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The Root Habits of Desert Plants

BY

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WASHINGTON, D. C.

PUBLISHED BY THE CARNEGIE INSTITUTION OF WASHINGTON

1911

QK
922
C255

CARNEGIE INSTITUTION OF WASHINGTON

PUBLICATION NO. 131

Copies of this Book

were first issued

MAR 28 1911

PRESS OF GIBSON BROS.

WASHINGTON, D. C.

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The Root Habits of Desert Plants.

INTRODUCTION.

It is now generally recognized that the arid and semi-arid regions are especially favorable areas in which to study the habits of plants. This is partly because the vegetation of the less humid countries represents the most advanced type of land forms—that is, those farthest removed from the primitive water-loving plants—and partly because, as the environmental features are severe, so the response on the part of the plants is correspondingly effective in order to bring about survival. The shoot habits of desert plants have received considerable attention from botanists, but the reaction of roots to desert conditions has, in a large measure, been neglected. That this neglect is illogical and without good reason is apparent when it is recalled that the connection between the plant and a most important feature of the environment, the soil and its water content, is sustained only through the roots.

The fact is well known that the roots of plants have a twofold function. They at once afford safe anchorage and support and at the same time are the means by which water and inorganic food materials are acquired. The dual nature of roots does not find separate organic expression in the most primitive plants, and in certain of them, the algæ, organs answering to roots serve the purpose of anchorage only. In the low land plants, the roots, morphologically rhizoids, are, from this point of view, quite undifferentiated, but as the scale of plant life is ascended we find these functions separated both in time and in space, at first on the same root and its immediate branches, and finally there is differentiation in the root-system of the plant, by which the anchorage is largely taken over by one set of roots and the absorption by quite another set. The last is the advanced condition found in the extreme xerophytic desert plants, such as many of the cacti. Thus the extent and the character of root development will reveal, in a measure, the degree of xerophily of a plant.

The prevailing idea that the roots of plants of the deserts, or of semi-arid regions, are of great length, especially that they penetrate the ground to great depths, doubtless has its origin largely in the belief that desert plants are obliged to develop a deeply placed root-system in order to obtain water during long dry seasons, and also in the few striking examples of really long roots of plants of arid countries which are accepted as representing the root condition of all desert plants.

On this point Schimper (Plant-geography, English edition, p. 612) says:

This second category of desert plants exhibits its dependence on subterranean water nearly universally by the immense length of its root-system, which the depth of the level of the subterranean water renders vitally necessary. A considerable length of root is, to a more or less extent, common to all desert plants and has attracted the notice of all travelers.

This statement is substantiated by a quotation from Volkens, who says (Die Flora der aegyptisch-arabischen Wüste auf Grundlage anatomisch-physiologischer Forschungen, p. 7):

Often as I have tried to dig up old bushes of perennial plants to the extremity of their roots, I have never succeeded in doing so. The most that I could establish was, that the root was thinner at the depth of one or two meters than at the surface of the ground. One can safely assume that, in this case, the length of the subterranean part was at least twenty times that of the epigeous part.

Volkens then goes on to say that certain species of *Acacia* were said to have been seen at the time of the digging of the Suez canal, whose roots were found in its bed, although the trees to which they belonged were growing on eminences on its banks.

Isolated observations indicate that the roots of certain trees of the arid regions of the southwestern part of the United States may, under favorable conditions, form long or deeply penetrating roots. Thus Prof. R. H. Forbes, director of the Arizona Experiment Station, informs me that he has seen roots of the mesquite (*Prosopis velutina*), by an irrigating ditch, extend very near the surface of the ground as far as 15 meters, and roots of the same species, where exposed by the washing away of river banks, which penetrated as deep as 8 meters. These figures may be taken as probably representing the deepest root penetration in this vicinity, although it is no unusual thing to see mesquite roots 5 meters in length. Dr. V. Havard is quoted as writing that sometimes in the Southwest camps were pitched on the plains where there was no fuel of any sort to be seen. It is there that the frontiersman, armed with a spade, went digging for wood. Speaking of the deep-penetrating roots of mesquite Havard says:

Of the vertical roots, the tap root is the only long and conspicuous one. It plunges down to a prodigious depth, varying with that at which moisture is obtainable. On the side of gulches one can trace these roots down thirty or forty feet. (American Naturalist, vol. 18, p. 451, 1884.)

It will appear from facts given in this paper that the root-systems of different perennials growing in the vicinity of the Desert Laboratory are extremely variable as regards depth of penetration, lateral extent, and other characteristics, and that no one type of root can be said to be the prevalent one.

The opposite extreme in the position of the roots of desert perennials is to be found in a highly specialized class, the succulents, in which the roots are uniformly near the surface of the ground. Volkens, for example (Die Flora der aegyptisch-arabischen Wüste, p. 24), states that *Euphorbia* has

laterals which are superficially placed, and Weiss and Yapp (Sketches of vegetation at home and abroad, III. "The Karoo" in August. The New Phytologist, vol. v, May and June, 1906) have reported the formation of superficial in addition to deep-growing roots in *Mesembrianthemum*. In a brief account of the habits of several cacti of Arizona Preston also describes the shallow placing of the roots of several of them (Botanical Gazette, vol. 30, p. 348, 1900).

The dwarfing of the shoots of the perennials of the deserts, resulting from excessive evaporation and inadequate water supply, does not indicate the best conditions for maximum root development. It is probable, on the contrary, that the longest or the most deeply penetrating roots are found where there is considerable rainfall and where the penetration of the rain is considerable and the water table relatively deep. In California, under field conditions, the roots of the grape may reach a depth of 22 feet (Hilgard: Soils, p. 167), and in Nebraska the roots of *Shepherdia* are said to attain a depth of 50 feet (Merrill: Rocks and Rockweathering, p. 181).

CERTAIN FEATURES IN THE ATTEMPTED CLASSIFICATION OF ROOTS.

From the point of view of this study any classification of root-systems which has for its final aim a better understanding of the habits of plants should receive attention, while those classifications which are purely systematic, although of value in other lines of research, may in this place be neglected. Attention will be called, therefore, merely to the work of Rim-bach, Büsgen, and Freidenfeldt, mainly as reviewed by von Alten (Wurzel studien, Bot. Zeit., vol. 67, 1909, p. 175), which is to be largely interpreted in physiological terms.

The researches of the authors referred to indicate that the root-systems of flowering plants may be separated into two groups according to the character of the terminal roots—they are either intensive or extensive. Intensive root-systems are such as have fine terminal roots; they are richly branched and occupy a relatively small soil volume. Extensive root-systems, on the other hand, are such as have coarse ultimate rootlets, are not richly branched, and occupy a relatively large soil volume. An important additional distinction, advanced by Freidenfeldt, is that of the diameter-quotient, or the relative diameter of the central cylinder of such rootlets to that of the entire rootlet. Von Alten states that the diameter-quotient in intensive root-systems is greater than in extensive root systems. For example, the difference may be from one-third or one-fourth to one-fifth or one-sixth, respectively, for the two types. In addition, there are structural differences which need not be given in this place.

Freidenfeldt, in place of the term intensive, classifies plants having these root types as xerophytes, and in place of the term extensive, classifies plants with this type of root-system as hydrophytes. The beech is given as an example of the former and the ash as an example of the latter, but

the terms xerophyte and hydrophyte denote more than intensive and extensive, as von Alten points out, and from a physiological standpoint, the latter terms are more useful.

How susceptible to modification, through a variation in the soil medium or its water content, the two classes of roots may be, has not yet been determined. It is believed, however, that the conservative inheritance tendencies are more powerful here than the influence of changing environment, and that the types will remain essentially constant under whatever condition they may be found.

Among plants with intensive form of root-system are: *Mentha piperita*, *Digitalis purpurea*, *Artemisia vulgaris*, *Imperatoria ostruthium*. Plants having the extensive form of root-systems include: *Helleborus purpurascens*, *Solidago canadensis*, *Polysoma integrifolium*, *Valeriana officinalis*, *Arnica chamissonis*, *Ranunculus acris*, *Adonis vernalis*, and others.

SCOPE OF THE STUDY AND METHODS.

When it was proposed some time ago to take up the study of the roots of desert plants, the work was laid down on broad physiological-ecological grounds, and it was realized that as an introduction to such studies, which would be in the nature of things mainly experimental, a knowledge of the habits of annuals and of perennials afield was a prerequisite. As an exact description of the root-systems of the most characteristic forms was wanting, the prosaic task of excavating roots was undertaken, and the present paper includes an account of the results of this work.

While the plants selected for study have been such as are presumably representative of all types, they do not include many which would be of interest, but an account of which would in a degree duplicate results already attained. Aside from the usefulness of the bare descriptions of root-systems in later experimental work, they will probably be found of value in comparative root studies, where the root-systems of other arid regions, in which the physical conditions are otherwise different from those of the Southwest, are carefully worked up and mapped. Much interest has been found in comparing the nature of the root-systems and their variability as observed in the field with the leading and obvious characters of the environment, and it has been found, as will be related later, that in certain instances there is a very clear relation between root type and plant distribution, as well as between root type and other habits of the plant. The root-systems, therefore, have been studied only in the field, and natural conditions have uniformly been described.

In the course of the research different methods have been developed to suit the particular form of roots studied. In the case of annuals, the entire root-system, or as much of it as could be removed from the ground, was measured and photographed, the photographs being somewhat under life size.

The root-systems of perennials had to be studied in another way and always *in situ*. After the earth above the most important roots was removed, the root-area of the plant was considered as a square and was surveyed in the following manner. Tapes divided according to the metric system were stretched along the east and west sides of the imaginary square, in a north-and-south direction, always at a certain distance, 1.5 meters from the base of the stem. These tapes were firmly fastened to the ground. A third movable tape was extended in an easterly and westerly direction so that it connected the two permanent tapes. This was also ruled metrically. By means of moving the latter tape and noting its position on the stationary tapes, the north-and-south as well as the east-and-west extensions of the roots were learned with fair accuracy. The record was made on a square of metrically ruled paper, each square on the paper corresponding with an imaginary square of the root-area as delimited by the divisions of the tapes. Wherever possible a reduction to one-tenth was employed in sketching the roots and preparing the field charts.

The data on the temperature of the air and soil, on water in the soil, and on its physical nature are taken from records made at the Desert Laboratory or from studies made elsewhere but now available at the Laboratory. The soil temperatures are mostly from the continuous soil-thermograph record which has been kept since 1904-05, and partly from thermometer readings made by Dr. V. M. Spalding. The other data on the soil are mainly from studies by Dr. B. E. Livingston (*Distribution and Movements of Desert Plants*, Carnegie Institution of Washington, Publication 113, pp. 83-93). Acknowledgment should also be made to Prof. J. J. Thornber, University of Arizona, for the determination of several of the plants studied, as well as for much information on the distribution of the plants of the domain of the Desert Laboratory (*Vegetation Groups of the Desert Laboratory Domain*, Carnegie Institution of Washington, Pub. 113, pp. 103-112).

ENVIRONMENT OF THE ROOTS.

LEADING CHARACTERISTICS OF THE SOIL.

In the vicinity of Tucson there are several sharply distinguishable physiographic areas which have well-defined characteristics as to soils, water and temperature relations, exposure and plant covering. For the present purpose these areas may be described as follows: (1) Tumamoc Hill, upon which the Desert Laboratory is situated; (2) the flood-plain of the Santa Cruz river; (3) the bajada or mesa*; (4) West Wash. In addition to these areas a portion of the high bajada which lies about 15 miles east of Tucson and the upper bajada slopes at the western base of the Rincon mountains, an altitude about 1,300 feet above Tucson and 20 miles distant, were observed. These areas are among the most sharply defined of all of those of low altitude in the vicinity of Tucson.

TUMAMOC HILL.

Tumamoc Hill is a low mountain rising about 800 feet above the surrounding bajada, and is an isolated member of the Tucson range. The northern slope is fairly gentle; the other sides are more or less precipitous. A wash or arroyo, which heads in the southeastern part of the mountain, runs along the eastern base, and another wash, called here West Wash, is along the western side. Bold outcrops of volcanic rock occur on the west, south, and east sides particularly, and irregular masses of rock form descending steps along the northeastern face. In crevices of the rock and incrusting thinly the surface of the upper rocks which are not exposed is a hardpan, the caliche, which is practically impervious to water.

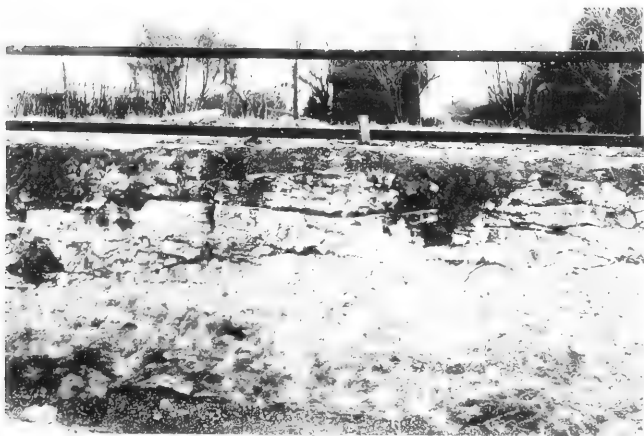
The soil of Tumamoc Hill is an adobe clay, malpais, which is derived from the lava rock. It contains small particles of volcanic rock and of caliche, about equaling the malpais in volume. The soil as thus constituted varies greatly in depth. In places it merely covers the rocks, while at others it lies in pockets and may be 50 cm. or more deep.

FLOOD-PLAIN OF THE SANTA CRUZ RIVER.

The flood-plain of the Santa Cruz river at Tucson is about a mile in width. Toward the eastern side of the plain the river has in recent years cut a channel 3 to 5 meters deep; formerly the water which washed down from the mountains to the south, from the Tucson mountains, or from the bajada to the east and north, spread over the entire floor of the flood-plain. This alteration of the river course has probably affected the water table of the plain in a marked degree, causing it to sink to a level lower than that formerly occupied.

The soils of the plain have been exposed along the banks of the river so that examination of them to the depth attained by the river is an easy

*The term bajada is used to designate the gently sloping masses of detrital material, which depend from the bases of mountain masses, and form such a prominent feature of deserts.



A. Upper soil, adobe clay, of Santa Cruz flood-plain, over 4 m. in thickness at the place shown.

B. Adobe clay, the darker soil overlying the caliche hardpan with "rotten" caliche, broken masses of the hardpan between. From the bajada, 1 mile east of the Santa Cruz River.

matter; and through the digging of two wells, one on the pump lot and one on the experimental garden of the Desert Laboratory, both within 70 meters of the western side of the flood plain, a soil section to a depth exceeding 12 meters has been obtained.

Along the course of the river the soils are adobe clay and apparently homogeneous to the depth examined. At the western side to the same depth, that is, about 5 meters, the soil is of a character similar to that near the river, but below 5 meters the adobe gives place to stratified sands and gravels. Caliche was not found in the soils of the flood-plain to the depth observed and probably none exists there.

WEST WASH.

West Wash lies along the western base of Tumamoc Hill and separates it from the benches of the bajada which stretch farther west to the main part of the Tucson mountains. It receives the drainage from the western face of Tumamoc and from a small portion of the Tucson range. The wash, for the present purposes, may be said to be differentiated into a channel from 5 to 10 meters in width and a small plain which separates the channel from the benches to the west.

The soil of the channel is a coarse sand which reaches to an undetermined depth. The soil of the plain is a sandy loam to a depth exceeding 2 meters. In both channel and plain the water quickly disappears from the surface; hence, as will appear repeatedly, the conditions of plant life here are markedly different from those of the river flood-plain, as well as from those of the other habitats to be described.

The only plant seen growing in the channel of the wash was a specimen of *Curcubita digitata*, with a fleshy root. Along the banks of the channel, which are less than a meter below the level of the adjacent plain, there is a fairly heavy growth of *Acacia constricta*, *A. greggii*, *Covillea tridentata*, *Ephedra trifurca*, *Parkinsonia torreyana*, *Prosopis velutina*, and *Zizyphus parryi*, with occasional specimens of *Echinocactus wislizeni*. The flood-plain of the wash contains all the species named as occurring along the channel, but the growth is more scattering and the plants may be somewhat smaller.

THE BAJADA.

The bajada is the drainage slope of the mountains and constitutes the mesa, or *Covillea* plain. In places in this vicinity it extends in a gentle gradient, said to be about 4 per cent, for distances of 10 miles or more. The slope of the bajada from the base of a mountain range, when viewed in profile and at a distance, constitutes one of the most striking features of desert topography. Where the slope of the bajada is short there are practically no cross-drainage channels, but where it comprises a wide extent of territory, physiography, soils, and other physical characteristics peculiar to it are developed which serve to greatly increase the diversity of this

formation. No physiographic area of this vicinity has so great diversity as the bajada.

The portions of the bajada brought into this study comprise the upper slope at the north base of Tumamoc Hill, the drainage slopes west of West Wash, the high mesa about a mile east of the Santa Cruz river, a certain locality about 15 miles east of Tucson, and the upper reaches of the bajada at the west base of the Rincon mountains. The range of the bajada in altitude at the stations mentioned runs from 2,500 feet, at the north base of Tumamoc, to about 3,500 feet at the west base of the Rincons.

The soils of the bajada are unlike in the localities mentioned, but a study of them, aside from observations in the field, has been confined to that portion which lies just north of Tumamoc Hill. The soils of the different localities, however, have certain features in common, some of which are as follows: The upper soil layer, to a depth of 30 cm., more or less, is of adobe clay. Underlying the adobe is caliche, a calcareous hardpan, which extends to an indefinite depth. The lower portion of the adobe, perhaps 10 cm., is composed of fragments of caliche and frequently of rock, and for convenience is here referred to as "rotten" caliche. It is a common occurrence that the caliche hardpan is cracked, or is wanting in small areas, so that the adobe which replaces it is consequently of considerable thickness. Plate 1, taken from a photograph of a cut in the bajada a mile east of the river flood-plain, shows variation in the depth of the soil which had been brought about in the manner indicated. The adobe is also of greater depth where it has accumulated in depressions as a result of the erosion of higher areas.

Although certain general conditions are shared by all of the bajada soils examined, even a superficial examination and comparison of them shows great differences. On the portions of the bajada where the distance from the mountains is relatively great, the adobe is practically homogeneous; but near the base of the mountains, as at the north base of Tumamoc, it may be shot through with fine rock fragments and caliche which may about equal half the volume of the whole. On the slopes west of West Wash there is little adobe, and what is comparable to the rotten caliche of the other parts of this formation there comes very close to the surface, thus causing a larger percentage of caliche and rock fragments at this place.

A special characterization of the soil conditions in the habitats of each plant examined will be given with the account of the root-system of the plant.

MOISTURE IN THE SOIL.

TUMAMOC HILL.

The water relations of the plants of Tumamoc Hill are in part conditioned by the configuration of the hill, in part by the character of the soil and the vegetal covering, and in part by its relation to the rest of the Tucson mountains.

Tumamoc Hill is an outlying spur of the Tucsons and is lower than many peaks of this range, for which reason the rainfall on Tumamoc is probably less and the temperature probably higher than on the more elevated parts of those mountains. Owing to its isolation, Tumamoc, although lower than the rest of the range to which it belongs, does not profit from the run-off from these mountains.

Tumamoc is flat-topped and has a gently sloping northern side, where there are two or more shoulders, and sharply descending eastern, southern, and western faces. The soil is deepest where the slope is least, that is, on the northern shoulders. Here, also, because of the slight gradient and because of seepage and superficial run-off from higher portions of the Hill, the water relations are most favorable.

Besides these factors the character of the rains, which are seasonal and often torrential, and the want of a heavy plant-covering operate to render much of the water which falls of no avail to the plants on the hill. The rainfall and its amount and character for a period of 15 years at the city of Tucson are given month by month in the following table.*

TABLE 1.—*Rainfall at Tucson (in Inches).*

Month.	Rainfall.	Month.	Rainfall.
January.....	0.79	July.....	2.40
February.....	0.90	August.....	2.60
March.....	0.27	September....	1.16
April.....	0.14	October.....	0.64
May.....	0.14	November....	0.87
June.....	0.26	December....	1.00

Thus the heaviest fall of rain occurs in midsummer and in midwinter, with little or no rainfall between. The character of the rains of the two seasons is unlike, that of summer is frequently torrential, while that of winter comes with less force. Much of the rain in the summer season, therefore, is lost as superficial run-off. Consequently, rain falling in equal amounts in winter and in summer probably produces unequal effects in moistening the soil and in providing the plants with water.

The penetration of the soil by the rain is not a fixed amount, but depends on a variety of factors, among which are the amount and duration of the rain. The depth of penetration is usually from 2 to 5 times the registered

*Coville and MacDougal: *The Desert Botanical Laboratory*, Publication No. 6, Carnegie Institution of Washington, 1903, p. 26.

precipitation, but the total penetration naturally does not exceed the thickness of the adobe, that is, 50 cm. more or less, usually less.

The studies on the movements of the moisture of the soil, on which this account is mainly based, comprise observations from October 3, 1907, to April 11, 1908, and include, therefore, only the dry autumn and dry early winter, the winter rainy season and the early spring. Studies on the conditions for the remainder of the year are not now available. The special studies were made on soils at two depths, namely, 15 and 30 cm.⁵ The soil was removed at frequent intervals, placed in stoppered bottles, and dried in an oven at the laboratory.

The following summary gives the water movements during the period under consideration, together with the rainfall recorded on Tumamoc Hill at the time:

From October until the latter part of January 1.68 inches of rain fell, and the curves of soil moisture at this time were fairly flat; that for the deeper soils fluctuated less than that for the shallow soils. Between January 13 and February 11, 1.54 inches of rain were reported at the laboratory. The soils on the first of February were the driest of the period under observation. At the 15 cm. depth they contained 15 per cent water; at the depth of 30 cm., 14.5 per cent (dry weight). During the period between February 1 and February 11, when the next soil observation was made, 1.49 inches of rain fell. On February 11 the amount of water in the soil at the 15 cm. depth was 34.8 per cent, which was the largest amount at that depth found at any time during the season. At this time there was 19.1 per cent water at the 30 cm. depth. Between February 11 and March 23, 0.87 inches of rain fell, in small amounts. During this period the amount of water in the soil at the higher level had fallen to 18.9 per cent, but the water content at the depth of 30 cm. had slightly increased.

Although the data for the year are not available to show it, it is fair to assume that, as the dry summer approached, the soils at both depths became more dry and reached their extreme desiccation in July when the summer rains began. The per cent of water in the soils at the time is not known, but observations on the soils at the laboratory made 4 years previously in July, gave the following results: The water content was 17.83 per cent at a depth of 30 to 40 cm.; at a depth of 40 cm. it was 15.8 per cent of the dry weight of the soil. At the same time, at the 15 cm. depth the moisture content was only 9.1 per cent. The significance of these last figures becomes apparent when it is recalled that the minimum moisture content of this soil which can be available to plants not possessed of water-storage organs is 10 per cent its dry weight.

From these data, admittedly inadequate, we can understand some of the characteristics of the environment and the conditions of growth of the flora of Tumamoc Hill. The soil to a depth of 15 cm. probably does not retain sufficient moisture for absorption by plants whose roots do not

reach deeper than this, for a period much exceeding six weeks following storms. This defines the limit of life of most annuals, both those of winter and of summer, and probably also the season of absorption of perennials with shallowly placed roots. Plants having roots which reach to greater depths than 15 cm. can obtain some moisture at all seasons. In order to survive, seedlings must send their roots below 15 cm. within six weeks following the close of a stormy period.

THE BAJADA.

The water relations of the bajada are very diverse, because of differences in soils, in topography, and in its relations to other physiographic areas. The nearly impervious caliche hardpan which underlies the bajada everywhere prevents at once the deep penetration of the rains and the opportunity of tapping subterranean water. Save where the bajada constitutes a drainage slope from a higher area, and well-defined channels are not formed, the only water available to the plants growing on it is what falls upon it directly. The water table of the bajada varies considerably in its position with relation to the surface of the ground. That in the vicinity of the University of Arizona, about a mile east of the Santa Cruz river, is approximately 25 meters deep. In other portions, where the general level of the bajada is higher, the perennial water is considerably lower than this figure.

The depth of the penetration of the rains is apparently entirely conditioned on the thickness of the upper soils and on the presence of cracks or rifts in the caliche hardpan which are filled with adobe. In favorable places on the mesa, where there has been a considerable accumulation of adobe soil, enough water is present to allow the growth of small specimens of such perennials as are most abundant on the flood-plain, such as *Prosopis velutina*, *Acacia greggii*, and *Ephedra trifurca*.

Where the bajada nears higher areas, as Tumamoc Hill, the most favorable water relations are to be found. This may be attributed partly to the larger rainfall in such areas, but mainly to seepage and to superficial run-off from the higher ground. The adobe soil from the bajada north of Tumamoc Hill has an admixture of fragments of caliche and of rock so that its moisture-retaining capacity is about 20.1 per cent of its dry weight. For this reason it is air-dry, to a depth of 20 cm., most of the year, and the perennials which are to be found on it, mainly *Covillea tridentata* and certain cacti, must get their water during dry seasons from the rotten caliche stratum and from the more deeply placed cracks in the underlying caliche itself.

During the period in which observations were made on the water content of the soils of the bajada, October 3, 1907, to April 11, 1908, it was learned that there was much less water in the soil on the bajada than in the soils on the Hill. Soil samples were taken at two depths, 10 cm. and 20 cm. From the beginning of the study until February 11, the water in the soil at either depth was less than 10 per cent of its dry weight. On February

11 the sample at a depth of 10 cm. had 17.3 per cent water, and that from a depth of 20 cm. had 18.6 per cent its dry weight. Ten days later the percentages had fallen to 11.7 and 14.3, respectively, for the two depths. Following this date the amount of water diminished rapidly until, four weeks after the maximum water content, it was no more than immediately before. The readings on March 12 for the depths of 10 and 20 cm. were 7.9 and 9.5 per cent dry weight. This was considerably under the amounts of water found on Tumamoc at the time and shows the bajada to be the more arid of the two areas.

The period during which the adobe clay of the bajada at this situation contained sufficient water to be of use to shallow-rooted plants was thus not more than three weeks of the year in question. This period would probably be somewhat extended and might be comparable to the Tumamoc Hill soils in portions of the bajada where the soil contains less rock and caliche fragments and also has the advantage of position near higher areas. The brevity of the period in which the bajada soil contains sufficient water for the growth of annuals, or of perennials without water-storage organs, is therefore an important feature of the xerophilous conditions of this physiographic area and indicates that it is the most intensely arid of any examined.

THE WEST WASH.

Tumamoc Hill, as above noted, is situated apart from the main range of the Tucson mountains. At both the east and the west bases of the Hill are washes, of which the former heads in the hill, while the latter receives drainage also from portions of the main range. The West Wash, therefore, drains a large area and during seasons of heaviest storms carries a large amount of water which may overflow its banks and flood the bordering plain.

The soil of the wash is coarse sand and allows water to percolate through it very rapidly. It is possible that there is a water table underlying the wash and its flood-plain, but this has not been demonstrated. The sandy loam of the plain has a water capacity of about 25 per cent its dry weight, or considerably higher than that of the upper reaches of the bajada.

The soils of the plain only have been studied; the studies were made from October, 1907, to April, 1908. The studies on the loams of the plain showed that up to February 11 they contained less than 10 per cent of water. On February 11 the soil at a depth of 15 cm. contained 14.9 per cent. At a depth of 30 cm. the soil during the entire period did not contain over 8.2 per cent water. On March 2 the soil at the lesser depth had 9.3 per cent and that at the deeper location 6.2 per cent water. April 11 the percentages of water for the two levels were, respectively, 5.3 and 4.6. The dryness of the upper soil is due to its sand-loam nature, which permits the rapid sinking of water and its rapid evaporation. In this place the soil is over 2 meters deep, and had studies been carried out on the deep

soil, as, for example, 2 meters beneath the surface, a much higher water content would probably have been found.

The relation of the roots of the plants of the area will be spoken of later in the paper, but it may be mentioned here that of non-fleshy forms only those with deeply penetrating roots are to be found, and that only here does a deeply penetrating root develop in a thoroughly normal and typical manner.

FLOOD-PLAIN OF THE SANTA CRUZ RIVER.

