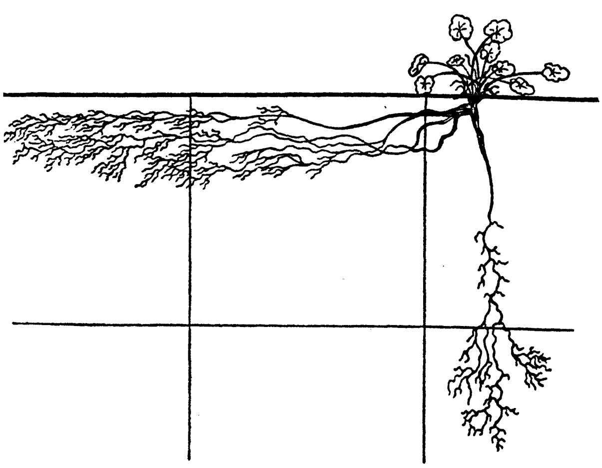


Fig. 49.—*Heuchera parvifolia.*

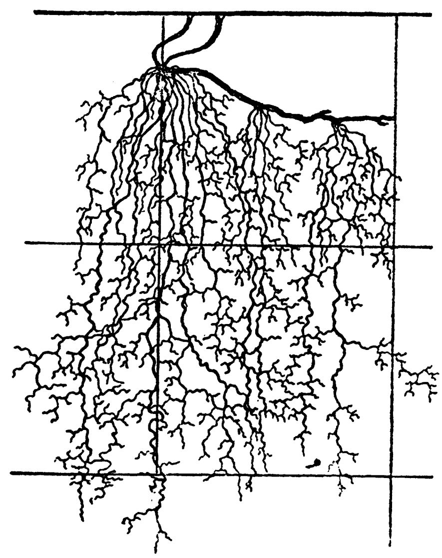


Fig. 50.—*Haplopappus parryi.*

Haplopappus parryi.—This composite forms dense societies in the shady woodland, the rosettes of long leaves almost completely covering the surface over local areas (plate 27, B). It is supplied with a system of stout, much-branched rhizomes that vary in diameter from 2 to 8 mm. and extend from just beneath the surface to a depth of from 6 to 8 inches (fig. 50). From these rhizomes arise large clusters of roots ranging in diameter from 2 mm. to less than 0.5 mm. These roots descend rather vertically or somewhat obliquely and completely fill the soil to a depth of 25 inches, while some reach a maximum depth of 28 inches. The younger roots are supplied with many branches from their point of origin and are reenforced by a great network of branches arising from the older roots in the deeper soil at 6 to 10 inches. The deeper roots and their network of fine branches spread widely, often running for several inches horizontally through the moist gravel soil. The whole root system is surprisingly well developed, considering the habitat conditions under which the plant grows.

FOREST ROOT SYSTEMS AND THE FOREST ENVIRONMENT.

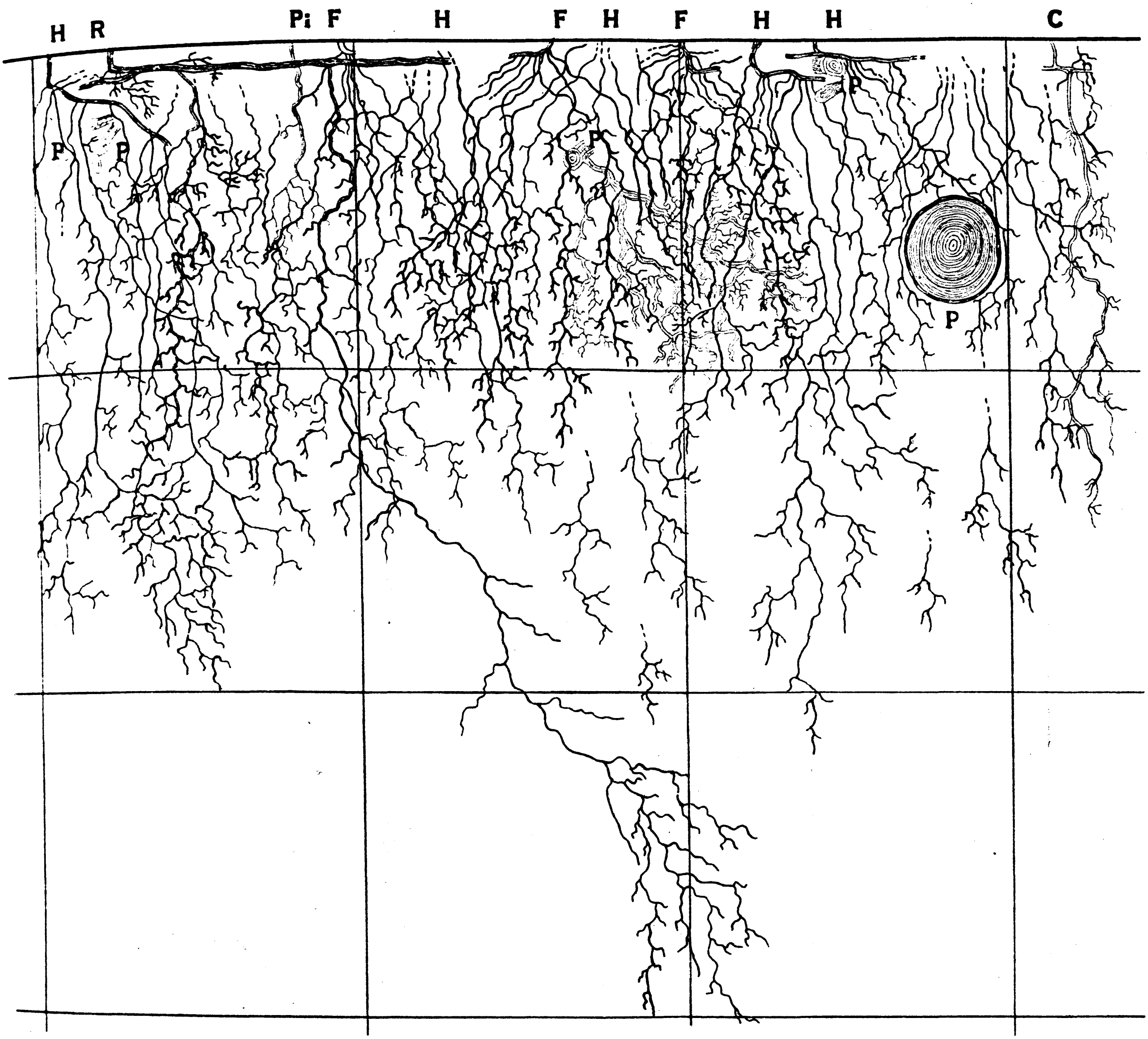
A survey of the preceding data reveals the fact that the herbs and shrubs of the forest floor are relatively shallow-rooted. Almost without exception the bulk of the absorbing system lies within the surface 18 inches of soil. *Arctostaphylos* and *Rosa* have roots which penetrate deeper. The former, however, shows its xerophytic tendencies by being the typical half-shrub of the open pine forest and often forming large mats in the half-gravel-slide. In the Douglas fir forest it occurs only in the most open places and disappears entirely in the spruce. *Rosa* is a relict from an earlier stage of succession. It makes a much better growth in full light, even in dry situations, where it forms dense thickets. Even the roots of many of the Douglas fir and spruce trees, including seedlings, saplings, and mature plants which were incidentally encountered in the course of the work, were found to possess many shallow roots (plate C). The root relations of forest dominants offer an exceedingly profitable field for investigation.

The water-content of the soil offers the logical explanation for the shallow root development of these forest plants. The forest soil is usually deeper and always much richer in organic matter than that of the half-gravel-slide. Usually there is a layer of 1 or 2 inches of duff, beneath which the soil is very rich in decomposed humus to a variable depth of 8 to 18 inches or more. Such a substratum furnishes

TABLE 20.—*Average daily evaporating power of the air in the forest communities.*

Date.	Douglas fir.	Engelmann spruce.	Date.	Douglas fir.	Engelmann spruce.
	c.c.	*c.c.*		*c.c.*	*c.c.*
June 10–17	28.8	21.6	July 22–29	11.3	8.5
June 17–24	11.1	7.1	July 29 to Aug. 5	16.0	11.4
June 24 to July 1	20.4	15.0	Aug. 5–12	8.6	6.2
July 1–8	15.2	11.1	Aug. 12–17	8.5	6.3
July 8–15	5.7	4.4	Aug. 17–23	11.6	8.8
July 15–22	6.1	5.2			

an excellent medium with a high water-holding capacity to catch the precipitation of winter as well as that of the frequent summer showers. The shade of the trees and various forest layers reduces the evaporating power of the air (table 20), while the water-loss from the soil is further retarded by the layer of duff.



Quadrat-bisect showing root systems of shrubs and herbs of the forest floor. This was made along the front edge of the quadrat shown in plate 27 B: H, *Haplopappus parryi;* R, *Rosa acicularis;* Pi, *Pinus flexilis;* F, *Fragaria virginiana;* C, *Chamænerium angustifolium;* P, *Picea engelmanni.*

That sufficient water ordinarily does not enter the soil to penetrate deeply is shown by the following series of soil-moisture determinations made during the summer of 1918:

TABLE 21.—*Water-content of the soil in the forest communities.*

Date.	Depth of sample, 0 to 6 inches.		Depth of sample, 6 to 12 inches.		Depth of sample, 12 to 18 inches.		Depth of sample, 2 to 3 feet.	
	Fir.	Spruce.	Fir.	Spruce.	Fir.	Spruce.	Fir.	Spruce.
June 10.......	6.6	12.7	3.1	8.1	....	....	....	....
June 15.......	5.3	8.5	2.1	7.2	1.7	5.6	1.7	4.6
June 24.......	19.8	19.2	6.2	10.0	3.5	9.2	....	....
July 1.......	13.1	15.3	7.3	5.2	5.8	4.4	....	....
July 8.......	8.1	12.8	5.4	5.2	4.8	8.4	....	....
July 15.......	14.7	15.1	7.1	8.9	4.6	5.1	3.6	7.3
July 23.......	9.2	....	3.9	....	2.7	....	....	....
July 29.......	16.4	18.8	11.3	9.2	8.6	5.8	....	....
Aug. 5.......	16.5	16.3	7.0	7.7	6.2	7.7	....	....
Aug. 12.......	*18.0	10.3	*9.1	7.0	*6.7	4.3	*5.6	6.9
Aug. 19.......	16.4	21.0	7.8	11.2	3.2	8.2	....	....

* Samples taken the day following a rain of 1.84 inches.

An examination of table 21 makes clear the fact that the greatest amount of available water is in the surface 18 inches of soil. This should account for the shallow root habit of forest herbs and shrubs. The lesser extent of the root systems of these forest plants, when compared as a group with the species of any of the preceding habitats, is correlated with the more favorable aerial conditions for water conservation on the forest floor. Indeed, not only is the temperature much lower, but the wind movement also is greatly checked. In the fir forest the average daily wind velocity was only 29 miles as compared with 67 miles on the half-gravel-slide. Likewise, in the forest diffuse light and low evaporating power of the air are the rule. Compared, for example with the half-gravel-slide habitat, the aerial conditions in the Douglas fir forest are only 54 per cent as severe. The evaporation in the spruce forest is only 40 per cent as great as that on the half-gravel-slide.

IX. ECADS.

During the course of these investigations, a number of species were encountered and excavated in two or more different habitats. While a few of these have already been described in explaining the root habits of plants of the several plant communities, others have been reserved for comparison in this place. Differences in ecads were always determined by actual comparison of plant materials from the two habitats at the same time, and these differences are expressed wherever possible by means of photographs or drawings. Any personal error was further checked out by the judgment of a second person, no statements being made until there was a consensus of opinion.

Smilacina stellata.—The shade form was excavated in a spruce-fir forest 24 feet from the brook bank and 3.5 feet above the water-level. The ground was covered with about 0.5 inch of raw humus underlaid with about 2 inches of well-decomposed humus mixed with sand. Below this was very moist sand with gravel and rocks. The light value was only 0.02.

The roots were much sparser and shorter, although somewhat greater in diameter than those of the gravel-slide form (page 85). While an inch of the rhizome of the latter form gave rise to 18 roots averaging 3.5 inches long, an average inch of the shade rhizome showed 8 roots only about 1.5 inches in length (plate 29, A). The longer roots, which have their origin near the base of the vertical stems, were likewise both fewer and shorter. In the gravel-slide form they varied from 2 to 5, in the shade form there was frequently none and seldom more than 2. The maximum length of the latter was only 16 inches, with an average length of about 11 inches; in the former case roots were traced to 44 inches in depth, with an average depth of about 32 inches. An intermediate stage was found in the fir forest, a habitat which has been shown to be somewhat less meosphytic than the spruce. The roots were nearly as sparse as those in the spruce forest but somewhat longer.

Chamænerium angustifolium.—This cosmopolitan plant is found in habitats of all degrees of mesophytism, from the gravel-slide and bare burn to very moist dark places in the spruce forest. A large group of these plants was examined at the foot of a slope near a stream and 4 or 5 feet above water-level. They were growing in the half shade of Douglas fir and mountain maple on one side. Below the first inch or two of duff and humus the soil consisted of a rich black sand intermixed with gravel and rich in humus to a depth of 2 or 3 feet. The plants are connected by means of strong, tough, well-branched rhizomes from 5 mm. to more than 10 mm. in diameter. These lie at depths varying from only 0.5 inch to 6 or 8 inches. The subterranean portions of the erect stems are practially free from roots. At rather distant intervals along the rhizomes, roots varying from 1 to 5 mm. in diameter arise. Many of these pursue a more or less vertically downward course, with but a few major branches, and reach depths of 35 to 48 inches (fig. 51). They taper very gradually and are only fairly well clothed with small rootlets. The latter usually occur in clusters of from 3 to 7 and are frequently less than an inch long. In addition to these, however, other longer and abundantly branched laterals supplement the absorbing system. These extend from 3 to 10 inches. Sometimes these deep roots break up into numerous branches, all of which are similar to those already described. In addition to these larger roots, the rootstock also gives rise to smaller, shallower, and frequently obl'que laterals. In fact, the larger roots also sometimes take an oblique course. As indicated in the figure, the root system is somewhat meager. The older roots may be identified by their brownish-yellow and somewhat flaky cortex and the tough, rope-like stele within, while the younger roots can be told by the clustered arrangement of their branches.

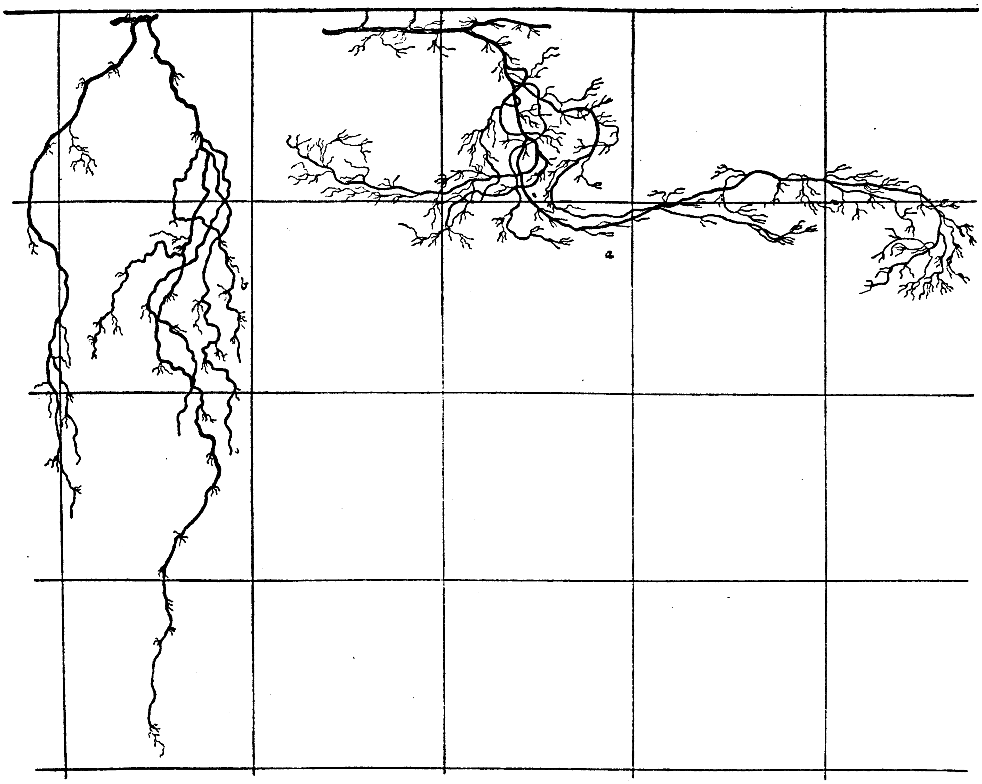


FIG. 51.—Root systems of ecads of *Chamænerium angustifolium: a*, gravel-slide; *b*, forest.

A number of plants were examined on a steep gravel-slide. Like those in the fir forest, they were mature and in full bloom. Those on the gravel-slide ranged from 1.5 to 2 feet in height, while the shade forms were 4 to 5 feet tall. The most noticeable differences in the underground parts were the shallowness and linear extent of the root systems and the remarkable difference in number and fineness of the smaller roots. Of the several plants examined on the gravel-slide, all sent roots up the slope at a depth of 2 to 10 inches or more. These frequently ran rather parallel with the surface, often branching into major branches, for a distance of 3 to 6 feet or more. From these rather shallow roots some of their branches pursued an obliquely downward course. None of them reached a depth greater than 20 inches, but almost invariably turned and ran parallel with the surface of the soil.

A comparison of the two root systems emphasized the paucity of small laterals in the forest ecad and their abundance in the gravel-slide. In the latter habitat, great clusters of fine rootlets (resulting from the repeated branching of the main roots, especially near their extremities) filled the soil with a web-like network in marked contrast to the rather sparse, absorbing rootlets of the shade form.

Elymus triticoides.—A family of *Elymus triticoides*, which formed a sod completely covering the ground under a canopy of Douglas fir, was examined. The soil was fairly well decomposed and filled with humus to a depth of 18 inches. The underlying soil was very similar to the second foot of soil in the half-gravel-slide. A trench 4 feet long was dug through the midst of the community and careful examination showed that no roots penetrated to a depth greater than 38 inches, while in the half-gravel-slide a maximum penetration of 46 inches by the larger roots was found (page 92). A marked difference was evident both in the density and coarseness of roots, especially in the first 2 feet of soil. In the half-gravel-slide the roots were not only much coarser, but they also filled the soil much more completely. In the shade form the flowering stalks were also much less abundant. The ecads of this species show differences in depth of penetration and in the number of roots per given area, as well as in size.

Bouteloua gracilis.—This widely distributed and important grass has been studied under four different habitat conditions. In the prairies of eastern Nebraska it occurs often in fairly pure stands on the lighter soils of gravelly ridges and is also frequently found dominating areas of alluvial soil on bottom lands. One of the several plants obtained from a gravelly ridge at Belmont is shown in plate 6, B, while the root system is fully described on page 8. A few roots reached a maximum depth of 46 inches, although below 2 feet they were very sparse. Great masses of roots occupied every cublic centimeter of the soil to a depth of 18 inches. Other groups of plants examined in two locations on alluvial soil showed a somewhat poorer development of the root system, but the general distribution and depth were very similar to those growing in the gravelly soil.

This grass was again examined on the plains of Colorado, where *Bouteloua* is the dominant, but where societies of *Aristida purpurea, Psoralea tenuiflora,* and *Artemisia frigida,* with other deep-rooted plants, indicate rather favorable water-content conditions. Here the soil was found to be well filled with these rootlets to a depth of 30 inches, while in the next 6 inches they were still fairly abundant, some of the longer ones penetrating to a maximum depth of 48 inches. The lateral spread in the surface soil was much more pronounced than in the plants examined near Lincoln. The plains species have many wide-spreading and exceedingly well-branched roots filling the surface soil and extending to 1.5 feet or more on all sides of the clump.

This grass was likewise studied in the typical hard-land or short-grass country about 25 miles southeast of Colorado Springs (p. 65, plate 20, A), where *Bouteloua* again dominates and the shallow-rooted *Opuntia polycantha* is the principal species, a community conspicuous for the almost entire absence of *Psoralea, Gutierrezia, Chrysopsis,* and other deep-rooted dicotyledons. A number of roots were found to penetrate to a depth of 51 inches, while they were very abundant to a depth of 40 inches. Their wide-spreading habit and their position in the soil was almost identical with those in the plains habitat just described.

Finally, a fourth group of these plants was excavated in the sandhills (p. 68), about 40 miles southeast of Colorado Springs but under the same general condition of rainfall. A trench 8 feet long and 5 feet deep was dug on a well-covered sandhill where this species was the dominant and formed rather pure stands. From the short, tough rhizomes, usually only an inch or two in length, great numbers of tough, fibrous roots a millimeter or less in diameter arise. On 4 cm. of one of these rhizomes 53 roots originated. While some of these pursue a rather vertically downward course to a maximum depth of 27 inches, or wander out somewhat obliquely, great numbers, perhaps half, run off more or less horizontally with the surface of the soil, reaching distances varying from 10 to 25 inches on either side of the clump (plate 29, B). Some of these ended only 2 to 4 inches below the soil surface, the tips of the growing roots being characterized for a distance of 1 to 3 inches by the entire absence of lateral branches. In fact, some of these had penetrated so near the surface that the soil had dried out and the root-tips had died. However, on mature roots, not only are the tips but also the entire root system densely clothed with great masses of capillary, much-branched rootlets of varying lengths, exclusive of the first 2 to 4 cm., which lie in the dry sand. Most of these branches are only 1 to 3 cm. in length, but frequently the main fibrous roots, especially the deeper-lying ones, repeatedly give off laterals many inches long, which run off at various angles from the course of the main root. While the first 8 inches of soil are literally filled with great masses of this wonderfully efficient absorbing system, the lower soil stratum to 2 feet is also abundantly supplied with fine roots.

The marked difference in the root penetration of the sandhill ecad as contrasted with those of the plains may be explained upon the basis of a fairly abundant water-supply in the shallower soils (first 2 feet) of the sandhills as contrasted with the uniformly drier soils of the plains. As pointed out on page 79, the surface sand forms a splendid mulch which inhibits water-loss by evaporation. It may be noted that the plants from the gravelly soils of the knoll in the prairie near Lincoln are intermediate in root depth between the sandhills and the plains ecads.