The conditions of soil moisture of the river flood-plain are relatively favorable for plants, perhaps the most so of any area under discussion, which is partly owing to the character of the soil and partly to the comparatively level surface. In earlier times the flood waters covered the plain, making of it a cienega; but comparatively recently the river has cut a channel and the only flood waters that go over the plain, at times not inconsiderable, are derived from the adjoining bajada. The river channel carries water only part of the year, and yet during seasons of storms it may be a yellow torrent with great erosive power. The water table of the flood-plain lies from about 5 meters, near the channel of the river, to about 12 meters at the western edge.

The top soil of the plain is an adobe loam with a water-retaining capacity of about 38.5 per cent its dry weight, the largest retaining capacity of any soils of the different habitats so far examined.

The digging of a well on the western side of the flood plain afforded an opportunity of determining the water content of soil to a depth of 5.25 meters, although the upper adobe stratum did not attain a greater depth than 5.10 meters. It was found that the water content increased with depth to the limits of the adobe. Following are the determinations: At the depths of 0.20, 3.30, 4.00, and 5.10 meters the water contents per dry weight of soil were 12.9, 19.0, 22.6, and 23.1 per cent respectively. At the depth of 5.25 meters, where sand was encountered, the water content was 7.1 per cent. It would appear from these determinations, therefore, that sufficient water is present in the adobe, at whatever depth examined, to be of use to plants, probably throughout the year. But, as will appear repeatedly in later portions of the study, the plants at the present time do not as a rule actually penetrate to the deeper levels except only close by the river; for the most part, the roots are confined to the upper two meters of soil.

Determinations of the water in the plain soils were made from October 3, 1907, to April 11, 1908, and revealed the fact that the moisture content of the soil at both depths taken for study, 15 and 30 cm., was greater most of the time than 10 per cent its dry weight. The sample taken February 11 showed a moisture content of 26.00 per cent at the depth of 15 cm. From this date until April 11 the water content gradually fell away until it became 10.9 and 11.6 per cent for the two depths respectively.

TEMPERATURE OF THE SOIL.

The observations on the temperature of the soil have been confined to two series, namely, to a continuous one by means of thermographs and to a fairly large number of readings of thermometers. The thermometric readings are for depths of 1, 2, and 12 inches. The thermograph records date from the summer of 1905 and the spring of the following year, and give the temperature for one station, close by the laboratory building, on the north slope of Tumamoc Hill, and for two depths, 15 and 30 cm.

RECORD OF THERMOGRAPH: 15 CM. DEPTH.

An almost continuous record of the temperature of the soil at the 15 cm. depth is at hand for the years 1905, 1906, 1907, 1908, and 1909. An examination of these temperature graphs shows interesting features, some of which will be noted.

The record shows an undulating line of which the curve-crests correspond to the warmest for each day, and the depressions the coldest. The crests for any record (each one is for 7 days) are remarkably uniform in height, as also the depressions are uniform in depth. The difference between the crests and the depressions is about 8° F., with 12° as the greatest variation, which usually occurs in March and July. Owing to the lagging of the soil temperatures, as compared with those of the air, the maximum at this depth is not attained until about 6 p. m. and the minimum about midnight.

The uniformity of the daily temperature range is broken during stormy periods, particularly in the winter season. In summer, the undulating curve of daily variation, even during stormy periods, may be identified, although its amplitude is greatly decreased. The extreme yearly range of temperature for this depth, for any year since the records began, is 69° F.; and the extreme range for the entire period, 1905 to 1909, is 73° F. The following table gives the greatest range in temperature for each year.

TABLE 2.—*Maximum and Minimum Soil Temperatures at a Depth of 15 cm.*

Year.	Maximum.		Minimum.	
	Date.	Temp.	Date.	Temp.
		° F.		° F.
1906. . . .	July 18	98	Jan. 3	34
1907. . . .	July 2	105	Jan. 7	36
1908. . . .	July 6	101	Dec. 22	42.5
1909. . . .	July 12	99	Dec. 25	42

If we follow the course of the temperature record throughout the year, we shall see that the period of greatest heat is during the latter part of July, or immediately preceding the rainy season of midsummer. With the advent of the rains, the temperatures suddenly decline, the decline con-

tinuing until midwinter. As great a fall as 14°F. has been recorded in a day. In January the temperature begins to rise, and the rise is gradual until the last of March, when it becomes accelerated, so that by May the soil approaches the temperature characteristic of early summer and is probably as great as that of the germinating period of midsummer. The course of the temperature for the year is fairly well illustrated by that of the minima for 1908. From January 4 to March 29 the minimum lay between 50° and 60°F. ; between April 5 and April 26 it was between 60° and 70° ; in May the minimum was between 70° and 80° ; in the first half of June it was between 80° and 90° , and from then until July 15 the thermograph did not record any temperature under 85° . With the coming of the summer rains the minimum began to fall and was near 80° until October 4; it fell to about 60° until November 26. The minimum was about 50° until December 14, and between 40° and 50° the remainder of the year.

RECORD OF THERMOGRAPH: 30 CM. DEPTH.

The soil temperatures for the depth of 30 cm. were recorded under the same conditions, except only the greater distance from the surface, as those of the 15 cm. depth just described. The sensitive bulbs of both instruments were only a meter apart. It needs but a glance at the records of the two instruments to reveal their most striking difference: the daily curve of the more deeply placed instrument has slighter undulations. In addition, the annual variation of the two and the course of temperature throughout the year are also markedly dissimilar.

The usual daily range in temperature of the soil at a depth of 30 cm. is about 2°F. ; the maximum daily range for 1908, which may be accepted as approximately the maximum for the period under observation, was a drop of 4° in July. But as this followed as a result of the rains it may be taken to represent the unusual rather than the usual temperature variation for the depth. The maximum temperature for the entire period, 1905-1909, occurred July 3, 1907, when the thermograph recorded 99°F. ; the minimum was on January 3, 1907, at which time the temperature was 44° . The annual extremes in temperature are presented in table 3.

TABLE 3.—Maximum and Minimum Soil Temperatures at a Depth of 30 cm.

Year.	Maximum.		Minimum.	
	Date.	Temp.	Date.	Temp.
		$^{\circ}\text{F.}$		$^{\circ}\text{F.}$
1905....	Aug. 7	97	Dec. 23	49
1906....	July 23	95	Jan. 4	46
1907....	July 3	99	Jan. 3	44
1908....	July 4-7	96	Dec. 21	50
1909....	July 12-13	96	Dec. 5	50

The course of the temperature for the year at the depth of 30 cm. is somewhat different from that at the lesser depth. This is graphically shown by the figure below, which was made from an inspection of the records for the year 1908-1909, and is accurate only in general form, not in detail, but illustrates the facts. As fig. 1 indicates, the highest temperature for the year is in July, or August, just prior to the rains of midsummer. With the coming of the rains the temperature falls and continues to decline until the middle of March, when it begins to rise and quickly reaches the degree characteristic of summer. There is thus a grand maximum, which precedes the time of the germination of the summer annuals and the active growth of the summer perennials, and a grand minimum which follows the most active period of vegetation of the winter season. Broadly speaking, therefore, when the activities of the two large classes of plants are awakened, there is seen to be a difference of approximately 30° F. in soil temperature at the 30 cm. depth.

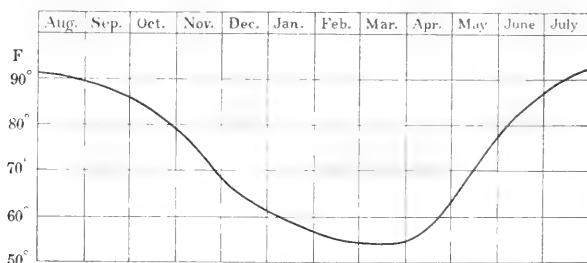


FIG. 1.—Temperature of the soil, at a depth of 30 cm., for the year 1908-1909. Desert Laboratory.

SOIL TEMPERATURES: 2.5 CM. DEPTH.

The only available records of temperatures of the soil at less depths than those above given are thermometer readings made at a station less than 50 meters from the location of the thermograph records given above. These readings extend from March 22 to May 10, 1907, and owing to the rather brief period covered by the thermometer record a discussion of it *per se* is precluded. However, it will be of interest to compare the thermograph record and that of the thermometer for the same days, as shown in table 4.

The most interesting facts revealed by the records are the differences in temperatures which the soil shows at any moment, and the relatively high temperatures of the least depth. During the days of which the temperature record is available the greatest difference of temperature between the depths referred to is shown in the following summary: At the 30 cm. depth the variation was 3° F.; at the 15 cm. it was 11° ; and 2.5 cm. it was 40° . The greatest difference in maximum temperatures at any moment

was observed on April 15, when there was a variation of 23.5° between the upper two levels; unhappily the record for the greatest depth for the time is missing, or the difference would doubtless be much more. From these records it appears that the roots of a plant which reach as deep as 30 cm. may at one moment in springtime experience a range of temperature as great as 22.50° F., and in other portions of the year probably a much greater range.

TABLE 4.—*Soil Temperatures at Different Depths, March-May, 1907.*

Date.	2.5 cm.		15 cm.		30 cm.	
	Thermometer.*		Thermograph.		Thermograph.	
	Min.	Max.	Min.	Max.	Min.	Max.
	$^{\circ}$ F.	$^{\circ}$ F.	$^{\circ}$ F.	$^{\circ}$ F.	F.	$^{\circ}$ F.
March 22.....	63	83.5	62.5	88.5	64	67
March 25.....	50	90	64	75	66.5	67.5
March 29.....	50	80	58.5	66.5	63.5	64.5
April 12.....	71	103	75	85		
April 15.....	71	103.5	74	80		
May 1.....	65	98	75	84.5	75	77
May 8.....	65	97	76	84	76.5	77.5
May 10.....	64	97.5	76	87	77	79

*Maximum and minimum thermometers were employed in the study.

SUMMARY OF ENVIRONMENTAL CONDITIONS.

The habitats, which have been studied in connection with the observations on the roots of plants inhabiting them, comprise mesa, or bajada, and include locations on the flood-plain of the Santa Cruz river, the West Wash (near Tumamoc Hill), and on Tumamoc Hill. The studies on the soils, the moisture in them and their temperatures, adopted from various reports, have been limited to Tumamoc Hill, or the bajada and flood-plain near by.

The surface soils are an adobe clay with a varying admixture of rock fragments, either of volcanic origin or of caliche, and the leading apparent differences in the soil are dependent on the amount of this coarser material present. The upper soil is usually from 15 to 30 cm. in thickness. Beneath, to a considerable but varying depth, lies a hardpan caliche. Between the upper stratum and the hardpan is an intermediate zone in which there are large fragments of caliche, or other rock, mingled with adobe. The intermediate stratum is usually not more than 20 cm. in thickness. The total soil generally available for the roots is thus 50 cm., and frequently (usually on the bajada) it is much less than this.

The depth of perennial water varies with the habitats, although on Tumamoc Hill no water table exists. On the bajada it lies 25 meters or more beneath the surface, and on the flood-plain of the river the water table is 5 meters deep, or more.

The rainfall on each of the areas, in the vicinity of Tucson, is approximately the same, but the differences in the mutual relation of the areas, the character of the soil, and its depth, as well as the surface configuration, operate to make the water relations of the habitats very unlike.

The flood-plains of the Santa Cruz river and of West Wash, in addition to the rains which fall on them directly, receive the run-off and seepage waters from the bajada, and the bajada, in turn, those from Tumamoc Hill or other higher elevations. In former years at flood time the Santa Cruz river overran its banks and covered the bottom lands, but now the river has cut a deep channel and flooding from this cause never takes place. The change is probably associated with the cutting of the mesquite forest, which was once a rather heavy one, and the conversion of the bottoms into ranches or waste lands, with second-growth mesquite.

The water retaining capacity of the soils of the river flood plain is the highest, below which should be placed the adobe of the bajada, at the north base of the Hill, with the loamy sand of the flood-plain of West Wash as the least.

So far as is known from studies on the water content of the superficial soils, the amount of water present during the dry autumn and winter on the bajada north of Tumamoc and on the flood-plain by West Wash is insufficient to be of direct benefit to the plants whose roots do not penetrate deep, while at the same time the soils of Tumamoc Hill and of the river flood-plain have moisture present in usable quantity.

The period of optimum moisture content of the upper soil includes the rainy period and a relatively short time after the beginning of the dry season. The upper levels dry out soonest, and on the bajada were air-dry three weeks after the close of the rains, while the soils on the river flood-plain and Tumamoc Hill remained moist for a period exceeding six weeks. This places the limit to the growing period of most annuals and the most active vegetative period of all perennials without water storage capacity, or deeply penetrating roots.

The temperature of the soil has been observed on Tumamoc Hill only, and chiefly at 15 cm. and 30 cm. The highest temperatures immediately precede the summer rains. With the advent of the rains the temperature falls quickly and continues to decline until January-February, at a depth of 15 cm., or March-April at the greater depth—30 cm. The time of the germination of the summer annuals and of greatest vegetative activity of the perennials, therefore, is below the maximum heat, as that of the winter-spring plants is above the minimum.

The daily fluctuations of temperature for the two depths is unlike; that at the greater depth is about 2° F., while that at the lesser depth is about 8° F. The yearly range at the 15 cm. depth is about 34°, and that at 30 is about 44° F., with the maxima at 99° and 105° for the two depths respectively.



a. *Amaranthus palmeri*, Tumamoc Hill, August 10, 1909.
 b. *Anoda thurberi*, Tumamoc Hill, August 10, 1909.
 c. *Aster tanacetifolius*, Tumamoc Hill, August 26, 1909.
 d. *Aster tanacetifolius* showing, at left, root-formation at base of lateral of first order. The figure at right has segment of tap-root bearing lateral of first order with its branches.

ROOT HABITS OF DESERT PLANTS.

In presenting descriptions of the root-systems of the desert plants, it seems best to be guided by the biological grouping—that is, to bring plants together which are naturally segregated either in time or in space. Accordingly perennials which are typical of the leading habitats treated are grouped under the respective habitats, but since the annuals of winter and of summer occupy the same areas and are separated only by time they are divided into winter and summer forms. By summer annuals is meant those which appear in midsummer, and by winter annuals those which come after the winter rains, although some of them might more truly be called spring annuals than those of winter.

SUMMER ANNUALS.

In early July the different habitats show only perennials, and the bare ground between them shows the dried remains of the annual vegetation of the preceding rainy season. With the coming of the rains of late July or August, however, the appearance of the land is suddenly changed. Seeds which have lain dormant for nearly 11 months promptly germinate, and hill and plain are speedily clothed with a growth of evanescent forms which are in great variety and, for desert forms, of surprising density.

The study of the summer annuals was carried on in the following manner. The roots of typical forms, mostly mature, were carefully washed out by a small jet of water, and the entire plant, or as much as was recovered by this means, was preserved in weak formaline for subsequent study. By this method the entire root-systems were rarely to be had, but enough was always saved to give the general character. More than one plant as a rule was preserved of each species so that a control on the observations might be had. A very serious drawback to this method of study lay in the impossibility of surely determining the extreme depth to which the main root (or the laterals) penetrated the soil, although in many cases this feature was learned with close accuracy. The following summer annuals were examined:

<i>Amaranthus palmeri</i> S. Wats.	<i>Dysoda papposa</i> Lag.
<i>Anoda thurberi</i> Gray.	<i>Euphorbia glyptosperma</i> Engelm.
<i>Aster tanacetifolius</i> HBK.	<i>Kallstroemia grandiflora</i> Torr.
<i>Boerhaavia</i> sp.	<i>Pectis prostrata</i> Cav.
<i>Cladostrix lanuginosa</i> Nutt.	<i>Solanum elaeagnifolium</i> Cav.
<i>Datura</i> sp.	<i>Trianthema portulacastrum</i> L.
<i>Ditaxis humilis</i> (Engelm. and Gray) Pax. (perennial).	<i>Vicia</i> sp.

AMARANTHUS PALMERI.

The species of *Amaranthus* studied was growing near the Laboratory building and was removed from the soil on August 10, at which time the shoot was 21 cm. long. The plant was not in flower.

The root-system consists of a tap root and several large laterals which bear filamentous branches. The roots do not intergrade in size, certainly

not in diameter. Only 10 cm. of the main root was recovered, but it may have been much longer than that, since, where it was broken, it was 0.5 mm. in diameter. The root was 4 mm. in diameter at the crown. From the main root 5 leading laterals take their origin. These are coarse and over 25 cm. long. The laterals of the first order bear numerous long delicate roots, which in turn are branched. The ultimate roots are long and filamentous, but rudiments, mere root tips, are also very numerous.

The root-system of *Amaranthus* thus is characterized by two classes of roots, coarse and fine, without intergradation, and by the presence of rudiments (plate 2).

ANODA THURBERI.

The specimen of *Anoda* which was studied was procured August 10; it was an unbranched shoot 22 cm. in height and bore several large leaves. The root-system is characterized by a prominent main root and several delicate secondary ones. The tap root was over 18 cm. long and was forked. From the tap root arise numerous laterals, mostly within 4 cm. of the surface of the ground, of which the largest is over 6 cm. in length. The laterals of the second order bear filamentous branches. No rudiments are present. As a rule the roots arise singly, although a few of the ultimate ones are in groups (plate 2).

ASTER TANACETIFOLIUS.

On August 26 the roots of *Aster* were removed from the soil. The plant has a dense habit of growth and bears many leaves. The shoot was 25 cm. high. The tap root is especially well developed. It is 4 mm. in diameter at the crown, and over 15 cm. was recovered. The laterals form a dense tuft 3 to 6 cm. beneath the surface of the ground and are uniformly slender. There are no rudiments.

A peculiarity, not observed in other species, was the place of origin of the laterals of the second order. All of the laterals of the first order, which were in the dense tuft referred to, were short—that is, less than 3 cm. long—and the tips were dead, but they all bore long and delicate branches, as shown in plate 2. The cause of this was not definitely ascertained, although laterals with branches near the somewhat enlarged base were seen with the tips yet living, so that the condition noted may be the usual occurrence in the species. The ultimate roots of *Aster* are of the fourth order.

Below the tuft of absorbing roots just described are scattered slender laterals arising from the main root. The root habit, with the relation of the laterals to the main root, is shown in plate 2.

BOERHAAVIA SP.

The specimens of *Boerhaavia* examined were from Tumamoc Hill near the Laboratory building and were washed out August 10. The shoot of the plant to be described, which was in bud, was 12 cm. high and bore numerous large leaves.

The main characters of the root-system are the relatively large size of the laterals of the first order and the paucity of filamentous roots. The ultimate roots are of two sorts, a longer and a shorter kind. The latter are rudiments and are borne in the axils of the former; they are shown, but imperfectly so, in plate 3. The plant thus shows a tendency to produce roots in groups.

CLADOTHRIX LANUGINOSA.

The specimens of *Cladothrix* studied were removed from the soil on August 19, and were mature plants with large leaves and shoots about 19 cm. in length. The main root was over 2 mm. in diameter at the crown and was 6 cm. in length with the tip atrophied, but it was continued 17 cm. farther by two successive laterals, so that the depth attained was over 23 cm. The laterals are numerous and rather fine and for the most part arise within 4 cm. of the surface of the ground. They bear laterals of the second order, which, in turn, are branched. The ultimate roots are represented in very numerous cases by rudiments.

As a whole, the root-system of *Cladothrix* is characterized by the slenderness of its roots, a large number of which are filamentous. Root hairs are present in great abundance. The absorption faculty, therefore, is a feature strongly developed.

DATURA SP.

The specimen of *Datura* studied was collected on August 10 and was immature. The shoot was 15 cm. in length and bore several large leaves. The root-system is characterized by the very large number of fine roots, which are usually long. At the crown the main root is 4.5 mm. in diameter, but tapers rapidly and is under 10 cm. in length. At a point 8 cm. beneath the surface of the earth it was less than 0.5 mm. in diameter. The laterals are all long and of two diameters, a few are noticeably heavy, and many are very slender. All of the laterals of the first order bear filamentous branches which are long and branch but little. The roots of the third order are especially fine. Plate 3 shows only imperfectly the density of the absorption system of *Datura*.

DITAXIS HUMILIS.

The species of *Ditaxis* examined is a perennial herb, which was in flower when collected, August 10. The shoot is leafy and over 12 cm. long. The roots reach deeper than those of the other herbaceous forms studied and the absorption system is poorly developed. The main root is relatively slender; it is over 23 cm. in length and is only 2.5 mm. in diameter at the crown. Four large and numerous small laterals of the first order arise within 8 cm. of the surface of the ground. Very few laterals are given off from the main root below this. The laterals may extend 11 cm. and over, and mostly are in groups of three or four. The laterals of the second order are filamentous and rarely branch. There are no rudimentary roots.

DYSODA PAPPOSA.

Specimens of *Dysoda* in flower were procured August 26. The shoots were 12 to 15 cm. in length, much branched, and well covered with leaves. The tap root dominates the root system. This evidently reaches deep, although unfortunately but 10 cm. of the root was uncovered. The laterals are filamentous and are given off from the main root somewhat farther from the surface of the ground than is usually the case in summer annuals. The laterals of the first order bear branches and these also are branched, but the entire extent of the filamentous roots is relatively slight (plate 4).

EUPHORBIA GLYPTOSPERMA.

Euphorbia glyptosperma is most abundant on Tumamoc Hill, where the specimens examined were collected August 26, but, like most of the other annuals it also occurs in the other habitats in the vicinity of the Laboratory. The specimens studied were about 7 cm. high, much branched, with a large leaf surface, and in flower. The roots grade in diameter from the main root, which is somewhat over 1 mm. in diameter at the crown, to the ultimate filamentous ones, although as a whole the roots are relatively coarse. The laterals of the first order arise for the most part within 3 cm. of the surface of the ground. They occur singly; no rudimentary roots were observed.

KALLISTRÉMIA GRANDIFLORA.

Kallistrémia is one of the less abundant but most striking of the summer annuals. It is of a semiprostrate habit, which varies with its stage of growth or with the conditions under which it has developed. If the summer rains are slight, so that the period of growth of the plant is short, its habit is nearly upright, but should the stormy season be prolonged, or should rains occur after those of early summer have passed, and before the plant dies, growth is renewed if the latter is the case, or in the former case growth is so active that the plant becomes vine-like and prostrate. Under such favorable circumstances it may cover as much as 16 square meters of surface, and perhaps even more than this. The plants whose roots were removed either were young or had attained the first stage of growth described above, that is, they were upright and mature.

The plant to be described was collected on Tumamoc Hill on August 10. The shoot consisted of two branches and several compound leaves and more numerous flower buds. It was 27 cm. long.

The root-system consists of a main root, with a relatively stout crown, and one long and one short branch, together with slender laterals, which are mainly close to the surface of the ground, and their proper branches. The longest lateral is over 21 cm. in length and bears two branches over 10 cm. each. Most of the laterals of the first order and all of the higher orders are filamentous. The main root penetrated the ground more than 22 cm.

The leading features of the root system, which is a rather extensive one, are shown in plate 4.



c



a



b



d

a. *Boerhaavia* sp. b. *Cladothrix lanuginosa*. c. *Datura* sp. d. *Ditaxis humilis*.





a. *Dysoda papposa*, flood-plain of Santa Cruz. b. *Euphorbia glyptosperma*, Tumamoc Hill. c. *Kallstroemia grandiflora*, Tumamoc Hill. d. *Pectis prostrata*, Tumamoc Hill. e. *Solanum eleagnifolium*, Tumamoc Hill.

PECTIS PROSTRATA.

The specimens of *Pectis* studied were growing on Tumamoc Hill near the Laboratory building. They were from 7 to 12 cm. in length and in flower. The general habit of the plant is shown in plate 4. The main root is very delicate and bears several long laterals within 3 cm. of the surface of the ground. The longest of these were over 13 cm. and bore numerous branches, which also were branched. The root-system as a whole may be characterized as being little branched, the laterals of all orders are relatively few, and composed of delicate roots only.

SOLANUM ELÆAGNIFOLIUM.

Immature plants of *Solanum* were collected August 22, of which one had a shoot 6 cm. high and bore several large leaves. A tap root dominated the root-system; it was traced over 15 cm. Laterals were given off at occasional intervals along as much of the main root as was examined, but they were mainly confined to the upper 4 cm. The laterals of the first order are fine and bear filamentous branches. There are also roots of the third order present. The roots arise singly; there are no rudiments. The leading characteristics of the root-system are the rather stout tap root and the delicate laterals, with no roots of intermediate diameter between (plate 4).

TRIANTHEMA PORTULACASTRUM.

The specimens of *Trianthema* which were studied were collected on the western edge of the Santa Cruz flood-plain, August 26. The shoot of the plant to be described was about 17 cm. high and bore 9 branches and numerous large leaves, and therefore possessed a large transpiration surface. The root-system is characterized by a preponderance of coarse roots. The tap root is 3 mm. in diameter at the crown, is over 15 cm. long, and bears (within 4 to 5 cm. of the surface of the ground) 5 prominent laterals, the longest of which was more than 17 cm. At intervals of about 1 cm. the laterals of the first order bore short filamentous roots and rudiments of roots. The number of rudiments is large, a feature which distinguishes this plant from nearly every other one examined. The rudiments appear as faint dots along the laterals in plate 5.

VICIA SP.

The specimen of *Vicia* whose roots were examined was growing near the Laboratory and was collected August 10. The shoot of the plant was mature and bore fruit and flowers. The specimen studied bore 7 branches and numerous linear leaves. The root-system is characterized by a prominent tap root, which was 2 mm. in diameter at the crown and over 20 cm. long, and large laterals arising rather far beneath the surface of the ground. A portion of the laterals of the first order are in groups of 2 or 3, although they mainly arise singly. The laterals branch but little and leave the impression that the absorption system of the plant is a rather meager one. A few tubercles are borne on the larger laterals.

WINTER ANNUALS.

Between the months of November and March, and occasionally one month before and one month after that period, if the moisture conditions are favorable, a large number of annuals make their appearance in the different habitats considered in this study. These are for the most part of different genera and species from those which occur in summer, and like the latter have to a large degree a generalized type of distribution. Often the same species of winter annuals are to be found wherever the soil and the water conditions are suitable irrespective of the habitat, whether Tumamoc Hill or the lower-lying bajada, but they may be present in greatest profusion on the lower slopes of the Hill. The following winter annuals were examined:

<i>Amsinckia spectabilis</i> Fischer and Meyer.	<i>Hordeum murinum</i> L.
<i>Astragalus nuttallianus</i> DC.	<i>Malva borealis</i> Wallm.
<i>Bowlesia lobata</i> R. and P.	<i>Malacothrix clevelandi</i> Gray.
<i>Brodiaea capitata</i> Benth.	<i>Medicago denticulata</i> Willd.
<i>Daucus pusillus</i> Michx.	<i>Mentzelia albicaulis</i> Dougl.
<i>Eritrichium pterocaryum</i> Torr.	<i>Microseris linearifolia</i> Gray.
<i>Erodium cicutarium</i> (L.) L'Her.	<i>Monolepis chenopodioides</i> Moq.
<i>Festuca octoflora</i> Walt.	<i>Orthocarpus purpurascens</i> Benth.
<i>Gilia bigelowii</i> Gray.	var. <i>palmeri</i> Gray.
<i>Harpagonella palmeri</i> Gray.	<i>Parietaria debilis</i> Forst.

AMSINCKIA SPECTABILIS.

Amsinckia spectabilis is one of the most abundant of the winter annuals and, as far as its local distribution is concerned, one of the most generally distributed. It also is one of the most drought-resistant, a condition which is illustrated by the following note on its behavior. In the spring of 1907 one of the staff of the Desert Laboratory was studying the invasion of plants into a denuded area. On March 19 the storms of winter were over and the arid conditions were rapidly becoming marked; on that date the temperature out-of-doors in the shade was 94° F. with a relative humidity of 20 per cent. The winter annuals were for the most part already dead. On the periphery of the denuded plot mentioned there had been a heavy growth of *Sisymbrium reflexum*, *Bowlesia lobata*, *Amsinckia spectabilis*, and *Phacelia tanacetifolia*. Of these annuals the first two were nearly all dead and were shedding their seed, while the last two were apparently unaffected by the drought, though all of these plants were apparently under similar conditions.

Amsinckia has a deeply penetrating main root and numerous laterals, all of which, especially in the young plants, are slender and branch but little. The root-system is extensive rather than intensive.* As the plant becomes older the tap root becomes heavier, and the difference in diameter between it and the laterals is somewhat accentuated.

As in the summer annuals, the length of the main root as given in this paper is usually somewhat less than the actual length, owing to the diffi-

*Where roots are thus characterized it is not intended to classify them after Büsgen, unless so stated, but the words are merely used in a descriptive sense.

culty in removing the root-system and keeping it intact. However, great care was always taken to obtain as much of the roots as possible. A shoot of a mature plant of *Amsinckia* 13.5 cm. in length had a tap root over 8 cm. long; a plant with a shoot 18 cm. long had a tap root more than 12.5 cm. in length. Thus, although the greatest penetration was not learned, it was sufficient to enable the plant to reach and to tap a relatively good water supply at a time when the upper layers of the soil were too dry to provide a sufficient amount of water for plants whose roots were entirely restricted to the surface soil layers (plate 5).

ASTRAGALUS NUTTALLIANUS.

In this vicinity *Astragalus* grows under a large variety of conditions as regards exposure, kinds of soil, and relations to other plants. It is practically cosmopolitan in its local distribution. A mature plant with a shoot 6 cm. long, together with young specimens, was preserved for examination. The leading character of its root-system was the well-developed tap root, 13 cm. in length. The laterals were few and coarse, and little branched. Tubercles were present in considerable abundance.

BOWLESIA LOBATA.

Bowlesia is to be found on Tumamoc Hill and on the lower detrital slopes, and usually occurs under the protection of a shrub or tree or in other situations where the water relations are relatively favorable. The leaves are large and the plant has the appearance of being ill-adapted to successfully withstand very severe arid conditions. The root-system is not an extensive one, and is characterized by having a main root and laterals of the first order of about the same diameter and by the relative coarseness of all the roots. The main root does not go straight down, but zigzags downward in a very irregular fashion. From the main root there arise, at intervals of about a centimeter, rather coarse laterals which branch sparsely. It seems probable, although not proved by actual experiments, that the restricted distribution of *Bowlesia* may be directly associated with the shallowly placed and poorly developed root-system of the plant.

BRODIAEA CAPITATA.

Brodiaea is restricted in its distribution to Tumamoc Hill and to the upper bajada slope, and does not occur in the other habitats, namely, Santa Cruz flood-plain or that by West Wash, or on the bajada as a whole. It is a bulbous perennial with the vegetative and flowering periods in the winter season. Its bulbs are somewhat over 1 cm. in diameter, and are 5 cm., more or less, beneath the surface of the ground. The roots are adventitious, coarse, and unbranched. They are relatively few and are usually more than 5 cm. in length. The depth to which the roots of the plant penetrate, therefore, is approximately 10 cm.

No forms of roots other than that just sketched were seen in the field, but dimorphic roots appeared in greenhouse cultures. Although this will be referred to later, it will be well to describe these roots in this place. The conditions under which the unusual form of roots occurred were as follows: Among preliminary experiments, looking to a study of the aeration of roots, was one which was arranged with two kinds of soils, namely, sand from a wash and fine adobe clay (sifted) from the river bottoms. The bulbs were planted, or were intended to be planted, on the line, which was a vertical one, separating the two kinds of soil, but on removing the plants at the end of the experiment one bulb was found to have been planted in sand and the other in adobe, about 1 cm. in each instance from the opposite kind of soil. The culture was running during a portion of November (1908) and all of December, which was a rather cold period and unusually cloudy. The green-house was not heated.

When removed from the soil, the plant of the adobe side of the culture had two leaves, 25 cm. long. The bulb had nearly or entirely disappeared and in its place was the fleshy base of a stout root from the upper end of which, or from the portion of the bulb remaining, was springing the usual type of roots. The relation of the two is shown in plate 23. Of the ordinary type of roots there were 13, which ranged from 2 to 11 cm. in length and were wholly confined to the adobe side of the culture. The central fleshy root was about 10 cm. long. It was 1.1 cm. in diameter at its crown and narrowed rapidly as it approached the tip, which was attenuated. The position occupied in the soil by the root was peculiar. In place of going straight down—as did the root of the sand grown plant—or of taking a horizontal position, like the other secondary roots, it went downward but at the same time inclined sharply away from the source of water supply, and ended in a curl as shown by a figure of the plate.

The plant on the sand side of the culture in certain particulars behaved in a manner somewhat different from that described for its adobe-grown fellow. The 2 leaves were 22.5 cm. long. The bulb was not resorbed, and from it there sprang two sorts of roots, the relations of which are indicated in plate 23. There were 7 rather coarse absorption roots, from 1 to 7 cm. long, and a single fleshy root. All were of secondary origin; the fleshy root, however, as in the case of the plant described above, sprang from a point on the bulb very near its base and went straight down from the bulb; it was 7.2 cm. long and 0.4 cm. in diameter at the crown. None of the roots entered the adobe side of the culture.

An explanation of the transformation of fibrous into fleshy roots of *Brodiaea* will not be attempted in this place. It may, however, be associated with the unusually large amount of water available to the two plants rather than to unfavorable conditions of aeration. A parallel instance, referred to later, was observed in cultures of several arborescent cacti, in which the formation of tuberous roots in species which do not normally produce tuberous roots was induced in cultures conducted much as that just described.



a. *Trianthema portulacastrum*, flood-plain of Santa Cruz. b. *Vicia* sp.
c. *Amsinckia spectabilis*. d. *Daucus pusillus*.



a. *Festuca octoflora*, March, 1908. b. *Gilia bigelowii*, March, 1907. c. *Malva borealis*, showing development of root-system, February, 1907. d. *Medicago denticulata*, February, 1907. e. *Microseris linearifolia*, March, 1907.

DAUCUS PUSILLUS.

Daucus pusillus, one of the most generally distributed of the winter annuals, is abundant on both Tumamoc Hill and the upper portion of the bajada north of the Hill. Its root-system can be characterized as being extensive rather than intensive. The main root dominates the root-system, although it is never fleshy, or even very coarse, and the laterals are relatively few and branch but little.

Young as well as mature plants were studied. The tap root of a plant whose shoot was 18 cm. long and which was in flower was over 15 cm. long. Just beneath the surface of the ground, where the tap root was slightly over 1 mm. in diameter, several fine roots, but not filamentous, were given off about 3 cm. from the surface of the ground, and 3 to 4 cm. deeper a prominent lateral, 7 cm. in length, had its origin. Roots of the second order were few in number. As plate 5 shows, there is no great difference in diameter between the main root and the laterals, or between the laterals of the first and the second order.

The leading feature which marks the mature plant is characteristic of the young plant as well. Thus a seedling with seed leaves and only one leaf of the adult type had an unbranched tap root over 5 cm. long, while another of about the same age had a tap root over 6 cm. in length, which every 3 to 12 mm. bore laterals about 2 mm. long. This type of root-system was seen also in a somewhat older plant. It may be concluded, therefore, that *Daucus* not only penetrates the ground deeply (how deep was not determined), but also quickly, and is thus admirably adapted to endure after more shallow-rooted annuals have perished.

ERITRICHIMUM PTEROCARYUM AND HARPAGONELLA PALMERI.

Eritrichium and *Harpagonella*, two boraginaceous winter annuals, although relatively small, usually considerably under 15 cm. in height, and thus inconspicuous as to individuals, occur in such great numbers that they constitute an important element in the plant covering of their favorite habitats. These are common on Tumamoc Hill as well as on the upper portion of the bajada to the north of the Hill. Plants of different ages and from different localities were examined. A mature specimen of *Eritrichium*, with the shoot 13 cm. long, had a filamentous tap root which penetrated over 8 cm. The laterals were borne in the region between 3 and 6 cm. from the surface of the ground, and were 4.5 cm., and less, in length.

The root-system of *Harpagonella* was somewhat better developed; plants from dry and moist situations were studied. Those from the drier locations had unbranched shoots 7, 9, and 10 cm. in length. The roots of the smallest plant penetrated over 11 cm. The laterals were given off from the main root from 1 to 4 cm. beneath the surface of the ground. The specimen of *Harpagonella* from the more moist soil, with a shoot 19 cm. long, had a tap root which was followed over 15 cm. The laterals, like those of the plant from the drier situation, were unbranched.

ERODIUM CICUTARIUM.

Erodium cicutarium, which is an introduced species, has already a wider distribution in this vicinity than most native plants and promises to become one of the most successful of the winter annuals (Spalding, Distribution and Movements of Desert Plants, Carnegie Institution of Washington, Publication 113, 1909, p. 27). Although its root-system was not studied closely, there are some points of interest that may be referred to. The dominant features of the root-system are the prominent tap root and the poor development of the laterals. How deep the tap root penetrated was not accurately learned, but its length is believed to equal that attained by the roots of most perennials occupying the same habitats. The laterals were most numerous about 4 cm. beneath the surface of the soil, and in the specimens examined averaged only 1.7 cm. in length.

FESTUCA OCTOFLORA AND HORDEUM MURINUM.

Two biologic types of grasses, annuals and perennials, occur on Tumamoc, each of which appears to have its characteristic distribution. The annual grasses, both those of summer and those of winter, are generally distributed, but the perennial forms occur where the water relations are especially favorable. Of the grasses only two winter-growing ones were examined. The type of the root-system of the grasses is well known so that there is no need of presenting a description of it in detail; but it will be instructive to compare the extent of the root-system of the grasses with that of the other annuals which appear at the same season.

In the mature plants the roots are entirely of secondary origin, and there is no main root to dominate the system. The length of the roots is variable but considerable. In a plant with a shoot 17 cm. long there were 3 large roots, each about 5 cm. in length, with numerous branches 2 cm. in length, more or less. Another plant (both were of the genus *Festuca*) 19 cm. high had 4 roots over 12 cm. long. The laterals borne on these roots were filamentous and varied greatly in length (some being 10 cm. or more), and bore in turn long and short filamentous branches (plate 6).

The root system of *Hordeum* was similar in character and approached in extent that of *Festuca*. A plant with a shoot 22 cm. in length had 4 large roots, all of which were over 14 cm. long; and another specimen with a shoot 30 cm. long had 7 large roots, of which the longest was over 17 cm. All bore numerous filamentous branches. The depth of penetration of the laterals was not learned. It may be safely assumed, however, from other observations as well as from those just presented, that the roots reach at least 15 cm.; perhaps still deeper in the largest specimens.

GILIA BIGELOWII.

Gilia bigelowii, one of the smallest winter annuals, is generally distributed on Tumamoc Hill. The roots of *Gilia* are admirably adapted to enable the plant to reach relatively deep, while at the same time it takes advantage

of available moisture near the surface of the ground. The leading feature of the root-system is the long and slender tap root which carries numerous rather short filamentous laterals. The general character of the root-system is shown in plate 6. The length of the tap root varies with the age of the plant from 5 cm. in one 4 cm. high to over 9.5 cm. in a plant with a shoot 8.5 cm. long. The laterals of the first order are usually less than 2 cm. long, and branch infrequently, so that as a whole the root-system corresponds very well with the "extensive" type of Bűsgen* (plate 6).

MALVA BOREALIS.

Malva, one of the most common of the winter annuals, was studied on Tumamoc Hill only, although it occurs on the flood-plain of the Santa Cruz also, where it is perhaps most abundant along the irrigating ditches. The root-system of the mature plant is characterized by the prominence of the laterals, which are coarse and relatively long. Several characteristic changes should be noted, leading to the formation of the mature root-system as shown in plate 6.

In the development of the root-system of *Malva* there are two fairly well differentiated stages, of which the immature is very different from the mature. The seedling plant sends down a tap root which penetrates the soil to a depth of about 8 cm. before laterals become prominent, or indeed appear in numbers. The prominent tap root, therefore, is the leading feature of the seedling. As the plant increases in size the tap root strikes down quickly and strongly until a condition shown in plate 6 is reached. After this the laterals begin to grow and from this time they constitute the chief feature of the system. At first the laterals arise singly, and close to the surface of the ground, but in time they become of importance by their increase in length, by the formation of branch roots of the second order, and by the formation secondarily of laterals of the first order along the main root axis. But the tap root is always an important feature, since in the mature plant it may attain a length exceeding 16 cm.

The secondary formation of laterals of the first order, by which groups of three or more roots are formed, which are of unequal age, has also been noticed in several other annuals and probably also occurs in many perennials. This not uncommon character of plants must greatly increase the efficiency of the root-system by adding much to the absorbing surface without greatly increasing the distance of water transport or of bringing the roots into more active competition with those of neighboring forms.

MEDICAGO DENTICULATA.

Medicago, one of the introduced forms which have their period of greatest activity in winter, is abundant on the flood-plain of the Santa Cruz. The plant examined, however, was growing on Tumamoc Hill in the vicinity of the Desert Laboratory. *Medicago* has a generalized type of root-system,

*Compare von Alten, Wurzelstudien, Bot. Zeit., vol. 67, p. 192, 1909.

characterized by few roots which are rather coarse and which branch infrequently. In the young plant the tap root predominates, but as it matures the laterals become important; the behavior of the root-system in its development recalls that of *Malva*. Tubercles were not present on the plants examined. Plate 6, slightly less than life-size, shows the main features of the root-system so that further description in this place is not necessary.

MENTZELIA ALBICAULIS.

Mentzelia albicaulis occurs on Tumamoc Hill and on the upper bajada-slopes. The leading character of its root-system is the prominent tap root. The root-system of the plant was studied mainly in young individuals, and the penetration of the roots of the fully developed plant was not learned. A young plant of *Mentzelia* with a shoot 2.3 cm. in length had a tap root 11.5 cm. long. The laterals in young plants are numerous, unbranched and occur singly. In older plants the laterals are in groups, as in *Malva* and other annuals.

MICROSERIS LINEARIFOLIA.

Microseris is abundant on Tumamoc Hill and on the slopes of the bajada to the north. The specimens examined were growing near the Desert Laboratory on Tumamoc Hill. The root-system, as shown in plate 6, is characterized by the prominence of the tap root and by the slenderness of the laterals of the first order. The root-system of a mature plant, with a shoot 20 cm. in length, consisted of a tap root, 2 mm. in diameter at the crown and over 11 cm. long, and a few filamentous laterals which were borne for the most part within 5 cm. of the surface of the ground. The laterals branched sparingly. *Microseris* is among the most deeply rooted of the winter annuals.

MONOLEPIS CHENOPODIOIDES.

Monolepis chenopodioides was collected for study in February from the immediate vicinity of the Desert Laboratory where it was growing in abundance. Its tap root, as plate 7 shows, is the most prominent feature of its root-system, although laterals are early developed. The laterals of the first order, although small as compared with the tap root, are, however, rather coarse, and branch but little. Thus the root-system of *Monolepis* should be classified as extensive.

ORTHOCARPUS PURPURASCENS.

Orthocarpus occurs on the upper slopes of the bajada especially, and only appears in abundance if, as happened in the spring of 1908, when the root-system of the annual was studied, the rains have been copious. It is a low annual, seldom above 15 cm. in height, of a gray-green color, and has lately been found to be an habitual root parasite.*

*Cannon: The Parasitism of *Orthocarpus purpurascens* Benth., Plant World, vol. 11, 1909, p. 259.



a. *Monolepis chenopodioides*, February, 1907. b. *Orthocarpus purpurascens* parasitic on *Astragalus* sp. c. *Orthocarpus purpurascens* on *Lupinus* sp., March, 1907. d. *Parietaria debilis*, mature plants from favorable and unfavorable moisture conditions. e. *Phacelia tanacetifolia*, March, 1907. f. *Plantago fastigiata*, March, 1906.



a. *Sisymbrium canescens*. b. *Streptanthus ciliatus*.

Parasitism of the plant has been observed on the following species:

<i>Astragalus nuttallianus.</i>	<i>Eschscholtzia mexicana.</i>	<i>Pectocarya linearis.</i>
<i>Bigelovia hartwegii.</i>	<i>Festuca octoflora.</i>	<i>Phacelia tanacetifolium.</i>
<i>Bowlesia lobata.</i>	<i>Gilia bigelowii.</i>	<i>Plantago fastigiata.</i>
<i>Daucus pusillus.</i>	<i>Lesquerella gordonii.</i>	<i>Silene antirrhinum.</i>
<i>Delphinium scaposum.</i>	<i>Lupinus sp.</i>	<i>Streptanthus californicus.</i>
<i>Eritrichium pterocaryum.</i>	<i>Mentzelia albicaulis.</i>	<i>Sisymbrium canescens.</i>

The typical root-system of *Orthocarpus* may be described as consisting of well-developed tap root and few laterals, but greater variation in the character of the root-system of this species was seen than was observed in that of any other annual. Three leading modifications of the roots were seen. These were: (1) roots with short and coarse laterals; (2) those in which the laterals were filamentous and either long or short; (3) root-systems in which the tap root is broken up into three or more forks.

While the immediate causes of these variations were not investigated, it is thought that they may be connected with the nature of the root-system of the host plant, as will seem probable from the following.

In association with *Astragalus*, *Orthocarpus* has a prominent tap root with both long and short laterals which are rather coarse. The long laterals are independent of the host plant, but the short ones bear haustoria. In the case of the length of the laterals, it is presumably directly dependent on the distance by which the parasite and the host are separated, which, however, would not account for the coarseness of the roots of the parasite.

When growing in association with *Festuca octoflora* as the host, the roots of *Orthocarpus* are filamentous and the root-system is poorly developed. On *Eritrichium* the roots of the parasite are also filamentous, but very numerous. In connection with *Silene*, the main root of *Orthocarpus* is broken up into several relatively large roots and the laterals are very few.

Whatever may be found to be the chief causes in bringing about the modifications in the character of the root-system of *Orthocarpus*, as described above, it is of interest to note that the soil conditions were as uniform as one would expect to find in a single habitat, and that the root-systems of the host plants had specific differences which the roots of the parasite to a degree reflected. Thus the roots of *Astragalus* are coarse and those of *Eritrichium* are filamentous, and the roots of *Orthocarpus* when attached to these plants are coarse or fine, as the case may be. Whether *Orthocarpus* can live independently is not known, so what its root-system would be as an independent plant can not at present be told. However greatly *Orthocarpus* changes the character of its root-system with differences in the roots of its hosts, it does not modify its life-cycle if that of the host chances not to coincide with that of its own. When associated with annuals, the plant would naturally not be influenced to prolong its period of existence, and when connected with a perennial, as with *Bigelovia*, it appears not to do so (plate 7).

PARIETARIA DEBILIS.

Parietaria occurs almost exclusively in the shade of rocks, or elsewhere where it enjoys protection either against excessive light or severe aridity. The plant closely resembles the eastern clearweed (Spalding: Distribution and Movements of Desert Plants, Carnegie Institution of Washington, Publication 113, 1909, p. 20) and has a very high water content; though growing in the desert it has no characteristics which ally it to typical desert plants. *Parietaria* varies greatly in size and appearance, a feature depending on water relations more than on any other environmental condition. This may be illustrated by the following observation. In March, 1906, many annuals were seen to be of very unequal size; the difference was so great in many instances as to make sure recognition of well-known species difficult. Among forms exhibiting this condition, none showed so extreme modification as *Parietaria*, mature specimens of which, growing under favorable and unfavorable conditions as regards water relations or protection by neighboring plants or rocks, were found whose shoots were from 8 mm. to 39 cm. long; that is, there was a difference of 1 to 49 in stature (plate 7).

The root-system of *Parietaria* is an extremely meager one. It does not penetrate far either horizontally or vertically. The main root of the plant with the longest shoot seen was over 4.3 cm., or about one-ninth the length of the shoot. The length of the main root of the smallest specimens was about 5 times the length of the shoot. The relation of the length of root and of shoot in these instances, together with the general character of the root-system, is shown in plate 7.

PHACELIA TANACETIFOLIA.

Phacelia is one of the most common of the winter annuals on Tumamoc Hill, and one of the most generally distributed, although it may be most abundant and attain greatest development on the northern slope and in the protection of larger plants and of rocks. A prominent tap root is the chief characteristic of its root-system. A mature plant with a shoot 15 cm. high had a tap root 2 mm. in diameter at the crown and over 18 cm. long. The laterals of the first order are fine, usually short, and arise singly. Under certain circumstances, however, the laterals become a more pronounced feature of the root-system, as, in a younger plant than that above described, laterals 6 cm. in length were seen within 3 cm. of the surface of the ground. With its prominent tap root and fine laterals, *Phacelia* is to be classed among the plants with an extensive root-system, like the most of the annuals examined (plate 7.)

PLANTAGO FASTIGIATA.

Plantago is abundant on Tumamoc Hill and on the upper bajada at its northern base. It grows everywhere in the open where it is exposed to the sun and is among the most drought-resistant of the winter annuals. The

leading characteristics of its root-system are the long tap root and the small development of laterals. The tap root of the young plant may reach as deep as 13 cm. before laterals appear to any extent (compare plate 7), and even in the mature form there are few laterals, and these branch but little. The extreme depth to which the tap root of the mature plant reached was not learned, but it may safely be considered among the most deeply placed of the roots of any annual.

RAFINESQUIA NEO-MEXICANA.

Rafinesquia occurs on the bajada at the northern base of Tumamoc Hill and on the hill itself. Its root-system is characterized by a prominent tap root which bears filamentous laterals. The tap root is 2.5 mm. in diameter at the crown. The laterals of the first order are 5 cm. long, more or less, and branch infrequently; laterals arise singly and cultures (to be mentioned below), in which attempt was made to induce the formation of laterals secondarily and in groups, were not successful. In *Rafinesquia*, therefore, the appearance of laterals singly should be considered a fixed character.

STREPTANTHUS ARIZONICUS, SISYMBRIUM CANESCENS, AND SISYMBRIUM REFLEXUM.

The three cruciferous annuals whose root-systems were studied occur both on Tumamoc Hill and the upper reaches of the bajada at its northern base. *Streptanthus*, however, appears to be limited to the Hill. *Streptanthus* and *Sisymbrium* have similar root-systems. The tap root is a prominent feature, and the laterals are fine and long, and branch but little. The roots thus are extensive rather than intensive, enabling the plant to reach out as well as to penetrate the ground a considerable distance. Plate 8 shows well the general character of the young and of the mature plant of *Streptanthus* and does not need further comment.

A specimen of *Sisymbrium* with the shoot 15 cm. long and fruiting was examined. The tap root was relatively heavy and was traced over 16 cm. into the soil. The laterals of the first order were either fine or filamentous and were 10 cm. or more in length, and were borne for the most part within 2 to 6 cm. of the surface of the ground.

Both in *Streptanthus* and in *Sisymbrium* the laterals arise singly; there are no groups of laterals and no rudiments.

GENERAL CONCLUSIONS AND SUMMARY OF STUDIES ON ANNUALS.

On Tumamoc Hill, and that portion of the bajada and the flood-plain of the Santa Cruz river within the Laboratory domain, as well as by the West Wash, 223 species of annuals are reported. Of these, 122 are winter annuals and 44 appear in summer. Representative species both of winter annuals and of summer annuals, as well as one or two perennials and long-lived annuals, were examined in connection with the present study. In looking over the results of observations on root-systems, several facts were brought to light, of which the following appear at present to be the most important.

A feature of several species of both winter and summer annuals is the presence of rudimentary roots in certain species and their consistent absence in others. Among the plants with rudimentary roots are *Amsinckia*, *Eritrichium*, *Harpagonella*, *Pectocarya*, *Erodium*, and *Malva*, among the winter annuals, and *Amaranthus*, *Boerhaavia*, *Cladothrix*, and *Trianthema* among those of summer. Frequently associated with the presence of the root rudiments, perhaps always so, is the appearance of laterals, particularly those of the first order, in groups of three or four; another feature is the precocity of rudimentary-root formation in several species, particularly in *Amsinckia* and its relatives. With the desire to throw some light on the causes underlying the appearance of the rudiments the following experiments, which are regarded as preliminary, were set up.

On February 14 two pots were planted with seeds of *Amsinckia spectabilis*. At the time of the sowing of the seeds the pots were thoroughly watered, after which one was not given water again and the other was watered frequently. About April 6 the young plants in the dry pot were seen to be in a wilting condition and were removed from the pot and their roots examined. It was found that the laterals of the first order were borne singly on the main root and that at the base of each lateral there were one or two rudiments. The rudiments of the smallest plants in the pot were best developed. The root-systems of the plants growing in the well-watered pot had the following characters: the laterals of the first order were mostly in pairs, and at the base of each group there was at least one rudimentary root. It would appear, therefore, that the organization of the rudiments in *Amsinckia* is not dependent on an improvement of the water conditions, although their subsequent development is, and that they are to be considered a constant character in the root-system of the species.

In many of the plants no rudiments were seen at any time; experiments were set up, consequently, to learn whether the formation of rudimentary roots might be induced; the experiments were confined to *Rafinesquia neo-mexicana* and the conclusions are not assumed to be applicable to any other species. In December a pot of suitable earth was prepared and was thoroughly soaked with water, and seeds of *Rafinesquia* were sown. After

the seedlings appeared no more water was given the pot until February 2, when by wilting in the daytime the plants showed that more was required. On February 2 the earth of the pot was well watered. Very shortly after the watering, the plants recovered and began growing vigorously, and on February 9 they were removed from the pot and their roots were examined. It was learned that the main root bore laterals of the first order singly; no rudimentary roots were present. It would therefore appear that in *Rafinesquia* not only are rudimentary roots not present in the natural condition, but their formation may not be induced by improved water relations.

The root-systems of the winter annuals are usually easily distinguishable from those of the summer annuals. The most striking characteristics of the roots of the former are the prominently developed tap root and the meager development of the laterals, which are generally filamentous or at least thin. The annuals of summer, on the other hand, have root-systems which are frequently of a more generalized form; that is, the laterals are developed well and are frequently rather coarse, and the main root is often forked. The absorbing surface of the summer annuals appears to be greater than that of the winter forms, although the depth of penetration of the roots of the two classes is apparently about the same.

The causes leading to the differentiation in the root-systems of the winter and the summer annuals are not surely known, but on the probability that they lie in the nature of the species as well as in the difference in the environment of the two classes of plants the following hypothesis, as a basis for subsequent experimentation, is offered. The facts in addition to those presented in the foregoing paragraph are as follows. The rains of summer, in addition to thoroughly wetting the soil, serve to cool it as soon as they come. The air temperature also immediately falls, and the relative humidity at once becomes high. In brief, the conditions for a tropical luxuriance of growth are at hand, and the shoots of the plants which appear at this season bear a noticeably large number of large leaves; the transpiration surface is relatively great.

In the winter season, however, the general character of the annuals, and that of their environment, are strikingly different from those just described as obtaining in summer. As was shown in the discussion on soil temperatures, the temperature of the soil begins to fall with the coming of the summer rains and continues to decline until March-April. Therefore, the rains of the winter season do not materially change the course of the curve, as is the case in summer. The air temperature at the time of the winter rains is relatively high, but much lower than in summer. There are also occasional periods of really high temperatures and drying winds. The winter plants, so far as I have observed, usually do not grow as quickly and do not have as large leaf surface as the summer annuals.

Given a sufficient amount of water both in winter and in summer, it is possible that the difference in the relative temperature relations of soil and

of air of the two seasons is mainly the operating cause in bringing about the difference in the root-systems. The leading factors in this process would be as follows. In summer the temperatures both of soil and of air permit, on the one hand, very rapid growth, and on the other the best conditions for water-absorption, with the result that the root-system of a plant is well developed. In winter, on the other hand, the soil at the 20 to 30 cm. depth is in daytime colder than the air, which operates directly to depress the rate of water-absorption, to limit the development of the roots, and thus to make the conditions unfavorable for the fullest growth of the shoot, with the result that in turn the demands on the root-system are relatively low. Could the winter soil be warmer than the air, the growth of the shoot would probably be much more vigorous and the root-systems of the plant much more extensive and of a different character than they actually are.

From the foregoing brief statement of the leading general differences between the annuals of summer and those of winter, it will appear that the summer season may be conceived as favoring hygrophily more than the winter season; so that the root-systems of the summer annuals can be said to tend toward hygrophily and those of the winter forms toward xerophily. With these differences in mind, it is of interest to classify those of the winter annuals which have a generalized type of root-system, or one which approaches the type of the summer plants. As a fact, we find that *Bowlesia Parietaria*, and *Malva*, the only plants examined with a marked generalized type of root-system, are limited in their normal distribution to situations where they enjoy relatively favorable water relations. The winter annuals with specialized or winter type of root-system, that is, deeply penetrating, have the widest distribution.