Stipa comata.—As described on page 53 and illustrated in plate 19, A, this species is deep-seated in the hard, dry plains soil. The surface 28 inches of soil is thoroughly occupied by the main roots, which are only a few millimeters apart, the interstices being completely filled with horizontal branches. Even to a depth of 32 inches the soil is fairly well filled with much kinked and rebranched threadlike rootlets, while not a few reach a maximum depth of over 5 feet. In addition, the lateral spread of the shallower oblique roots is 18 inches or more on either side of the base of the clump. The sandhill ecad of this species, while having a similar surface-root distribution, stands out in marked contrast as regards its superficial position in the soil, a condition already explained upon the basis of a relatively high water-content of the shallow soil.

Tufts of *Stipa comata* about an inch in diameter were abundant on the slopes and tops of captured sandhills. Of the 5 clumps examined, rather large roots (to the number of 15 to 25) originated from the base of the crown. None of these exceeded a millimeter in diameter. While some of them descended rather vertically to somewhat obliquely, a few reaching a maximum depth of 23 inches, the remainder ran off much more obliquely, having a lateral spread of 10 to 15 inches and reaching depths varying from 3 to 20 inches. Although the roots are not branched in the first 1 or 2 inches of soil, they are densely covered with hairs. Upon entering the moist soil they immediately begin to branch, giving off countless numbers of very fine, mostly rebranched short laterals only a few millimeters to an inch in length. At a distance of from 8 to 12 inches from the tip, the main roots frequently break up into 3 to 5 laterals several inches in length. These spread out in all directions and their profusely branched and rebranched network of finer absorbing rootlets lays hold upon considerable areas of soil.

Yucca glauca.—The root systems of numerous individuals of this species were examined in the plains soil (page 51) and also in the half-gravel-slide of the mountains. The main roots, which are more abundant in the half-gravel, slide ecad, are much more profusely branched. Great clusters of long, well-branched sublaterals fill the soil in sharp contrast to the poorly branched laterals characteristic of the half-dozen yuccas examined on the plains (fig. 52). A marked difference was also noted in the diameter and the fleshiness of the system of roots. While most of those of the plains were rather dry and often papery, those of the gravel-slide were generally more turgid, thicker, and fleshy. The rhizome system is somewhat more branched and is nearer the surface than on the plains.

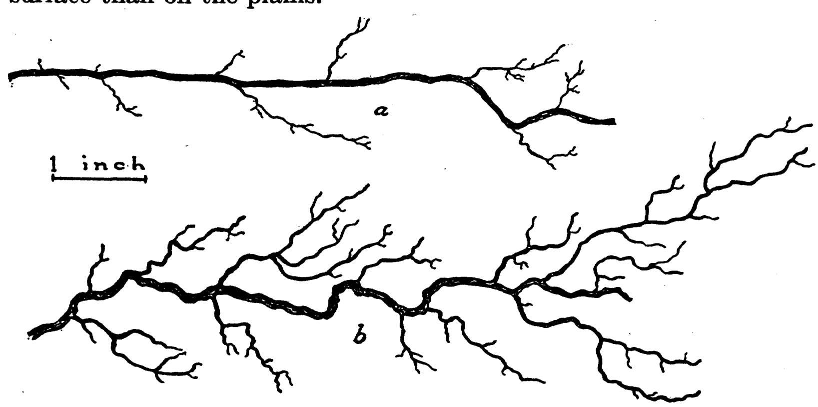


FIG. 52.—Fragments of the roots of *Yucca glauca: a*, plains form; *b*, half-gravel-slide form.

Allionia linearis.—This four-o'clock is a widely scattered secondary species on the plains and also occurs rather abundantly in the sandhills. Of the 8 or more plants examined in the former situation, all had strong and rather fleshy tap-roots, the largest 12 mm. in diameter. However, the tap is not uniform, often contracting at the top and being largest at a depth of from 8 to 16 inches. At about 2 feet in depth it narrows down abruptly to scarcely more than 2 mm. Except for small curves and kinks, it pursues a vertically downward course, some to a maximum distance of 5.5 feet. The first 18 to 24 inches of the root are practically unbranched, and in fact the lower part of the root system has no long laterals. Those that do occur at irregular intervals consist of groups of hairlike laterals, seldom more than a centimeter in length and usually only 4 or 5 mm. long. These are very minute in diameter and rather well branched. The tip ends abruptly with only a few short branches. The root is dark brown in color and very brittle, the interior parts being glistening white. At a depth varying from 6 to 14 inches, usually one or sometimes two laterals arise. These may be as large as 2 mm. and run off horizontally or slightly upward, ending 18 inches to more than 2 feet from the base of the plant. Like the main root, they are only poorly clothed with clusters of short branches (fig. 53).

Other specimens were examined in the sandhills from a half-captured blowout. Five roots were examined. In general they were very similar, the strong taps (which were about 5 to 8 mm. in diameter) descended rather vertically to a depth of 4 or 5 feet. A typical specimen is shown in figure 54. One to three branches, usually only one, occurred in the first foot of soil. The lower portions of the roots had a few branches or were in some cases almost destitute of them. The tops were both greater in diameter and taller than the plains specimens examined. The leaf surface also was greater.

From the above, as well as from figures 53 and 54, it may readily be seen that *Allionia linearis* is a rather stable species as to root system, the root habit differing only slightly in the two habitats. The clusters of small branches were quite pronounced in the plains ecad, while this was compensated for in the sandhill form by a somewhat greater degree of branching. The habit of sending off one or more large and rather horizontal branches in the surface foot of soil was characteristic in both habitats, as was also the strong taproot, which showed about the same degree of penetration in both groups.

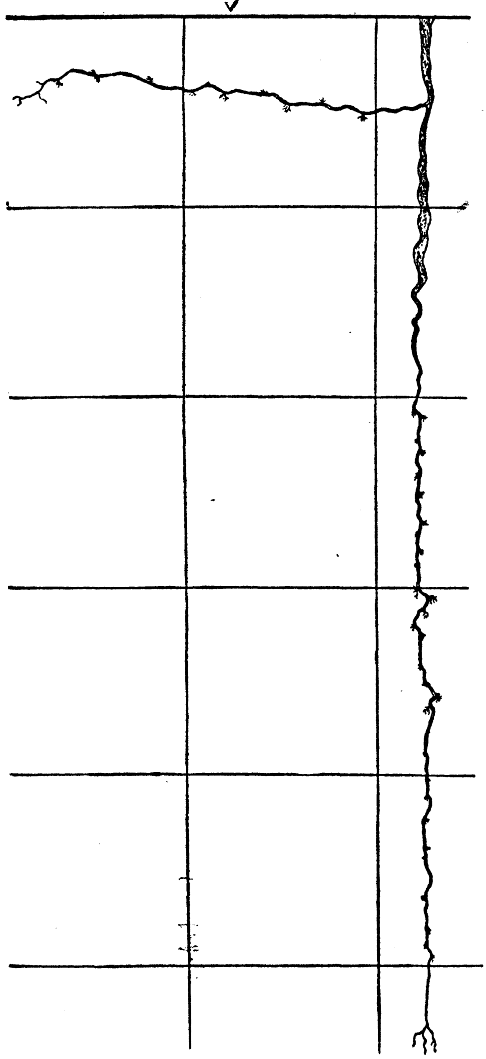


Fig. 53.—*Allionia linearis* from the plains.

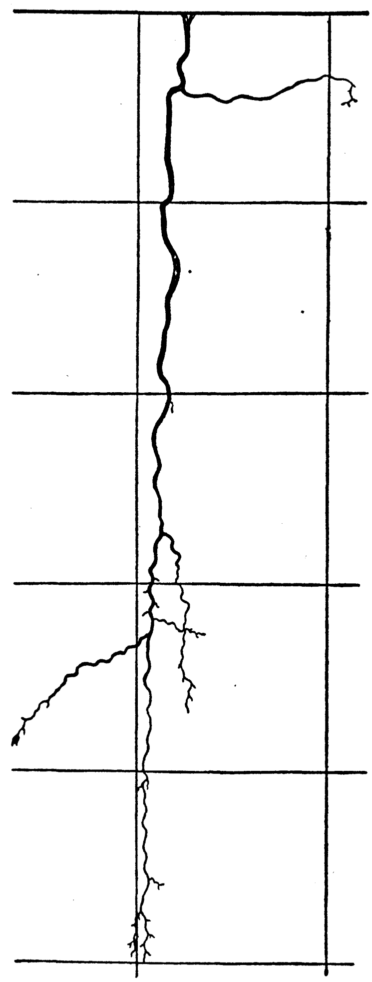


Fig. 54.—*Allionia linearis* from the sandhills.

Abronia fragrans.—This plant is rather widely distributed over the plains in disturbed areas, where, as in the sandhills, it frequently forms socies. The large, showy, hemispherical clusters of flowers make it very conspicuous.

Three plants were examined. The description for one will answer in general for all. The two largest had tap-roots 6 and 7 mm. in diameter respectively; the smaller was only 3 mm. in diameter. Both of the larger plants had 3 stems which reached a height of 14 to 16 inches and were either in blossom or in fruit; hence these may be considered typical mature plants. The tap-roots, except where they twist and curve irregularly back and forth for an inch or more in crevices of the cloddy soil, pursue a vertically downward course. The smallest reached a depth of 34 inches, the largest 40 to 43 inches respectively. As a whole the root is very poorly branched, no large laterals being given off. Beginning near the surface, however, and extending quite to the tip, short threadlike laterals, seldom exceeding 0.2 to 0.3 mm. in diameter and often

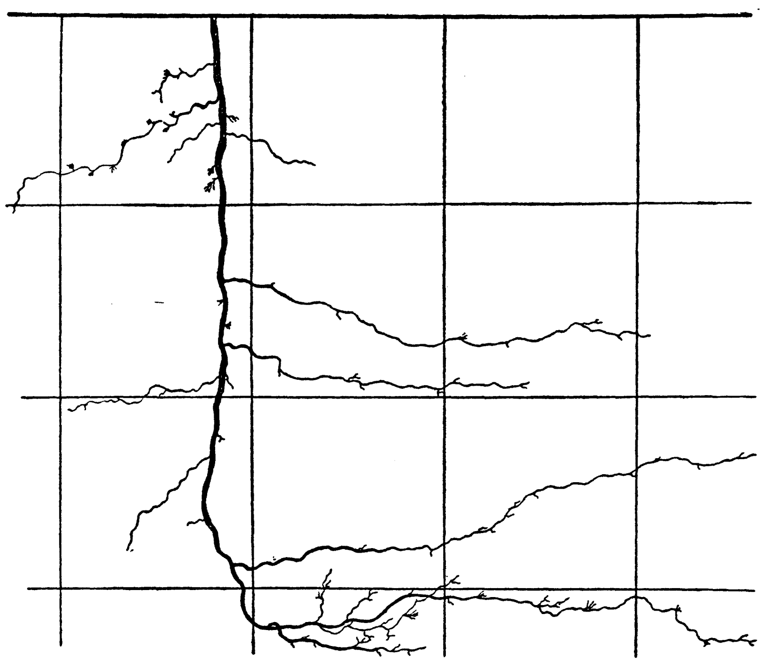


FIG. 55.—*Abronia fragrans* from the sandhills.

arising in groups of 2 or 3, run out laterally for a distance of less than 1 cm. to more than 4 inches. The longer ones occur within the surface foot of soil. These branches are very scattering, often 3 or 4 cm. of root having no branches whatsoever. The tip is only poorly branched. The older roots are black in color, this being confined to the outer layer of cortex, the interior being white. The younger roots vary in color from brown to yellowish. They are removed only with extreme difficulty from the hard soil. The tiny lateral rootlets are seldom branched beyond the second order and do not form a network (plate 29, c).

Four more rather large plants, all in flower or fruit, were examined. They were growing on a captured sand-dune and had tap-roots varying from 6 to 10 mm. in diameter. One of the largest of these is shown in figure 55. The tap is prominent throughout and tapers slowly to the tip, which reaches a depth of from 40 to 48 inches. The plant is characterized by 2 types of branches; the shorter ones vary from 2 to 20 mm. in length and occur in tufts or clusters, both on the main root and larger branches. Besides these, all of the roots examined had 3 to 6 or more larger branches, which ran off from the tap somewhat horizontally at all levels and to distances varying from a foot to over 3 feet. As shown in figure 55, the root system as a whole is poorly branched, although the sandhill ecads were much better provided with laterals and smaller rootlets than were the specimens examined in the plains soil. The root is yellowish-brown to nearly black in color. It is very brittle, the laterals especially being followed with extreme difficulty.

A comparison of these descriptions, together with an examination of the two figures, reveals the fact that the sandhill form, while showing the same habit of a strong tap-root which penetrates to about the same depth as the plains species, differs in its more abundant branching as well as in the great lateral spread of the branches. In these respects the modifications are not unlike those of other sandhill ecads already described.

Kœleria cristata.—This very important and cosmopolitan grass was first examined in the prairies of eastern Washington, where it is a common bunch-grass. Under the prevailing conditions of rather moderate precipitation (about 21 inches), most of which falls in winter and is followed by a season of summer drought, it flowers in late June, soon dries up, and remains dormant until revived by the autumn rains. In this region the deepest root found was at 28 inches and 15 inches was determined as the average maximum depth. In the prairies of eastern Nebraska it is also an important grass, growing under an annual precipitation of 28 inches, much of which falls during the growing season. Here none of the roots of the 7 plants examined reached depths of over 21 inches, while the average maximum root depth was about 15 inches.

Kœleria was further examined in the hard plains soils of east-central Colorado and under an annual (summer) precipitation of about 15 inches. Here the root distribution was almost identical in lateral spread and depth with those already described. The greatest depth was 26 inches and the average maximum depth about 14 inches. Finally, the same species was excavated on a half-gravel-slide at an elevation of 9,000 feet in the Rocky Mountains. As was characteristic in the other habitats, the first 6 to 8 inches of soil was completely filled with the profusely branched and matted root system. Roots were quite abundant to a depth of 12 inches, while some of the longest penetrated to 18 or 20 inches.

A comparison of plates 5, A, and 26, A, showing the roots of plants from the prairies of eastern Nebraska and from the gravel-slide respectively, reveals the fact that they are almost identical. Compared with the profound differences in the ecads of *Stipa comata* and *Elymus triticoides*, *Kœleria* is a remarkably stable species.

Chrysopsis villosa.—This composite is widely distributed throughout much of the grassland formation, occurring abundantly in the sandhills (plate 21, A). On the plains several plants were examined. All had strong tap-roots, which were woody for 2 or 3 feet. The height of the plant above ground was 6 to 10 inches. A second plant had a tap-root with a diameter of 12 mm. It penetrated almost vertically downward, except for local curves and kinks, usually less than an inch from a vertical line, to a depth of 8.6 feet (fig. 56). The first 18 inches of the tap, beginning about an inch below the soil surface, is abundantly supplied with threadlike laterals, mostly less than a millimeter in diameter, which run out in a horizontal direction from a distance of 1 inch to more than a foot. These laterals are practically free from branches. At a depth of 6 to 18 inches, half a dozen stronger laterals, each about 1 mm. in diameter, ran off rather horizontally for a distance of 18 inches or so before turning downward. At 2 feet the root had a diameter of only 2 mm. and was very much twisted and curved, as is characteristic of many plants in penetrating the hard soil. Practically no branches were given off to the very tip, which was threadlike and unbranched. At a depth of 6 feet, where the soil became looser and more moist, the roots pursued an even course, in striking contrast to the twisted parts in the harder soil. The younger portion of the root is almost white in color and covered with a dense coat of root-hairs. The older parts are dark brown. This description answers for two other plants which were growing near it.

Another plant gave off two laterals at a depth of 18 and 21 inches respectively. These were each a millimeter in diameter and ran rather horizontally to a distance of 2 and 2.5 feet. At a depth of 34 inches another lateral, 2 mm. in diameter, came off and ran almost parallel with the tap. This plant had a woody tap 3 cm. in diameter, which split at the top and gave rise to three clusters of stems. It tapered rapidly, however, and at a depth of 2 feet was only 4 mm. in diameter. The main root outside of branches already mentioned branched but little, as indicated in the drawing. It reached a depth of 13 feet.

On a half-captured dune in the sandhills, 5 or 6 large mature plants were examined, all of which agreed in having a multicipital crown arising from the 2 to 5 upper forks of the thick, woody tap-root. The surface branching was exceedingly well developed. From the very base of the plant numerous lateral branches arose, varying from 0.5 mm. to 6 or 8 mm. in diameter. All were fairly well rebranched, the smaller laterals and the larger branches of the major ones being densely clothed with root-hairs. In most cases the tap-root, owing to the enormous numbers of large lateral branches, rapidly diminished in size, so that at a depth of 18 inches none were larger than 5 mm. in diameter. This stands out in marked contrast to the stout, deep-seated tap of the plains. Indeed, the deepest root examined penetrated to a depth of only 6 feet 11 inches, while most of them reached depths of only 4 to 6 feet. The lateral branches, both large and small, formed a dense network of roots filling the soil from 18 to 24 inches on either side of the plant. All of the larger roots were well supplied with small, well-branched absorbing laterals. The divisions of the tap-root were themselves branched and rebranched to such an extent that, as they passed downward, great numbers of roots were found penetrating the soil to depths of 4 or 5 feet. Still other plants were examined which confirm the above descriptions, the taps and larger branches having a strong tendency to run obliquely or even horizontally, rather than vertically downward as in the plains ecads (plate 30, B).

This affords a very clear case of the effect of the habitat upon root development. The plains form has a root which is approximately twice as deep-seated as those in the sandhills. While the tap is prominent throughout in the former, it soon loses its dominance in the sandhill form and often scarcely exceeds in importance some of the stronger laterals. While both forms are supplied with rather abundant surface laterals, in the plains form these are largely confined to the surface foot, while in the sandhills they occur to a much greater depth and are abundant along all of the major branches. The branches in the first foot of the plains soils were mostly less than 1 mm. in diameter and had a horizontal spread seldom exceeding 18 inches. They were practically free from branches. In the sandhills the laterals ranged from 0.5 to 8 mm. in diameter and were rather well branched. In number these lateral branches, both large and small, formed a dense network of roots

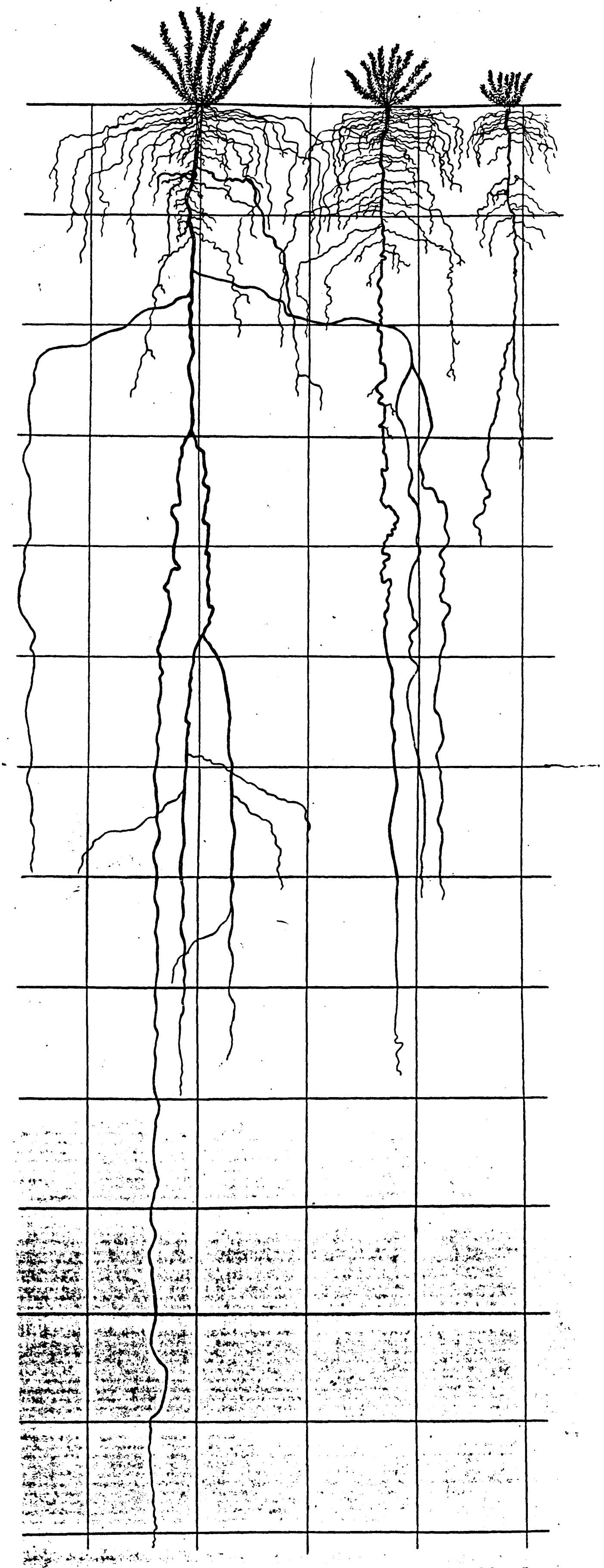


FIG. 56.—*Chrysopsis villosa*, showing various stages of development in the plains soil.

filling the soil to a distance of 18 to 24 inches on either side of the plant. Such marked differences in root habit are probably accompanied by marked changes in the aerial parts. This is a rich field for future investigation.

Euphorbia montana.—This spurge is rather widely distributed throughout the plains and mountains and is often locally abundant. Those examined on the plains had a strongly marked tap-root, which started with a diameter of 6 mm. and pursued a tortuous and zigzag course downward to a depth of 7.5 feet, where it ended in pearly white, hairlike branches (fig. 57). Within the first foot there were 4 short branches from 4 to 8 inches long, which were themselves slightly branched. The larger branches from this point downward were very sparse, there being only one of note, which came off at a depth of about 20 inches and pursued an obliquely downward course for a distance of about 2.5 feet. Along the whole course of the root below the first 21 inches, very fine, pearly-white, hairlike branches were found in abundance. Particularly was this true from 21 to 55 inches deep. In this region a large soil fissure occurred, and these pearly-white branches, oftentimes arising in pairs, were matted and profusely branched, extending horizontally from the main root to a distance of 10 inches in some cases. The matting of these small branches in the fissure was probably due to the excess of water which came down from the surface. Below this fissure these branches continued, but much fewer in number, to a depth of 60 inches, where a very moist, easily penetrable stratum of soil was encountered. In this stratum the small branches again occurred in great numbers, being sometimes 6 to 8 inches long and as many as 25 per linear foot. Here, too, they often occurred in pairs. The root is light brown in color. It has a fleshy cortex and a tough, fibrous stele; when broken a very small amount of latex exuded.