Although no attempt has been made in this study to group plants according to the various types of root-systems, or to describe the roots from the standpoint of classification, such, for example, as has been done by Freidenfeldt (Studien über die wurzeln krautiger Pflanzen. I. Ueber die Formbildung der Wurzel vom biologischen Gesichtspunkte, Flora, 91, 1902), it has been noted that each species examined had its peculiar form of roots. So striking is the individuality of the root-systems that it may be possible, and probably would be possible, to determine the form solely from the character of its root.

The most striking roots of autotrophic annuals examined were those of *Aster tanacetifolius*, although those of *Amsinckia* and its relatives were also very individual. The root-system of the parasite *Orthocarpus purpurascens*, which was found in connection with 18 hosts, was more diversified than that of any other annual. The roots were either coarse or fibrous, with a single main root, or broken up into several main roots. Whatever may have been the determining cause of this diversity, it was observed that the roots of the parasite reflected in a degree the characters of the roots of the host plants.

ROOT-SYSTEMS OF PERENNIALS.

The problem of studying the roots of the larger plants in the field, and of recording the results, is naturally quite different from that of examining the root-systems of annuals. The environment to which the roots of perennials are exposed and to which they should be related, is likewise much more varied than that of the smaller plants of briefer life span. In the case of the annuals the entire root-system might by appropriate means be brought under the eye, photographed, measured, and examined microscopically; but such procedure is impracticable in perennials, and choice had to be made arbitrarily between minute examination of ultimate roots, as Büsgen studied the roots of Javanese and German trees, and a study of the more permanent portions of the root-systems. Since the survival means successful resistance to desert conditions, and, further, as the study was primarily one in which the plant was to be compared to its environment, the latter method was decided on.

Accordingly, in this report on the results of the investigation, the mature root-systems are characterized and the more obvious relations to temperature and water are presented.

The perennials selected for study comprise the most striking ones only, and probably do not include many which will be found worthy of subsequent examination. The list includes trees and shrubs, mainly the latter, and among these is a great diversity in habits and habitats. There are fleshy as well as non-fleshy forms; plants with shallow and those with deeply placed roots; plants deciduous as well as evergreen; those which come into leaf in summer only and those which form leaves whenever there is adequate amount of water whatever may be the time of the year, and finally there is one parasite (*Krameria*).

Following is a list of the species examined, together with the habitats in which they were studied:

TUCAMOC HILL: *Echinocactus wislizeni* Engelm., *Enecha javinosa* Gray, *Jatropha cardiophylla* (Torr.) Muell. Arg., *Opuntia discala* Griffiths, *Opuntia leptocaulis* DC., *Opuntia versicolor* Engelm.

THE BAJADA: *Carnegia gigantea* (Engelm.) Britt. and Rose, *Covillea tridentata* (DC) Vail, *Fouquieria splendens* Engelm., *Franseria deltoidea* Torr., *Krameria canescens* Gray, *Krameria glandulosa* Rose, *Opuntia arbuscula* (?) Engelm., *Opuntia fulgida* Engelm., *Riddellia cooperi* Gray.

THE BAJADA, RINCON MOUNTAINS: *Davallion texanum* Scheele, *Montonia scabrella* Gray, *Yucca* sp., *Yucca radiosa* Engelm.

FLOOD-PLAIN OF SANTA CRUZ AND WEST WASH: *Condalia spathulata* Gray, *Ephedra trijurca* Torr., *Kerberlinia spinosa* Zucc., *Opuntia vivipara* Rose, *Zizyphus parryi* Torr.

Besides these forms some observations were made also on *Prosopis velutina* Wooton, *Lycium* sp., *Oleña tesota* Gray, *Parkinsonia microphylla* Torr., and a few other forms which will be given incidentally in the account of the root-systems below.

PLANTS FROM TUMAMOC HILL.

Of the areas under consideration in this paper, Tumamoc Hill is the richest in the number of species of perennials and the bajada in annuals. The same species frequently occur on all of the habitats, but to this there are numerous exceptions. Of the plants studied on Tumamoc Hill the following do not grow in the other areas: *Jatropha cardiophylla*, *Opuntia discata*, and *Opuntia versicolor*. On the other hand, some forms which are most typical of Tumamoc Hill, such as *Carnegia gigantea*, but which are in other areas also, were studied where the soil conditions were most favorable for excavating, and not necessarily on the Hill exclusively.

ECHINOCACTUS WISLIZENI.

Two specimens of *Echinocactus wislizeni* were selected for special study, one of which was growing by West Wash and the other on the north shoulder of Tumamoc Hill about 60 meters north of the Laboratory building.

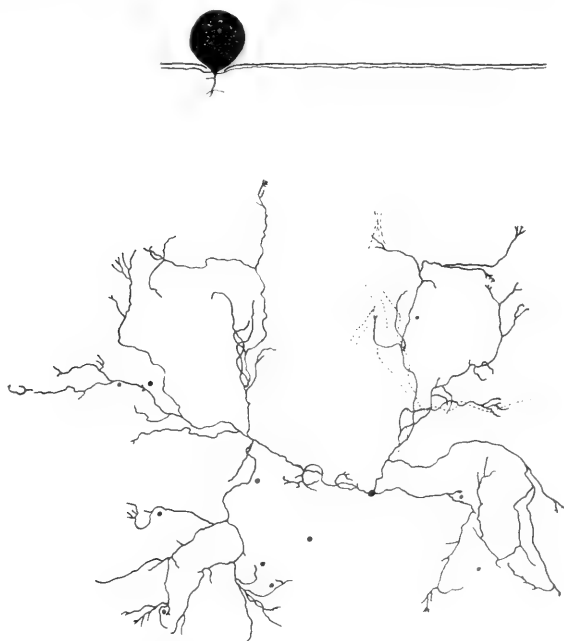


FIG. 2.—Root-system of *Echinocactus wislizeni*, horizontal and vertical extension. Intruders are represented by broken lines, *Acacia constricta* by large dots, *Menispermata*; and *Opuntia discata* by dotted lines.



ROOT-SYSTEM OF ECHINOCACTUS WISLIZENI.

- A. Showing anchoring and absorbing roots in natural position, from West Wash.
- B. Bird's-eye view of roots from which overlying soil has been removed.



a



b



c



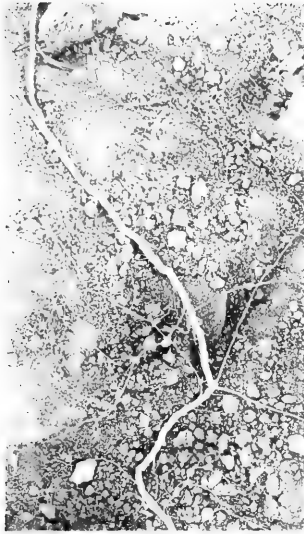
d

a. Root and shoot habit of *Opuntia leptocaulis* which was growing under the protection of *Acacia constricta*, Tumamoc Hill.

b. *Opuntia versicolor* showing habit of plant and character of environment. A small specimen of *Echinocactus wislizeni* is to be seen at base of main stem.

c. Bird's-eye view of a portion of the central part of the root-system of the plant shown in b, with the overlying soil removed, leaving roots as far as possible in their natural placing.

d. This and figures on plate 11 are of one main lateral and some branches of the plant shown above.



Continuation of plate 10. Bird's-eye view of root-system of *Opuntia versicolor*.

The general soil conditions of Tumamoc Hill have already been described and need not be repeated here. It will only be necessary to add that, at the precise spot where the specimen of *Echinocactus* was growing, the bed rock was so deep that it was not encountered in the course of the excavation of the plant's roots. The roots were wholly confined to the upper soil layer or the malpais, which here was relatively heavy. In West Wash (the soil conditions of which are also described above) the soil is somewhat lighter, owing to an admixture of sand, and exceeds 2 meters in depth. The water and the temperature relations of the habitats are unlike, and as far as studied are also characterized in the section above referred to.

The *Echinocactus* examined on Tumamoc Hill, April, 1907, was 38 cm. high and of about the same diameter. As plates 9 and 10 and fig. 2 indicate, the root-system of the plant has a very meager anchoring portion and a very extensive absorbing portion. The main root went straight down 20 cm. and gave off several short laterals between its tip and its crown, which latter was 10 cm. beneath the surface. The most deeply placed of the short laterals extended 12 cm. away from the main root axis and attained a depth of 25 cm.

The main absorbing system consisted of three laterals of the first order which left the tap root at its crown and extended in two directions, namely, uphill and downhill. The larger portion was that which extended up the hill. The uphill portion originated from a single lateral, as shown in the figure, and consisted of numerous roots of the second, third, and fourth orders, which were so disposed as to cover the ground included by them fairly thoroughly.

The roots of the main absorbing portion of the system were of a light brown color, and were rope-like and tough; they were slender throughout their length. The depth of the roots may be learned from the following measurements, which were made on the portion which was placed uphill from the main axis of the plant. At a distance of 40 cm. the lateral was 3 cm. deep; 3 meters distance it was 3 cm.; and at 3.5 meters the roots were 1.5 cm. beneath the surface of the soil. Thus the roots of the absorbing portion of the system are all extremely shallow, so shallow that they are often exposed by the eroding effects of severe storms.

In order to observe the possible range of variation of the root-system of *Echinocactus*, other specimens were examined, one of which was growing by West Wash. The leading points in the study of this plant may be summarized as follows: The horizontal system was sharply differentiated from the vertical system, both of which, particularly the latter, were densely branched. The horizontal portion of the root system lay for the most part within 5 cm. of the surface. It was apparent that the anchoring roots were also very actively engaged in absorption, and that the absorbing roots were relatively not so important as the corresponding roots in the specimen from Tumamoc Hill.

The relation of the specimen of *Echinocactus* from Tumamoc Hill to other perennials included within the radius of its horizontal roots was as follows: One specimen of *Acacia constricta* was placed 1 meter from the main axis of the plant; one specimen of *Opuntia discata* was slightly farther than *Acacia*; and 10 specimens of *Menodora scabra*, a shrubby form, occupied various positions nearer than the other species named. The neighboring forms, however, held very unlike relations to the *Echinocactus*, a fact, in this case, dependent on the character of the root-systems. The roots of *Menodora* penetrated deeply and there was little development of the laterals corresponding to the horizontal or absorbing system of *Echinocactus*. Only a few of the roots of *Acacia* were encountered while excavating for the root-system of *Echinocactus*, but two long and a few short roots of *Opuntia* were seen to lie in close proximity to the downhill roots of *Echinocactus*. From the positions occupied by the roots of these plants it may be concluded that only the species of cactus enter into active competition with one another for water. Competition between plants whose roots occupy horizons 20 to 30 cm. apart, as between the cacti and other plants, is not to be considered as direct.

The story of the developmental changes which take place in the root-system of *Echinocactus* was not learned, although it is undoubtedly different from that of such a fleshy form as the sahuaro (*Carnegiea gigantea*) in which the horizontal portion of the root-system becomes modified secondarily to meet the demands of the plant for mechanical support, as will be described below. The root-system of *Echinocactus* is not suited to enable the epigeal portion to withstand severe lateral strains, as is the case with the sahuaro, for which reason the plants are often found uprooted, and are usually easily overthrown by a well-directed push. It is a matter of common observation that in falling, or in leaning, the plant generally leans or falls in a southerly direction. It thus may be called the compass-plant of the desert. The consistence of this position is without doubt founded on normal developmental changes to which the plant is subjected, such as the greater growth of tissues on either the north or the south side, as in the sahuaro (E. S. Spalding: Mechanical adjustment of the sahuaro, *Cereus giganteus*, to varying quantities of stored water, Bull. Torr. Bot. Club, vol. 32, page 64, 1905), by which an asymmetrical distribution of weight takes place.

ENCCELIA FARINOSA.

Encelia has a very decided habitat preference. Not only is the species limited to Tumamoc Hill, but it is most abundant on the southern face of the hill, though occurring also on the west and east, and to a limited extent on the north side. As the most typical habitat was not favorable for examination of the roots of the plant, on account of the rock exposures and the steep gradient, it was studied on the northern slope where the soil is deeper and the roots more easily removed.

Encelia is a very striking shrub, less than 1 meter high, with a close and rounded contour. The ends of the rather sparingly branched shoots, which are of a yellow-green color, bear large grayish leaves during the more moist seasons, and drop all but the terminal small ones when the arid conditions set in. Both leaves and flowers are formed whenever the water relations are favorable.

At the place where the specimen of *Encelia* was studied the malpais, about 15 cm. in thickness, was underlaid by hard caliche of about the same thickness, with a stratum of rotten caliche between, and this in turn was resting on a layer of sandy malpais of undetermined thickness.

The specimen selected for study was 90 cm. in height and was composed of 12 shoots, all of which bore large leaves. The plant was mature and was a very vigorous one. Its root-system was composed of a rather stout tap root, running directly downward, and numerous laterals which arose comparatively far from the surface of the ground. The main root went straight down through the malpais to the rotten caliche, where it narrowed abruptly and ran through the rotten caliche to the hard caliche, through a crack in which it made its way to the more deep-lying sandy caliche beneath. When the latter was reached it turned abruptly and took a horizontal course for a distance exceeding 50 cm. It was followed to a depth of 55 cm. beneath the surface of the soil.

The laterals of the first order, with no noteworthy exception, were given off in the malpais stratum, that is, within 20 cm. of the surface, and were placed between 15 and 30 cm. deep. There were about 5 main laterals; they branched but little. The diameter, length, and position of the laterals may be learned from measurements on one of the typical roots. The lateral in question left the main root 15 cm. from the surface; 15 cm. distant it was 6 mm. in diameter; at a distance of 60 cm. it was 2 mm. in diameter and lay 24 cm. deep; 1 meter from the main root axis it was 24 cm. deep, and at the tip, 1.5 meters distant, it lay 22 cm. beneath the surface. In addition to the larger laterals there are about 6 shorter ones of the first order which are wholly confined to the malpais.

All of the laterals bore groups of filamentous roots, recalling those of *Aster tanacetifolius*, 5 cm. more or less in length, and about 1 cm. apart. At the time the root-system of *Encelia* was studied, February 11, these rootlets were no longer living, and the time of their origin is not known, but is supposed to be much later than the formation of the mother laterals that bear them. To judge from their appearance only,* one would suppose them to have been in part produced during the preceding year, probably summer, and to constitute an important element in the absorbing system of the plant. Further comment on this type of roots, which were observed on several species, will be given below.

*On January 4, 1910, after rains had moistened the ground well, the roots of *Encelia* were seen to bear young and growing rootlets of the kind described in the above paragraph.

Figure 3 shows the horizontal and vertical extensions of the root-system of *Encelia parviflora*.

The specimen of *Encelia* studied had very little competition from its perennial neighbors. No other perennial grew within reach of its roots, but the roots of two plants, *Opuntia discata* and *Parkinsonia microphylla*, reached into or passed through the area occupied. The roots of the former were more shallow than those of *Encelia*, while those of *Parkinsonia* ran beneath the roots of *Encelia*. It should not be concluded, however, that the plant is without competitors for ground water since during two seasons, covering three months or more, annuals with deeply penetrating roots occur in large numbers and probably extract more moisture from the soil than *Encelia* itself does. The relative thickness of the 3 upper soil layers, adobe, rotten caliche, hard caliche, are shown diagrammatically in fig. 3b.

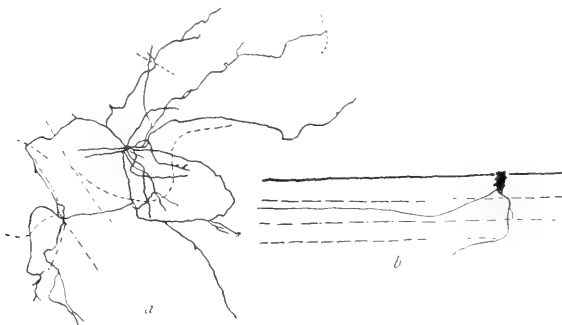


FIG 3.—*Encelia parviflora*.

OPUNTIA DISCATA.

Several types of flat-stemmed opuntias are native on Tumamoc Hill, and certain of them, as far as the habitats considered in connection with the present paper are concerned, are restricted to the Hill. Among these is *Opuntia discata*, a plant of varying habit, with prostrate branches when young, and with branches free of the ground when older. Two specimens of this plant were selected for study, one mature and the other young. The latter was growing on the north face of Tumamoc and the former on the west side. The soil conditions where the cacti were placed were apparently alike; the upper soil to a depth of 15 to 20 cm. is malpais, with rotten caliche beneath, all lying on the bed rock.

The plant from the northern exposure had two shoots composed of two and three "joints" each. Both branches were lying on the ground, so that the main stem bore none of their weight. The root-system consisted of several main roots, which either ran straight downward from the base of the main axis of the plant, or at an acute angle, and also about 8 laterals,

which arose from these vertical roots and extended in a more or less horizontal direction for various distances not far beneath the surface. There was no well-defined tap root, or supporting roots, all roots functioning mainly as absorbing roots.

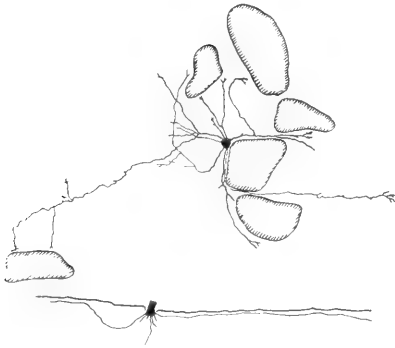


FIG. 4 - *Opuntia discata*. Horizontal and vertical extension of root system

The main points are shown in fig. 4, which represents the horizontal as well as the vertical extension of the root-system. For the most part the roots are confined within a radius of 50 cm. from the central axis, but two laterals, the one going uphill and the other down, were approximately 1.5 mm. in length. The root reaching southward maintained a depth of 20 cm. for a distance of 20 cm. and then ascended rapidly until it lay at the 10 cm. level, about which it remained during the rest of its course. The roots extending east were approximately 15 cm. deep. Those to the west ran along the face of a boulder at a depth of 15 cm., and after leaving this protection quickly rose and occupied a position near the surface. The roots of the *Opuntia* were slender throughout their course and branched very little.

The roots were seen frequently to be in intimate association with boulders whose presence and position greatly affect the branching and probably other habits of the root-system. Where the rocks are shallow the roots run beneath, but where they are as deep as 25 cm., for example, they run alongside. The roots which are placed under rocks are closely appressed to them and form intricate patterns as they there branch very densely; such roots also remain functional for a longer period than those of the same plant less advantageously situated. These features are clearly to be associated with the better water relations that are obtained beneath the rocks which serve to retain as well as to conduct water better than the bare soil. As illustrating this statement the following observation on the penetration of water may be noted. Soon after a rainfall of half an inch, by which the soil would usually be moistened to a depth approximately 8 to 12 cm., that underneath

a boulder was perceptibly wet to a depth of 25 cm., while less than 1 meter distant the soil, free of large rocks, was air-dry at this depth.

The root-system of the older plant, which grew on the western side of Tumamoc was different in some particulars from that of the plant just described. The shoot of the plant consisted of two main branches and three secondary ones, with a stout central axis, and the weight of all of the branches was born by the stem. There was no main or tap root, as in other cacti, but several roots, constituting a brush, left the base of the stem and penetrated the ground at an acute angle. Of these roots, the longest attained a depth of 15 cm. in a horizontal direction. From the central group there arose 8 leading roots which formed the superficial portion of the system; these varied in length from 50 cm. to 1.3 m.; the longest were those extending uphill. The superficial roots varied greatly in depth, some being as close to the surface as 2 cm. and others penetrating as deep as 20 cm., but the deeply placed ones uniformly ran underneath boulders, while the more shallow roots were situated where the soil was free from large rocks. The bases of the superficial roots were somewhat enlarged; for example, a root 50 cm. long was 1.5 cm. in diameter at its base, but the roots as a whole were very slender. The enlargement of the bases of the roots probably represents a regulatory response on the part of the roots by which the weight of the shoot is borne and the strains incident to winds successfully withstood. Thus roots functioning primarily as absorbing organs become, in the absence of a well-developed tap root, the most important mechanical support of the heavy shoot.

The superficial roots of the cactus favor absorption of water even when the rains have been slight, as may be illustrated by one or two instances. On October 17 half an inch of rain was recorded as having fallen at the Desert Laboratory. Within 3 days the joints of *Opuntia discata* lost the shriveled appearance which they had during the dry season and became plump. On another occasion the response was noted within 24 hours after a rain of 0.54 inch; also, 24 hours after irrigating a certain plant it showed by its increased turgidity that it had taken up water. In none of these instances had the water penetrated sufficiently to be of benefit to plants the absorbing system of whose roots was 10 cm. below the surface.

OPUNTIA LEPTOCAULIS.

Opuntia leptocaulis grows mainly and was studied only on Tumamoc Hill; it has very slender shoots, as is indicated by the specific name, and has certain biological relations, probably associated with the character of the shoot, which are of much interest.

As a rule the cacti in the vicinity of the Desert Laboratory do not hold close and fixed relations with other plants; they grow near or remote from other plants, apparently wholly according to chance. But the species *leptocaulis* is a very striking exception to this, in that it rarely occurs alone or remote from other and larger forms. The shoot habits of *Opuntia* vary

with the position which it occupies relative to other plants. When it is isolated, the shoot is rounded and much-branched; where the plant is protected by another plant, the branches are few and may be much elongated, and we shall see that the roots also of the plant vary with its position.

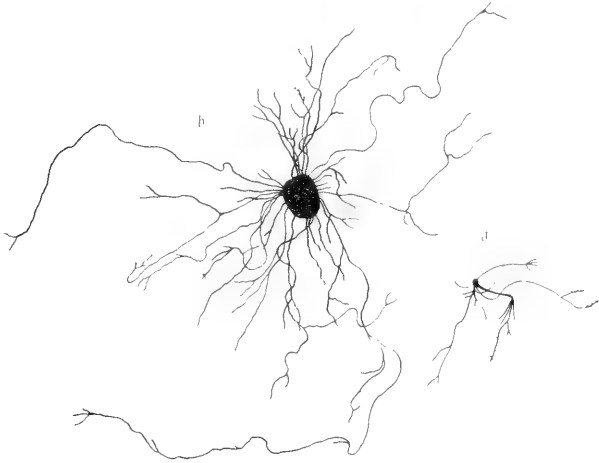


FIG. 5.—Root systems of *Opuntia leptocaulis*. a, plant growing at the base of *Acacia constricta*. b, plant growing apart from other species. Both figures are of mature plants.

Another character of the species is the presence of short branches, shown in plate 10, which constitute the chief chlorophyll-bearing organs. Under favorable water conditions, these short branches may be very numerous, but where the moisture conditions are otherwise, they are few. The branches really function as leaves, in that they are formed at times of active growth and that their subsequent history varies with the moisture relations; if favorable, they are long retained; if unfavorable, they early fall away. This effect can be quickly achieved by uprooting a plant and hanging it in a dry place, under which treatment the short branches to a large extent soon drop off. The exfoliated branches do not commonly, if ever, act as propagative bodies, as is the case in other species, notably in *O. vivipara*, as will be shown below.

The root-systems of two specimens of *leptocaulis* were studied in February, 1907; one was growing at the foot of *Acacia constricta* (fig. 5a) and the other independently (fig. 5b). Both plants were on the northern slope of Tumamoc Hill under the same conditions of soil and moisture as described above for *Encelia*. The protected plant was 80 cm. high, and the sub-aerial portion consisted of a central axis with a few long slender branches that carried many short ultimate ones of the character spoken of in a preceding

paragraph. The entire habit of the plant was symmetrical and loose. Figure 5 and plate 10 show the extension of the roots in the ground and their appearance when removed. There was a tap root, which penetrated 15 cm. and which bore a few laterals not over 10 cm. long, and about 4 main laterals 3 of which extended from the main axis as far as 30 cm. and varied in depth from 5 mm. to 5 cm. All of the laterals were slender and bore almost no branches. Thus the root-system was very meagerly developed.

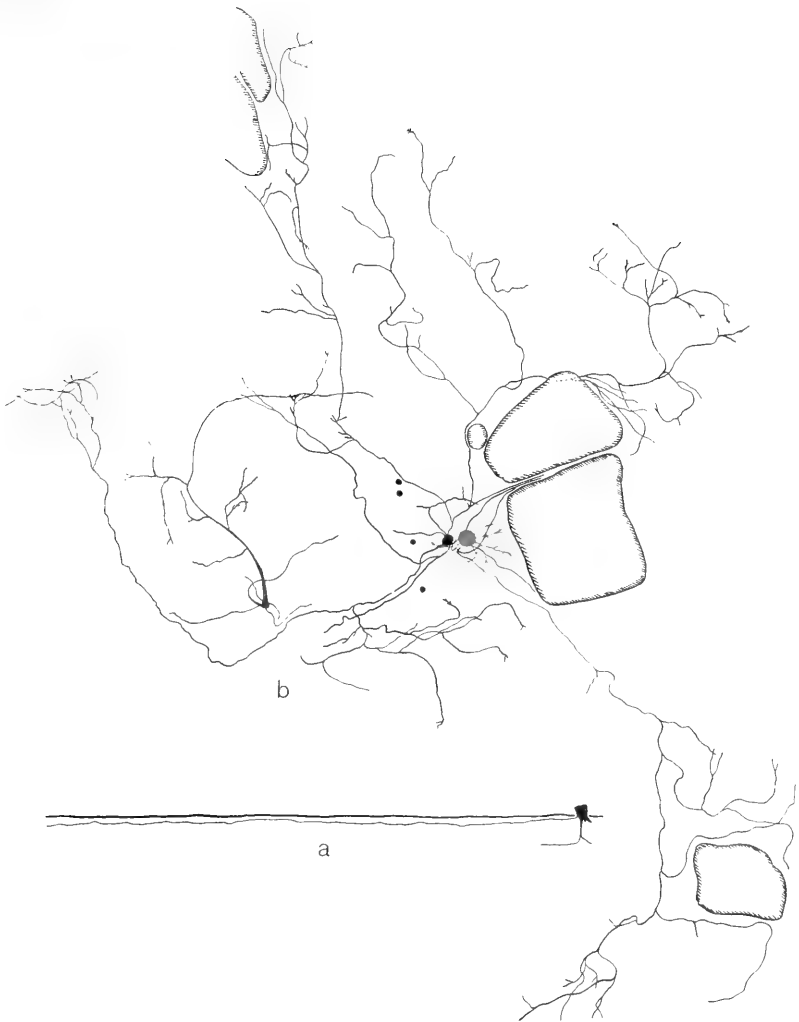
The specimen which was growing apart from other plants was 50 cm. high, of a compact growth-habit, and was much branched. The root-system of this plant may be briefly described as follows. There was no well-defined tap root, but there was a brush of slender roots varying much in length. The roots radiated out from 60 cm. to 2.8 meters and the longest was less than 1 cm. in diameter at its base. The depth attained by the longest roots ranged from 4 cm. to 14 cm., with the usual depth between 5 and 8 cm. The roots branched hardly at all.

In contrasting the root-systems of the two specimens it will be seen that that of the protected plant is composed of fewer and shorter roots than that of the unprotected one, and that the roots of the former are also nearer the surface of the soil. In either instance it is probable that the character of the root-system, at least as far as regards the number and the length of the roots, is immediately connected with the development of the shoot, and that the character of shoot development and the vertical position of the roots are intimately associated with the protected or unprotected condition of the plant.

OPUNTIA VERSICOLOR.

Opuntia versicolor, one of the cylindro-arborescent forms, is one of the best represented species on Tumamoc Hill, although in no place does it occur in large enough numbers to constitute the dominant plant type. The habitat where the plants studied were growing was in the main similar to that described for *Encelia farinosa*, although it differs in certain details. The upper malpais soil is relatively deep and carries, on its surface and embedded in it, stones and boulders in some abundance. The water conditions are better than where *Encelia* grew, owing to the nearly level character of the ground, the rather deep soil, and also to the fact that the place receives considerable water as superficial run-off and as seepage from higher portions of the hill.

Two specimens of *versicolor* were studied, of which one was young and the other mature. The younger plant was less than 50 cm. high and had few branches. There were two well-defined root types in the plant, namely, those shallowly placed and extending horizontally, and those extending vertically and reaching rather deep. The latter, the anchoring or supporting system primarily, consisted of a tap root, with short and long laterals, which penetrated to a depth of 20 cm. One branch of the tap root attained a depth of 30 cm. The superficial portion of the root-system was



a, Vertical and, b, horizontal extensions of root-system of *Opuntia versicolor*, Tumamoc Hill, views of which are shown in plates 10 and 11. One-fortieth natural size. The root-area of the cactus contained other perennials of which one specimen of *Echinocactus wislizeni*, at the base of the cactus studied, is shown in yellow, one specimen of *Jatropha cardiophylla* in purple, and the tips of the roots of a neighboring *Opuntia discata*, on margin of plate, are in yellow.



Root-habit of *Jatropha cardiophylla*, of which the horizontal extension of the root-system was shown in plate 12.

composed of two laterals which left the main root just beneath the surface of the soil and ran in opposite directions each for about a meter. These roots were little branched and lay within 5 cm. of the surface. In addition to the difference in the position of the two portions of the root-system there was a further difference in size: the deeper part being uniformly of greater diameter than the more shallow horizontal portion.

The older plant whose roots were examined was situated about 10 meters south of the one just described. It was 1 meter high and bore several branches, and although mature was somewhat under the average size for the species. The habit of the plant is shown in plate 10.

In the immediate neighborhood of the cactus, or growing within the reach of its roots, were numerous perennials, *Echinocactus wislizeni*, *Menodora scabra*, *Jatropha cardiophylla*, *Cassia bauhinoides*, *Acacia constricta*, and *Parkinsonia microphylla*. There also were several species of annuals. The position of specimens of *Menodora* and the census of the species within the *versicolor* area are as follows: (1) 50 cm. northeast; (2) 1.4 meters north; (3) 2 meters north; (4) 2.2 meters southwest; (5) 2.6 meters west; (6) 50 cm. south; (7) 60 cm. southwest; (8) 1.5 meters west; (9) 1.6 meters east; (10) 2.1 meters east; (11) 1.2 meters southeast. Of these plants, only one was placed so that the roots of the cactus did not go near it. The situation of *Jatropha* and *Echinocactus* are indicated in plate 12. Of other perennials growing in the area, two specimens of *Cassia* were 2.8 meters southeast and 2.2 meters south respectively, one specimen of *Acacia* was 2.7 meters northwest, and one *Parkinsonia* was 2.2 meters southeast. Among the herbaceous forms *Astragalus nuttallianus*, *Daucus pusillus*, *Brodica capitata*, *Harpagonella palmeri*, and *Hilaria* sp., all of which except *Astragalus* and *Daucus* were in flower at the time the roots of the cactus were examined. No record was to be had of the number or kind of the summer annuals which belonged to the area. In addition to the perennials and annuals, both of summer and of winter, which were growing within reach of the cactus roots, the roots of a neighboring specimen of *Opuntia discata* invaded the area. Thus within a space of little more than 20 square meters there were 16 perennials belonging to 6 genera, and numerous herbaceous forms, of which those appearing in winter belonged to 5 genera. This area was the richest in variety as well as in number of plants, both perennials and annuals, of any observed during the course of this investigation.

The root-system of the older cactus was an extensive one, the leading characters of which are shown in plates 10 and 11 and require little further description. The root-system is composed of a widely extending horizontal portion and a rather deeply penetrating portion. The former system was not seen to attain a depth greater than 5 cm., but the latter reached as deep as 25 cm. The horizontal roots of the first order are slender except at the bases, which, as the plates show, are rather heavy. The laterals branch but little except where they run underneath stones, where, as in

Opuntia discata, they are much branched. Besides the more prominent roots, such as those just referred to, there are filamentous ones which occur in groups and which are usually about 1 cm. long. Such filamentous roots are to be seen throughout the most of the course of the superficial larger laterals.

Growing within the compass of the roots of the cactus, as described in an earlier paragraph, there were several perennials whose position would indicate, if other conditions were favorable, that they competed with the cactus for water. An examination of the roots of these plants indicated that this might be the case in some species, but that it probably was not true in others. *Menodora*, for example, has a tap root which penetrates deep but has little extension of laterals, and the roots of *Parkinsonia* also penetrate the ground more deeply than those of the cactus. These plants, therefore, did not enter into close competition with the cactus.

Of the other aliens, *Echinocactus* would be supposed to have superficial roots which would be placed similarly to the corresponding roots of *versicolor*, but owing to the fact that the specimen was young, the anchoring roots, and not the widely extending ones, were developed, and competition between the two species of cacti had not yet begun. The case was different, however, with the specimen of *Jatropha* and the neighboring *Opuntia discata*. The distal roots of one lateral of the *discata*, as the plate indicates, occupied the same horizon as those of *versicolor*, and were mingled with the roots of the latter cactus. There must have been active competition for water, therefore, between the roots of the two cacti. The root-system of *Jatropha* was of the sort that, had the plant been more fortunately placed, active competition with it must also have occurred.

The root-system of *Jatropha* is entirely superficial and placed fairly close to the surface of the ground. As shown in plates 12 and 13, the root system of the plant was composed of a long and fleshy main root, which ran horizontally, and several shorter roots, some of which were fleshy also. There were also two relatively short fleshy roots which arose from the enlarged shoot-base and ran horizontally. At a point 10 cm. from its base, the main root was 2.5 cm. in diameter. The terminal rootlets of *Jatropha* were placed at about the depth of the small superficial roots of the cactus, and the plant would have competed with the cactus actively had the roots of the two species chanced to occupy the same territory. Thus it seems that despite the large population of the area the roots of *Opuntia versicolor* were in close relation with those of but one alien, and that one with its central axis relatively remote. However, this statement would undoubtedly be modified if consideration were given to the relation of the roots of the cactus and those of the numerous summer and winter annuals that also occupy the area, as the roots of many of them must be in close relation, if not in physical contact, with those of the cactus.

THE BAJADA.

The plants of the bajada which were studied either were peculiar to or characteristic of the bajada although not confined exclusively to that habitat, or, being characteristic of other formations, occurred nevertheless on the bajada where for different reasons they were found most convenient for study. *Covillea tridentata* is found in greatest numbers on this habitat, where it may in places produce almost a pure growth, but the species is to be found on the other areas also and in fact attains its largest development on the flood-plain or close by streamways. *Riddellia cooperi* occurs mainly on the bajada, and *Opuntia arbuscula* and *O. julgida* grow only there. Of other species whose root-systems were examined, *Carnegiea gigantea*, *Fouquieria splendens*, *Franseria deltoidea*, *Krameria canescens*, and *K. glandulosa* are found on Tumamoc Hill also, and occasionally, on the flood-plain save *Fouquieria* which was not seen on the last named formation.

Two species of *Yucca*, an *Agave*, and a *Dasyliirion* from the bajada to the west of the Rincon mountains, about 20 miles east of Tucson, were also studied.

CARNEGIEA GIGANTEA.

The root-systems of several specimens of the sahuaro have been observed, but the study has been carried on mainly on plants from the bajada immediately west of West Wash, and from the flood-plain of the wash itself. The soil conditions comprise very shallow as well as fairly deep surface soils, as a result of which the extreme variability of the roots might be expected. The water relations, also, were very diverse, and probably the temperature conditions as well. However, it should be stated that this cactus not only avoids the habitats where the soils are shallowest, but also the opposite extreme, where they are the deepest; or, briefly, it does not occur as a general rule on the bajada or the flood-plain, but rather on rocky areas, chiefly on the southern, the western, and the eastern exposures.

The bajada habitat is at the eastern end of the long slope which leads away from the main range of the Tucson mountains. The soil at the place where the cactus was studied is of a dark color, closely resembling the malpais of Tumamoc Hill, and is rather thickly strewn with large and small stones. A section of the soil shows the following leading characters: The uppermost soil, about 30 cm. in thickness, is of the adobe-malpais referred to above; beneath the superficial stratum is a thinner one of caliche which rests on bed rock. (See figure to the left, plate 14.) Numerous stones and boulders are embedded both in the adobe and in the caliche layers. The contour of the ground at the place is such that little if any water comes to it by seepage from higher ground, or by superficial run-off, the plants obtaining all of the water supply directly from the rains.

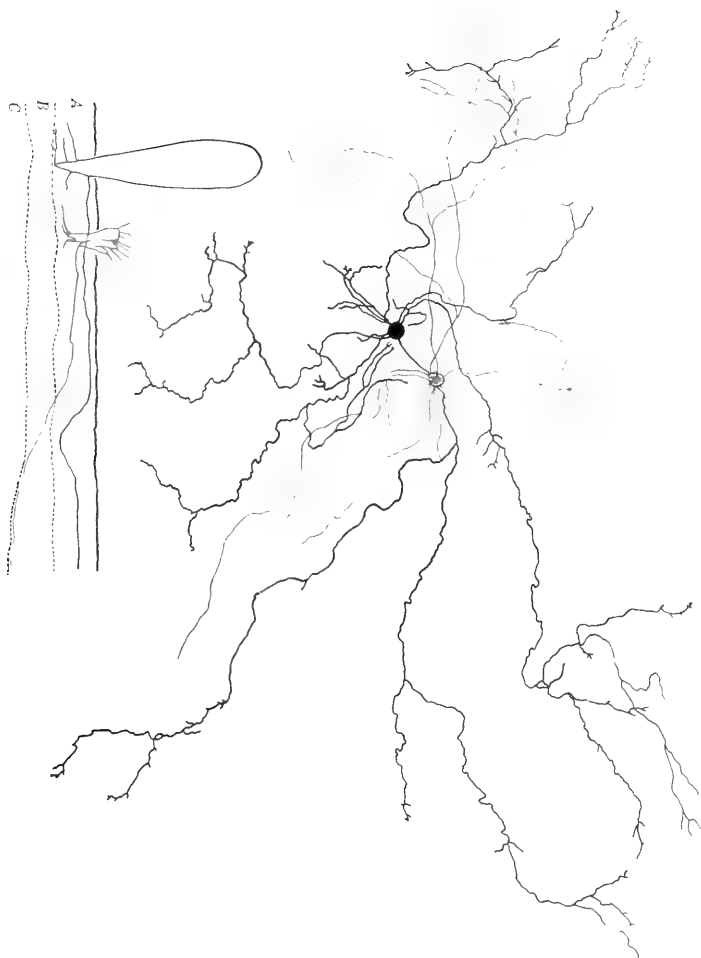
The root-system of the plant is differentiated into an anchoring portion, which is the more deeply placed, and a superficial portion, which is pre-eminently the part engaged in absorption, although it has other functions.

Of the specimens of sahuaro studied, the first to be described was a healthy and very vigorous plant 1.2 meters high and 35 cm. in diameter at the largest part. The anchoring system consisted of a stout tap root which went straight down to a depth of 30 cm., or to the caliche, and a few laterals, of which one ran horizontally about 25 cm. The superficial system arose from the main root close to the surface of the ground and was composed of about 6 main laterals which radiated from the main axis so as to divide fairly equally the available area between them. They extended from 1.5 to 5 meters from the central axis, and branched but little. As an instance of the latter characteristic it may be stated that four of the laterals did not give off branches during 1.5 meters of their course, and one root, which branched freely at the tip and was 3 meters long, bore only 4 branches. The superficial roots end in a tuft of fine rootlets, nearly all of which die with the advent of the drier season, and groups of delicate rootlets are borne by the superficial roots the greater part of their length. It is probable that these fine rootlets are produced each year with the coming on of favorable conditions of growth and water absorption, as in *Franseria deltoidea* and other desert plants. The plant is thus enabled to exploit thoroughly more of the root-area than would otherwise be possible.

The superficial portions of the root-system penetrated the ground to a depth which was fairly uniform, although in no case very great. For example, one root left the main root at the surface of the ground, and both it and its three main branches, with little deviation, ran 7 cm. from the surface. Another root ran from 3 to 40 cm. from the surface, but gave off a branch which went straight down to a depth of 17 cm. Others of the superficial system varied between 5 and 15 cm. in depth, and one dipped under a large boulder, whose lower surface was 30 cm. from the general ground-level, after which it ascended to about the depth characteristic of the older parts.

Where the larger of the superficial roots left the tap root they were relatively heavy, but they tapered rapidly until a small diameter was reached which was maintained with little change for a long distance. A few measurements will show the point. One of the larger laterals was 1.6 cm. in diameter at its base; another was 7 mm. in diameter; another root, 45 cm. from its base, was 1 cm. in diameter, and it extended 2.5 meters beyond the point of measurement. Roots not above 50 cm. long were about 3 mm. in diameter at the base. A root 5.5. meters in length was 2 cm. in diameter 30 cm. from its base.

In a sahuaro of the size of the one under discussion, it is probable, therefore, that the tap root constitutes the main support by which the plant successfully withstands the pressure of the wind, which at times is heavy, and that the superficial roots function mainly as absorbing organs. With the growth of the plant, however, the need of anchorage is greatly increased and the tap root no longer suffices as the sole stay, so that the laterals assume the added rôle of mechanical supports and become much changed in size, perhaps in other regards also, to meet the new demands. This develop-



Horizontal and vertical extensions of root-systems of *Carnegiea gigantea*, *Covillea tridentata*, and *Parkinsonia microphylla*, from the bajada west of West Wash, December, 1906. The *Carnegiea* is represented by black, the *Covillea* by yellow, and the *Parkinsonia* by green.





B



C



A

A. Anchoring roots and bases of some lateral roots of *Carnegiea gigantea*, 6.8 m. high, from the bajada near West Wash.

B. Tap-root and secondary roots making up the anchoring system and the bases of some of the superficial roots of a specimen of *Carnegiea*, 1.2 m. high, from same habitat as the cactus shown in A.

C. Tap-root and bases of laterals of *Parkinsonia microphylla* which was growing near *Carnegiea* shown in B, and which appears in plate 14.

mental modification can be shown by the main characters of the root-system of a larger specimen. A sahuaro 6.8 meters high and bearing 4 branches, from 40 cm. to 1 meter in length, and growing in a situation apparently similar to that of the cactus above described, had a relatively heavy root-system. The roots of the anchoring system were sharply differentiated from the superficial roots and were composed of a cluster of 10 main roots with their branches which ran directly downward about 77 cm., and ended abruptly on reaching the bed rock. Of the superficial system three leading laterals were uncovered, one of which ran southeast over 9.7 meters, one northeast over 4 meters, and one west over 4.5 meters. All of these roots were very heavy, especially at the base, as plate 15 indicates. In this, and in other specimens examined, it is clear that the increased diameter of the superficial roots is connected with the large size of the sub-aerial portion of the plant and its need of better support than would be afforded by the "anchoring" roots alone. A proof of the importance of the laterals as mechanical supports of the stem is often afforded by the spectacle of uprooted plants, whose laterals have become diseased and no longer function as efficient props or stays.

A specimen of sahuaro growing on the flood-plain of West Wash was also examined. The root-system did not differ materially from either of those above described; that is, there was an anchoring portion and a superficial portion, which in the plant seen (which was less than 2 meters high) were not as yet sharply differentiated either in function or in position. The main root did not penetrate deep, although the soil was somewhat deeper than at either of the other habitats mentioned. This was the leading point of interest: the root-system of the sahuaro is essentially superficial even if the soil conditions are such as to permit deep penetration.

From the brief discussion of the root-system of the sahuaro it will be seen that there is no sharp distinction in function between the superficial roots and the anchoring roots, as is to be found in *Echinocactus* especially, but that as the plant increases in size the superficial system gradually assumes the rôle of supporting the sub-aerial portion in addition to its chief rôle in the absorption of water.

In the immediate vicinity of the cacti growing on the bajada were also the following perennials: *Echinocereus fendleri*, *Covillea tridentata*, *Encelia farinosa*, *Krameria canescens*, *Parkinsonia microphylla*, and some other plants, especially species of cacti.

The relation of the roots of sahuaro to those of other perennials was examined closely only in connection with the study of the sahuaro which was 1.2 meters high. In this case one specimen of *Parkinsonia* and one of *Covillea* were situated within the proper root-area of the sahuaro, as plate 14 shows. The *Parkinsonia* was growing 1.3 meters distant from the stem of sahuaro. The following were the leading points in the character of its roots. There was a tap root which went straight down to the caliche, where it terminated

abruptly. Several slender roots left the main root between 5 and 10 cm. from the surface of the ground and either extended fairly horizontally or dipped downward to a depth of 45 cm. and even deeper, where they penetrated the caliche. The root-system of *Covillea*, so far as its position was concerned, was similar to that of *Parkinsonia*; that is, it extended downward through the malpais and the caliche, and ran on the surface of the bed rock.

The relation of the root-systems of the three species is shown graphically in the cuts of the horizontal and vertical extension. It will be seen that, although growing in close proximity to one another (the *Covillea* was only 50 cm. from the cactus), the roots are not in physical contact anywhere, so that competition for water in the soil is probably not keen in this instance, notwithstanding the proximity of the plants.

COVILLEA TRIDENTATA.

Perhaps the most widely distributed perennial in the vicinity of the Desert Laboratory is *Covillea tridentata*, which occurs not only on the bajada, where it is the most characteristic shrub, but on the flood-plain of the Santa Cruz river and West Wash, and on Tumamoc Hill. It attains its most luxuriant growth on the flood-plain, or elsewhere where the soil is deep and the water conditions relatively favorable. The specimens specially studied were situated on the flood-plain of West Wash and on the bajada at the northern base of Tumamoc Hill. In these locations the extremes of soil conditions, as far as concerns its depth, were met, together with the greatest differences in water relations to be found in the four habitats under consideration.

The upper soil at the bajada habitat is of adobe clay, with an admixture of rock fragments and larger stones, about 20 cm. in thickness, below which is a layer of rotten caliche, also about 20 cm. thick, and the latter is underlaid by hard caliche of undetermined depth. A section of similar soil conditions, made from a photograph of a cut not far from the habitat in question, is shown in plate 1, and illustrates the conditions which obtain here.

The larger plants of the vicinity were all of the genus *Covillea*, of which those nearest the specimen were 1.5 meters northwest, 2.6 meters southwest, and 3.1 meters south. The roots of each of these plants, and probably the roots of others also, invaded the root-area of the specimen specially studied.

The *Covillea* examined was 95 cm. high and was composed of numerous branches. It was a typical and vigorous plant. The leading characters of its root-system were found to be as follows: A main root went down to the hard caliche, about 35 cm., where it forked. One branch was traced about 3 meters northwest and lay from 35 to 53 cm. beneath the surface of the ground. The other branch was followed about 1 meter and lay from 35 to 45 cm. deep. These were the longest roots of the plant and extended to pockets in the hard caliche.

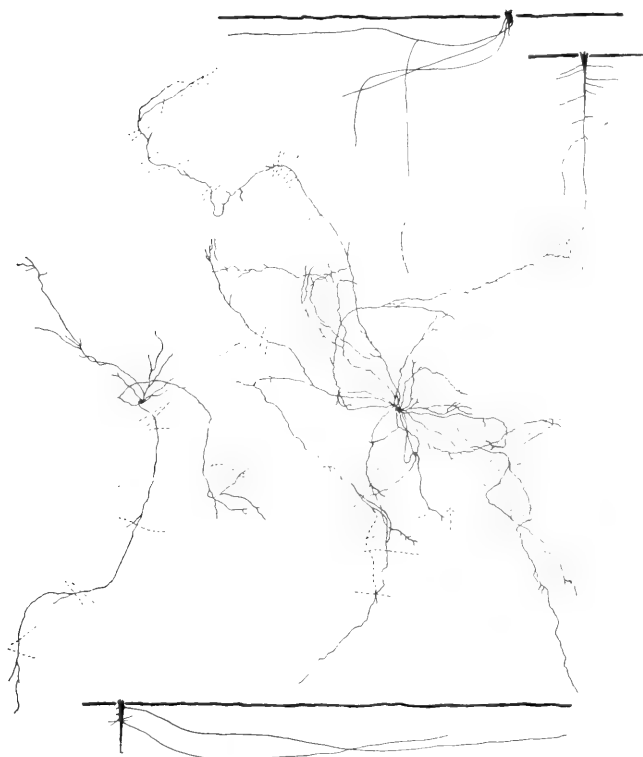


FIG. 6. Root systems of *Cotillea tridentata*, from various locations on the domain of the Desert Laboratory.

a and *b*, Horizontal extensions of root system of one plant, separated for sake of clarity. Dotted lines indicate the intruding roots of neighboring *Covilleas* encountered on the same level, or nearly so, as the roots of the plant studied.

c, Vertical extension of bajada-grown plant.

d and *e*, Vertical extensions of root-systems of two plants from the flood-plain of West Wash. Entire length of laterals in *c* is not shown.

About 10 large and numerous small laterals were given off from the main root within 15 cm. of the surface of the ground. These roots were from 5 mm. to 1.1 cm. in diameter at the base, and the longest extended as far as 4 meters from the central root axis. This, the longest lateral, branched from the main root 3 cm. from the surface, and lay 21, 39, 31, and 28 cm. from the surface of the ground at various distances from its base. The position of this root with relation to the surface is fairly illustrative of all of the rest. The mutual relations of the principal roots,

together with vertical extension of two plants from West Wash, are shown in fig. 6. The general character of the bases and the number of smaller laterals are adequately shown in plate 16. Besides the larger branches of the main laterals, which, as fig. 6 shows, were relatively few, there were groups of filamentous roots occurring along their course as in *Franseria* and other plants. Although not specially studied in *Covillea*, these rootlets were of limited growth, serving the plant for a short period only, as in the species mentioned.

The soil of the flood-plain by West Wash, where the other specimen of *Covillea* studied was growing, was of adobe and sand to a depth exceeding 2.1 meters. The perennials of the habitat, both as regards kinds and numbers, were more numerous than on the bajada. Near the specimen of *Covillea* from the flood-plain, whose roots were examined, were *Acacia greggii*, *Lycium andersonii*, *Parkinsonia torreyana*, *Prosopis velutina*, and other forms, mainly shrubs.

The *Covillea* studied by West Wash was 1.65 meters high, or somewhat larger than the bajada specimen examined, and, from the size and number of the leaves and the character of the branching, it gave evidence of having a better water supply than the bajada-grown plants. An examination of the root-system of this plant showed that in certain ways it was very different from that of the plant from the bajada. The points of difference appear well in comparing the vertical extension of the roots of the two plants, as shown in the figures. The tap root was traced to its end at a depth of 30 cm., although in another specimen growing near by the tap root went down 1.7 meters, indicating that in the specimen under consideration some calamity had brought about the untimely end of the main root. The laterals were, in part, given off from the bases of the shoots and, after leaving the main plant axis, had little uniformity in position. Some lay 20 to 45 cm. from the surface, others were still deeper. Such roots took a more or less horizontal position. From these laterals branches were given off, one of which went straight downward as far as 2.1 meters.

Although the laterals of the first (?) order ran fairly horizontally as a whole, they were not as long as the corresponding roots of the bajada-grown plant; the radius included within the root-area did not exceed 2.2 meters, as opposed to nearly twice this figure in the other form studied. In addition to the larger laterals just described, many smaller ones arose from the bases of the shoots or from the bases of the larger laterals. As plate 16 shows, there were in the plant from the flood-plain many more small adventitious roots than in the plant from the bajada. The laterals bore relatively few branches.

The root-system of the specimen of *Covillea* from the flood-plain may be characterized, therefore, as having a deeply penetrating main root and laterals which run in a fairly horizontal direction, although they may lie as deep as 53 cm. and may give off branches that go straight downward.

The number of small laterals at the bases of the plant is especially large. The roots are mainly either horizontal or vertical, without being at any intermediate angle, a character so strong in the root-system of *Prosopis*, to be described later, and of so wide occurrence among the larger plants, where the soil conditions are favorable, that it forms one of the most striking of the general root characters of desert plants.

The lateral extension of the roots of the *Covillea* from the flood-plain is considerably less than that of the plant from the bajada. Those of the latter reach out over 4 meters, while the roots of the former, as mentioned above, extend hardly half as far. The root-area, or the area included within the reach of the roots of the bajada-grown *Covillea*, was about 50 square meters, while that of the plant from the flood-plain was only one-fourth as much. These differences make it imperative that fewer plants occupy a given space on the bajada than on the flood-plain. It is of interest, however, to note that the mass of earth compassed by the root-system of the two specimens of *Covillea* was approximately equal.

With the characteristic differences in root development and root position of the bajada and flood-plain plants are associated differences in the relations of these plants to their neighbors. In excavating the roots of the specimen from the flood-plain no roots of other woody plants were encountered within the root-area of the plant studied. But the condition of the bajada-grown *Covillea* was quite otherwise. No fewer than 60 roots of neighboring *Covilleas* were encountered at the same level, and frequently in physical contact with the roots of the plant studied, and very many more were met between the levels of these roots and the surface of the ground. Therefore the competition between neighboring *Covilleas* on the bajada, for soil water, is presumably keen, while, on the other hand, competition between neighboring *Covilleas* on the flood-plain, for soil water, is at best indirect, and may be so slight as to be negligible.

FOUQUIERIA SPLENDENS.

Fouquieria occurs most abundantly on the northern slope of Tumamoc Hill, on its lower drainage slope, or the upper portion of the bajada, and on the bajada near West Wash. It was not found on the flood-plain of West Wash or of the Santa Cruz, that is, in other words, the species in the vicinity of the Desert Laboratory does not grow where the soil has considerable depth, so that the "normal" behavior of its roots is not known.

The soil conditions where the specimens of *Fouquieria* specially studied were growing, the bajada to the north of Tumamoc Hill, are nearly the same as those of the *Covillea* habitat above described, except that the superficial adobe clay is somewhat thicker and there may be a greater admixture of small stones. The superficial soil is underlaid by rotten caliche and the latter by hard caliche, as in the habitat referred to.

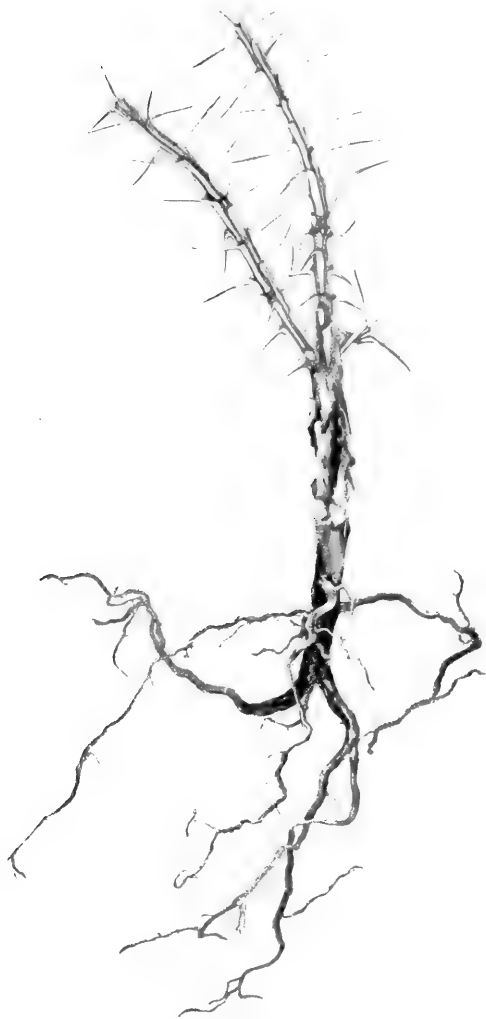


FIG. 7. Root and shoot habit of *Loupina splendens*.

The other woody plants growing near *Fouquieria* were mainly *Covillea tridentata*, and an occasional specimen of *Parkinsonia microphylla*.

Two specimens of *Fouquieria* were specially studied, of which one was young and the other mature. The younger plant had a shoot 24 cm. high, which had a central main axis and two branches 3 cm. and 15 cm. long. The habit of the plant is well shown in fig. 7.

The roots of *Fouquieria splendens* are coarse and brittle, and bear relatively few branches. The tap root was large and penetrated the ground 8 cm., where it forked, one branch extending horizontally 13 cm. and the other going down 18 cm. before branching. Each of the main forks of the main root branched only two or three times.