Compared with this root type, that of the half-gravel-slide, with its shallower but more widely spreading and much more profusely branched roots, stands out in marked contrast. It shows a profound series of modifications in adapting itself to this very different habitat. This is evident from a comparison of figures 57 and 58, notwithstanding the fact that the half-gravel-slide plant here illustrated was exceptionally deep-rooted, and from the following description, which is typical of one of several other half-gravel-slide plants examined.

This was a large plant, with a tap an inch in diameter, which divided at a depth of 1 inch into two nearly equal parts. The one ran up the slope in a horizontal position and at a depth of only 4 to 10 inches. It soon broke up into many smaller branches, which diverged in all but a downward direction and extended to distances of 3 to 4 feet, and mostly only a few inches below the soil surface. The second descended vertically, but gave off 2 branches 5 and 8 mm. in diameter, respectively, at a depth of 2 and 3 inches, while the tap was now only 5 mm. in diameter. The largest of these branches ran off at a depth of only 8 inches to a lateral distance of 5 feet. At 16 inches from the base of the plant it broke up into numerous equal-sized branches which rebranched profusely. None of these reached a depth greater than 14 inches, while many of the obliquely upward running branches filled the soil to near the surface with great masses of finely branched rootlets. The tap tapered very gradually and after branching considerably, mostly with vertically descending or oblique or even horizontal branches, reached a depth of 58 inches. The spread of the deeper branches on either side of the tap was only about 12 inches. Tiny, fragile, glistening-white mats of branches form a network of rootlets 2 to 8 inches long, surrounding all but the larger parts of the older laterals. Four plants were examined.

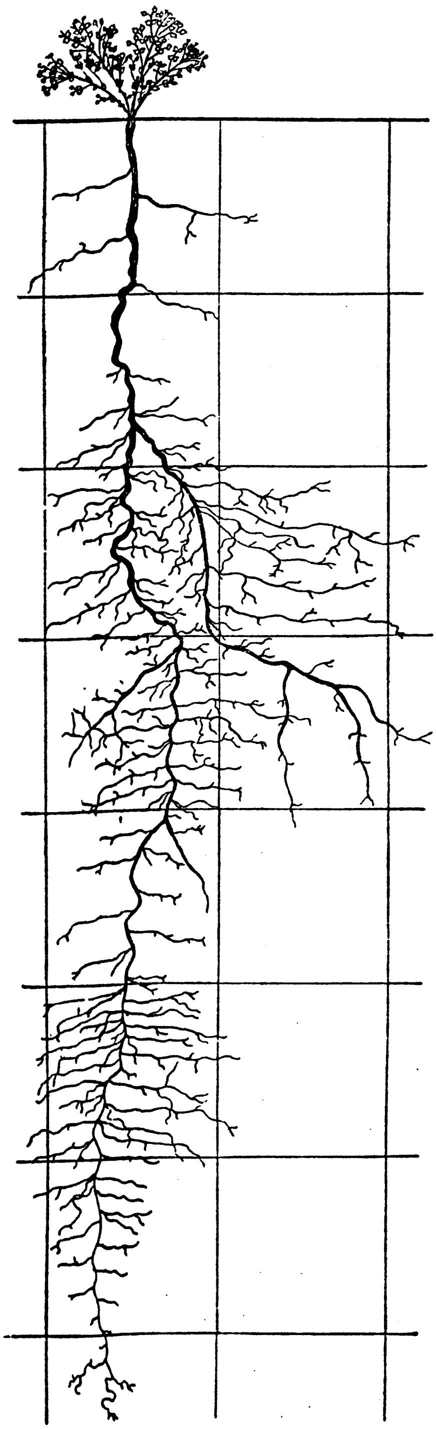


FIG. 57.—*Euphorbia montana* from the plains.

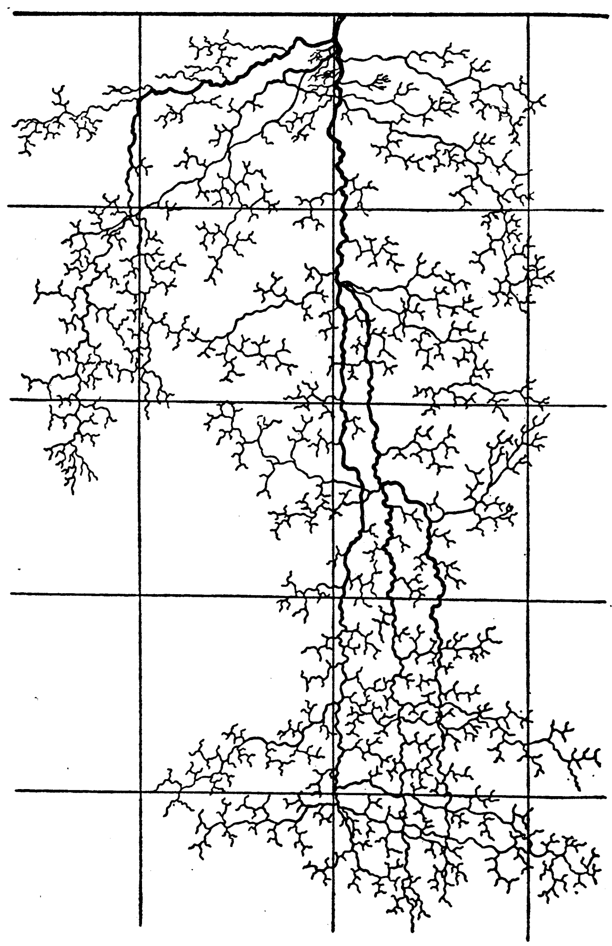


FIG. 58.—*Euphorbia montana* from the half-gravel-slide.

ROOT MODIFICATIONS OF POLYDEMICS.

Of the 10 polydemic ~~species here described~~, each growing in at least two different habitats, 7 show very striking changes in their root habits, 2 made practically no change, while 1 exhibited only moderate differences of root development.

Bouteloua, *Stipa*, and *Chrysopsis* growing in the plains soil were all deep-rooted species, the latter indeed reaching a depth of over 13 feet. In the sandhills they all conformed to the typical root habit of most plants of this habitat. None of them reached more than half their former depth, but the shallow lateral root development and lateral spread were much more pronounced, especially in *Chrysopsis*. On the other hand, the more stable species as regards root development, *Allionia linearis* and *Abronia fragrans*, when growing in these same habitats, were only slightly or not at all modified. The former showed practically no difference in the sandhill and plains ecads; the latter had a tendency to develop more and longer branches in the sand. These, with *Kœleria*, which was examined under four distinct sets of conditions in widely separated areas and found to be practically the same in all, form a very conservative group as regards root type, although, as shown by E. Clements (1905), the aerial parts of some are very plastic. This forms a unique problem for further investigation.

Euphorbia and *Yucca*, while conforming to the plains root habit in having a rather deep and widely spreading absorbing system, were found to be profoundly modified when grown in the half-gravel. In the former the depth of penetration was always much less, while the branching, like that of *Yucca*, was much more pronounced.

Of the three species, *Smilacina stellata*, *Elymus triticoides*, and *Chamænerium angustifolium*, examined in gravel-slide or half-gravel-slide and in the forest, all took on the typical root habit characteristic of the several habitats respectively. All had fewer branches, a smaller lateral spread, and a lesser depth of penetration in the forest than in the open. The rather great root depth of *Chamænerium* in the Douglas fir forest is an exception. This is somewhat puzzling and seems to be quite contrary to the usual rule of root development.

X. SUMMARY.

This study was undertaken to determine the root habits of dominant and subdominant plants growing under a wide range of climatic and edaphic conditions; to find the root relations of the plant communities as units of vegetation; and to determine the root distribution and root competition of the individual species in their relation to other species in the community. Other aims were to determine the relation between the root habits of plants in various communities and their successional sequence, and to obtain a more definite knowledge of the indicator value and the significance of various species used in classifying lands for grazing or for agriculture, as well as to aid the forester in selecting sites for afforestation or reforestation.

The investigation extended over four years, during which time more than 1,150 individual root systems of about 140 species of shrubs, grasses, and other herbs were excavated and studied. These species were members of 8 different plant communities widely separated geographically and growing under distinctly different climatic or edaphic conditions. The communities studied were the prairies of eastern Nebraska, the chaparral of southeastern Nebraska, prairies of southeastern Washington, the plains association and sandhill subclimax of Colorado, and the gravel-slide, half-gravel-slide, and forest communities of the Rocky Mountains of Colorado.

The trench or pit method was used in excavating the roots, the root system being removed with appropriate apparatus from the face of the trench. In case of roots extending to depths beyond 15 feet, two working levels were maintained. The quadrat-bisect method has been employed to show the root systems of communities in place and thus exhibit their interrelations in detail.

The root systems of 33 species were examined in the prairies of eastern Nebraska; 13 of these were grasses. All of the dicotyledonous plants were found to extend well beyond a depth of 2 feet, while the roots of 6 of the grasses were confined to the surface 2 feet of soil. Four of the grasses and 5 other species were found to penetrate well below the second foot of soil, but seldom deeper than 5 feet. More than half of the plants studied, including three dominant grasses, have roots which reach depths greater than 5 feet—indeed, most of them penetrate to distances of from 7 to 9 feet and a few to a maximum depth of from 13 to 20 feet.

These prairie species grow under a mean annual precipitation of about 28 inches, over 20 inches of which fall during the growing season. The soil is of the type commonly called loess, much of which, however, is confounded with glacial drift. Soil-moisture determinations for more than two seasons show that the water-content is sometimes reduced to such a degree that no moisture to a depth of 4 or 5 feet is available for plant growth. The wind, prevailingly from the south or southeast during the growing season, averages about 70 miles per day over the vegetation. The mean summer temperatures are high (70° to 75° F.), while the mean humidity is often low (58 to 70 per cent). The average daily evaporation throughout the growing season is about 21 c.c.

The plants of the prairie community, in response to these environmental conditions, have developed very efficient widely spreading and deeply penetrating root systems. The prairie community root habit emphasizes depth of penetration and widely spreading, deep laterals much more than the desert community (Cannon, 1911, 1913; Markle, 1917). The roots of prairie plants are grouped into more or less definite absorbing layers, many of the deeper-rooted species having few or no absorbing roots in the first few feet of soil. The layering of the roots reduces competition and permits the growth of a larger number of species.

The root systems and mechanism of invasion of several dominant shrubs of the chaparral community, which occupies the tension zone between forest and prairie, were examined. All are supplied with splendid absorbing systems which are somewhat variable as to depth (5.5 to 21 feet), but all of which are deep-seated. In addition, they all have excellent methods of vegetative propagation. Their presence indicates a soil richer in humus and higher in water-content than that of adjacent grassland areas. These differences, as well as a lower evaporating power of the air, are brought about by the reactions of the shrubs. These consist of the accumulation of wind-blown snow and plant débris, a lowering of the light values and a consequent disappearance of most or all of the prairie species, obstruction to wind movement, lower temperatures and higher humidity, in part due to shade, and a less rapid oxidation of the humus materials.

The root systems of 18 dominant and subdominant species were examined in the prairies of southeastern Washington. These prairies represent an extreme westward extension of the great grassland formation lying east of the Rocky Mountains. They are characterized by the absence of late-maturing grasses and in general by an earlier seasonal development. Three of the four dominant grasses have root systems confined to the surface 18 inches of soil. This is correlated with early seasonal growth and maturity. The fourth, like the other herbaceous species, has a deep, widely spreading root system. All of these reached depths from 4 to 6 feet, while some penetrated even deeper. However, the plants of the prairie community are not so deeply rooted as those of the prairies of eastern Nebraska. This may be correlated with the environment.

These prairie species grow under a mean annual precipitation of 21 inches, only about 7 inches of which fall during the growing season. But the silt-loam soil is extremely retentive of water, so that the precipitation, which occurs so gently that there is little run-off, is held as in a great reservoir that is rather thoroughly emptied during the following summer. Soil-moisture determinations for two seasons show that the water-content is sometimes reduced to the non-available point for plant growth, especially on exposed slopes, even to a depth of 3 or 4 feet. The wind, prevailingly from some southerly direction, averages about 96 miles a day just above the vegetation on south slopes. The air temperatures, which may reach 90° to 100° F., show a mean daily range varying from 25° F. in April and May to 38° F. in July and August. The mean daily soil temperatures at a depth of 3 inches vary from 40° to 50° F. in May to from 66° to 92° F. in August, depending upon the slope. The humidity, normally low, frequently falls to 10 or 15 per cent during afternoons. The average daily evaporation throughout the growing season is about 29 c.c. on southerly slopes and 20 c.c. on northerly ones.

Root penetration and the amount of branching were found in both the prairies of Washington and those of Nebraska to be profoundly affected by hard soil. Both the root length and the amount of branching of a prairie species growing under the two conditions of soil texture were found to be more pronounced in the less compact soil. Plants growing in the mellow loess soil of eastern Nebraska are deeper-rooted than those growing in glacial drift soils. Aeration may be an important factor in effecting these modifications. Roots show a marked increase in their output of branches upon leaving compact soil and entering earthworm burrows or small crevices.

The root systems of 28 important plains species were examined near Colorado Springs, Colorado. They were found to have deeply penetrating and widely spreading roots. The lateral spreading of roots in the surface soil at depths of from 2 to 12 inches is much more pronounced than in either of the preceding prairie communities. Only four plants, including two cacti, had their root systems confined almost entirely to the surface 2 feet of soil. One-third of the plains species penetrated to depths greater than 2 feet but seldom beyond 5 feet. This group includes such dominant grasses as *Bouteloua gracilis* and *Aristida purpurea*. Nearly 60 per cent of the plains species had roots extending to depths greater than 5 feet. The roots of several plants reached depths of 10 to 12 feet. Although as a community plains plants are deeper-rooted than those of the prairies, no roots were found at a depth greater than 13 feet, as was the case with several prairie species in Nebraska. It is probable that water never penetrates more deeply than 13 feet in the plains.

Like the plants of prairies and sandhills, the roots of plains species show a wide range in type from those with the tap as the principal feature or with the laterals placed near the surface and especially well branched, to roots with both tap and laterals well developed. However, the latter or generalized type is the most common. Notwithstanding these individual differences, each community, viewed as a whole, has as its own root habit the one best fitted to the particular environment.

These plains species grow under a mean annual precipitation of about 15 inches, 12 inches of which fall during the growing season. The soil is a sandy loam so compacted that ordinarily it can be removed only with a pick. Because of the great degree of compactness, run-off after rains is high. Moisture determinations during 1918 show that the soil to a depth of 7 feet is rather uniformly dry and that at certain periods during the summer no water is available for plant growth to a depth of 5 feet. The wind movement over the plants averages about 120 miles per day. The daily fluctuation of temperature among the plants is usually about 35° to 40° F., the air reaching a maximum of 90° to 95° F. Soil temperatures among the roots at a depth of 4 inches ranged daily from 60° or 70° F. to 90° or 95° F. The average daily evaporation throughout the growing-season is about 48 c.c.

The well-developed system of shallow, widely spreading laterals is undoubtedly a response to the moisture in the surface soils resulting from frequent light summer showers. These surface roots are especially well developed in cacti. Those of *Yucca* are remarkable for their great lateral extent, often reaching a distance of more than 30 feet on every side of the plant. Bisects show that root competition among plains plants, especially in the first 2 feet of soil, is very severe.

The root habits of 19 important sandhill species were studied in eastern Colorado, about 40 miles southeast of Colorado Springs; 8 of these have roots which are entirely or nearly confined to the surface 2 feet of soil. The deeper-rooted species, none of which were traced below 11 feet because of the caving sand, practically all show a striking profusion of long, widely spreading laterals in this surface-soil stratum. The lower parts of deeply penetrating roots are often much more poorly branched. Several deep-rooted plains species under sandhill conditions develop only shallow roots.

General climatic conditions are almost identical with those described for the plains; hence differences in root habit must be attributed to edaphic causes. Precipitated moisture is readily absorbed and there is practically no run-off, even in the heaviest showers. During dry weather the surface sand forms a very efficient means of retarding evaporation. Moisture determinations and observations show that the surface 2 or 3 feet of soil often is moister than the deeper strata, and thus offers a logical explanation for the typically shallow but widely spreading sandhill root habit. Several plants have in addition deeply penetrating roots; hence the deeper soils must receive moisture, perhaps during wet phases of the climatic cycle. *Ipomœa leptophylla* has the most extensive root development of any species examined in the eight communities studied.

In the Rocky Mountains, adjoining the plains at Colorado Springs, the root systems of plants were studied in the gravel-slide, half-gravel-slide, and forest communities respectively. These communities form a developmental series. All plants of the gravel-slide community are similar in possessing root systems adapted to secure moisture and nutrients from the surface foot, and few extend beyond a depth of 18 to 24 inches. They have a remarkably wide lateral spread, combined with a most profuse system of branching.

The surface soil consists of coarse, angular rock fragments, which are from over an inch to only a few millimeters in diameter. Below this lie a few inches of coarse gravel and sand which gradually give way, at a depth of 1 to 2.5 feet, to poorly disintegrated granite. The precipitation falls largely as frequent summer showers which seldom wet the soil below 18 to 24 inches. The surface gravel serves efficiently, both in preventing run-off and in retarding evaporation. Moisture determinations show that the soil moisture, while at no time high, is rather equally distributed throughout the surface 18 inches of soil. Plants are so sparsely spaced that relatively little water is removed by transpiration. Wind movement averaged 103 miles daily. The average daily evaporation throughout the summer was 34 c.c. The community root habit is clearly a response to the environment. The development of strong laterals, characteristically up the slope, seems to be due in part to a response to the soil slipping down the mountains. Root competition on the gravel-slide is not at all severe.

An examination of roots in the half-gravel-slide revealed quite a different type. In addition to the shallow, widely spreading root habit, most species had supplementary deep roots which penetrated from 2 to 4 feet. The soil of the former gravel-slide has now become deeper and richer in humus and much more densely populated. More than half of the surface is occupied by plants, dominant among which are certain grasses, while all of the soil to a depth of 3 feet is occupied by roots. The surface gravel has become more disintegrated and compacted and is less efficient in preventing evaporation. Because of competition for light, and especially for water, most gravel-slide plants have disappeared. Although wind movement is somewhat less and evaporation considerably lower than in the former barer habitat, the water-loss by transpiration from the denser plant population is higher. During periods of drought plants must rely largely upon the water in the deeper soil. More favorable deep-soil conditions, together with intense shallow-root competition, are factors largely determining root depth.

Through a transition chaparral stage, the half-gravel-slide gives way to forest. *Pinus ponderosa, Pseudotsuga mucronata,* or *Picea engelmanni* is the dominant, depending upon the amount of humus and moisture. The 19 herbs and shrubs examined on the forest floor were relatively shallow-rooted. Almost without exception the major portion of the absorbing system lies within the surface 18 inches. A few relicts from earlier successional stages had roots which penetrated somewhat deeper. Many of the roots of tree dominants were found to be superficial.

The water-content of the soil offers a logical explanation for this community root habit. The duff retards run-off as well as evaporation. The trees and shrubs reduce wind movement, lower the temperature and evaporation, and consequently greatly reduce water-losses by transpiration. Series of moisture determinations show that the surface 6 inches of soil usually have more available water than the underlying 6 inches, while the third foot is usually much drier than the second. This may be accounted for by the frequent summer showers. Not only are the herbs and shrubs of the forest floor shallow-rooted, but also as a rule the root systems are less extensive in proportion to the transpiring area than is the case with the half-gravel-slide and the gravel-slide plants.

The root systems of several species growing in two or more distinctly different habitats were studied. It was found that in most cases the root type conformed to the community root habit in which the species was excavated. Thus profound differences, both in root depth and position and number of branches, were determined for most ecads. In general root position conformed strikingly with the distribution of soil moisture. A few stable species were found which showed little or no variation of the root system when grown under different environmental conditions.

The general characters of the root systems of a species are often as marked and distinctive as are the above-ground vegetative characters. But the root systems of different species of the same genus, while often somewhat similar, may be of entirely different types.

A knowledge of the position and competition of roots is indispensable in explaining the phenomena of succession. Since root position so clearly reflects the moisture conditions of the soil, especially when interpreted in its community relations, a study of the root habits of plants greatly increases our knowledge of the value of various plants in indicating lands of agricultural or non-agricultural value. A knowledge of root habits is of further value in solving the problems of the competition of range species and the improvement of the range. Finally, root systems indicate the distribution of soil moisture in various habitats, and thus should aid the forester in selecting sites for reforestation or afforestation.

BIBLIOGRAPHY.

ALWAY, F. J., *et al.* 1916. The loess soils of the Nebraska portion of the transition region. Soil Science 1: Nos. 3, 4, 5.

BATES, C. G. 1910. Experiments in sandhill planting. Proc. Soc. Am. For. 5: 59.

CANNON, W. A. 1911. The root systems of desert plants. Carnegie Inst. Wash. Pub. No. 131.

———. 1912. Some features of the root systems of desert plants. Pop. Sci. Mon. 41: 90.

———. 1913. Botanical features of the Algerian Sahara. Carnegie Inst. Wash. Pub. No. 178.

———. 1918. The evaluation of the soil-temperature factor in root growth. Plant World 21: 64.

——— and E. E. FREE. 1917. The ecological significance of soil aeration. Science 45: 178.

CLEMENTS, E. S. 1905. The relation of leaf structure to physical factors. Trans. Am. Mic. Soc. 26: 19.

CLEMENTS, F. E. 1904. Formation and succession herbaria. Univ. Nebr. Studies 4: 329.

———. 1905. Research methods in ecology.

———. 1916. Plant succession. Carnegie Inst. Wash. Pub. No. 242.

KORSTIAN, C. F. 1917. The indicator significance of native vegetation in the determination of forest sites. Plant World 20: 267.

LOVELAND, G. A. 1912. Summary of climatological data for the United States, Sec. 37, Southern Nebraska.

MARKLE, M. S. 1917. Root systems of certain desert plants. Bot. Gaz. 64: 177.

POOL, R. J. 1914. A study of the vegetation of the sandhills of Nebraska. Minn. Bot. Studies 4: 189.

POUND, R., and F. E. CLEMENTS. 1900. The phytogeography of Nebraska.

PRESTON, C. E. 1900. Observations on the root systems of certain cactaceæ. Bot. Gaz. 30: 348.

ROBBINS, W. W. 1917. The botany of crop plants.

SAMPSON, A. W. 1914 Natural revegetation of range lands based upon growth requirements and life history of the vegetation. Jour. Agr. Res. 3: 39.

———. 1917. Important range plants; their life history and forage value. U. S. Dept. Agr. Bull. 545.

SHANTS, H. L. 1911. Natural vegetation as an indicator of the capabilities of land for crop production in the Great Plains area. U. S. Dept. Agr., Bur. Pl. Ind. Bull. 201.

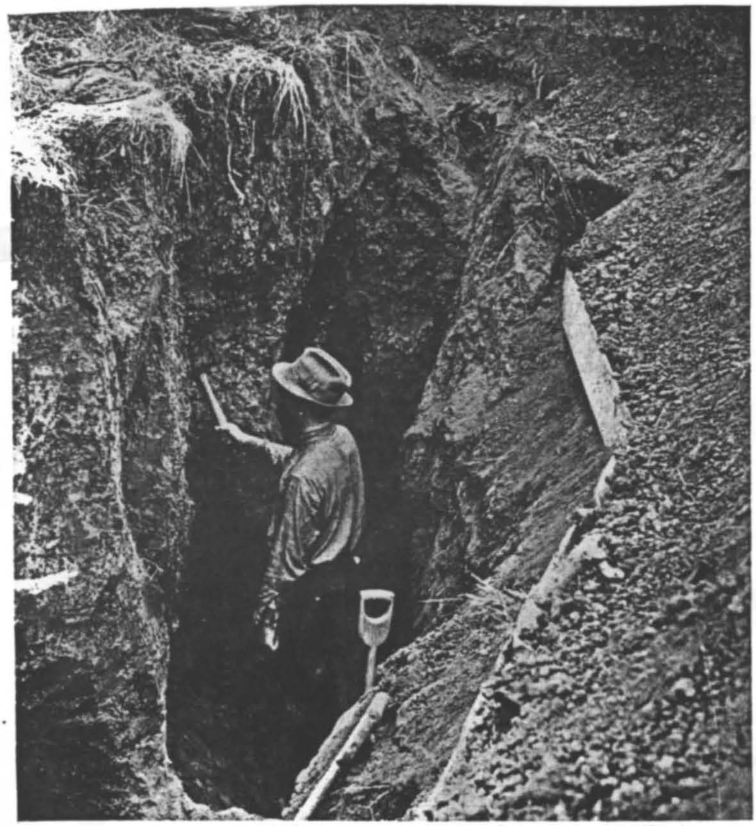
TEN EYCK, A. M. 1904. The roots of plants. Kans. Agr. Exp. Sta. Bull. 127.

THORNBER, J. J. 1901. The prairie-grass formation in region I. Rep. Bot. Surv. Nebr. 5: 29.

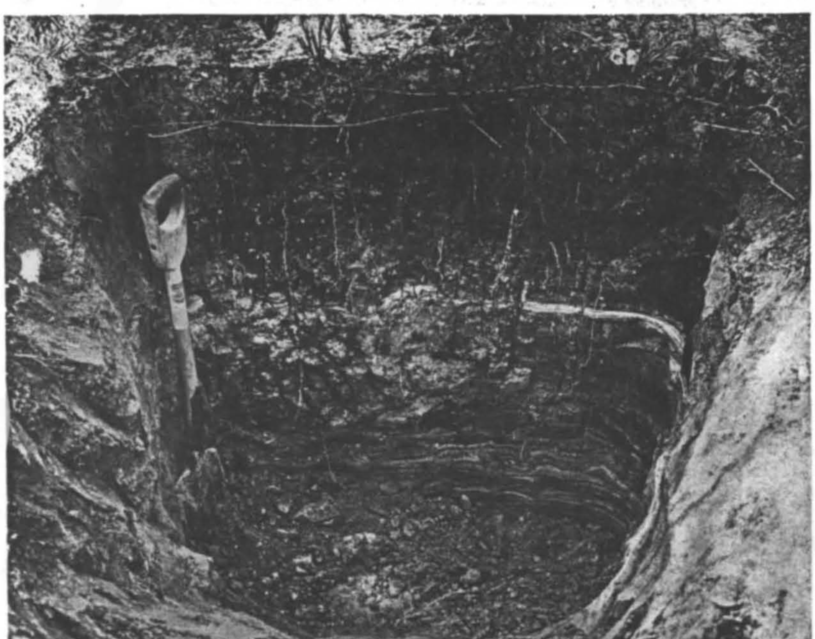
WEAVER, J. E. 1915. A study of the root systems of prairie plants of southeastern Washington. Plant World 14: 227.

———. 1917. A study of the vegetation of southeastern Washington and adjacent Idaho. Univ. Nebr. Studies 17: 1.

——— and A. F. THIEL. 1917. Ecological studies in the tension zone between prairie and woodland. Rep. Bot. Surv. Nebr., n. s. 1: 1.



A



B

A. One end of a trench used in excavating root systems.
B. *Distichlis spicata*, showing the long rhizomes and shallow roots.

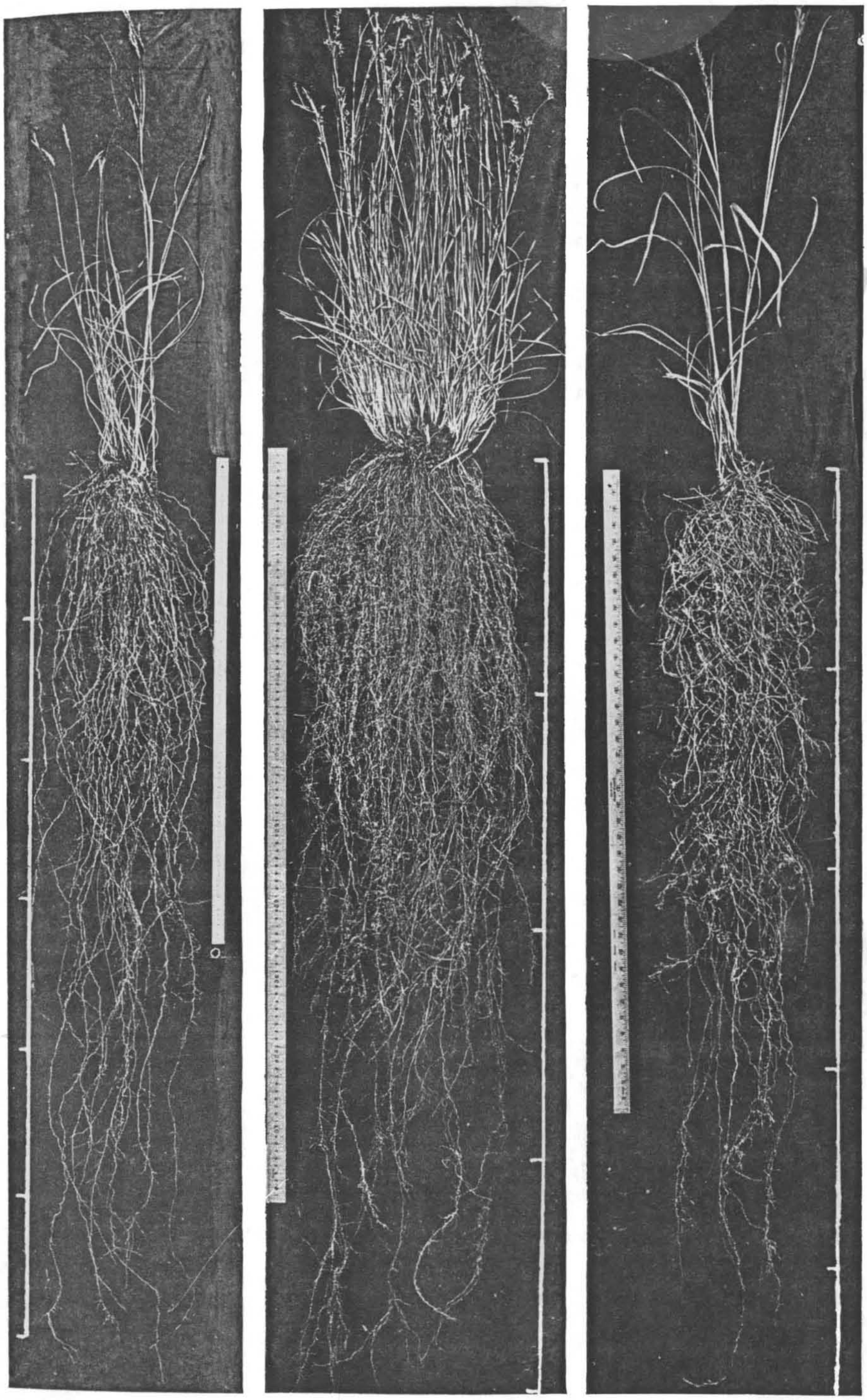
A

B

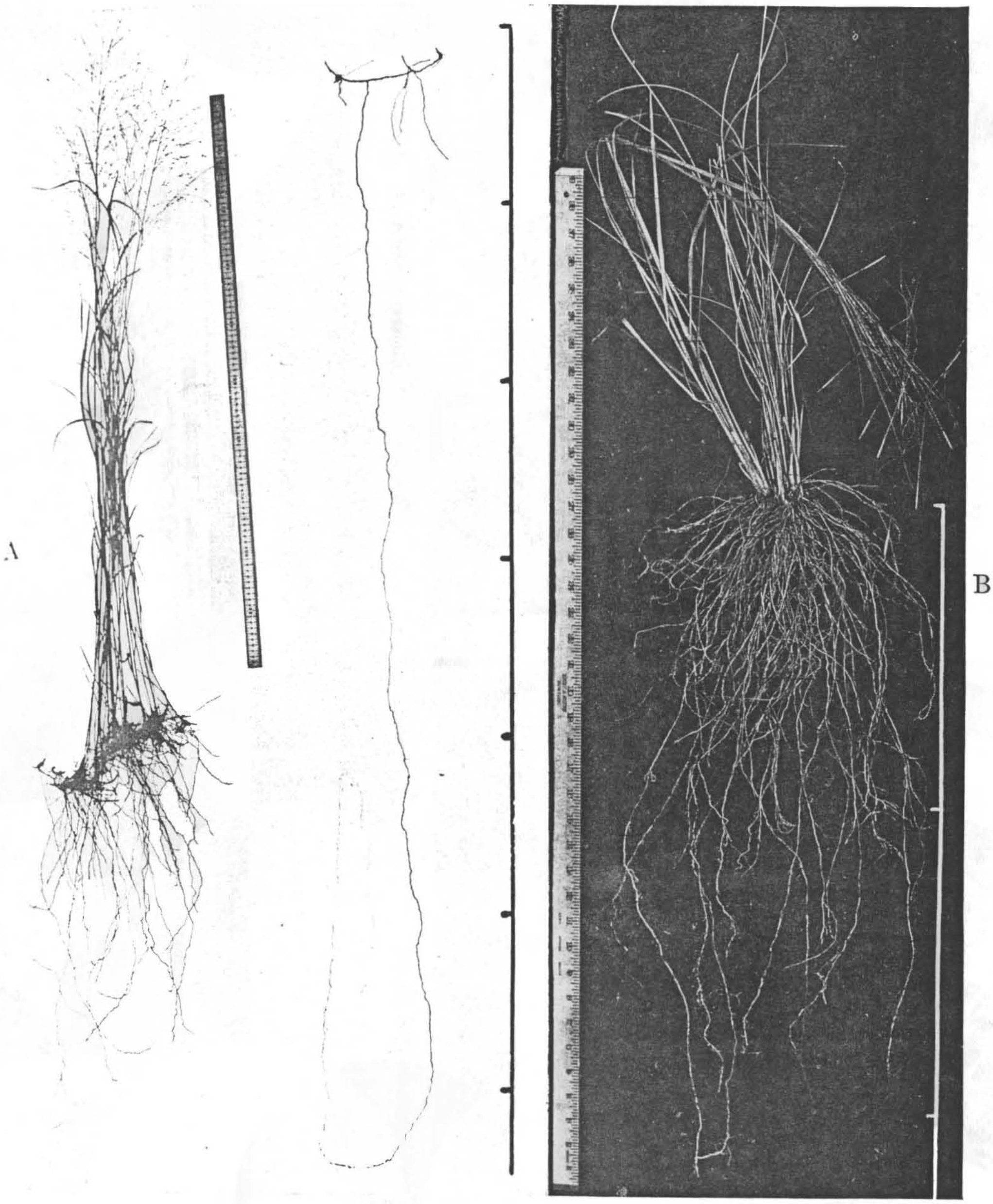
A. An eastern Nebraska prairie in June. *Erigeron ramosus* and *Meriolix serrulata* in the foreground and bushy *Psoralea tenuiflora* in the background.

B. An area dominated by *Agrostis hiemalis* with *Allium mutabile*, *Achillea millefolium*, and *Stipa spartea*.

A B C

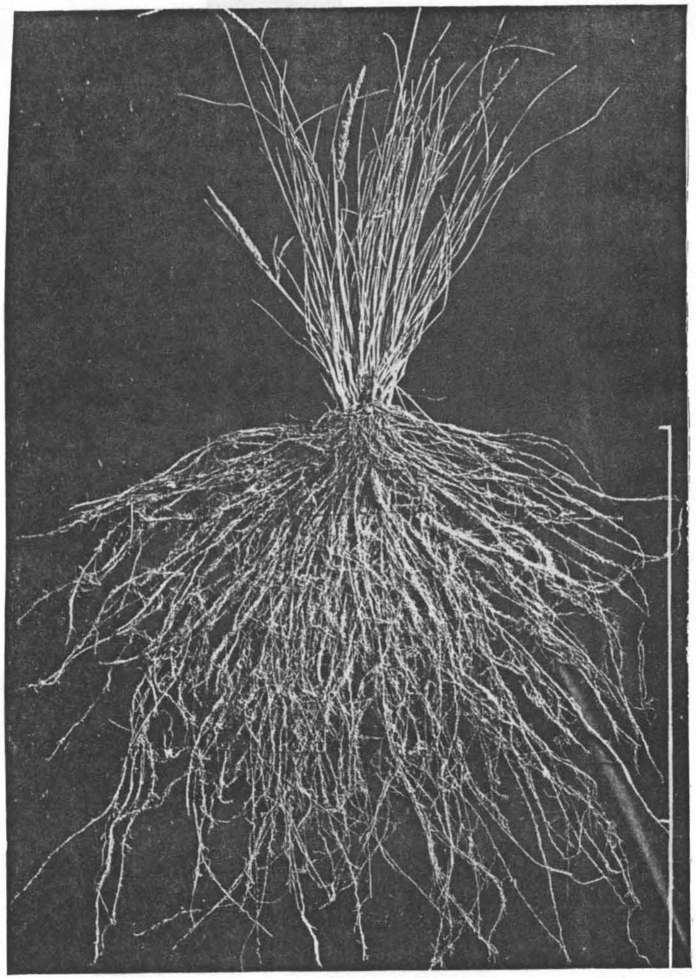


A. *Andropogon furcatus.* B. *Andropogon scoparius.* C. *Andropogon nutans.*



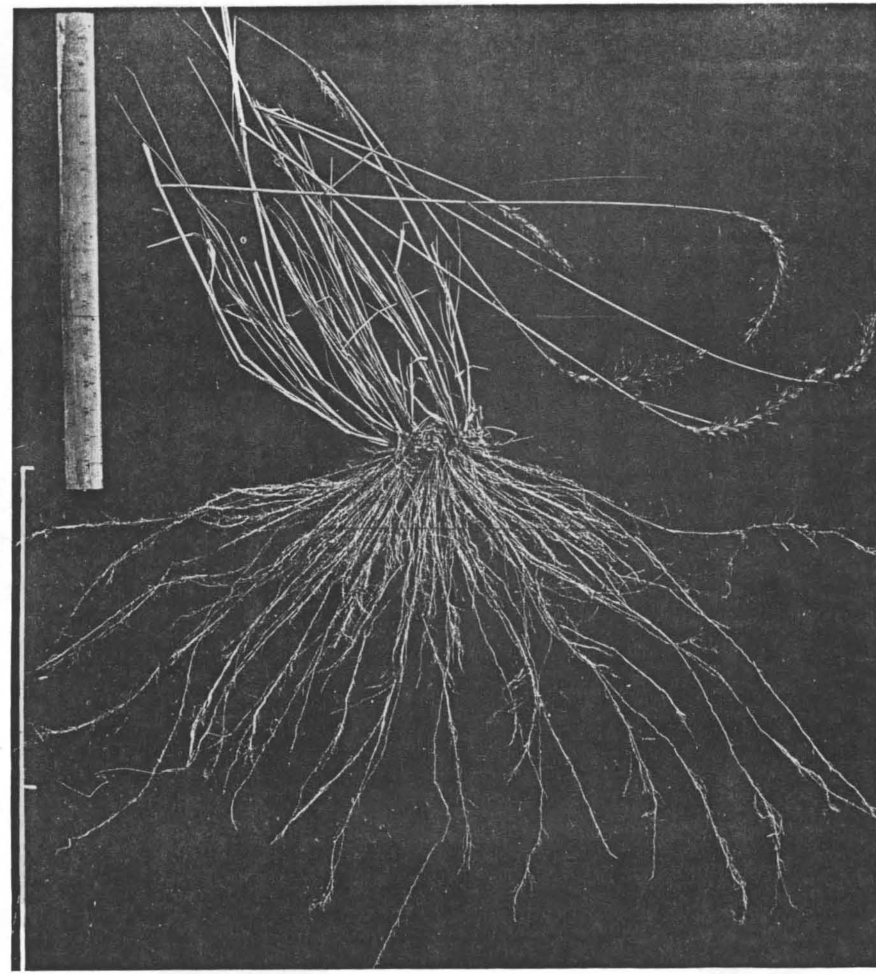
A. *Panicum virgatum*, showing rhizomes, coarse roots, and complete single root.
B. *Stipa spartea*.