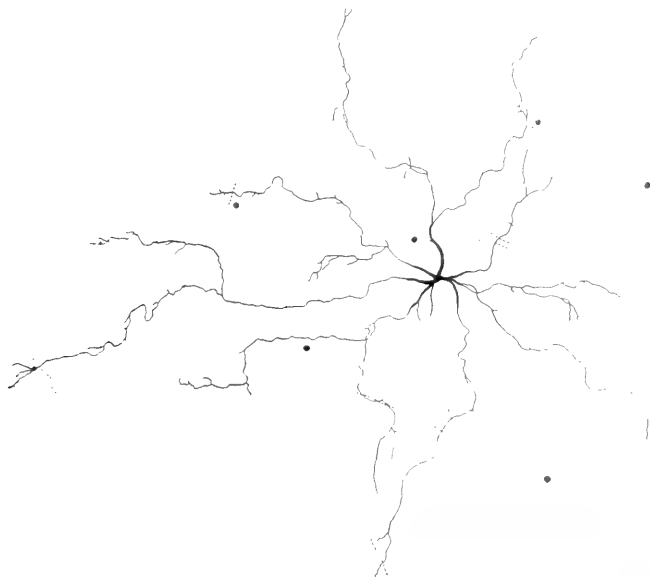


FIG. 8.—Horizontal extension of the root system of *Fouquieria splendens* from the barada at the north base of Tumamoc Hill. Dots represent position of *Covillea tridentata* which occurred within the root area of *Fouquieria*, and dotted lines such roots of *Covillea* as were found on the same horizon as the *Fouquieria* roots.

Above the forking of the tap root, about 3 to 4 cm. from the surface of the ground, two laterals arose, which, as far as traced, ran in a nearly horizontal direction. One of these bore 3 branches and was over 22 cm. long. At the base the laterals were less than 1 cm. in diameter, and, where broken off, they were slightly more than 1 mm. in diameter. Thus the roots of *Fouquieria* are so heavy that they may perhaps be termed fleshy.

A character of the smaller roots of the plant was the bearing of groups of filamentous, adventitious rootlets about 1 cm. in length. At the time the study was made, January, these rootlets were dead.

The only roots of neighboring plants which intruded on the root-area of *Fouquieria* were two of *Parkinsonia microphylla*, which lay 3 and 15 cm. from the surface of the ground.

The larger specimen of *Fouquieria* examined was 1.75 meters high and bore numerous long branches. In February, when the study was made, the plant was without leaves.

The following were the main characters of the root-system of the larger plant. A tap root penetrated the ground until it met a mass of caliche which lay immediately below the base of the plant. The depth attained by the root was about 15 cm. Five laterals arose immediately below the surface of the ground; they were 5 cm., more or less, in diameter, at the base. It is a characteristic of *Fouquieria* that the roots, although relatively heavy at the base, taper rapidly; for example, one 5 cm. in diameter at its base had a diameter of 1.1 cm. about 50 cm. away. After the diameter of 1.0 cm. is reached, the root maintains this very closely for a considerable distance.

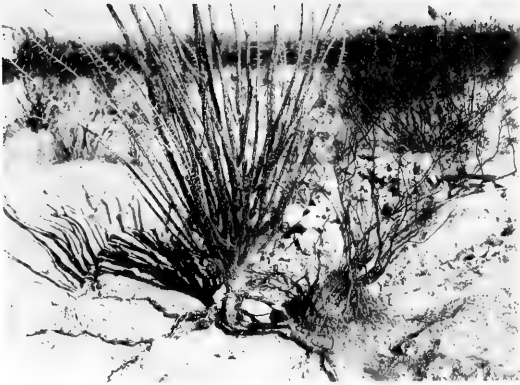
The depth usually attained by the laterals may be illustrated by a few examples. Taking a typical root, we find that while it leaves the tap root immediately beneath the surface of the ground, at a distance of 40 cm. it is 25 cm. deep; at 50 cm. it is 16 cm. deep; at a distance of 1 meter it is 23 cm. beneath the surface; and at a point 1.75 meters from the main axis, where it is 2 mm. in diameter, the root is 21 cm. deep. A branch of this root was traced downward to a depth of 37.5 cm., but at that point it was no longer living.

Groups of filamentous roots were not seen in the larger specimen. There were several specimens of *Covillea* in the area included within the scope of the roots of *Fouquieria*. One was about 25 cm. distant and its roots occupied much the same area as those of the *Fouquieria*, but they were deeper and, although the roots of *Fouquieria* were exposed with great care, only four instances were noted where roots of the neighboring *Covilleas* were found in the same horizon as those of the plant examined. Competition between the two species of shrubs, therefore, is probably not very active.

FRANSERIA DELTOIDEA.

Although perhaps as widely distributed locally as *Covillea*, the characteristic habitat of *Franseria deltoidea* on the domain of the Desert Laboratory is the bajada, just to the west of West Wash. In this habitat the population of *Franseria* for any given area is greater than that of any other shrub in its characteristic habitat in this vicinity. In fact, the species at the place in question fairly completely conceals the ground.

In the neighborhood of the *Franseria* examined, the following woody plants also occurred: *Covillea tridentata*, *Krameria canescens*, *Krameria*



C



A



B

A. *Covillea tridentata* from bajada at north base of Tumamoc Hill. Horizontal and vertical extensions of roots of this plant shown in fig. 6.

B. *Covillea* from flood-plain near West Wash, showing the large number of slender adventitious roots springing from upper part of roots and long tap-root, of which only a portion appears.

C. *Fouquieria splendens* from bajada near where *Covillea* shown in A was growing. Horizontal extension of roots of this plant shown in fig. 8.



a. *Franseria deltoidea* from flood-plain, February, 1909, showing part of tap-root. b. Lateral of the first order bearing filamentous roots in groups, which, at time photograph was made, were no longer functional. c. *Krameria canescens* from flood-plain near West Wash, February, 1909, showing essential superficial placing of roots. d. *Lycium andersonii* from near West Wash.

parvifolia, *Opuntia discata*, *Opuntia versicolor*, other species of *Opuntia*, and *Parkinsonia microphylla*.

The soil of the habitat is much like that of the portion of the bajada at the northern base of Tumamoc Hill, where *Covillea* was studied, adobe clay constituting the upper soil to about 20 cm. depth, under which is rotten caliche, the latter resting on hard caliche. The situation is probably the most severely arid of any habitat studied.

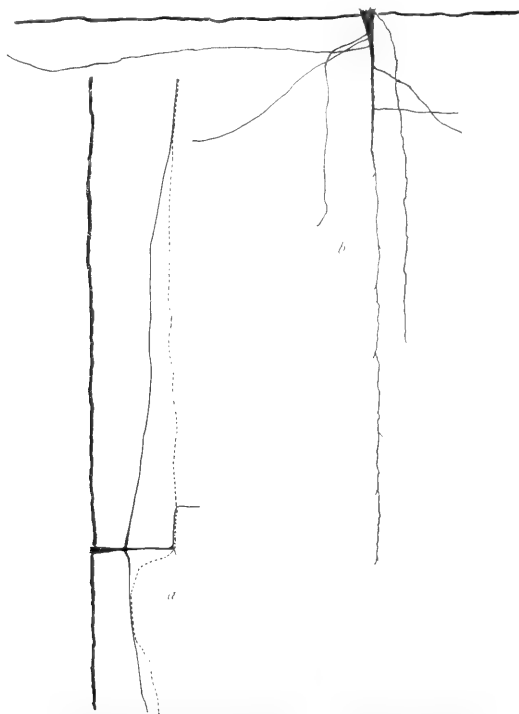


FIG. 9.—Vertical extension of the root system of *Franeria deltoidea* from different habitats. *a*, root-system of a bajada-grown plant. Upper surface of caliche hardpan indicated by dotted line. *b*, root system of a plant from the flood-plain by West Wash to show depth to which tap root penetrated, 1.8 m.

Two specimens of *Franeria* from the bajada habitat and one from the flood-plain of West Wash were examined. Therefore, as regards soil conditions and water relations, the two habitats present the greatest contrast to be found on the domain.

The shoot of the larger specimen of *Franseria* from the bajada was 50 cm. high and was composed of numerous slender branches. The species is well covered with leaves, so that, compared with most of the local shrubs, it has a large transpiration surface. The leading characters of the shoot are shown, but rather imperfectly, in plate 17.

The root-system consisted of a tap root bearing several laterals and of numerous adventitious roots originating from the bases of the shoot. The tap root went straight down 29 cm., where it forked, one root penetrating the rotten caliche to a depth of 38 cm. from the surface of the ground. About 12 cm. from the surface, the main root gave off several laterals which reached as far as 1.6 meters from the main axis and lay 12 to 30 cm. deep. Thus the roots are confined to soil above the hard caliche. The roots are dark brown, very brittle, and are ridged longitudinally with cork. They are always slender; the largest root, the tap root, 2 cm. from the crown, was only 8 mm. in diameter.

The younger specimen of *Franseria* studied was 3 meters distant. Its shoot was 14 cm. high and composed of four separate branches. Upon digging, it was learned that the surface soil was relatively deep, and that over a small area the hard caliche had given place to adobe, a condition similar to that shown in plate 1.

A main root of the young plant was traced down 1 meter, and evidently penetrated farther. The main root gave off one lateral 3 cm. long, another less than 10 cm. long, and a third which, shortly after leaving the main root, penetrated to a depth of 60 cm. The vertical extension of the root-system is shown in fig. 9. No roots of neighboring plants were seen in the root-areas of this plant.

For comparative purposes, the roots of a *Franseria* growing on the flood-plain not far to the east of the proper habitat of the species were also examined. The soil is a sandy loam, sand and adobe, of a depth exceeding 2 meters. No excavations have been made below this level. The place is occasionally flooded and the water-table is variable as to its depth, but probably the ground at a depth reached by roots is moist all of the year.

The leading woody plants of the flood plain in the immediate neighborhood of the specimen of *Franseria* studied were *Acacia greggii*, *Covillea tridentata*, *Ephedra trifurca*, *Lycium andersonii*, *Parkinsonia torreyana*, and *Prosopis velutina*. The flood-plain is the characteristic habitat of all of these except *Covillea* and *Franseria*.

The leading points of interest in the root-system of *Franseria* from the flood-plain were as follows: A tap root which went straight down to a depth of 1.8 meters was only 5 mm. in diameter at its crown. For the most part the laterals arose within 15 cm. of the surface, and one of these extended 1.4 meters in a fairly horizontal direction (see fig. 9); another took a downward course at an angle approximating 45° until a depth of 45 cm. was reached, after which it was approximately horizontal; a third root, after

reaching out about 20 cm. from its place of origin, turned directly downward to a depth of 78 cm.

Besides roots arising on the main root, and of primary origin, there were over 50 slender adventitious roots, about 3 mm. in diameter, which arose from the shoot bases and from the crown of the main root. For the most part, these roots took a horizontal direction, but one of them ran downward and was traced to its end at a depth of 1.3 meters. Such laterals as lay about 15 cm. from the surface of the ground bore groups of filamentous roots (plate 17), which were dead when the study was made. The rootlets were 2 cm., more or less, in length and were six or so in a group; the groups were from 5 mm. to 2 cm. apart.

Filamentous roots were seen also in the bajada-grown plants, and in others from Tumamoc Hill. In January, 1910, after the soil had been moistened some days by rains, freshly formed rootlets were seen on many roots of *Franseria*. These roots, therefore, are formed in winter, and probably in summer as well, and are very short-lived. No study has yet been made of the conditions under which the rootlets are developed, their period of activity, or whether, if conditions remained constantly favorable, they would be active indefinitely.

KRAMERIA CANESCENS.

One of the most generally distributed species in the vicinity of the Desert Laboratory is *Krameria canescens*, occurring as it does on each of the physiographic areas treated in the present paper. It attains its largest size where the water relations are most favorable, as on the flood-plain of the wash, on the bajada near it, and on Tumamoc Hill. As has been shown elsewhere* *Krameria* is an habitual parasite and this is probably the leading cause for the wide distribution noted.

The first specimen of *Krameria*, of which the root-system was examined, was an isolated plant on the flood-plain of West Wash. The soil conditions of the place have already been noted; in brief they were: a sandy clay over 2 meters deep and relatively favorable water relations, as evidenced by the occurrence of the most hygrophilous of the native species.

The specimen studied had a much-branched shoot, about 60 cm. high, which was leafless in February. The general character of the shoot is shown in plate 17. The root-system consisted of a short tap root, no longer living, and six, or more, laterals which extended as far as 2 meters from the main axis (fig. 10). Besides the main laterals there were about an equal number of more slender ones, less than 2 mm. in diameter and about 20 cm. long, which ran in a horizontal direction. The longer roots, from 4 mm. to 1 cm. in diameter at the base, lay from 13 to 18 cm. beneath the surface. In addition to these roots, several were dead and decaying. A very striking

*Conditions of Parasitism in Plants, by D. T. MacDougal and W. A. Cannon. Publication No. 120, Carnegie Institution of Washington, 1910.

feature of the root system of the plant was the almost total absence of branches, nor were the filamentous roots which occur in *Franseria*, *Encelia*, and in other perennials, observed in *Krameria*.



FIG. 10 —Root system of *Krameria canescens*.
The large laterals *d, d, d* were dead.

Only two foreign roots (shown as dotted lines, fig. 10) of an unknown species were encountered during the excavation of roots of *Krameria*.

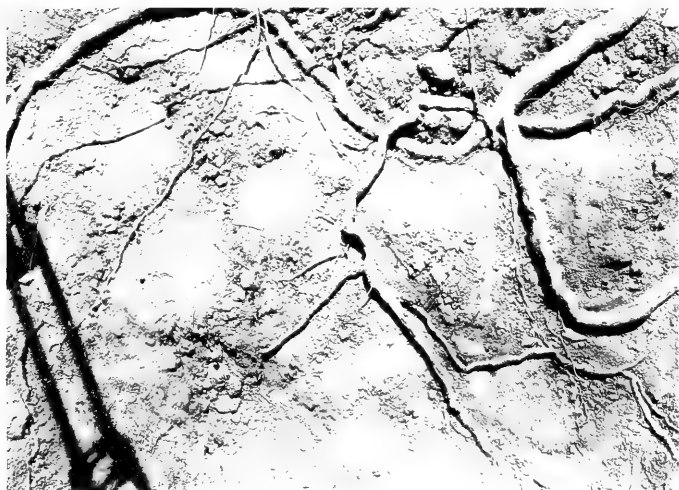
The presence of so many dead roots made it advisable to examine another specimen of equal age in order that a perfectly "normal" root-system should be described. Accordingly, another plant, also growing on the flood-plain, was selected for study. The results of the second excavation substantiated those of

the first, namely, that the tap root had reached a rather large size before dying, that there were many dead laterals, and that those yet living were near the surface, although the soil at the place was of considerable depth. In examining another plant, under circumstances which allowed the observation of the relation of the roots of the species to those of its neighbors, the fact of the parasitic habit of the plant was revealed.

After the discovery of parasitism in *Krameria* a very large number of specimens growing under widely different conditions were examined and root attachment to the following plants was demonstrated: *Acacia constricta*, *Covillea tridentata*, *Encelia farinosa*, *Ephedra trifurca*, *Franseria deltoidea*, *Lycium andersonii*, *Menodora scabra*, *Opuntia* sp., *Parkinsonia microphylla*, *Prosopis velutina*, and *Zizyphus parryi*. Subsequently parasitism of the plant on *Parkinsonia aculeata*, a species indigenous within 75 miles of Tucson, was induced in cultures.

The attachment to the host is usually by means of small roots and only rarely does one find the association of old roots of host and parasite. Thus the connection is probably made during the growing seasons, and persists if the conditions continue favorable during the subsequent dry periods.

The hosts already found are only trees and shrubs, and it is not at present known whether the parasite is strictly limited to such, or whether it may not derive temporary sustenance from annuals, some of which are very resistant to drought and endure for considerable time after the rainy seasons have closed.



Bird's-eye view of superficial roots of *Opuntia arbuscula*, from bajada, a mile east of the Santa Cruz, showing their fleshy character.

The root-system of the seedling has a pronounced tap root with relatively few and short laterals which do not bear haustoria if the plant is growing alone, but develop them if the roots of another form, such as *Parkinsonia aculeata*, are in close relation with its own. The root-system of the seedling, however, differs from that of autotrophic plants in the fact that it does not form root-hairs. As the plant develops, the tap root continues to be a leading feature, since in the old plants remains of the tap root have always been encountered. When or why this organ dies is not known. In the mature plant the superficial laterals become the most prominent feature of the root-system and include a large area within their compass.

In associating character of root-system with habit in any species, it has repeatedly been shown above that an autotrophic plant without water reserve is always provided with a deeply placed root-system, or as deeply as the soil permits, but that a plant with water-storage facility has a root-system which lies near the surface of the soil. In *Krameria* the roots are shallow, although the form is not a water-storing species—suggestive of unusual life-habit of the species.

OPUNTIA ARBUSCULA.

Among the species of cacti limited to or characteristic of the bajada are *Opuntia arbuscula* and *O. fulgida*, though the latter only occurs on the domain of the Desert Laboratory. The habit of the two arborescent cylindrical-opuntias is unlike. The species *arbuscula* occurs in groups of few individuals usually, of common descent, as will be shown, while *fulgida* at its best forms fairly dense growths, to the exclusion of other woody plants.

The specimen of *Opuntia arbuscula* chiefly studied was one of a small group growing on the bajada about a mile east of the Santa Cruz river, April, 1907. The upper soil is of adobe clay to a thickness approximating 20 cm. with a layer of rotten caliche beneath, of variable thickness, which rests on the hardpan.

In the vicinity of the cactus were *Acacia constricta*, *Bigelovia hartwegii*, *Covillea tridentata*, *Krameria canescens*, *Opuntia fulgida*, and *O. spinosior*. Of these species, 3 plants of *Covillea* and one of *Bigelovia* occurred within the root-area of the cactus. The *Covilleas* were 20 cm. west, 70 cm. south, and 2 meters northeast, all mature shrubs of large size.

The *Opuntia* whose roots were examined was a much branched and old plant about a meter high, apparently in perfect health and in every way a normal specimen. Its root-system was composed of an anchoring portion and a widely reaching horizontal portion (fig. 11).

The anchoring roots were not specially studied. The horizontal system consisted of 4 main members arising from the crown of the tap root just below the surface of the ground. They radiated from the main axis in such fashion that the ground around the base of the plant was fairly equally divided between them. These main laterals, as distinguished from the cor-

responding roots of all other opuntias seen, branched repeatedly throughout their course, in places forming a network closely covering the ground. The laterals extended for about 3 meters and lay so near the surface of the ground that the tips could be lifted out with a walking-stick, and they could be torn out of the ground their entire length. More exactly stated, the roots lie from 2 cm., and even less, to 8 cm. beneath the surface.



FIG. 11. Horizontal extension of root system of *Opuntia arbuscula*: Black dots indicate position of *Cylindropuntia tridentata* which had invaded the root area of the cactus.

As compared with the roots of other opuntias, those of *arbuscula* are large (plate 18). This will be appreciated from the following measurements. A meter from its base one of the larger roots had a diameter of 2.5 cm., 2 meters distant it was 2 cm., 3 meters distant it was 1.5 cm. The tips of these roots, excluding the most recent growth, were not less than 1 cm. in diameter. From the size and tuber-like appearance of the roots it was concluded that they function as water-storing organs. This conclusion was strengthened by the observation that inside of 48 hours after the roots of this plant were removed from the soil they were rapidly losing their plump aspect and had begun to shrivel strikingly. A noteworthy peculiarity of the larger roots was their frequent abrupt ending through the death of the more distal portion.

The fleshy roots of *arbuscula*, in addition to functioning as water-storing organs, a rare root-character among mature opuntias, further serve as propagating organs, and to this function the occurrence of the species in masses is due. The procedure, in brief, is this. One or more shoots may arise from a single lateral while the latter retains its connection with the parent,

The shoots put down roots, the connection with the parent plant is probably early cut off (when was not learned), and the daughter plant is independent. The result is that *arbuscula* frequently forms clumps several meters in diameter, to the total exclusion of other species.

From the previous description of the root-system of *Covillea* it is perhaps hardly necessary to point out that the roots of this species growing within the root-area of the cactus are much deeper than the roots of the latter plant, and hence are not in active competition with the cactus roots for their water supply.

OPUNTIA FULGIDA.

On the domain of the Desert Laboratory, *Opuntia fulgida* occurs only on the bajada near West Wash, where in places it forms fairly dense growths constituting the most prevalent species. This is an unusual habit for any cactus in this vicinity, since usually the cacti are either scattered in an apparently chance fashion, unless controlled by such external factors as temperature or other physical environmental conditions, or at best but few individuals of a species are congregated.

The soil in the habitat of *fulgida* is a sandy clay with an admixture of rocks of various sizes which appeared to be in stages of active disintegration. No caliche was found to a depth of 60 cm. The habitat, therefore, presents certain striking differences from that of *Fraseria*, not far distant.

In the immediate vicinity of the *Opuntia* studied were *Acacia constricta*, *Echinococcus jendleri*, *Covillea tridentata*, *Opuntia fulgida*, *Opuntia versicolor*, *Parkinsonia microphylla*, and *Riddellia cooperi*, and of these plants only one example of *Acacia* and two of *Riddellia* occurred within the root-area of the cactus. Since, as will appear directly, the roots of *fulgida* extended as far as 3 meters from the main plant axis, the perennial population of the habitat is relatively light.

The specimen selected for study was growing somewhat apart from the typical *fulgida* habitat, but the plant appeared to represent thoroughly the typical and mature species. The root-system, like that of *Opuntia versicolor*, has a somewhat deeply penetrating portion, the anchoring roots, and a widely reaching horizontal portion not far from the surface of the ground. The horizontal and vertical extensions of the root-system are shown in fig. 12.

The anchoring system consisted of about six stout roots which ran down at an acute angle to a depth of 35 cm. Of these the largest was 2.5 cm. at the crown; it tapered rapidly and gave off several branches which ran outward for a distance of 5 to 10 cm. The anchoring roots did not reach hardpan or bed-rock, or other material which might prevent deeper penetration.

The superficial root-system consisted of 6 main laterals, of which 4 ran 3 meters, more or less, in an easterly direction (down-hill), and the others took a fairly well defined up-hill direction. The roots branched but little; for example, one 3 meters long gave off no important branches, and a some-

what larger one branched only twice. The roots of no cactus studied, and in fact no perennial plant except the parasite *Krameria*, branched less than this one.

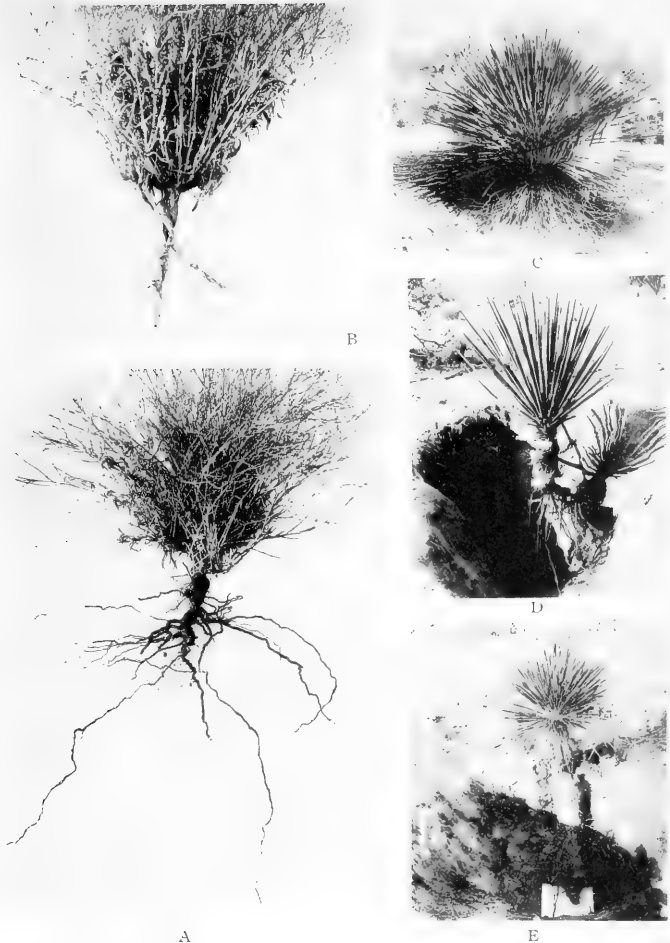
The roots were slender, as the following representative measurements will indicate. One of the superficial roots which was 3 meters in length was 6 mm. in diameter 35 cm. from the base; another long lateral, 1.2 meters from its base, was 3 mm. in diameter; and a third root, 1.5 meters from the point of origin on the main root, was 4 mm. in diameter. This



FIG. 12. Root system of *Opuntia julgida*. In the sketch of the horizontal extension of *O. julgida*, A, two specimens of *Riddellia cooperi* and one *Acacia constricta* (the one shown) are shown. The vertical extension of the roots of *O. julgida* is given in B, and of *Acacia constricta* in C.

system was also shallow, the main lateral running southwest, at a point 35 cm. from the central axis, was 4 cm. deep, and at a point 1.2 meters from the main plant axis it was 6 cm. beneath the surface of the ground. The other laterals also were found to lie 5 to 6 cm. below the surface, although, as was pointed out above, the soil at the place was relatively deep and would have offered no obstacles to deeper root penetration.

The roots of the 3 specimens of *Riddellia cooperi*, growing within the root-area of the cactus, were also examined. They each sent a tap root straight down, and in each root a few laterals were given off which ran in a more or less horizontal direction as far as 10 cm. How deep the tap root of *Riddellia* penetrated was not learned. At no place, however, did the root-systems of *Riddellia* appear to occupy the same horizon as the



A. *Riddellia cooperi*, from sandy loam east of West Wash, showing the large number of slender laterals arising from crown of tap-root and the branching feature of the bases of the main laterals. B. *Riddellia* from red clay soil near West Wash, to illustrate lack of slender roots at crown of tap-root.

C. *Dasyllirion texanum*, from bajada near Rincon mountains, with root-system partly exposed.

D. Shoot and root habit of *Yucca* sp., from bajada near Rincons. Plant supported by two props, one at side and one below, which should not be mistaken for roots.

E. Root character of *Yucca radiosa* from bajada near the Rincons.



roots of the cactus, so that active competition between the roots of the two species could hardly have taken place.

The specimen of *Acacia*, which was about a meter distant from the main axis of the cactus, had a generalized type of root-system. It consisted of 2 main roots and about 12 smaller ones. Of the larger roots, one ran north of the main axis of the cactus and extended beyond the east boundary of its root-area, as fig. 12 indicates, and lay from 9 cm. to 40 cm., where it was left, beneath the surface. The other roots descended rapidly and evidently penetrated deep, although they were not traced more than 60 cm. from the surface. The disparity in the position of roots of *O. fulgida* and of *Acacia* was so great that there could be no active competition between the two species for ground water.

RIDDELLIA COOPERI.

Riddellia cooperi is one of the widely distributed shrubs in the vicinity of the Desert Laboratory, occurring not only on Tumamoc Hill and on the bajada, but on the flood-plains both of the Santa Cruz river and of West Wash. It was studied on a slope separating the bajada west of West Wash from the flood-plain of the wash and also on the flood-plain east of the wash. The soil west of the wash is red clay containing coarse particles of sand, with the caliche hardpan at a depth of 55 cm.; the soil to the east of the wash is a sandy loam, apparently homogeneous to a depth exceeding 1.4 meters.

Riddellia is about 30 cm. high and consists of numerous shoots, the terminal portion only, equal to about half, bearing flowers, and the proximal portion only bearing leaves. This should be borne in mind when considering the stature of the plant as presented in the succeeding measurements, since, for various reasons, the measurements were made to include both the flowering and the non-flowering portions of the shoots.

The specimens situated west of the wash had a generalized type of root-system. There was a tap root, the lower portion of which was dead, which gave off a branch that descended gradually until it attained a depth of 48 cm. where its tip was 50 cm. distant from a line dropped straight down from the crown of the tap root. In addition to this root, 5 laterals arose within 20 cm. of the surface of the ground and extended in a fairly horizontal direction for a distance of 1 meter from the main plant axis. These laterals bore few branches and scarcely any filamentous roots, such as are a feature of the laterals in *Franseria*, *Encelia*, and other species, and the filamentous roots were not borne in groups, but occurred singly.