A



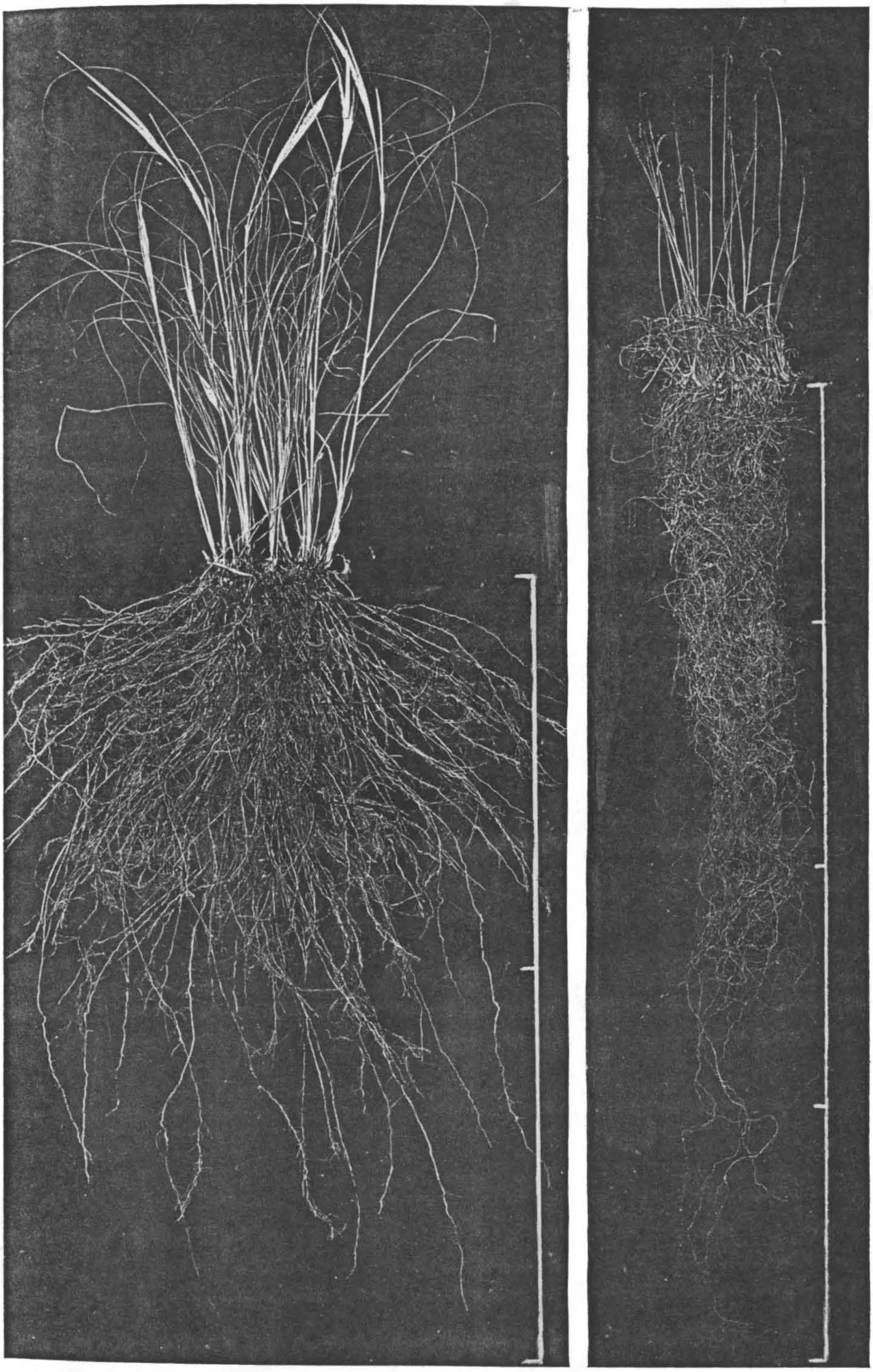
A. *Kœleria cristata.*

B



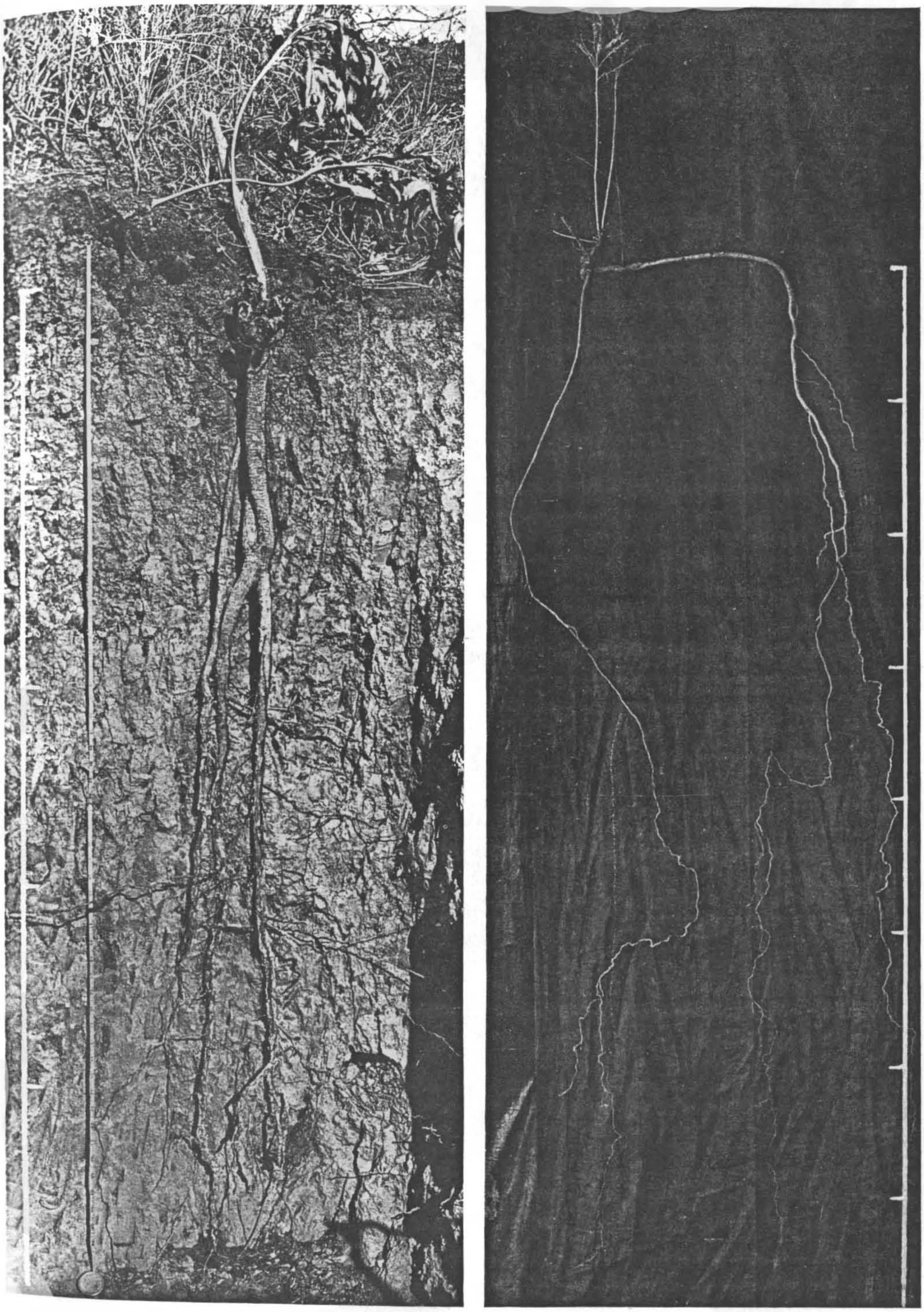
B. *Elymus canadensis.*

A



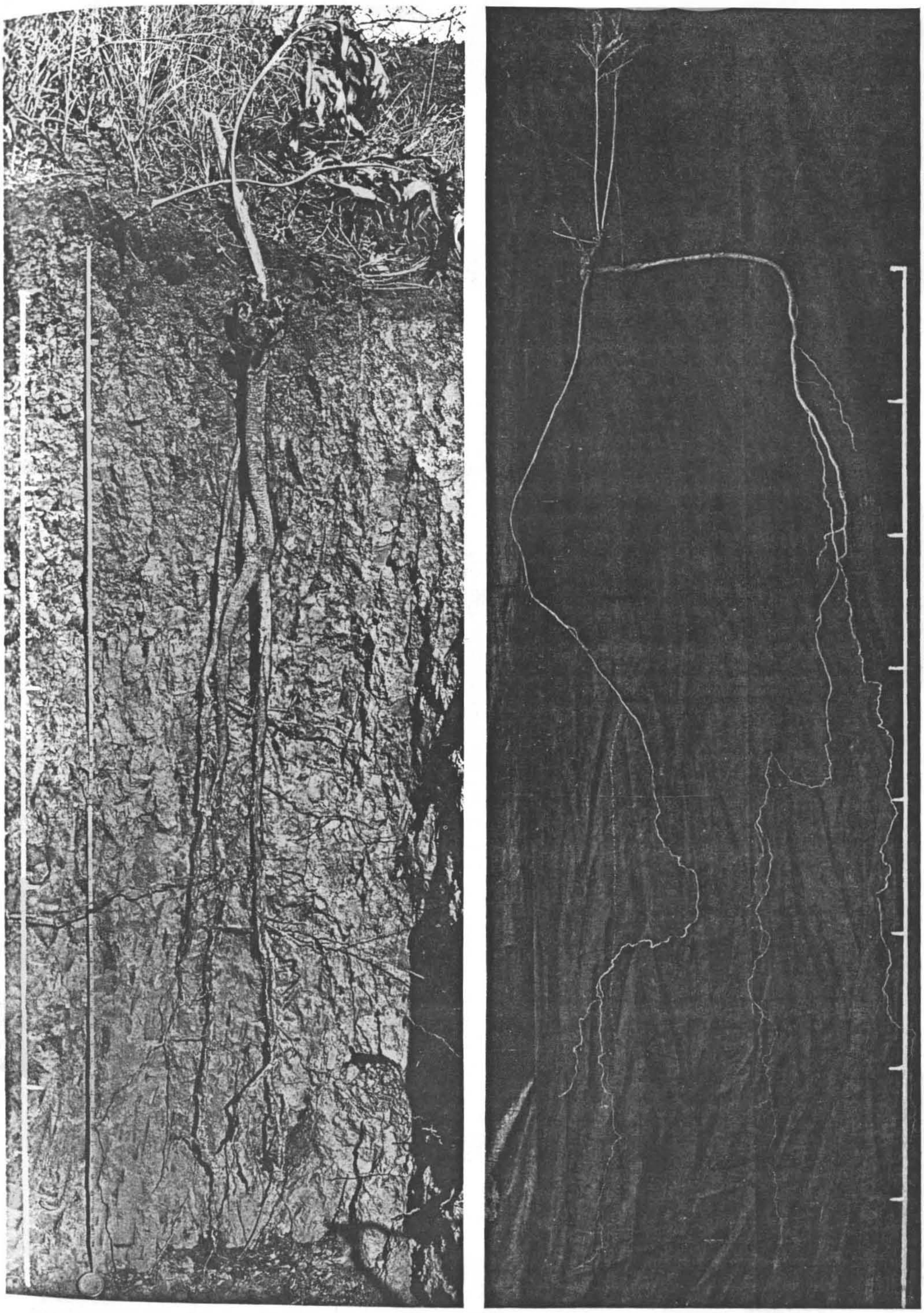
B

A. *Sporobolus longifolius.*
B. *Bouteloua gracilis*, excavated near the quadrat shown in figure 1.



A. *Silphium laciniatum*, roots partially excavated.
B. *Amorpha canescens*, showing wide lateral spread.

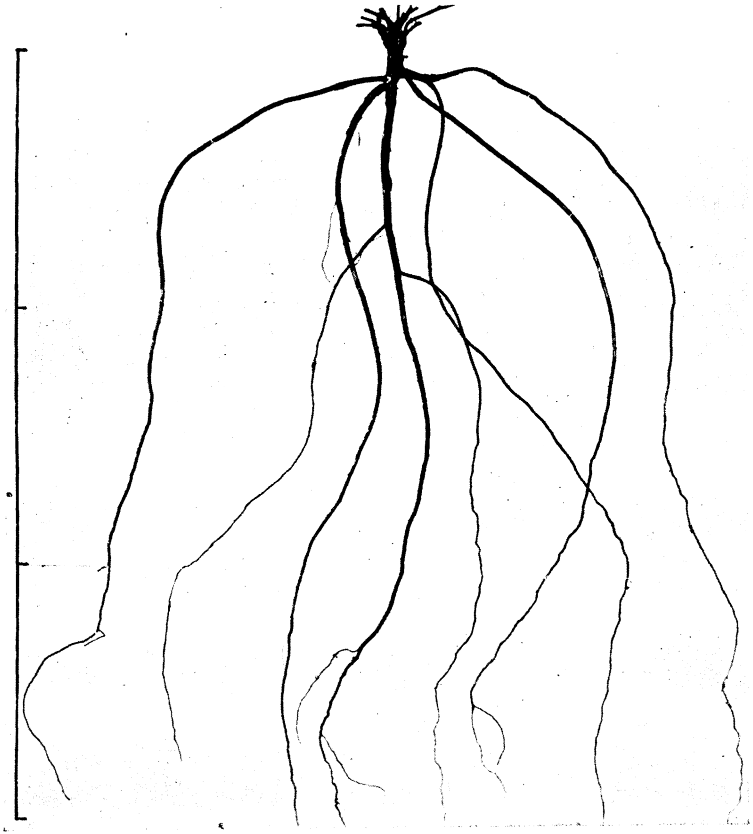
A



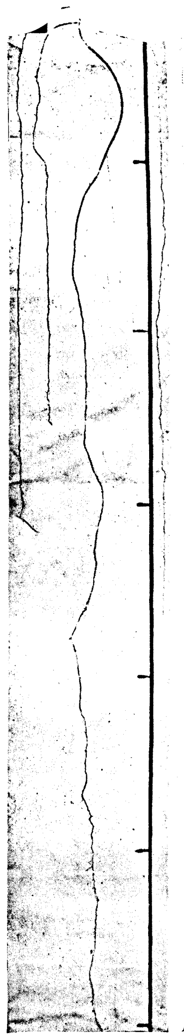
B

A. *Silphium laciniatum*, roots partially excavated.
B. *Amorpha canescens*, showing wide lateral spread.

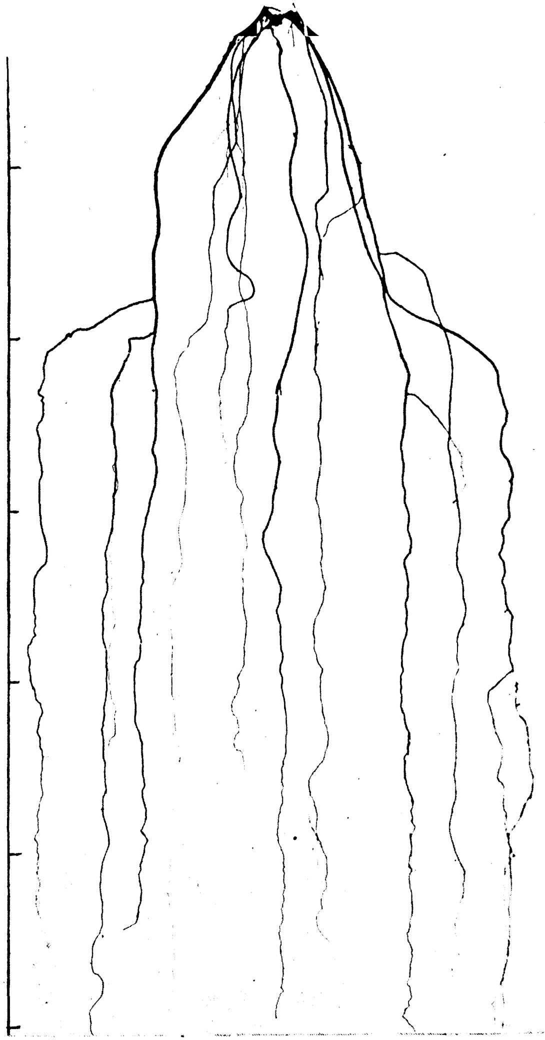
A



B



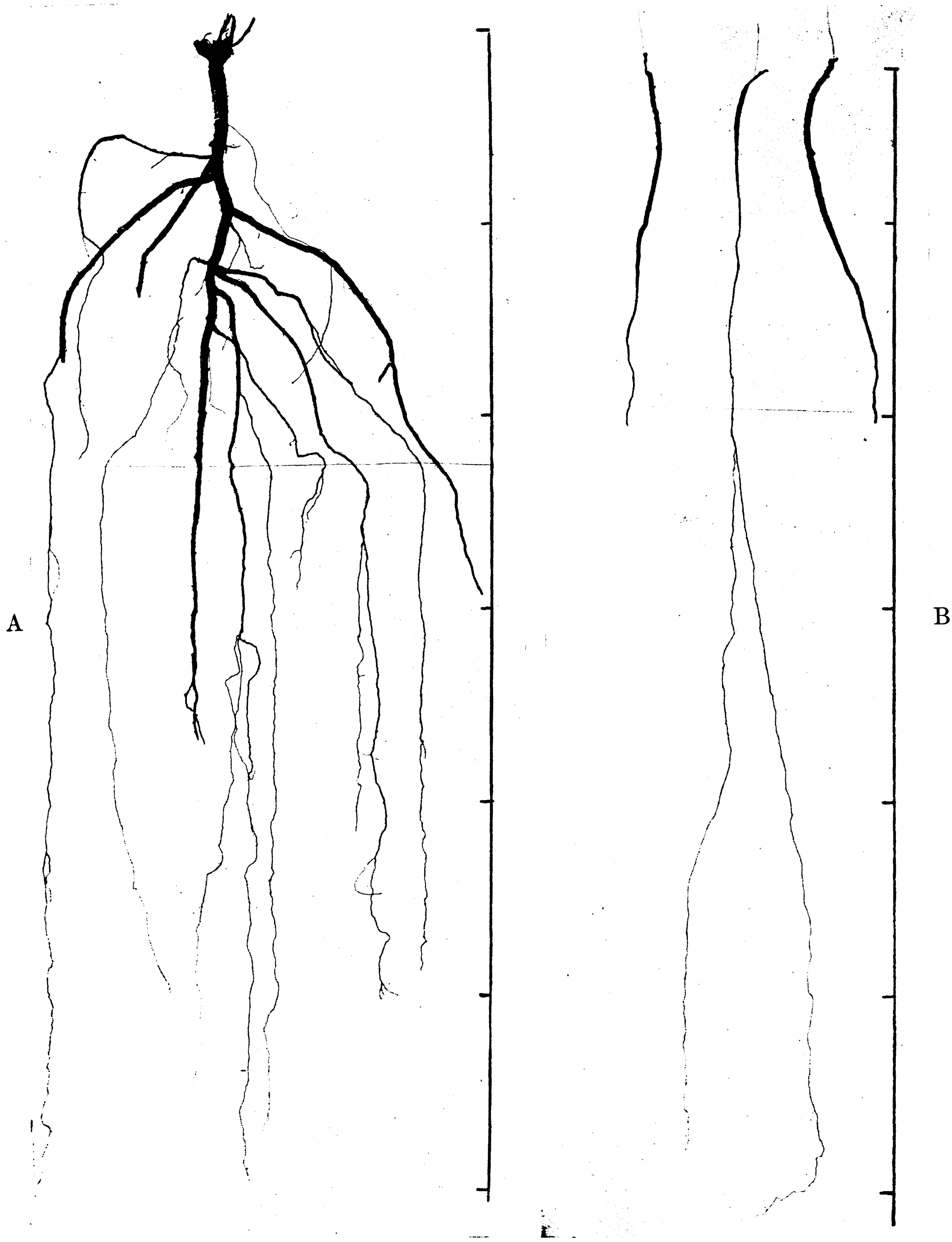
C



A. *Astragalus crassicarpus*, mature root system.

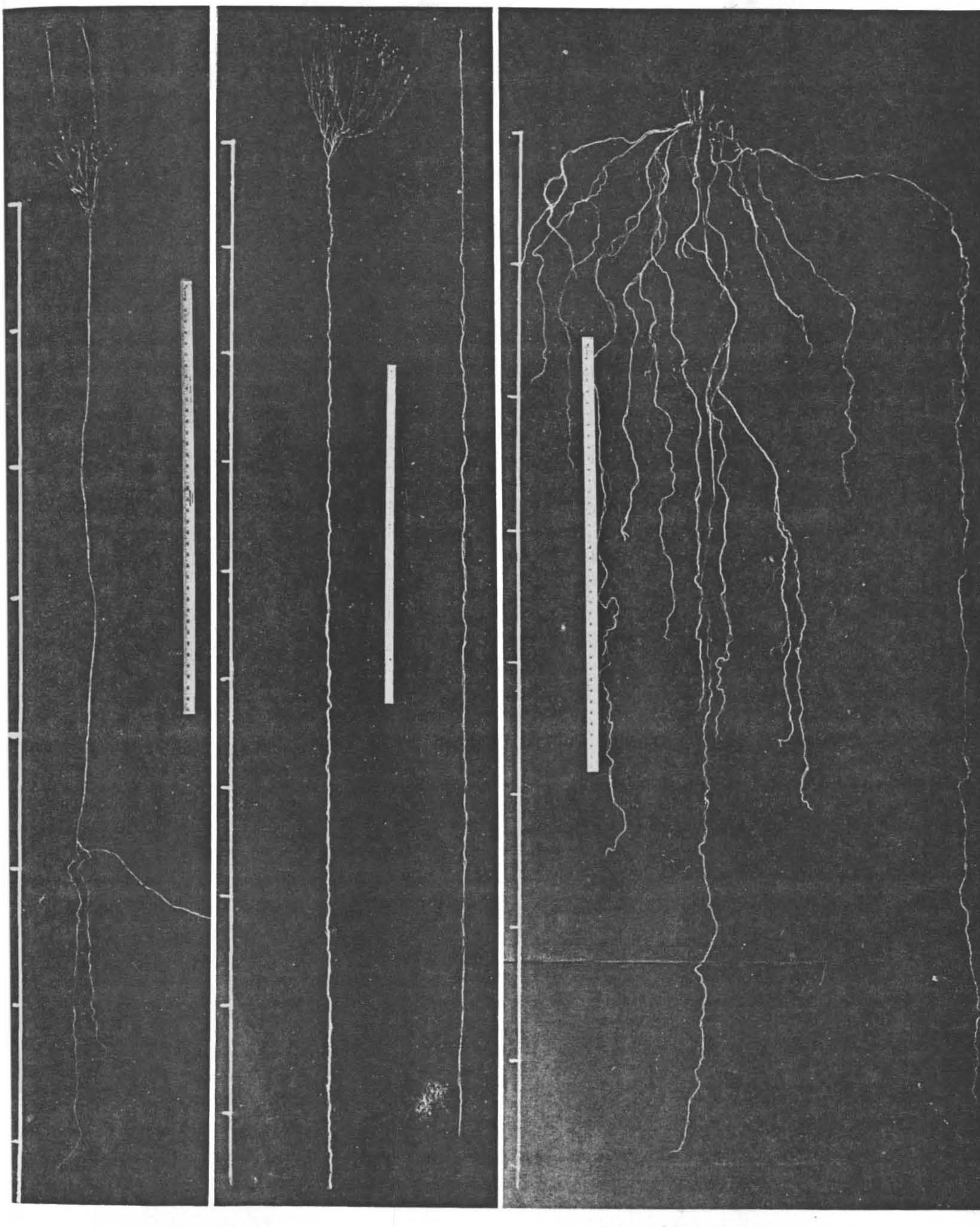
B. *Astragalus crassicarpus*, showing root of young plant.

C. *Baptisia bracteata*.



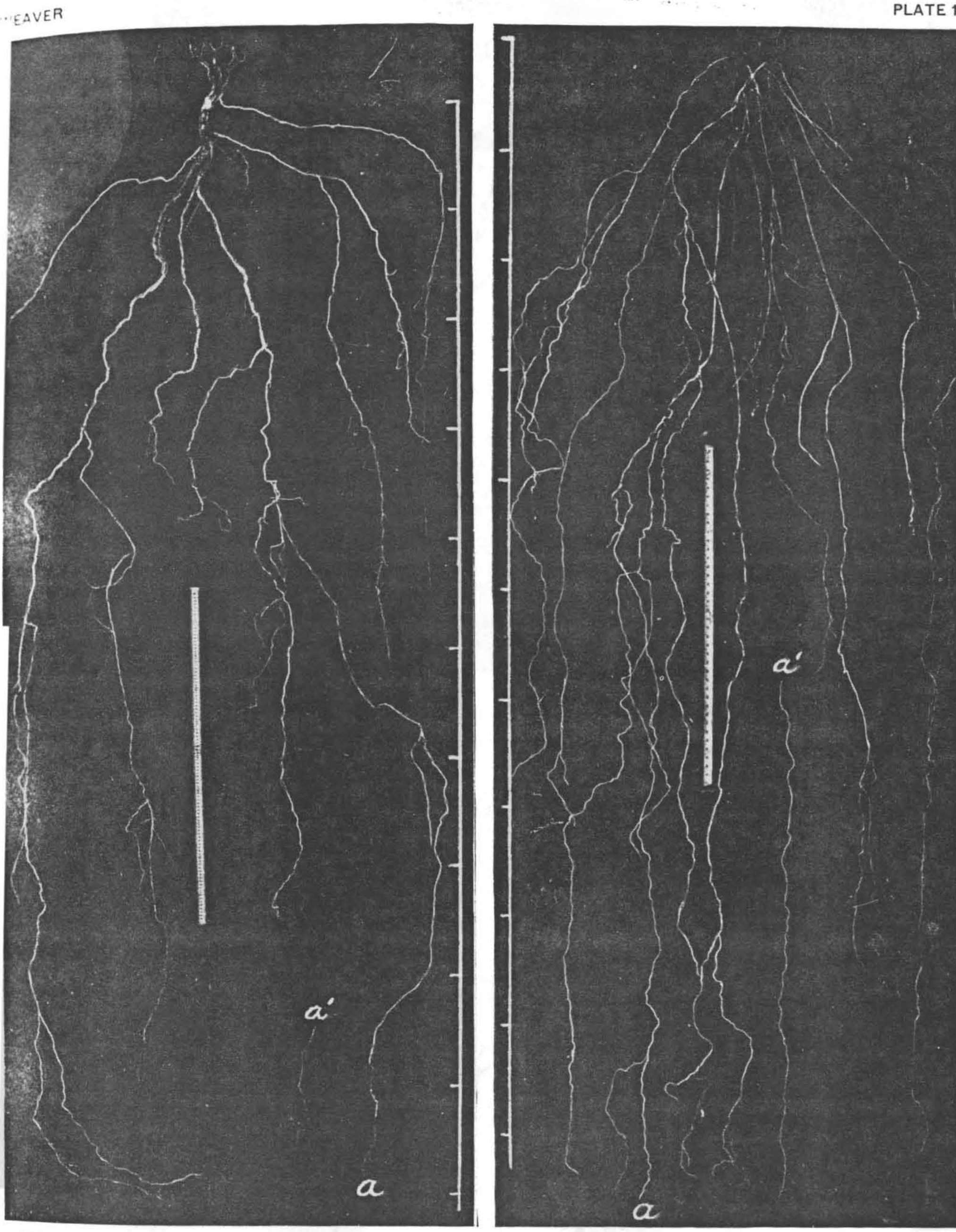
A. *Psoralea tenuiflora*, the tap-root decayed.
B. *Psoralea argophylla*, showing entire root in center.

A B C



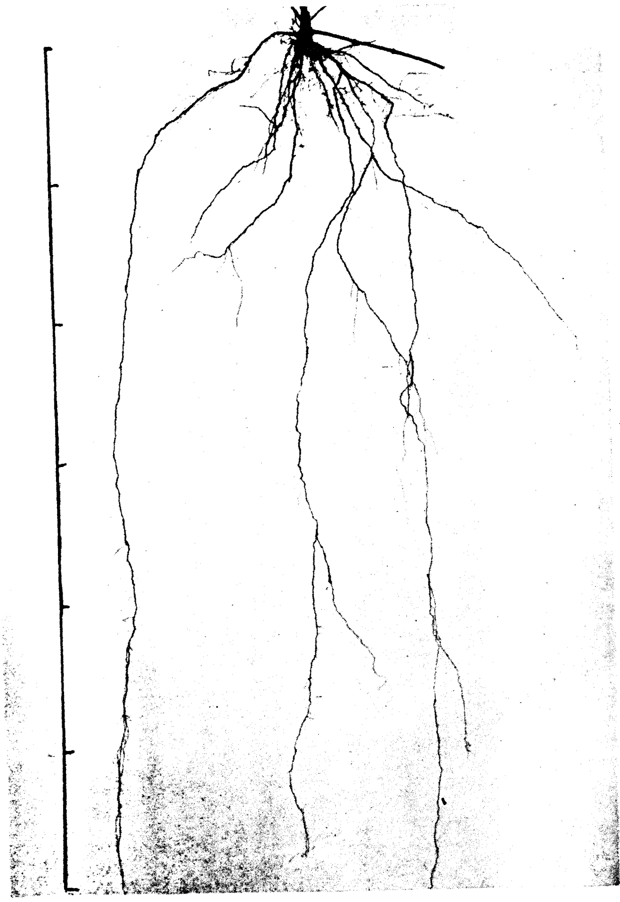
A. *Brauneria pallida*. B. *Lygodesmia juncea*, in two sections. C. *Lespedeza capitata*.

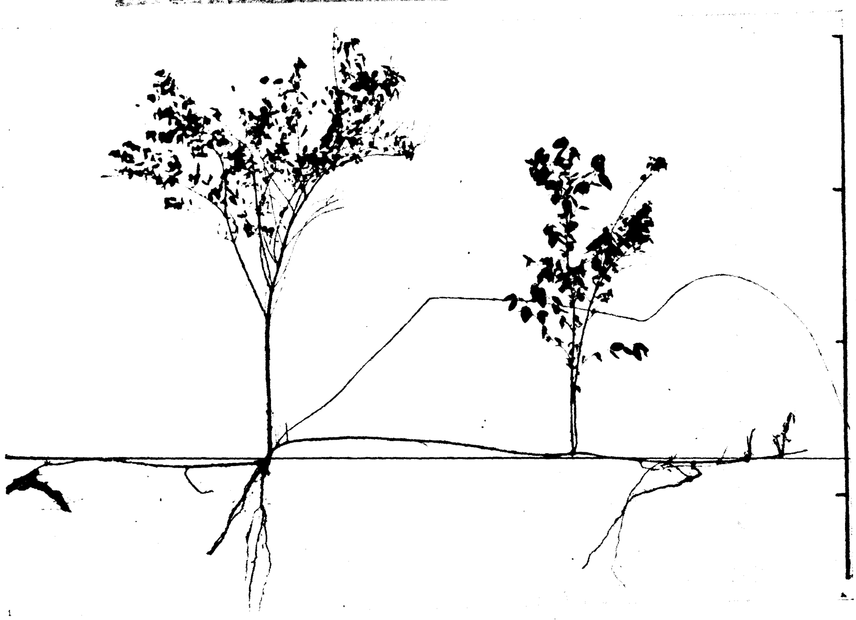
A



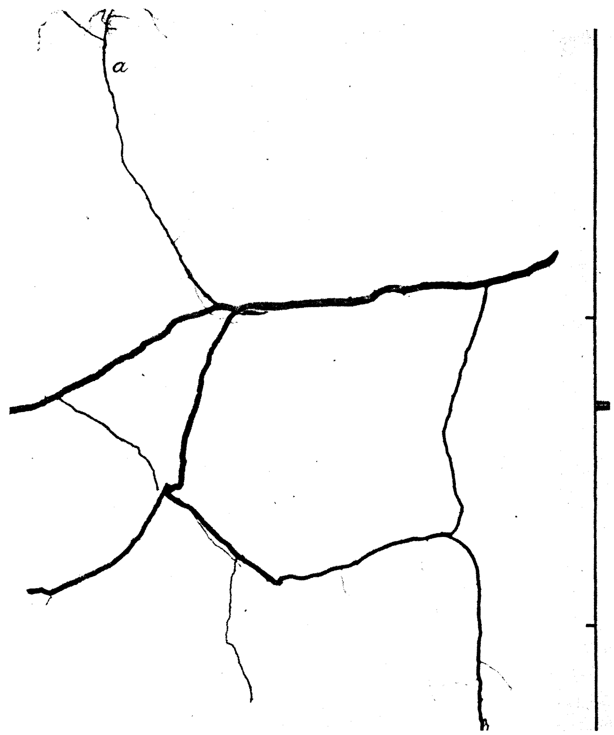
B

A. *Ceanothus ovatus;* root of a thirteen-year-old plant; *a′* is a continuation of *a*.
B. *Amorpha canescens; a′* is a continuation of *a*.

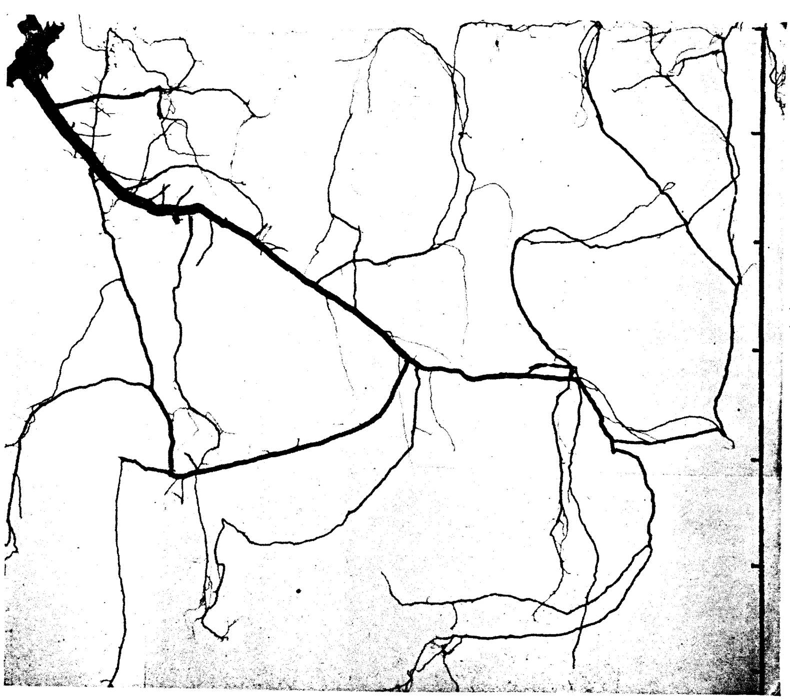

A


B

A. *Symphoricarpos vulgaris,* showing fine network in surface soil.
B. Rhizomes and runners of *Symphoricarpos vulgaris;* the horizontal line is the ground-line.



A



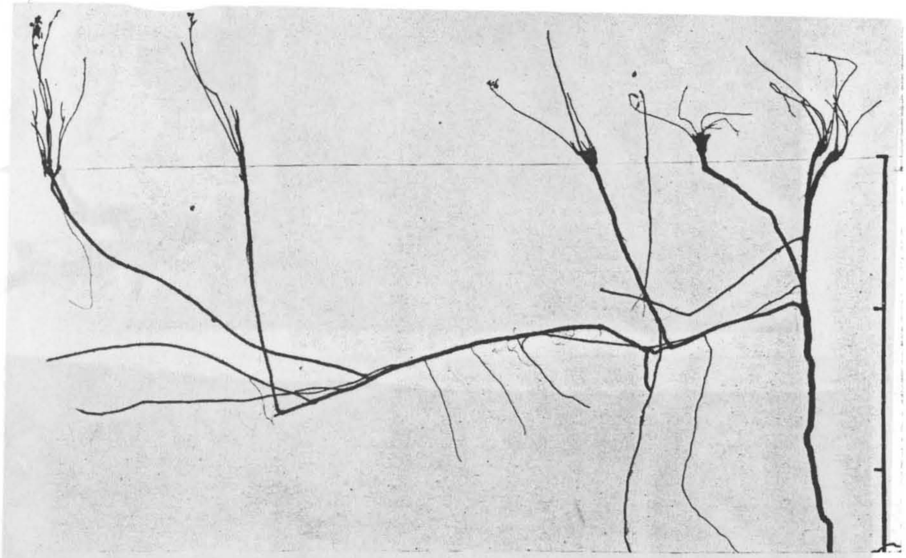
B

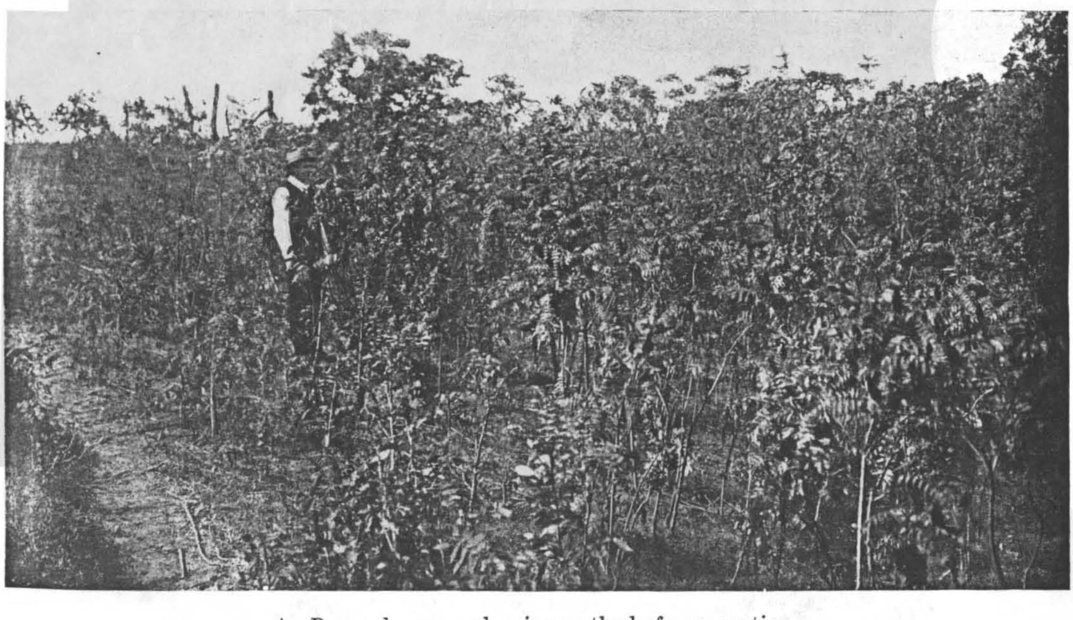
A. *Rhus glabra,* a portion of the root network with ascending rootlet *a*.
B. *Rhus glabra,* with ascending rootlets.

A  B

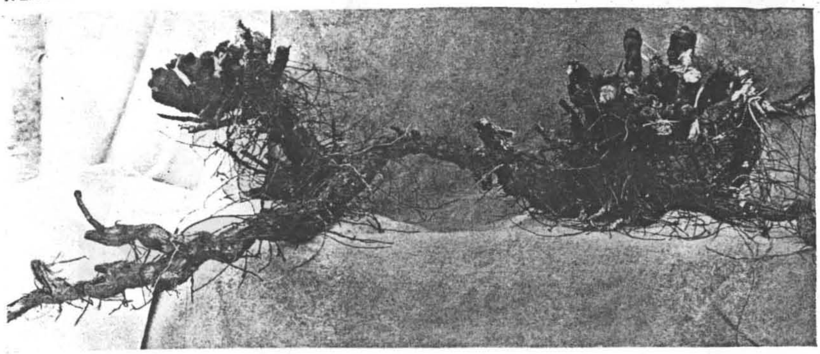
 C

A. *Corylus americana*, the roots shown in two sections.
B. *Rosa arkansana*, the roots shown in two sections.
C. *Corylus americana*, rhizomes and roots.

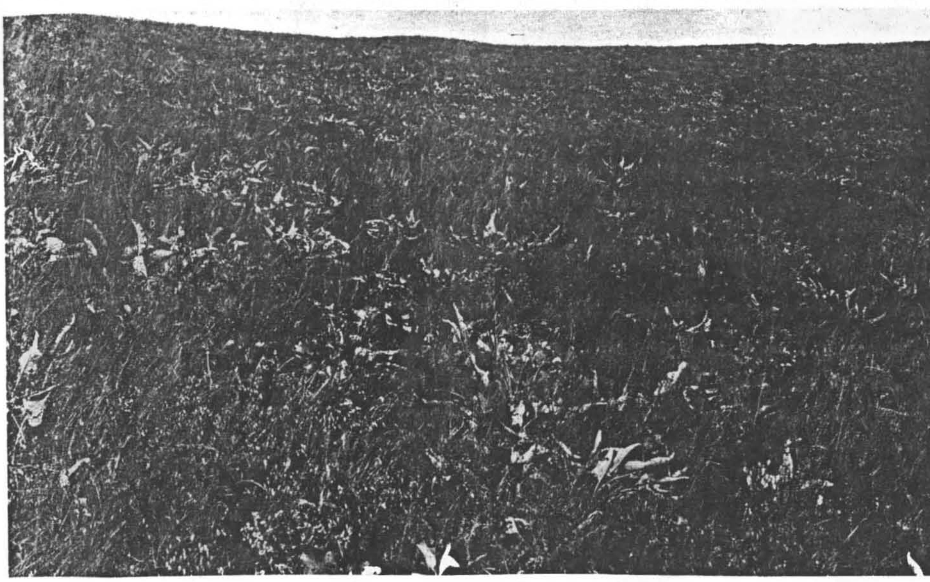

A


B

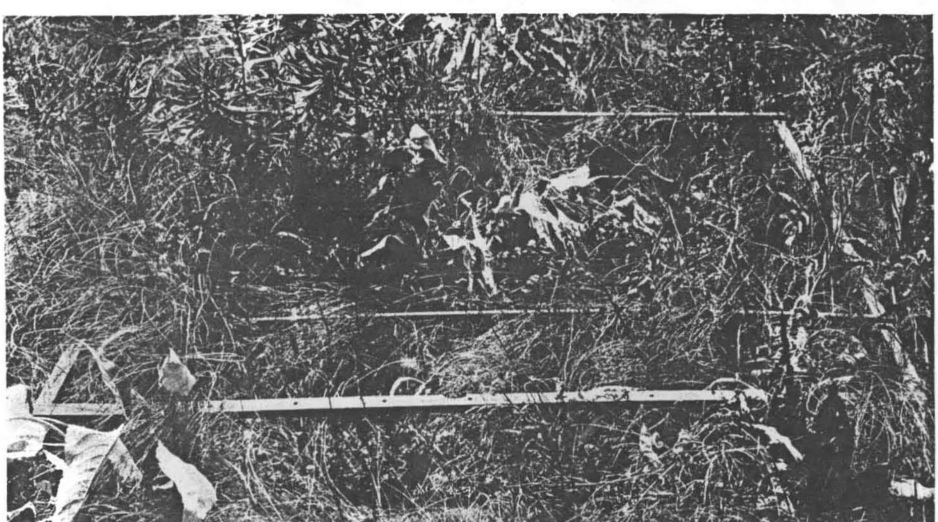
A. *Rosa arkansana*, showing method of propagation.
B. *Rhus glabra* invading subclimax prairie.



A



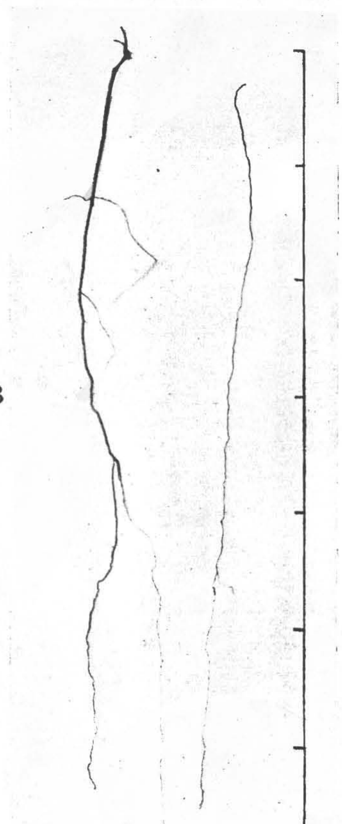
B

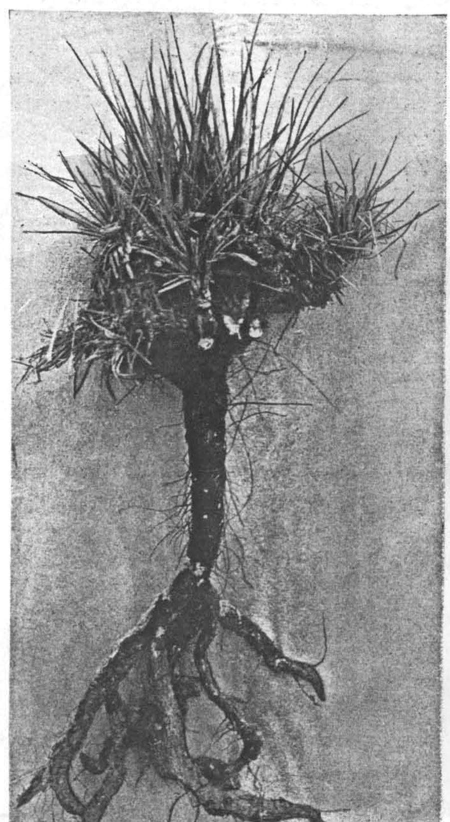


C

A. *Yucca glauca*, showing the multicipital stems and rhizome habit.
B. Prairie of southeastern Washington.
C. Meter quadrat in prairie, showing *Balsamorhiza*, *Festuca*, *Lithospermum*, and *Hieracium*.