The roots of *Riddellia* extended so short a distance in a lateral direction that the only root found within its root-area was a single one of *Acacia constricta* (fig. 13).

The specimen of *Riddellia* growing east of the wash had a shoot 32 cm. high, or the same length of the plant just described, but, as will appear directly, in several particulars its root-system was unlike that of the other

specimen. A tap root was traced down 40 cm. and gave off, within 15 cm. of the surface of the ground, 6 main laterals. These reached out less than 1 meter from the main root axis, and certain of them were inclined downward at a rather sharp angle. The laterals gave off frequent branches of two sorts, filamentous as described for the other specimen, and relatively large ones. In addition to the main laterals and their branches, there were very numerous slender roots close to the surface and taking their origin also from the tap root. The latter type of roots was entirely lacking in the first plant examined. The contrast between the two plants in this regard is shown, but not adequately, in plate 19.



FIG. 13. Root systems of *Riddellia cypripedium*.

- a. Horizontal extension of root system which was growing in the sandy loam east of West Wash, showing the most prominent laterals but none of the large number of slender ones which were at base of shoot.
 b. Vertical extension of plant shown in a. Tap root penetrated 1.44 m. beneath surface.
 c. Horizontal extension of root system of a specimen which was growing west of the wash in clay soil. Dotted line shows position of an intruding root of a neighboring *Acacia constricta*.

In considering the form of the root-systems of the two plants, both having a relatively short tap root, though the systems were such as to lead one to expect a deeply penetrating root, it was decided to excavate the roots of another plant with the view of observing especially the behavior of its tap root. Accordingly, a third plant was selected, growing east of the wash and close by the first specimen studied. The soil conditions where the second and third specimens examined were growing were apparently the same. The shoot of the last plant studied was 38 cm. high. The root-system of this specimen was dominated by a tap root, which was traced to its end,

1.44 meters deep. Like the root-systems of the other plants, this one also comprised several laterals which were borne about 15 cm. from the surface of the soil and which reached about 90 cm., but then, turning sharply, ran directly downward to an undetermined depth. The slender roots, so numerous on the last plant examined, were also a feature of this one.

DASYLIRION TEXANUM, YUCCA RADIOSA, YUCCA SP., AND AGAVE SP.

Up to this point the plants of the bajada, which have been described, grew in the immediate neighborhood of the Desert Laboratory, or at most not more than a mile distant, but the plants selected for the purpose of examining types other than had been seen heretofore, were found in the region west of the Rincon mountains, about 20 miles east of Tucson. The bajada at that point was perhaps 4 miles from the base of the main range of the mountains and at an elevation approximating 3,600 feet, or about 1,300 feet higher than Tucson. The greater altitude means lower temperatures and greater rainfall, although, as there are no records of the locality, the extent of the difference from Tucson in these regards is not known.

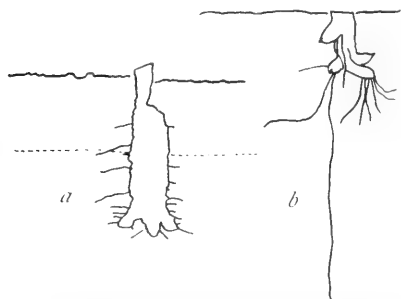


FIG. 14. a Vertical extension of root-system of *Yucca radiosa* from the bajada near Rincon mountains. Dotted line indicates boundary between adobe upper soil and underlying rotten caliche.
b Vertical extension of root-system of *Yucca* sp. from the bajada near the Rincos.

The soil conditions varied where the plants studied were growing. At the *Yucca* sp. habitat the upper soil, for more than a meter, was sand and red clay with caliche underlying, while in the habitat of *Yucca radiosa* and *Dasylyrion texanum* the upper soil, although of like character, was only about 20 cm. in thickness. The two plants first named were 50 meters apart, and were about 200 meters

from *Dasylyrion*. The *Agave* sp. was found on the upper bajada slope near the base of an outlying range approximately 2,000 meters south of the other plants. The soil was similar to that above described, except that there was a larger amount of sand and rocks.

In the immediate vicinity of the *Agave* studied were observed *Calliandra* sp., *Encelia farinosa*, *Fouquieria splendens*, *Hyptis* sp., *Opuntia blakeana*, and *Parkinsonia microphylla*. Of the two specimens of *Agave* examined, one was about 20 cm. high and the other somewhat larger. The roots of young agaves, and of the older ones as well, were borne in a cluster at the base of the shoot. All of the roots were of about equal length and very

coarse. The older ones were shriveled, and of a dark red color, but the young roots, which were put out from the base of the plant and not as branches of already existing roots, were stout and pinkish. The young roots ended abruptly and very evidently functioned more as storage than as absorbing organs. No tap root was seen in any specimen of *Agave* examined.

The bases of the leaves and the axis of the stem of *Agave* are fleshy and serve the purpose of storing both water and food-stuffs against the flowering season or other periods of need. The other plant studied at this time, which has storage facilities above the ground, *Dasyliirion texanum*, has, as will appear at once, a similar root-system.

Turning now to consider *Dasyliirion* and *Yucca* and the habitats in which they were growing, we shall find, as revealed by the character of the vegetation as well as shown by soil differences, that the bajada farther from the mountain base does not have uniform conditions. For example, in the vicinity of *Dasyliirion* there are *Acacia constricta*, *Bigelovia hartwegii*, *Opuntia blakeana*, *Riddellia cooperi*, *Yucca* sp. Besides these species, in the vicinity of the *Yucca* sp. studied, the following occurred: *Parkinsonia microphylla*, *Parkinsonia torreyana*, *Prosopis velutina*, and *Zizyphus parryi*. At lower altitudes, as at Tucson, these species do not occur together, but are characteristic of the different well-defined physiographic areas; for example, *Parkinsonia torreyana* grows only in the vicinity of washes, or where the water conditions are relatively favorable, while *P. microphylla* occurs on the bajada above the wash. Both *Zizyphus* and *Prosopis* are chiefly found on the flood-plain, occurring not at all, or as dwarfed specimens only, in the other and more arid areas.

In addition to the differences in the two habitats last considered, as revealed by the difference in the kinds of woody plants growing in them, the *Yucca* sp. habitat has far the larger population. Without further investigation it is assumed that this difference is wholly due to the fact that the latter habitat has deeper soil, and hence more water and for a longer time, than the alternate one. The root-systems of the plants growing in the first habitat, *Dasyliirion* and *Yucca radiosa*, will be first described.

The specimen of *Dasyliirion* examined was a meter high. The roots were exposed on the southern side only and had the following characteristics: A large number of roots, each about 5 mm. in diameter, formed a cluster at the base of the stem. The roots ran downward at an acute angle and also extended out into the soil in a more or less horizontal direction. The roots were all coarse; the most shallow were 15 cm. beneath the surface and the deepest about 36 cm. deep. The longest roots were the most superficial ones, of which some measured 2.25 meters, though they were mostly shorter than this (plate 19c).

Another specimen of *Dasyliirion*, with the shoot about 2 meters high, possessed a root-system essentially like the smaller plant just described, although the soil at the place was somewhat deeper than that in which the

smaller plant was growing. It therefore appears that the root-system of *Dasyliirion* is essentially a comparatively superficial one.

The shoot of *Dasyliirion* functions as an important organ for food and water storage, the storage apparatus being made up of the large central axis and the enlarged leaf bases. The entire organ, in the larger plant studied, was 25×30 cm. In another specimen, of which the stem axis was 2 meters long, the water capacity would be very considerable, easily comparable to that of the sahuaro.

The root-systems of two specimens of *Yucca* were studied. Both of these plants, although separated by some little distance, were growing under practically identical soil conditions. The old specimens of *Yucca*, of the type examined, have the habit of growing in colonies, to the exclusion of plants of other species, but the younger forms occurred singly.

The shoot of *Yucca* sp. was 70 cm. high and bore leaves 60 cm. in length. The subterranean portion of the plant consisted of a branched tuber-like root, from which arose several roots of the type characteristic of *Dasyliirion* and *Agave*, that is, coarse and little branched. The tuber measured 8×25 cm., and was richly supplied with sap. The branches of the tuber were also fleshy, and three or four of them bore buds destined to produce shoots. From the tuber 26 roots took their origin, wholly from the lower surface, which were of two sorts, namely, immature, which did not function as absorbing organs, and mature roots. The former were of a light pink color, 1.5 cm. in diameter and about 8 cm. in length, and were well filled with sap. The older roots were dark red and generally shriveled; they were unbranched and were devoid of groups of filamentous roots, a characteristic of many perennials of other families which were studied. The roots were variously placed. The one penetrating deepest was traced to its end 1.23 meters beneath the surface. Another, 1.22 meters in length, ran more or less horizontally and reached 8, 12, and 22 cm. beneath the surface at different points. It terminated abruptly. As compared with the root-system of *Dasyliirion*, that of *Yucca* sp. can be said to be poorly developed.

The specimen of *Yucca radiosa* studied had a shoot 64 cm. high and was situated about 50 meters from the other species of *Yucca* just described. It had a stout main root from which arose numerous laterals. The main root was 5 cm. in diameter about 10 cm. beneath the surface of the ground and expanded rapidly to a diameter of about 14 cm., which it maintained almost to its end, 56 cm. below. The tip of the root was expanded and divided into short forks. The entire root was thus 66 cm. in length and, as it was well supplied with sap, it must be considered an important water and food storing organ (plate 19, *d*, *e*).

Laterals were given off from the main root from a point about 20 cm. from the surface to the end of the root. They were all old and in appearance were like those of the other species of *Yucca*. As in the other species, they were comparatively close to the surface of the ground.

THE FLOOD-PLAIN.

The bottom lands which come into this study comprise not only the flats near West Wash and those along the Santa Cruz river, but also a branch of the latter, the mouth of a wash having no well defined channel, about 9 miles down the river, west from Tucson. The first two physiographic areas both have a deep surface soil, and in both cases, in former years before the Santa Cruz had cut itself a channel, flood waters at times spread over the bottoms. The water table of the two areas is at different depths: that of the flood-plain of the river is from 5 to 12 meters from the surface, while that of the wash is much deeper and probably fluctuates with the seasons or the years. While a certain amount of excavating has been done, reliance has also been put on authenticated reports and use has been made of natural excavations, as the caving of the banks of the river and the exposing of roots by other severe washouts. On the river flood-plain have been examined the roots of *Kerberlinia spinosa*, *Prosopis velutina*, and *Zizyphus parryi*; by the Wash those of *Panicum gracile*, *Ephedra trijuncata*, and *Lycium andersonii*; *Opuntia vivipara* was studied in its habitat near the Nine-mile Water-hole. The root-systems of some other trees or shrubs, as *Olneya tesota*, *Parkinsonia torreyana*, *Condalia spathulata* were seen in part or incidentally in connection with other plants.

THE FLOOD-PLAIN OF THE SANTA CRUZ

KERBERLINIA SPINOSA.

Kerberlinia is one of the most striking of the desert plants of the vicinity of Tucson. It is without leaves throughout its existence and the branches are reduced to rather short, stout spines. The plants are usually under a meter in height and occur in colonies which are frequently circular in form and 4 meters more or less in diameter. Where the species has formed such a thicket it is secure from injury by grazing animals and constitutes a safe retreat for small rodents. The distribution of the plant in this vicinity is somewhat limited. It does not occur on Tumamoc Hill or by West Wash, but on the flood-plain of the Santa Cruz, by the edge of the plain as well as nearer the river, and on the bajada where soil conditions are favorable.

The habitat of the specimen of *Kerberlinia* studied is on the line between the bajada and the flood-plain of the river and on the lower slopes of the bajada itself. The top soil, to a depth of 30 cm., is adobe clay with sand or gravel admixture and under this is the caliche hardpan. On the flood-plain just below, where the most perfect specimens of the plant were growing, the soil had a depth characteristic of the plain. The character of the specimens, as well as the greater depth of soil, made it impracticable to study the roots of the better-developed plants of the flood-plain.

The root-systems of three individuals, or groups, were examined with the purpose of learning not only the type of the roots but also the manner of development of the colonial character, a prevailing habit of the species.

The first plant studied was a separate individual with a shoot under 50 cm. in height, and extremely scraggy and thorny. It possessed a stout tap root which went down 75 cm. and then turning sharply ran for an undetermined distance horizontally. At its crown the root was elliptical in section and 2 to 3 cm. in diameter. It gave off a single branch about 12 cm. beneath the surface of the ground, and a single adventitious root was found which took its origin at the crown of the tap root. This root was 5 mm. in diameter and ran straight downward. Both the tap root and the adventitious root penetrated through the top soil, and the main root went to the caliche before turning from its vertical course. (See plate 20.)

The second study was made on a group of two plants of unequal size and with indications that they had had a common origin. The tap root of the larger plant went straight down, after the manner of the root of the plant examined earlier, and bore two main laterals, of which one had been partly exposed by the erosion of the soil surface, and one lay about 4 cm. beneath the surface. The latter root kept its distance from the surface fairly constant for the distance it was followed, 1 meter, and was seen to give off frequent branches. The function of this root was evidently that of absorption. The more superficial lateral was about 50 cm. long and along its upper surface bore numerous small shoots, and on its lower surface many short, slender rootlets. No deeply penetrating roots were found beside the tap root of the oldest, really parent, plant. It appears, therefore, in these two plants, that the younger one depended on the parent for its constant water supply, and that during the wet seasons this could be supplemented by what was obtained by small adventitious rootlets growing along the lower surface of the superficial root.

The third plant group studied consisted of two plants of unequal size, but both relatively small. The larger of the plants, the parent plant, had a pronounced tap root which gave off a single prominent lateral on which was borne, 15 cm. from its place of origin, the daughter plant. Midway between the two plants the connecting root was observed to be dead and partly decayed. An examination of the daughter plant showed that it had several slender and short absorptive roots, but that in addition there was one of larger diameter which ran straight down and functioned as a tap root (plate 20). The daughter plant, springing as a shoot from the sucker-like root of the larger form, had finally become independent and had developed a deeply penetrating root-system of its own.

Other plants were examined in which the daughter shoots were large and were borne on stout superficial laterals of the parent plant but which had not developed tap roots. In the largest of the shoot-bearing laterals no absorptive adventitious roots were seen, but such rootlets are present in large numbers on such laterals as the one shown.

It would appear from observations on the distribution and root habits of *Karberlinia*, that it must be in continuous connection with a water supply. This is effected either by each plant developing a tap root of its

own, or by maintaining its union with the parent and deriving the needed supply through the parent root. It is this requirement that confines the species, apparently of the extreme xerophytic type, to places where the soil is of considerable depth and the water relations relatively favorable.

PROSOPIS VELUTINA.

Prosopis shows a very marked power of accommodation to varied conditions of soil and water, especially the former, and when grown under extreme conditions, exhibits differences in growth habit so great as nearly to defy recognition. For instance, on Tumamoc Hill and on the bajada, the species occurring to a limited extent in both places, *Prosopis* assumes the form of an irregular bush, but on the flood plain, its proper habitat, it may become a tree 15 meters or more in height, with a well-defined bole. Frequently, however, along the river-bottoms the species takes the form of the cultivated eastern apple. By an earlier observer (Harvard, The Mezquit, American Naturalist, vol. 18, page 450, 1884) the variation in the size of *Prosopis* was taken as an index of the depth of the water table: if the tree was large, the water lay close to the surface; if it was small, the water table was very deep. That the species is an indication of the presence of perennial water is said to be the belief among native ranchers of southern Arizona, who, it is said, may even follow the roots of mesquite in digging wells—a "water-witch" which points unerringly to subterranean water. Although these beliefs are largely fanciful, they nevertheless have some foundation; where the mesquite grows large the perennial supply of water is relatively close to the surface, and where it is small the water-supply is limited but probably confined to the surface water.

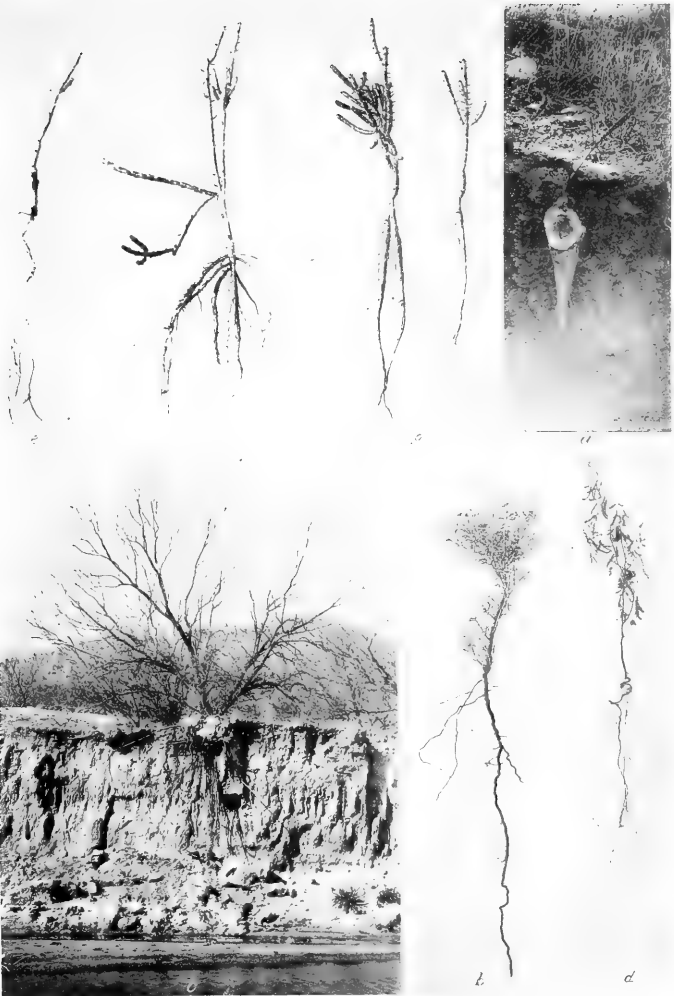
How deep the roots of *Prosopis* may penetrate the soil is difficult to learn, but it is conditioned on the character of the soil, the depth of the water table, and the penetration of the rains. Where a substratum, as hard caliche and possibly fine-grained adobe clay, makes difficult or prevents deep percolation of flood waters, roots of plants will not strike deep; but where it is such as to permit the deep sinking of the rains, or the rise of water from the perennial water supply, the plant roots may also penetrate to great depth. The most deeply placed roots of *Prosopis* known to the writer are those of plants growing by the Santa Cruz, which penetrate at least 5 meters, but I have been informed by a reliable observer that the roots of mesquite growing by a tributary of the Santa Cruz have been seen to reach to a depth of 8 meters. As one leaves the river and goes toward the sides of the flood-plain, *Prosopis* becomes smaller until, at the edges of the plain, it is little more than a large bush. The water table also is deeper at the sides of the flood-plain than near the river, and it is believed, although not actually demonstrated, that the roots of the mesquite reach perennial water only where the water table is relatively close to the surface.

Where the surface soils do not permit the deep penetration of the roots of *Prosopis*, as on Tumamoc Hill and the bajada, the plant derives all of its



ROOT HABIT OF *KOEBBERLINIA SPINOSA*.

- A. Isolated plant with prominent tap-root.
 B. Several shoots arising from a single sucker, which still keeps connection with parent tap-root.
 C. Adventitious absorption roots arising from a sucker which has not formed an independent tap-root.
 D. Secondary formation of tap-root in a group with connecting sucker root no longer living.



a. *Peniocereus greggii* from flood-plain near West Wash, showing fleshy main root and most important laterals.

b. *Condalia spathulata* from flood-plain of the Santa Cruz.

c. Root-system of *Prosopis velutina* partly exposed by the caving bank of the Santa Cruz. Vertical distance from surface of ground to water is approximately 5 m.

d. Young plant of *Prosopis*. The squares are centimeters.

e, f, g. Cuttings of *Opuntia arbuscula* (Tucson), *O. arbuscula* (Sacaton), and *O. vivipara*, all grown under similar conditions and with a large water supply.

water supply from the rains directly, and also, even where the roots may penetrate deep and actually do so, it appears from the abundance of superficial roots that the species growing under such conditions also derive their water supply mostly from surface waters. Thus, although it is characteristic of the young plant that a strong tap root is developed (plate 21), in the mature form many of the laterals remain near the surface of the ground and, with little change of level, may run 15 meters from the central axis under especially favorable conditions, as by an irrigating ditch. This observation was verbally communicated by Prof. R. H. Forbes, of the Arizona Experiment Station.

CONDALIA SPATHULATA AND ZIZYPHUS PARRYI.

Condalia and *Zizyphus* are both dwellers on the flood-plain of the Santa Cruz and of West Wash, but the characteristic habitat of both forms is on the river bottom. In this vicinity *Zizyphus* reaches its largest size in the forest of *Prosopis velutina* near the old San Xavier mission, 9 miles south of Tucson. Both species, however, were studied near the western edge of the Santa Cruz flood-plain about 6 miles west of the domain of the Desert Laboratory.

In the neighborhood of the plants examined the leading perennials, in addition to *Condalia* and *Zizyphus* which were fairly abundant, were *Acacia constricta*, *Bigelovia hartwegii*, and occasionally *Karberlinia spinosa*, with many arborescent specimens of *Prosopis velutina*.

Soil conditions where *Condalia* and *Zizyphus* were studied are characteristic of the edge of the flood-plain, that is, adobe clay with particles of rock fragments to a considerable depth. *Condalia* is evergreen, but *Zizyphus* is deciduous, dropping its leaves soon after the beginning of the arid autumn.

The specimen of *Condalia* studied was 74 cm. in height. The root-system of the plant consisted mainly of a tap root with numerous small and a few large laterals. The tap root was traced directly downward 1.3 meters and where left it was 8 mm. in diameter, so that it would not be possible to state the depth attained, but without question it was much more than actually demonstrated. At its crown the tap root was 2.5 cm. in cross-section. The leading laterals arose as follows: three, 5 mm. in diameter, originated just below the surface of the ground, three more were given off at a depth of 36 cm., and one arose 90 cm. beneath the surface. Throughout the first meter of the tap root there were, between the larger laterals, very many smaller ones about 1 mm. in diameter, but these were relatively long. The length of the larger laterals was not learned. Filamentous roots were not seen on the laterals.

The shoot of the specimen of *Zizyphus* examined was 1.4 meters high and bore numerous branches. At the time its roots were examined (April 22) it was not in leaf. The root-system closely resembled that of *Condalia*; it was characterized by a stout tap root from which arose several laterals; the main root was 3.5 cm. in diameter at the crown and was traced straight

down to its end, 1.36 meters deep, 18 laterals, 1 cm. or less in diameter, were given off from the tap root within 15 cm. of the surface of the ground; at a depth of 1 meter a larger lateral was given off. None of the laterals bore filamentous roots along their course, as did those of *Lucida*, *Franseria*, and other plants (plate 21b).

From this study of the root-systems of *Condalia* and *Zizyphus* it will be seen that, more than in any other plants examined, unless perhaps it is *Kaberlinia*, a well developed tap root appears to be an essential character, and it is due to this fact that these species are confined to places where the soil has considerable depth.

EPHEDRA TRIFURCA

Ephedra, on the domain of the Desert Laboratory, occurs exclusively on the flood plain, especially that by West Wash, where it attains large size. It is there associated with plants characteristic of the wash, *Acacia greggii*, *Prosopis juliflora*, *Parkinsonia torreyana*, and a few specimens of *Pentocercus megalis*, shown in plate 21, which is somewhat rare in the vicinity of Tueson.



FIG. 8.—Root system of *Ephedra trifurca* showing position of tap root and typical laterals.

The *Ephedra* whose roots were examined was about 1 meter high and the shoot was composed of numerous slender branches. The root-system was characterized by a stout tap root and few relatively slender laterals. The main root was 1.3 cm. in diameter at the crown, and was traced 75 cm. to the place where it forked; one fork was followed 25 cm. deeper, a total depth exceeding 1 meter, and the end was not found. The laterals were of two sorts, a larger and a smaller kind. The latter were confined to the crown and resembled the slender roots in an analogous situation in the plants of *Franseria*, growing by the Wash. The larger laterals originated from 15 to 50 cm. beneath the surface of the ground, and, as is usual with the roots of plants which grow where the soil is deep, either went straight down or fairly horizontally. The depths and the lengths of two of the laterals may be taken as being representative of all of the rest; one arose 15 cm. from the surface and kept this distance very closely to end, 1.8 meters from the main root; the other lateral, which arose at about the same depth, after running straight out 10 cm., turned downward at a sharp angle to a depth of 57 cm., when it took a horizontal course for a short distance.

OPUNTIA VIVIPARA.

In the vicinity of Tucson the cacti usually occupy the more arid situations as the bajada or Tumamoc Hill, and avoid the flood-plain, but among the exceptions to this condition should be included *Peniocereus greggii* and *Opuntia vivipara*. The former, owing to the fleshy main root, requires considerable earth-room for its full development, and usually occurs where the soil is relatively deep. *Opuntia vivipara* is known only

from a locality not far from the mouth of a wash which debouches on the flood-plain of the Santa Cruz near the Nine mile Water-hole.

Opuntia vivipara is of the cylindrical type and is remarkable especially for the great number of young plants which take their origin from fallen "joints" and which cover the ground, beneath every large individual of the species, with a fairly dense growth. The manner of origin of most of the plants is indicated by the figure in plate 21, which also shows something of the fleshy nature of the young roots.

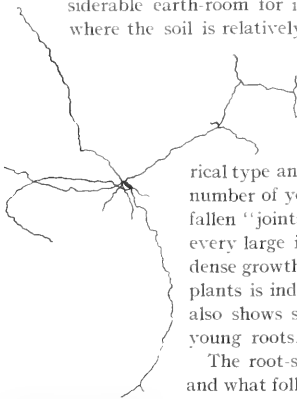


FIG. 16.—Horizontal extension of root-system of *Opuntia vivipara*. All laterals in this specimen were slender.

The root-systems of several plants were examined and what follows is merely a résumé of the observations made on them. In most regards the root-system of the mature plant of *vivipara* is similar to other arborescent opuntias, e.g., that of *O. versicolor*, as described in a foregoing paragraph; that is, there

is an anchoring system and an absorbing system, both well differentiated. But in a certain particular the roots of this species are unlike those of any other cactus examined: they are usually slender, but occasionally one is found which is fleshy, although the more distal portion as well as the proximal portion may be of the usual type. The departure from the usual root-type will appear in the following measurements. A lateral of the usual form, that is, 3 to 4 mm. in diameter up to a point 50 cm. from its place of origin, may then become 1.5 cm. in diameter and retain this larger size for 25 cm., while nearer as well as farther from the main root the lateral will be of the slender type. The peculiarity of the root-system of the species, in addition to the fact that fleshy roots are present, is that both slender and fleshy roots occur on the same plant.

It was shown in the case of *Opuntia arbuscula* that the fleshy roots of that species gave rise to plants as a regular habit, and it was learned that the fleshy roots of *O. vivipara* are capable of doing the same thing, although the characteristic has not been observed in nature.

EXPERIMENTAL CULTURES.

Although the primary object of the present research was to learn the most striking facts regarding the root-system of mature desert plants, as a necessary preparation to later experimental work, problems arose during the course of the study on which experiments were carried out intended to be suggestive rather than necessarily conclusive. The experiments naturally centered around the relation of the roots to water supply: (1) as regards formation of adventitious and temporary rootlets; (2) the direction of growth or position of the roots; (3) as regards the quality of fleshiness in the young as well as mature roots of certain opuntias.

The root-systems of many species of perennials and a few annuals are provided with filamentous roots in groups of about 6 each. In perennials these roots appear during favoring seasons and disappear when such seasons have passed. In annuals their behavior is not so clear but their presence is probably also associated with an increase of the water supply. The leading experiments undertaken along this line may be briefly stated. Among the perennials, *Franseria deltoidea* and *Encelia farinosa* form temporary rootlets in midwinter, if the ground is moistened, but other species such as *Covillea tridentata*, *Fouquieria splendens*, *Lycium andersonii*, and *Opuntia discata*, are not provided at this season with newly developed rootlets. Therefore, in certain of the species named, besides an improvement of the water relations, a condition has to be fulfilled before the temporary absorbing roots may be formed, and this very clearly is higher temperature, since freshly formed rootlets are to be found on these plants in early autumn. However, such a plant as *Opuntia discata* can absorb water in the winter season without the development of recognizably new rootlets, as a series of experiments in the winter season well shows.