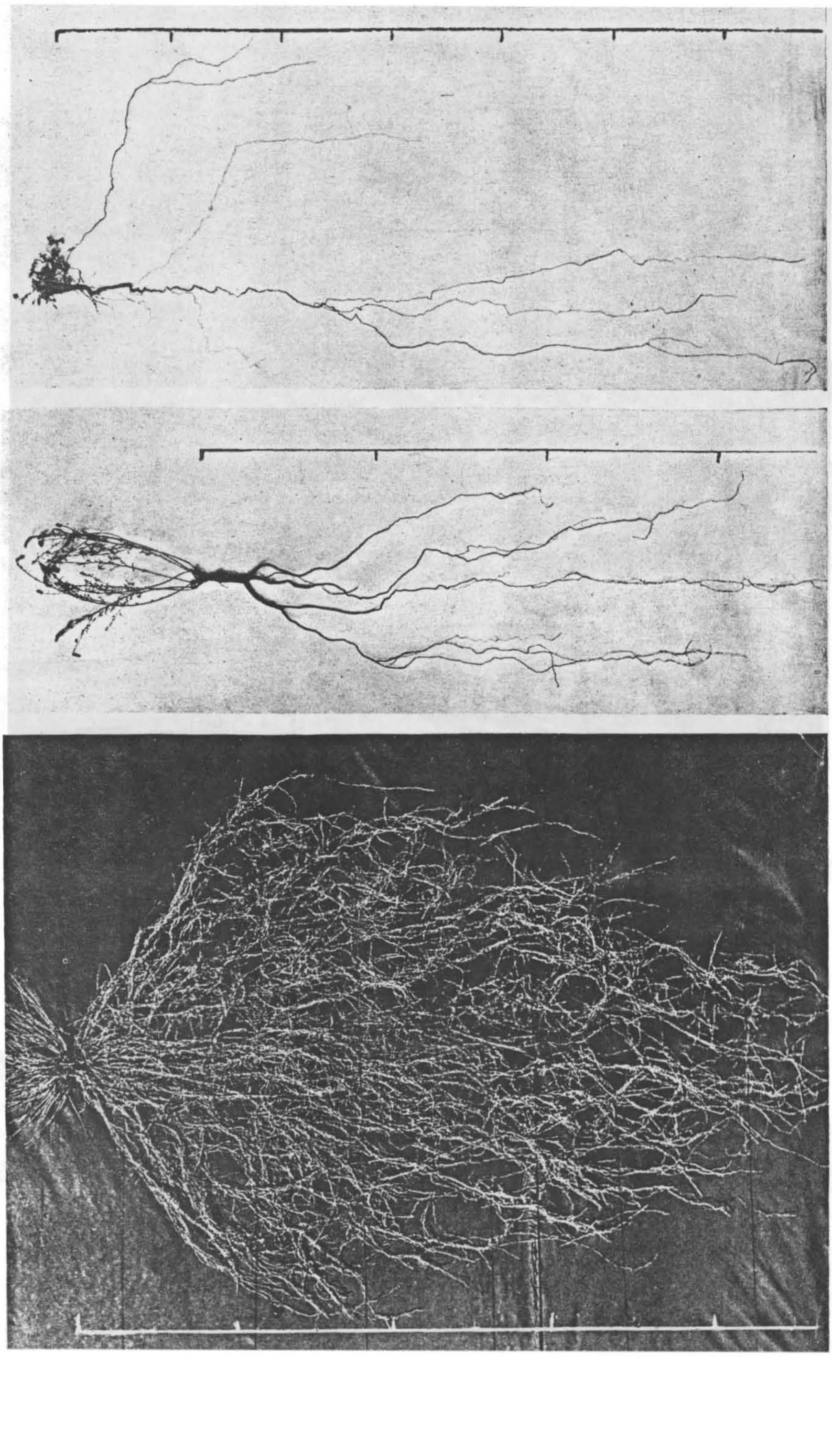
A


B


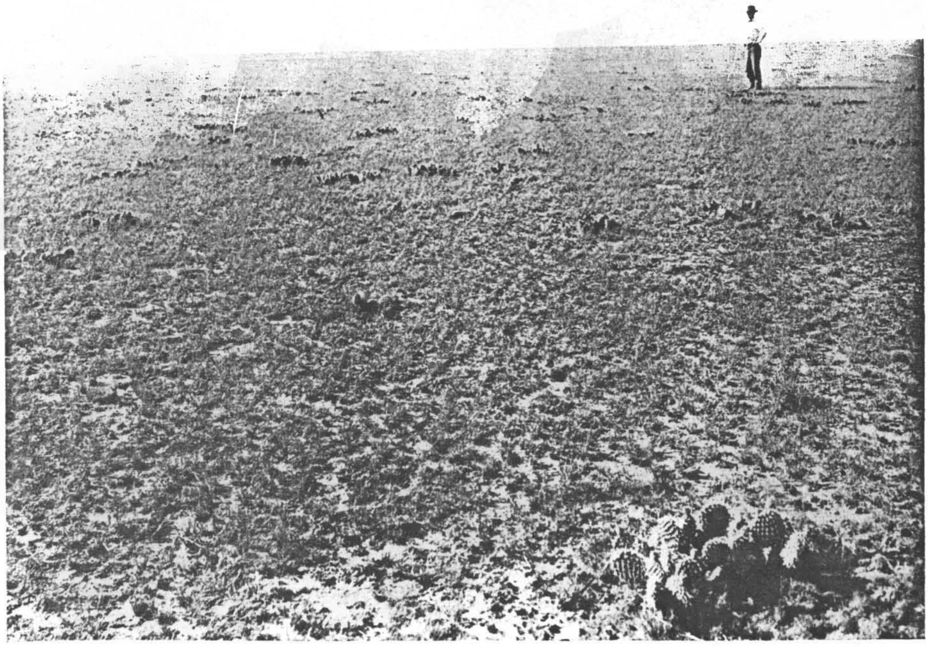
C


A. The plains association near Colorado Springs, showing *Aristida purpurea* bunches in *Bouteloua gracilis* turf.
B. *Psoralea tenuiflora* in two sections. C. *Yucca glauca*.

A B C



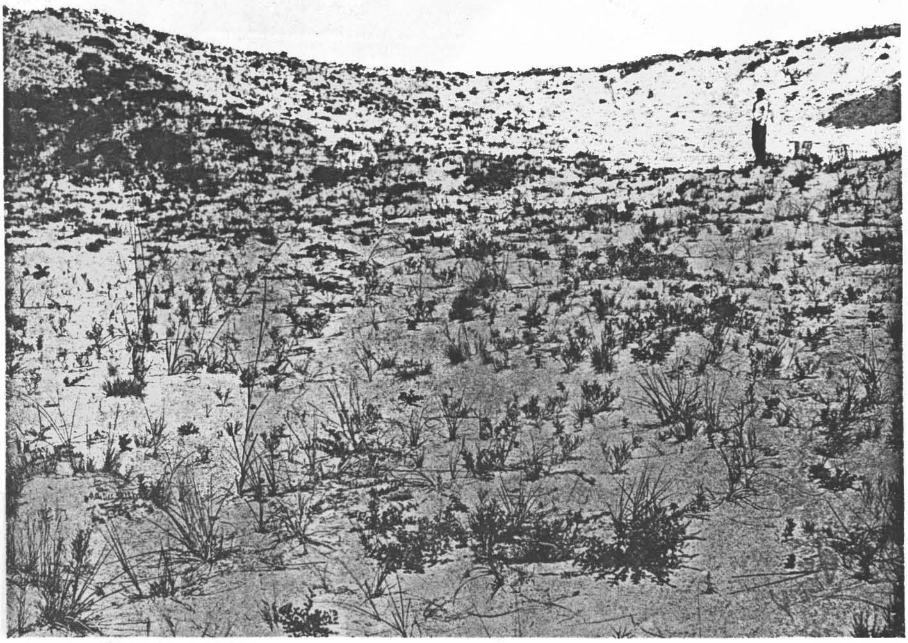
A. *Stipa comata.* B. *Petalostemon candidus.* C. *Erigonum jamesii.*



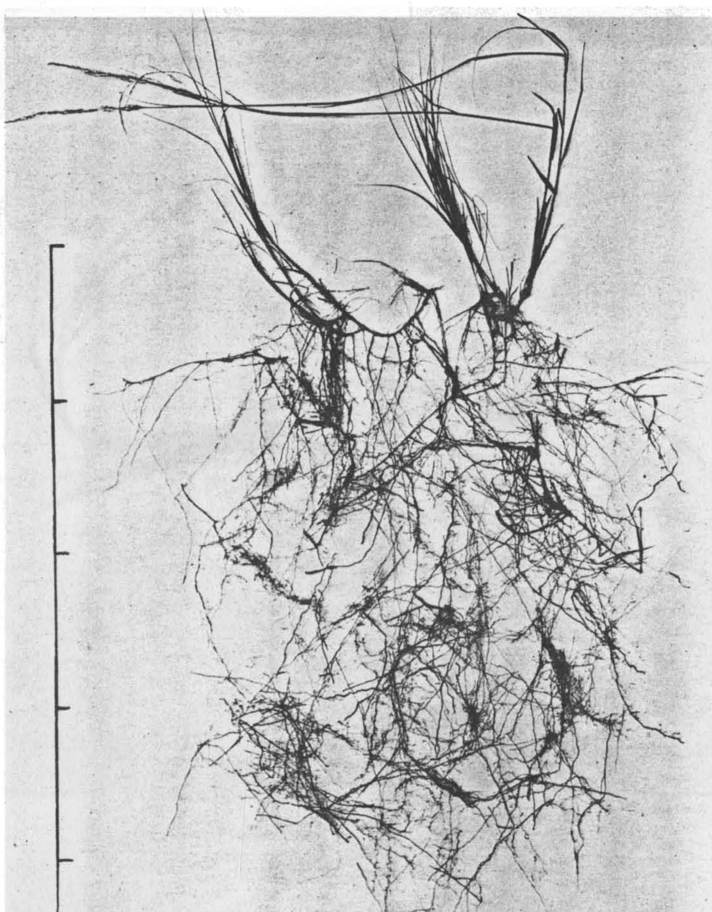
A

B

A. Short-grass plains, showing *Bouteloua gracilis* and *Opuntia polyacantha*.
B. General view of the sandhill community.



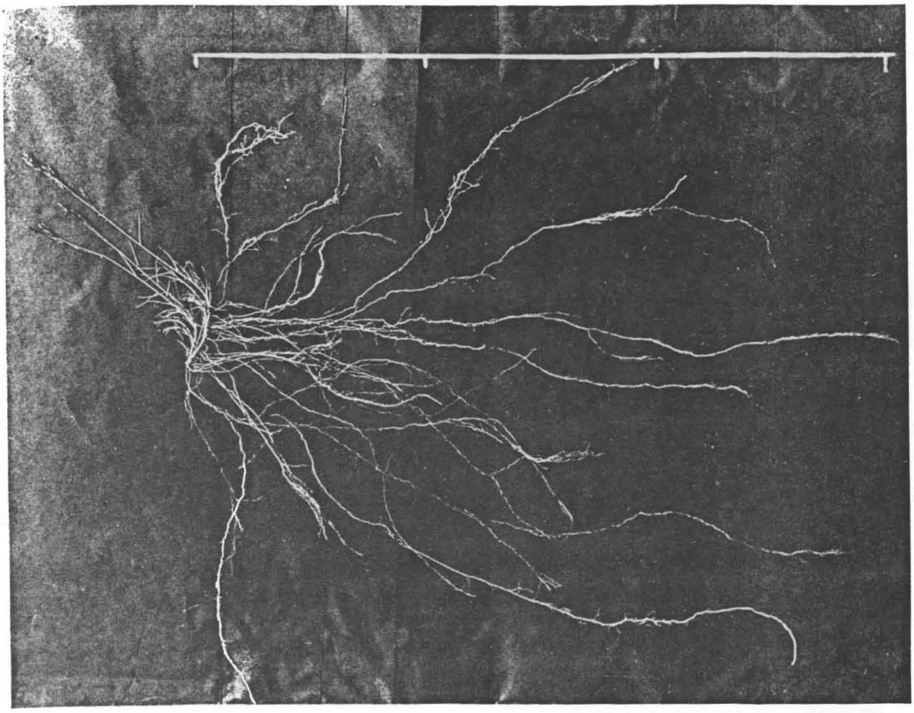
A



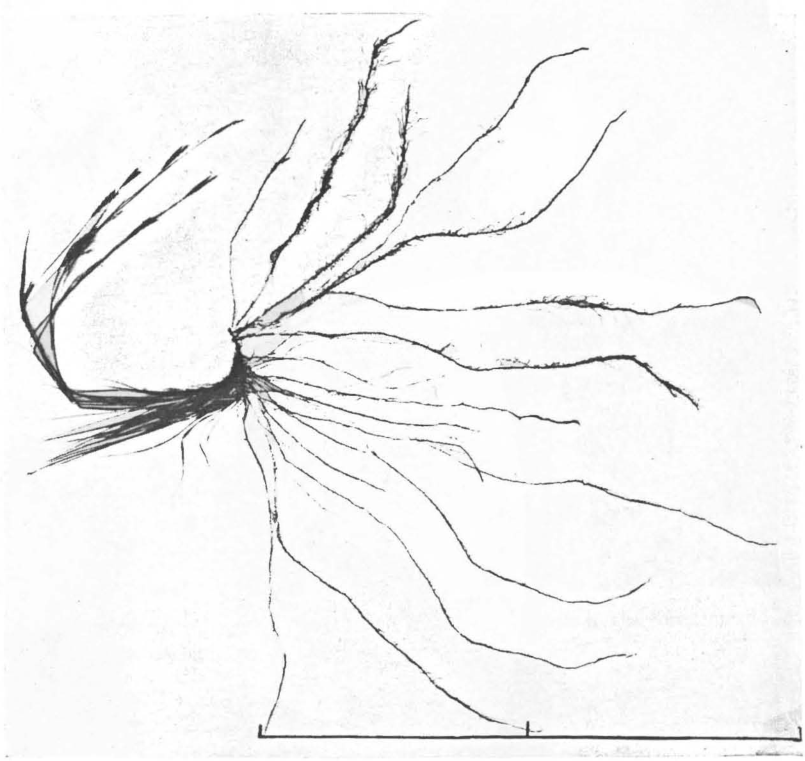
B

A. A sandhill community, showing *Redfieldia*, *Petalostemon villosus*, *Psoralea lanceolata*, and *Chrysospis villosa*, with a socies of *Eriogonum microthecum* at the left.
B. Roots and rhizomes of *Calamovilfa longifolia*.

B

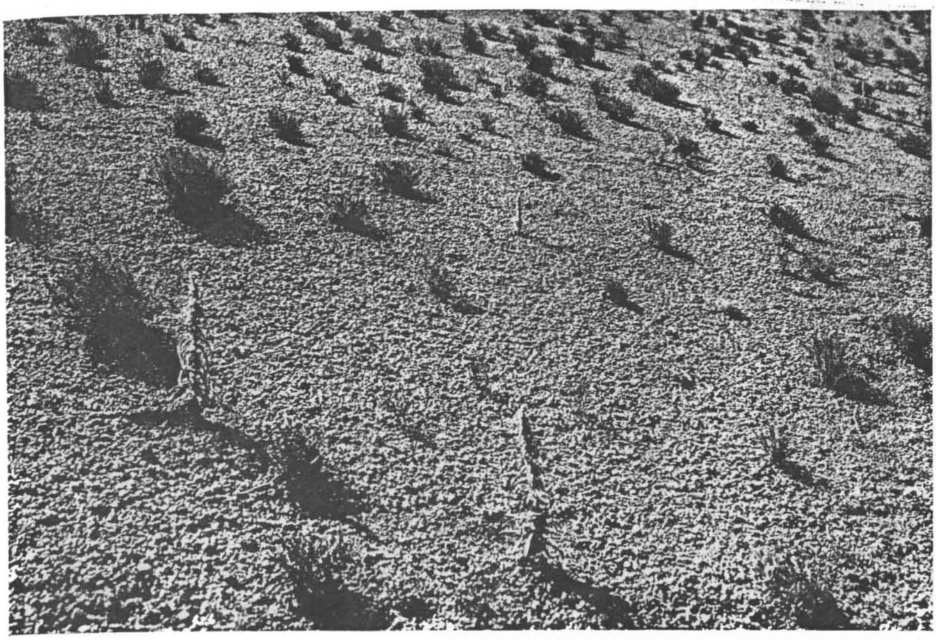


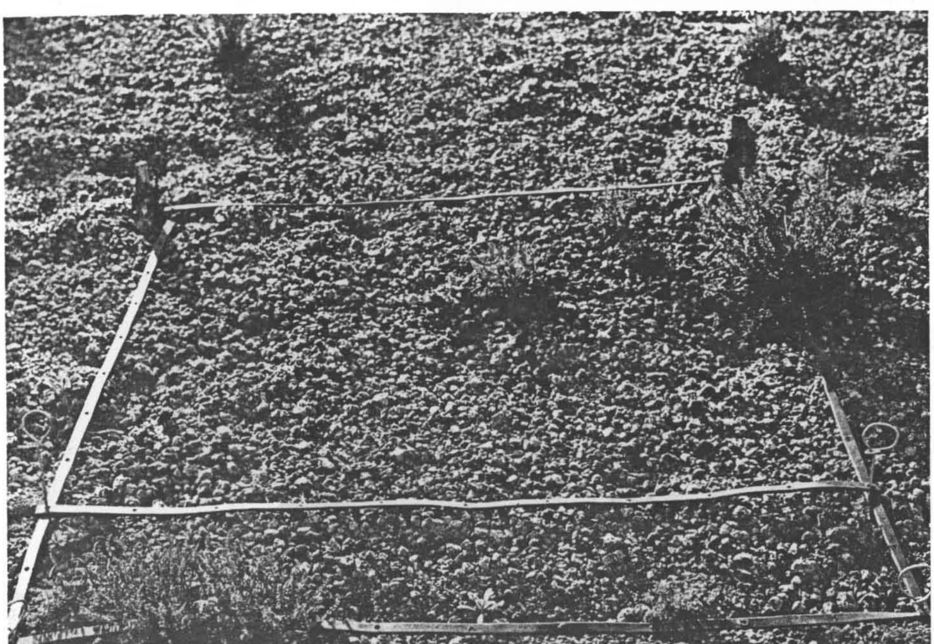
A



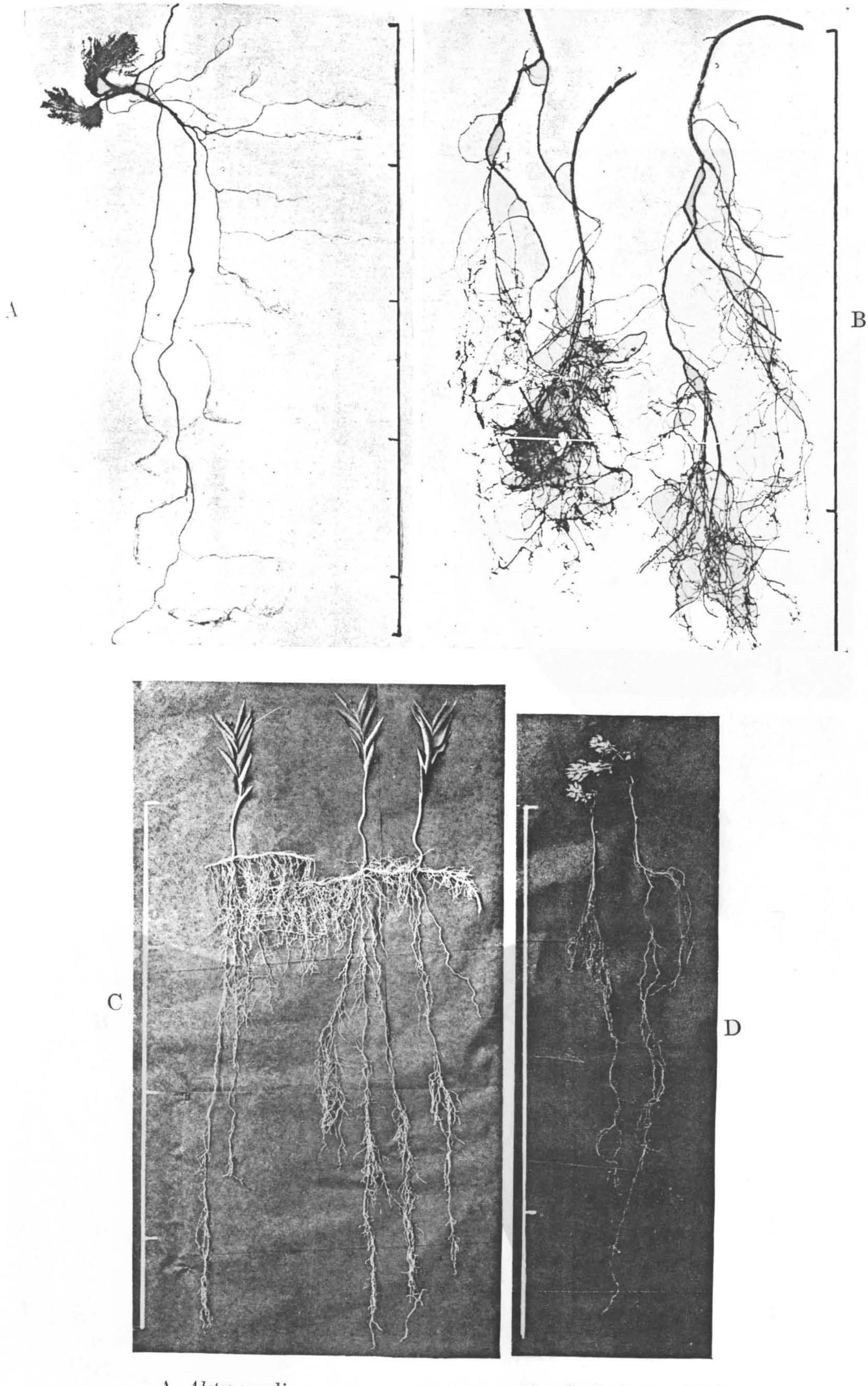
A. *Andropogon hallii.*

B. *Muhlenbergia pungens.*


A

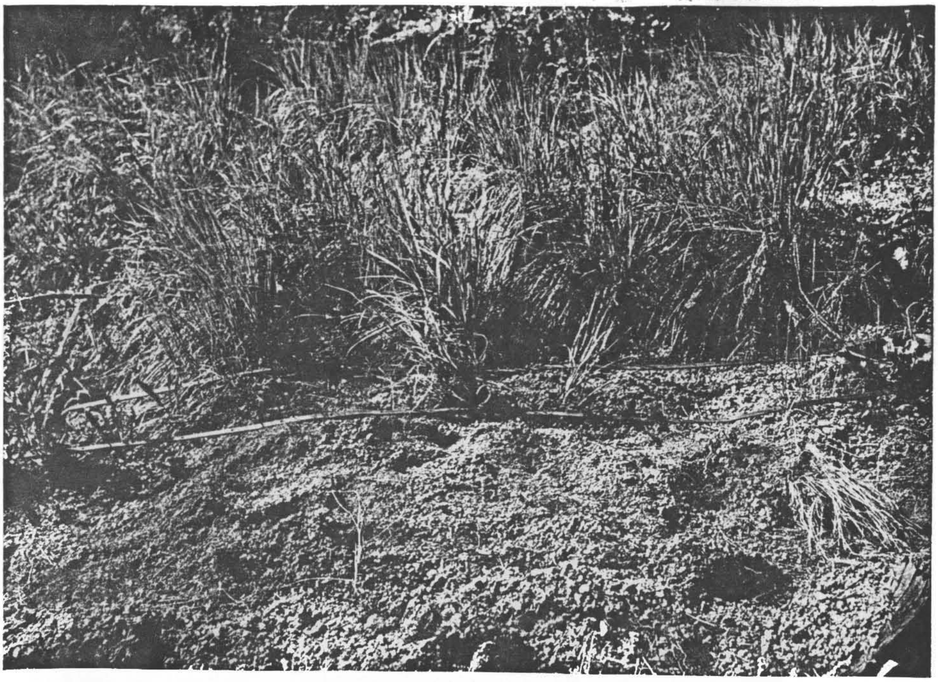

B

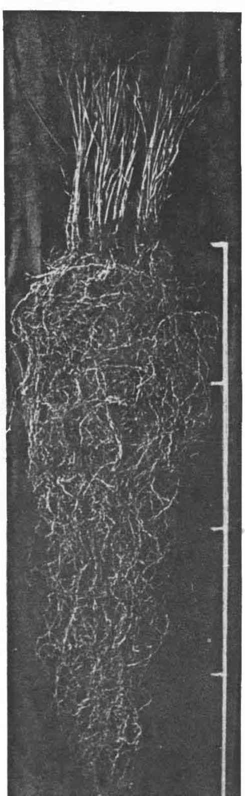
A. Consocies of *Aletes acaulis* on the gravel-slide, with *Krynitzkia virgata* in the foreground.
B. Quadrat on the gravel-slide, showing detail of surface.

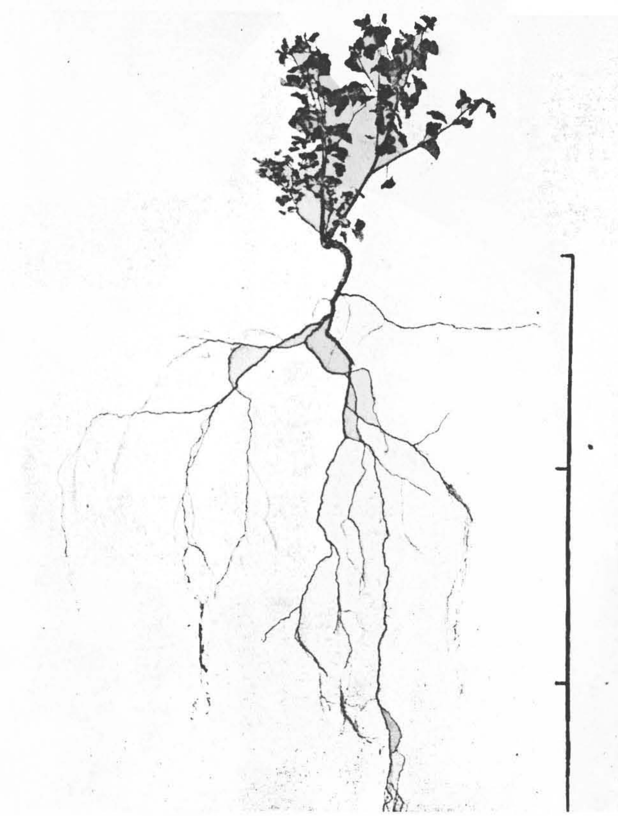


A. *Aletes acaulis*.
B. Network of fine rootlets of *Aletes*.

C. *Smilacina stellata*.
D. *Thlaspi alpestre*.

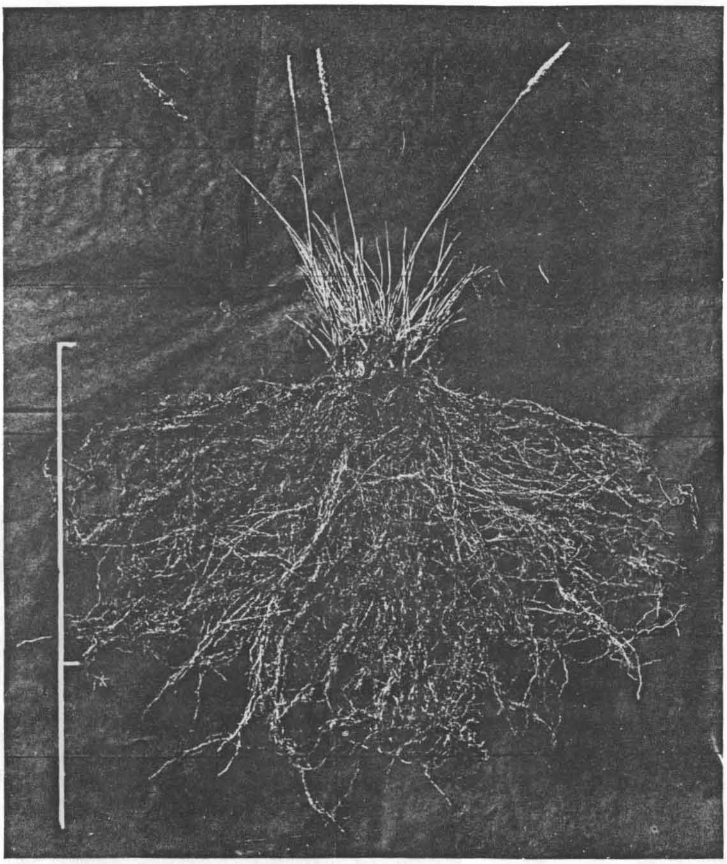
A


B


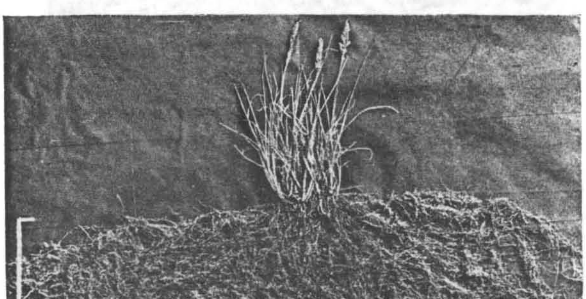

C

A. Half-gravel-slide, showing *Elymus triticoides* and the large bare intervals.
B. *Elymus triticoides*. C. *Rubus deliciosus*.

A

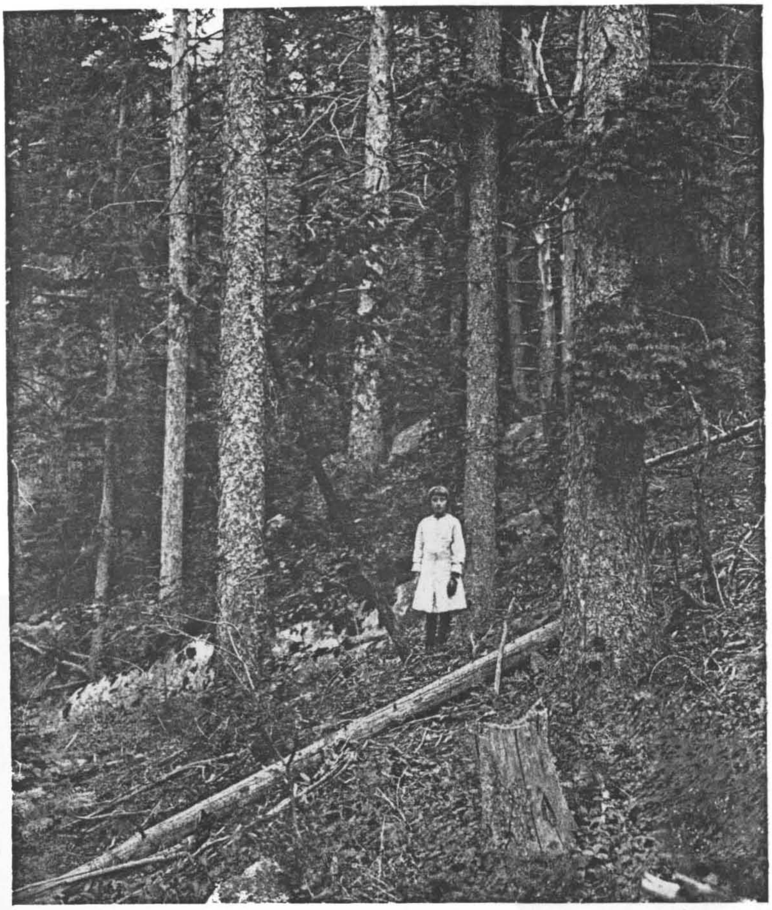


B

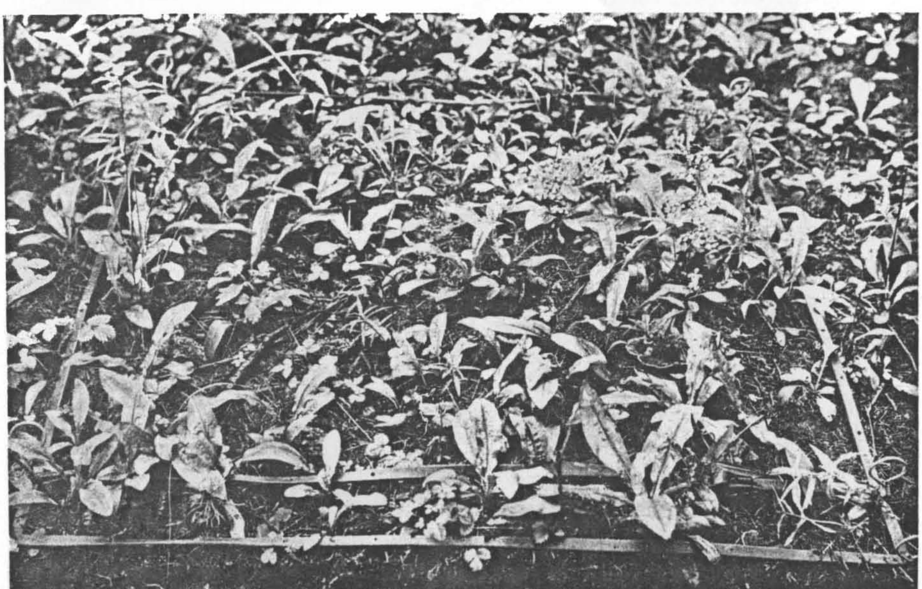


C

A. *Kœleria cristata.* B. *Calamagrostis purpurascens.* C. *Potentilla arguta glandulosa.*

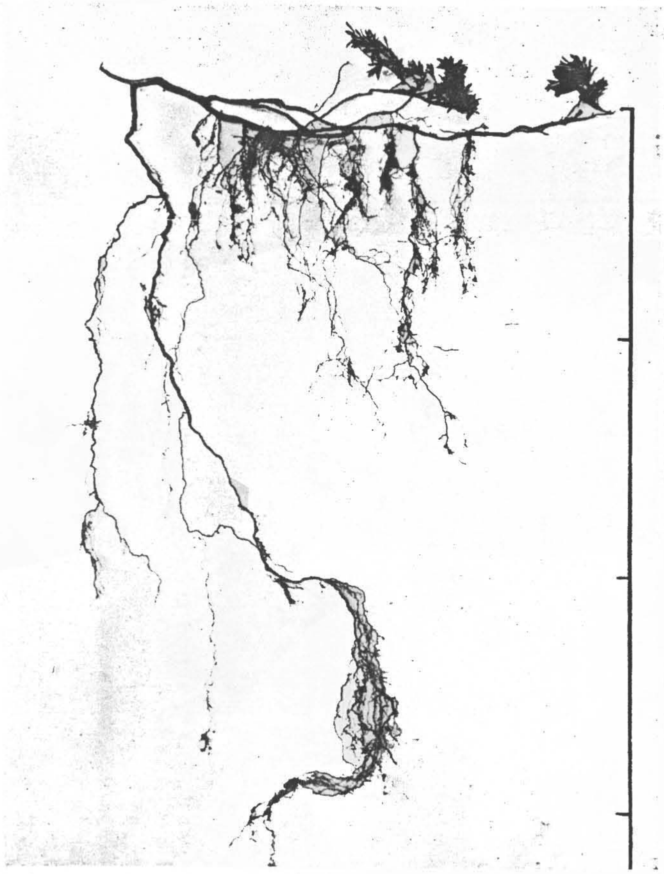


A

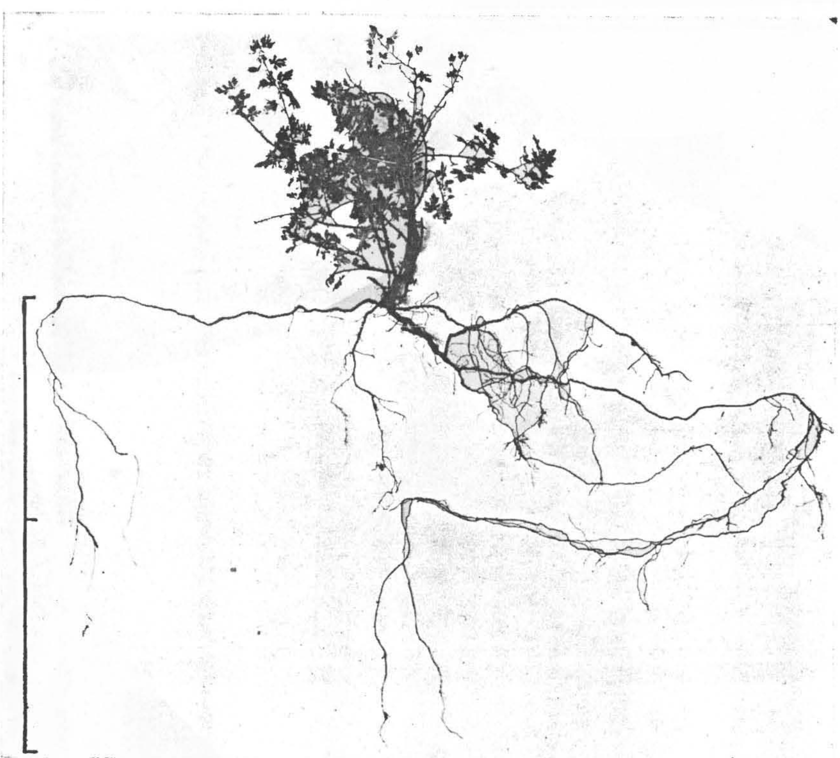


B

A. *Picea engelmanni* consociation, showing the forest floor.
B. Quadrat in the same spruce forest, showing *Haplopappus parryi*, *Fragaria virginiana*, *Thalictrum fendleri*, etc.



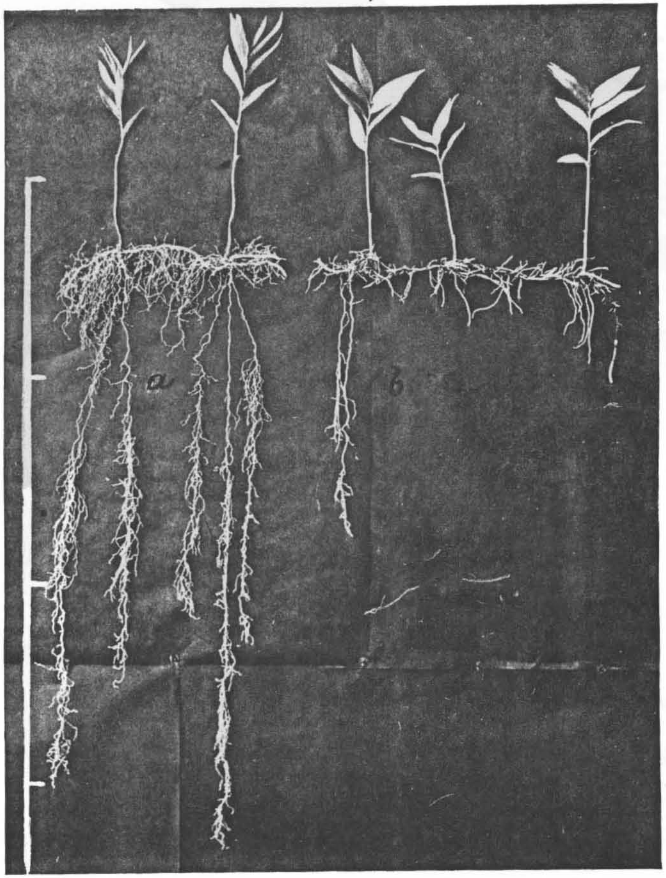
A



B

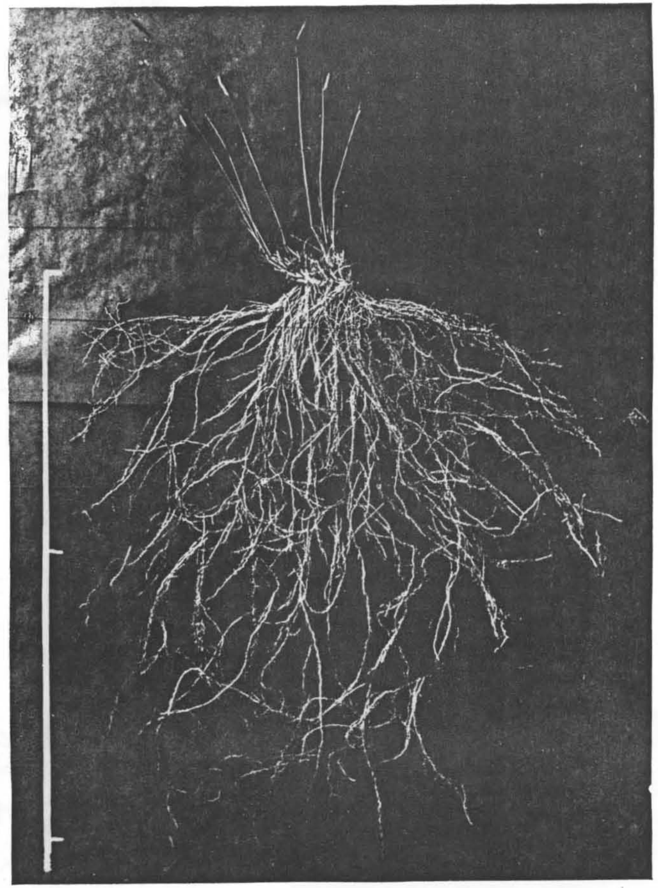
A. *Arctostaphylos uva-ursi*, showing a portion of the root system.
B. *Ribes lacustre*, seven years old.

A



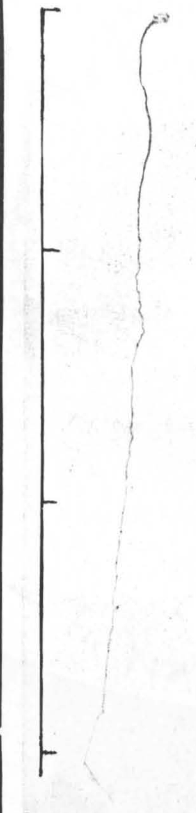
A. Root systems of ecads of *Smilacina stellata: a*, gravel-slide; *b*, spruce forest.

B

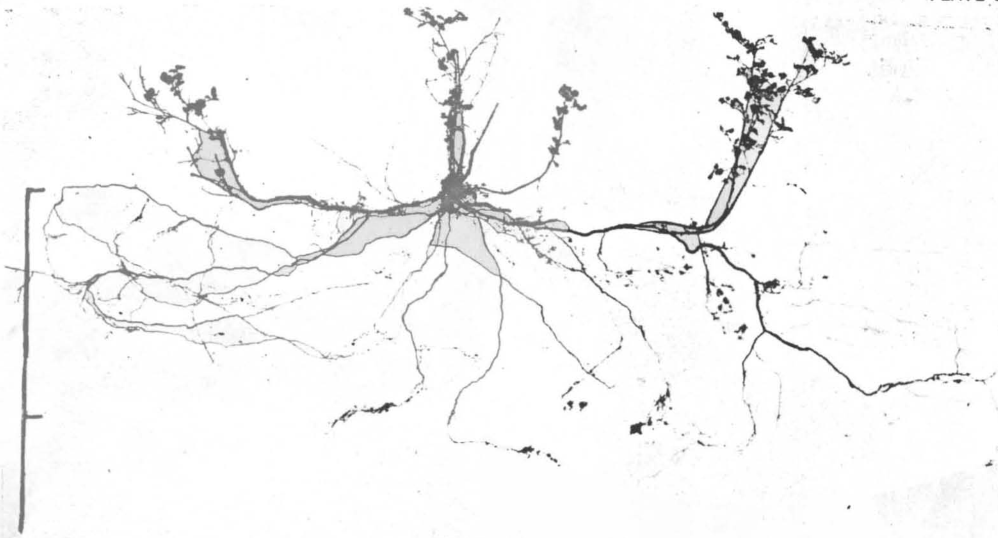


B. *Bouteloua gracilis* from the sandhills.

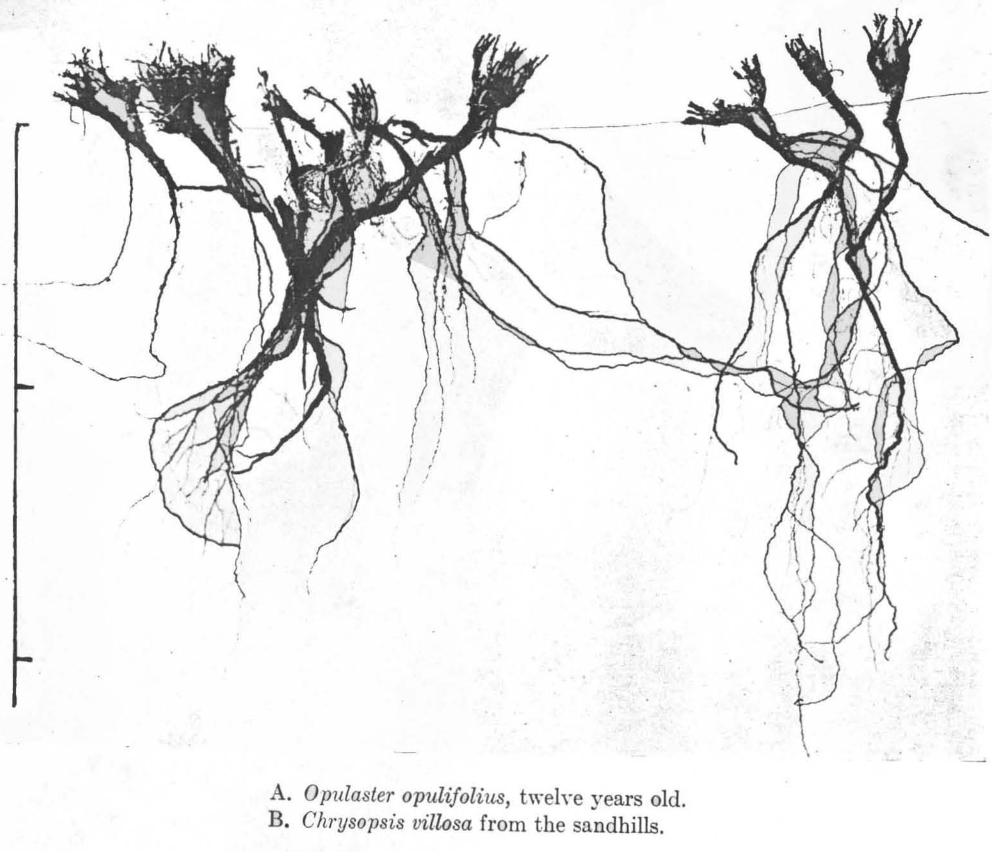
C



C. *Abronia fragrans* from the plains.



A



B

A. *Opulaster opulifolius*, twelve years old.
B. *Chrysopsis villosa* from the sandhills.