On November 11, 1908, after several weeks of drought, a small specimen of *Opuntia discata* was well watered, and the watering was repeated the following day. Six measurements on the thickness of the flat joints were made on as many different places; 31 hours after the water was applied the joints had begun to increase in thickness; the increase in thickness continued for three days, after which the maximum diameter was maintained for an unknown period. On the sixth day after irrigating, roots of the plant were carefully removed from the soil and examined. No newly formed rootlets were present. In summer, however, such roots are formed on this species, and the vegetative activity of the plant is very great, as shown by new growth, the formation of leaves, and a high rate of transpiration.

Among the annuals the behavior of the roots as regards the formation of adventitious rootlets also appears to be varied, although probably constant for any species. A large proportion of the annuals studied were seen



a. Cultures of *Fouquieria splendens* and of garden watermelon showing differences in character and development of extreme types of root-systems.

b. Shoot of *Opuntia vivipara* springing from a fleshy root; natural size.

to possess them, but they were not to be found in a few, and in one species their formation could not be induced experimentally. In *Amsinckia spectabilis*, these rootlets are present as rudiments, whatever may have been the water conditions, but are only brought to full development under favorable moisture relations; while in *Rafinesquia*, as stated above, no adventitious rootlets were seen in nature and none could be induced to form in experiments. The cultures were carried on in the plant house where the temperatures were higher than out of doors. (See page 40).

In December-February, 1907-8, a culture was set for the purpose of seeing the relative extent of the roots of a typical desert seedling and those of a pronounced mesophyte. The seeds planted were of the garden water-melon and of *Fouquieria splendens*. When the plants were taken up the

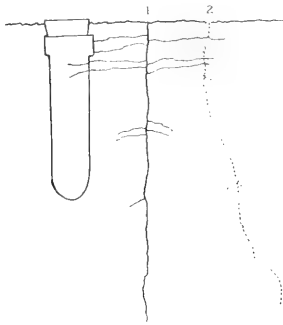


FIG. 17.—Culture of water-melon (1) and *Fouquieria splendens* (2) in a soil kept constantly moist by a porous clay cup shown at left.

shoots of each species were about of a height, although the transpiring surface of the water-melon, naturally, was much greater. The root-system of the seedlings of the two species was found to be very unlike; that of the water-melon was three to four times as long as the shoot and bore very many laterals of the first order, while that of the *Fouquieria* was only about as long as the shoot and bore few laterals. The relative development of the two is imperfectly shown in plate 22. The behavior of the roots of *Fou-*

quieria brought about the starting of another culture for the purpose of

learning the direction which the tap

root of a typical desert plant would take if provided with an abundance of water. Water poles of porous clay tubes were placed in opposite ends of a box and, after the soil moisture coming from the poles had reached an equilibrium throughout the box, seeds of water-melon and of *Parkinsonia aculeata* were sown at different distances from the centers of water supply (fig. 17). The root of the water-melon went straight down, while that of *Parkinsonia* inclined away from the water pole in a marked manner. The difference in reaction of the roots of the two plants is thus a striking one, whether the immediate cause is too much water or too little oxygen, or other causes not now suspected.

This form of culture was later repeated using bulbs of *Brodiaea capitata* in place of the other plants previously used, with the distribution of water from porous clay cups, of the kind employed by Livingston, arranged as before, but with fine and coarse earth arranged in alternating vertical columns. Bulbs were placed both in the fine soil and in the coarse, and on

the line separating the two. The results of this culture have already been given above and need only be summarized here.

The plant on the adobe-clay side of the culture had developed two sorts of roots: a fleshy tap root which inclined away from the water pole and ended in a curl, and several of the usual sort (plate 23). The bulb had entirely disappeared. The plant on the sand side of the box (both were very close to the opposite kind of soil) had developed two kinds of roots also, a large tap root and a few laterals. The tap root went straight down without regard to the water pole (plate 23). In the latter plant the bulb had not wholly disappeared.

In connection with the behavior of the *Brodiaea*, whatever may be the immediate underlying causes, it is of interest to review the reaction of certain cacti to analogous natural and cultural conditions. In the course of observations on the roots of the cacti it was learned that frequently the seedlings of the arborescent forms were provided with fleshy roots, and also that in the root-systems of the mature plants of *Opuntia vivipara* some of the roots were slender and some fleshy, and also that all of the laterals of *Opuntia arbuscula* were fleshy. In the latter species the description applies only to the plants from near Tucson; those seen near Sacaton are slender throughout. Cultures of cuttings from the Sacaton form of *arbuscula*, the Tucson representative of the same species, and of *Opuntia vivipara*, were grown in the experiment house during the spring and summer. The soil in which the plants were placed was sand and adobe, about equal parts. The culture was frequently watered throughout the entire period. On November 21 the plants were carefully removed from the soil and it was noted that all of the larger roots of *O. vivipara* were fleshy; the longer roots of the *arbuscula* from Sacaton, the species which does not possess fleshy roots in its natural surroundings, were fleshy also, as were those of the specimens from Tucson. But the fleshiness of the last was the least marked of any (plate 21). It would appear, therefore, that the character of fleshiness in these cacti and in *Brodiaea* is to be associated with an abundant water supply.

Besides serving as water-storage organs the fleshy roots of *Opuntia arbuscula*, from Tucson, also propagate the species, as mentioned above and described by Preston (Non-sexual propagation of *Opuntia*, Bot. Gaz., p. 128, vol. 31, 1901). This appears to be a very common way of increasing the number of individuals. To learn whether similar conditions might obtain in those roots of *O. vivipara* which were fleshy, one was brought to the experimental plantation and given water freely for some months. From this root a single well-developed shoot with roots appeared and continued to grow vigorously (plate 21).

PHYSIOLOGICAL FEATURES OF ROOT-SYSTEMS.

"CHARACTER" IN ROOTS.

The roots of desert plants, possibly to a greater extent than the roots of plants of the more humid regions, are remarkable for their individuality. The roots of each genus, often perhaps of each species, possess peculiarities of form, of branching habits, of color, of texture, of position in the ground, or of more subtle physiological reactions. In how far these features can be used for systematic purposes is yet to be shown, but there is no question of their importance in the field of plant biology, particularly in ecology.

It has been found convenient to group the types of root-systems into generalized and specialized forms with a physiological rather than a systematic bearing. By a generalized root-system is meant one that has both the tap root and the laterals well developed. Such roots penetrate the ground deeply and reach out widely. To this type belong most of the desert perennials, of which *Franseria deltoidea* and *Prosopis velutina*, among the shrubs and trees, may be taken as representative. Nearly all the annuals, also, belong to this type. There are two forms of specialized roots, those with the tap root the chief feature, as in *Ephedra trifurca* and *Kaerberlinia spinosa*, and those with the laterals, which are placed near the surface of the ground, especially well developed. Of the latter, the cacti are almost the sole representatives. So far as desert plants are concerned, it is probably true that generalization in root-systems looks toward mesophily, and specialization toward xerophily.

The specialized root-systems of either form are changed little with environment, but the generalized roots are often extremely variable, ranging from a pronounced tap root to a marked development of the laterals, dependent on soil characters and water relations. Thus it will appear clear that rigidity or plasticity of root-system may be an important factor in the local distribution of a species, a feature to be discussed below.

One of the most striking characters of the root-systems of perennials is the variation in the branching habit, although as the habit is a matter of degree rather than of kind it is not possible to express the difference in exact terms. Under parallel conditions, the roots of any species act consistently, and where the conditions are much changed, as from the bajada to the flood-plain, and modification of the branching habit results, still the induced variation is superimposed on the specific and familiar habit in such a way that the proper habit is easily recognized. The roots of *Covillea* branch repeatedly, wherever the plant is growing, but those of *Fouquieria* are little branched. The most richly branched root-system observed was of *Opuntia arbuscula*, which covered the ground so completely that it would

have been impossible for any other plant, perennial or annual, to gain a foothold without encountering the roots of this species. *Krameria canescens*, the parasite, however, has a root-system that is scarcely branched beyond the first order. Among the annuals it was observed that the root-system of those appearing in summer was more richly branched than the roots of the winter forms, and that the annuals both of summer and of winter varied greatly, but consistently in the species, so that genera at least could be distinguished merely by the branching habits of the roots.

The more superficial laterals of the generalized root systems of perennials and a few roots of the cactus type of the specialized root-systems are provided with filamentous roots, borne in groups, of limited period of activity. These temporary absorption roots, referred to in this paper as deciduous roots, are formed always during the rainy season, either of summer or winter, and persist until the soil about them becomes unbearably dry. The length of this period is not known, but probably is not far from the time which limits the growth of annuals, from three to six weeks, or even more. Similar roots are to be seen in some of the annuals, particularly in *Amsinckia* among those of winter, and *Triantha* of those of summer, but are regularly absent from certain other species.

THE RELATION OF ROOTS TO SOIL TEMPERATURE.

The relation of the roots of annuals and of perennials to the temperature of the soil can be presented briefly. As appeared in an earlier section of this paper, the grand course of heat movement finds its maximum just prior to the summer rains, and its minimum in late winter or early spring. With the coming of the rains in summer the soil temperature falls immediately and considerably, but the rains of winter do not appear to have so marked effect on the temperatures of the soil. However, when more complete temperature observations are at hand, the winter rains may be found to have a marked and important effect, particularly in the way of altering the temperature of the uppermost soil levels.

From what is known regarding the temperature of the soil at a depth of 15 cm., it appears that the summer annuals are not subjected to very intense heat, in fact not greatly exceeding 80° F., but those of winter may experience temperatures very close to the freezing point. At a depth of 30 cm. the soil is not as cold as at less distance from the surface, but the minimum is reached later in the season than at the higher level, so that the roots of the winter annuals may be subjected to the following conditions: During the warmer days of winter and early spring the superficial soil may attain a temperature relatively high, while the deeper soil is yet cold. The conditions for most favorable water absorption are not present in winter, therefore, and the effect is a limitation of the development both of root and of shoot. Reversed conditions are to be found in summer, when the lower soil layers at the time of the rains and the appearance of the annuals are



a. *Brodiaea caespitosa* grown in adobe clay, in b. in soil, in plant-house cultures.
 Main root of clay-grown plant curved away from source of water supply.

warmer than the upper soil layers. The growth conditions both of shoot and of root in summer, therefore, are most favorable, with the result that the summer annuals are very luxuriant, the shoots carrying a large leaf surface and the roots being especially well developed.

The relations of the roots of perennials to soil temperatures are at once similar and unlike the relations of the annuals. They are similar in that the deciduous roots, which are developed on the more superficial laterals, occupy the same soil horizon as the roots of the annuals, are developed at a time when the annuals appear, and die with their passing. The persistent portions of the roots of the perennials are subject to the greatest temperature extremes of the horizon they occupy, which in the most superficial roots, like certain of the cacti, must be very great, although the exact measure is not known. The peripheral absorption roots of perennials, both of the specialized and the generalized types of root-systems, have still other temperature relations. It is probable that these roots in the generalized root-systems, and in the *Ephedra* type of the specialized roots, remain active throughout the year, but that in the cactus type of the specialized roots, especially in such forms as *Opuntia arbuscula* and *Echinocactus wislizeni*, they are formed at the time that the deciduous roots appear and die when the latter kind of roots die. The temperature relations of these roots are thus seen to be extremely complicated.

Most, perhaps all, of the perennials are active during the summer rainy season, but many do not renew growth or come into flower in winter. This is clearly a temperature relation and finds its reaction in the formation of deciduous roots, and probably in other ways, in the root-systems. It has been found impossible, for example, to induce the formation of deciduous roots in *Opuntia discata* in winter, and deciduous roots have not been seen in *Fouquieria splendens* at this season, though when the examination of the roots of *Fouquieria* was made, temporary roots were seen in *Encelia farinosa*, *Lycium andersonii*, and other plants.

THE RELATION OF ROOTS TO WATER.

The water relations of the plants in the vicinity of the Desert Laboratory are very complex, owing partly to diversity in the plants themselves and partly to essential differences as regards soil water in their habitats. These differences lie chiefly in the origin of the water supply as well as in the length of time which the water of the soil is available for use. On Tumamoc Hill the entire supply is derived directly from the rains; on the bajada the water comes in the main directly from the rains, but some is also received as superficial run-off or by seepage from Tumamoc Hill or other higher ground; on the flood-plains, in addition to the rains and the water which comes from Tumamoc Hill and other higher ground, there is a water-table of unknown depth by West Wash, varying from 5 to 12 meters beneath the surface on the plain by the Santa Cruz. The water-table by the

Santa Cruz is sufficiently near the surface to permit its being reached by the roots of the larger plants, as *Prosopis juliflora*. It has been learned* that the Santa Cruz is at present lower than the water-table, so that the river acts as a ditch. In times not very remote there was no well-defined channel of the river, as at present, but the water spread over the plain, which might indicate that formerly the water table was nearer the surface than it is now and thus more easily reached by the roots of plants. The changes in the position of the water table have probably operated to modify profoundly the flora of this habitat.

Not only do the sources of water vary in the different habitats, but also the periods during which it is available for the use of plants. Tumamoc Hill and the bajada, partly for reasons of differences in water supply, are the most arid, and the flood-plain of the Santa Cruz the least so. The character of the soil and its depth are also important factors in this connection. The soil of the bajada and Tumamoc Hill is usually less than 50 cm. deep, while the soil by West Wash is over 2 meters and that of the flood-plain of the Santa Cruz is 5 meters, more or less. Thus the arid conditions of the bajada and Tumamoc Hill, with the least water supply, are greatly increased by the slight soil covering. The length of time elapsing after a through wetting before the soil of the bajada, at a depth of 15 cm., becomes air-dry, is about three weeks, but moisture at this depth on the flood-plain of the Santa Cruz remains for six weeks. In this instance, however, in addition to the fact that more water is present in the habitat, the character of the soil as regards its fineness is an important factor.

Annuals are directly affected by the rains of the particular habitats where they are placed, while the perennials are in part directly and in part indirectly dependent on obtaining water by this means. On the bajada and on Tumamoc Hill, water is mostly derived directly from the rains, and only such perennials as are provided with water-storage organs, or are the most resistant, can live or attain the best development in these habitats.

The depth to which the roots of annuals penetrate the ground is directly controlled by the depth of the penetration of the rains of the season and the persistence of the annuals is mainly directly dependent on the length of time the water remains in the soil where they are growing. As above stated, within a period of three weeks following the rains, the superficial soil on the bajada, to a depth of 15 cm., may become air-dry, while that of Tumamoc Hill and of the flood-plain may retain moisture for a period exceeding six weeks. Since the largest part of the roots of most annuals do not reach deeper than 20 cm. it is seen that the period of their activity is definitely fixed and comparatively brief.

Annuals having the most deeply penetrating root-systems, and which are provided with checks against excessive water loss, survive longest after the wet season has passed. *Kallstroemia grandiflora*, for example, a sum-

*Communicated to the writer by Prof. G. E. P. Smith, of the Arizona Experiment Station.

mer annual, outlives many other forms, and should additional rains occur somewhat out of season, but before the plant has succumbed, it will revive and accomplish an astonishing extent of growth. *Among the winter annuals, such deeply rooted forms as *Amsinckia spectabilis* and *Phacelia tanacetifolia* will survive long after *Bowlesia lobata*, or other plants with shallow roots, have perished.

How closely the character of the water supply, the amount of water, and the progressive drying out of the soil, are related to the character of the root-system of annuals, does not appear from the observations here reported. In certain instances, however, the root-system is greatly modified by the water relations. For example, it has been repeatedly seen that the longest and frequently the greatest number of laterals arise within 4 to 5 cm. of the surface of the soil. Without definite knowledge of the water movements at that depth, it may be assumed that during the period of greatest growth the soil at this depth has an adequate water supply and provides practically all of the water necessary for the plant, and that it is only later, when by progressive drying out the upper soil becomes too dry for benefiting the plant, that it obtains its water at the greatest depth and mainly by means of the elongated tap root. In certain cases, as in *Amsinckia*, where precociously formed root rudiments are present, the coming of unseasonal rains induces growth, and the superficial roots are again in condition to absorb water.

The reaction of the root-systems of the perennials is much more complex than that of the annuals, inasmuch as a portion of the roots live throughout the year and a portion endure during favorable seasons only. The situation is further complicated by the fact that each habitat differs from every other habitat as regards water relations. The great difference in the character of the root-systems of the perennials and their possible variability under different conditions have also to be considered.

The peripheral rootlets of the generalized root-systems are probably living throughout the year, since they are in soil which, even in dry seasons, contains sufficient moisture for absorption, but the deciduous rootlets, both of the generalized and the specialized root-systems, are present and functional only during the more favorable seasons, chiefly in summer. The peripheral roots of the specialized forms of the cactus type, however, like the deciduous rootlets, are present only during the more favorable seasons. From these circumstances it is seen that the active period of absorption of plants with the latter type of roots is a very restricted one, while the absorption period of the generalized root-system and of the *Ephedra* type of the specialized system, although most active during the existence of the deciduous rootlets, is continuous from season to season.

In plants having generalized root-systems, it is probable that the penetration of the roots, the character of the soil permitting, is equal to the penetration of the rains. On the bajada this is limited by the presence of

the hard pan which occurs within 50 cm., or less, of the surface, and on Tumamoc Hill by the underlying rock. On the flood-plain, where the soil is sand and adobe, as by West Wash, the penetration is probably about 2 meters, but on the Santa Cruz flood-plain water from the rains is thought not to penetrate the ground over 1 meter, although it probably goes below that depth in places.

The penetration of the roots of the cactus type apparently presents another problem, since certain of the cactus root-systems, *Opuntia arbuscula* particularly, lie within 2 to 5 cm. of the surface or well within the depth attained by water either during summer, when the most active growth occurs, or in winter. The relation in this instance may be with a proper air supply, rather than with the penetration of the rains alone.

Where there is considerable depth of soil and the water table is close to the surface, as in places near the Santa Cruz river, the conditions are most favorable for the deep penetration of roots. Under such conditions the water chain during the rainy season may be continuous from the water table to the surface and so favor deep penetration. It is here that *Prosopis velutina* and *Populus* sp. may be in position to obtain perennial water and attain a large growth. The roots of *Prosopis* have here been seen to reach 5 to 8 meters below the surface, which is apparently the greatest depth reached by any plant in this vicinity.

RELATIONS OF THE ROOTS OF NEIGHBORING PLANTS.

The desert plants vary greatly in their abundance. It is well known that shrubs inhabiting the bajada are comparatively remote from one another. On the flood-plain the same species may form a fairly dense thicket. In favorable seasons the annuals, both of the bajada and the flood-plain, are occasionally so numerous as to completely hide the ground. It is evident, therefore, that the roots of the different classes of plants, annuals or perennials, hold varying relations to each other, which are different in accordance with the kind of habitat they occupy.

The mutual relations of the roots of annuals and of perennials vary also with the character of the perennial roots, but only as the roots of annuals find sufficient room for full development in all of the habitats.

On the bajada and Tumamoc Hill the roots of such annuals as *Anoda thurberi*, *Kallstrœmia grandiflora*, *Solanum elaeagnifolium*, *Erodium cicutarium*, and others which have a deeply penetrating root-system, may reach as deep as the roots of the perennials having a generalized type of root-system. But on the flood-plain the roots of the two classes of plants do not occupy the same horizon due in part to the fact that the roots of the annuals differ little if any in habit from those on the bajada, but mainly because of the deep penetration of the perennials. This can be illustrated by a single example. The roots of *Covillea* on the bajada may extend away from the main axis as far as 4 meters, while on the flood-plain the

lateral extent may be less than 2 meters. In the latter case there is the additional fact that the root-system of *Covillea* is, as a whole, deeper than on the bajada. Competition between annuals and perennials on the flood-plain, therefore, may be considered a negligible quantity, but competition between the two classes of plants on the bajada during the vegetative seasons is undoubtedly very keen, and the presence of annuals on the bajada is probably an important factor in bringing about the sparse character of the perennial flora of the habitat.

Since the roots of the specialized type of the *Ephedra* form penetrate deep and reach laterally to but a small extent, the roots of the annuals do not come into close relation with them, but the relation of the roots of annuals and of the specialized roots of the cactus type is peculiar in that usually the roots of such perennials are more shallowly placed than those of the annuals. Owing, however, to the fact that in the root-system of annuals, laterals are ordinarily prominent 4 to 5 centimeters beneath the surface, during the rainy season, the roots of the two classes occupy the same horizon and undoubtedly enter into keen competition for water. Soon after the close of the rainy period the superficial roots of the annuals and the deciduous rootlets of the perennials, owing to the progressive desiccation of the soil, can no longer remain functional. With the drying of the surface layers the more superficial roots of the plants having the generalized root type also cease absorbing, and the entire amount taken in by the root-system of such plants comes from the deeper levels. At this period the most deeply placed roots of such annuals as mentioned above are placed in close relation with the deeper absorbing roots of the perennials with generalized roots, and the competition is transferred from the more superficial to the more deeply placed roots both of annuals and of perennials. Finally the annuals mature, their roots absorb in decreasing amounts, and competition with the roots of other plants ceases.

Where the growth of annuals is most dense, the roots intermingle and occupy the soil fairly completely. This, however, occurs only in the case of perennials when, as on the bajada, plants of one species, or plants having similar types of root-systems, are growing in proximity. The most striking instance observed of the encroaching of the roots of one species on the territory occupied by the roots of another plant of the same species was that of *Covillea*, where 60 roots of neighboring *Covilleas* were seen either in physical contact or lying very near the roots of the plant being specially studied.

The roots of plants with specialized root-systems of the cactus type do not occupy the same horizon as the roots of perennials having the generalized forms of roots, and therefore do not compete with them for water. This, however, is true only of such cacti as have the most superficial roots; those like *Opuntia fulgida*, with a root-system which approaches the generalized type in character, probably approach this type in their mode of distribution in the soil, particularly where the soil is shallow.

ROOT HABITS AND PLANT DISTRIBUTION.

The character of the root system of desert plants as an ecological factor is often of great importance. The direction taken by the roots as a factor in the causes underlying the distribution of plants may be illustrated in a simple manner, thus: Let *a*, *b*, and *c* represent the three leading root types, namely, those having both laterals and tap root well developed, generalized root system (*a*), those with the tap root as the most prominent feature (*b*), and those with the laterals of special prominence (*c*). Of plants having *a*, *b*, or *c* forms of roots, other conditions including temperature relations being equal, *a* will have the most general distribution, *b* will have the most limited distribution, while plants with *c* roots are in a measure intermediate in this regard. In plants with the last type of roots, however, it is probable that factors other than the root character exercise the controlling influence.

Of plants with generalized root-systems *Acacia*, *Celtis*, *Encelia*, *Lycium*, *Parkinsonia*, and *Prosopis* may be found to some extent in each habitat, both where the soil is deep and where it is shallow. With these forms should also be included the annuals except those with bulbous roots. Plants with this root type are either evergreen or deciduous, but all have a fairly large transpiring surface, and in certain of them, especially *Encelia*, the leaves are of good size.

Plants having a prominent tap root, the *b* type, include *Condalia*, *Peniocereus greggii*, *Ephedra*, *Karberlinia*, and *Zizyphus*. These forms are restricted to localities, preferably the flood-plain, where the soil has sufficient depth for the development of the main root.

The cacti are nearly all provided with the *c* form of roots, but to them should be added *Jatropha* and *Krameria*, the latter a parasite. The cacti occur both on the bajada and on Tumamoc Hill, and not on the flood-plain of the Santa Cruz or by West Wash to any extent. They are the plants *par excellence* of the bajada.

Summing up the relation between the type of root-system and the distribution of plants, according to the notation given above, we have the following: Plants with *a* type of roots may be found on the bajada, Tumamoc Hill, and on the flood-plains of West Wash and of the Santa Cruz. Plants having the *b* type of roots occur only on the flood-plains of the wash and the river. Plants with the *c* type are chiefly on the bajada, although they are common also on Tumamoc Hill, to which certain of them, notably *Carnegiea*, are, for the most part, confined.

The different root types are differently related to the distribution of the plants. The generalized roots (*a* type) facilitate distribution because of their plasticity, while the specialized roots of the *b* type restrict the distribution because of their rigidity and the need of considerable depth of soil.

SUMMARY.

1. On Tumamoc Hill there is sufficient moisture in the soil at a depth of 30 to 40 cm. to be available to plants all of the year. The soil of Tumamoc Hill and the flood-plain of the Santa Cruz at a depth of 15 cm. may be air-dry within six weeks following rains and that of the bajada within three weeks.

2. The highest soil temperatures are reached in July just preceding the summer rains; the lowest temperatures of the soil, at a depth of 15 cm., are reached in midwinter and a depth of 30 cm. in late winter.

3. The roots of most annuals do not penetrate the soil deeper than 20 cm. The largest development of laterals of annuals takes place 4 to 5 cm. from the surface of the ground. Rudimentary roots of the first order were seen in *Amsinckia*, *Erodium*, *Eritrichium*, *Harpagonella*, *Malva*, and *Pectocarya* among the winter annuals, and *Amaranthus*, *Boerhaavia*, *Cladostrix*, and *Trianthema* of the summer forms. These rudiments are further developed only under favorable moisture conditions, such as out-of-season rains, when they become of great importance to the plant.

4. The root-systems of the summer annuals, which are distinct from the winter annuals, are especially well developed. This characteristic is due to the great luxuriance of shoots of the summer forms, owing to the favorable vegetative conditions of this season, not least of which is the warm soil. In winter the soil at the depth attained by the roots of the annuals is colder than the superficial layers and does not present the most favorable conditions for water absorption. In winter, also, the shoot development of annuals is less than in summer.

5. Perennials have three types of roots, namely, the generalized type, with the tap root and the laterals both well developed, and two specialized forms, of which one type has a prominent tap root and the other prominent laterals. *Covillea tridentata* and *Prosopis velutina* are representatives of plants with generalized roots, while *Karberlinia spinosa* and a few other plants have specialized roots of the first type, and most of the cacti have specialized roots of the second kind.

6. The roots of perennials growing on Tumamoc Hill and on the bajada do not penetrate as a rule deeper than 30 cm., the depth of the available soil; while those on the flood-plain of West Wash attain a depth of 2 meters, and those by the Santa Cruz may reach as deep as 5 meters or more.

7. The most shallow rooted perennials observed were *Opuntia arbuscula* (whose roots frequently do not lie more than 2 cm. below the surface) and *Echinocactus wislizeni*. The arborescent opuntias have roots which approach the generalized type.

8. Most cacti have two divisions of the root-system: an anchoring and an absorbing system. In *Carnegiea gigantea* the anchoring roots, in old plants, are assisted in their mechanical function by the enlarged bases of the laterals. This to a certain extent is true of the arborescent cacti as well, but the lack of secondary development of this character in *Echinocactus wislizeni* is the chief reason why plants in age lean sharply, or fall.

9. Fleshiness in the roots of the opuntias is a condition resulting directly from an abundant supply of water. Whether some species exhibit greater tendency toward fleshiness than others was not determined. A similar reaction was seen in *Brodiaea capitata*.

10. The most superficial roots of the generalized type of root-systems and a few of the specialized type of the cactus-form bear, on the larger laterals, filamentous roots in groups of 6 or more. These are formed during the rainy season, especially in the summer, and die with the drying out of the soil. The deciduous rootlets are of great advantage to the plants in that they greatly and quickly increase the absorption surface, without at the same time increasing the distance of water transport—a factor of undoubted importance where the transpiration rate is high.

11. Competition as evidenced by the relationship of the roots of neighboring plants may be summarized as follows: The roots of annuals intermingle and often occupy the same horizon. Where perennials of a single species occur together on the bajada, the roots of one plant may reach to and intrude upon the root-area of its neighbor. Thus in studying *Covillea* on the bajada, 60 roots of neighboring *Covilleas* were encountered which either were in contact with the roots of the plant studied or were in the same horizon. On the flood-plain competition among the roots may not be so keen as on the bajada. The roots of annuals growing on the bajada reach as deep as most perennials in the same habitat, and since they occur in large numbers competition with them must be an important causal factor contributing to the sparseness of the perennial vegetation of the bajada. The annuals also come into competition with the shallow rooted perennials through the laterals which are developed on the tap root of the annuals 4 to 5 cm. beneath the surface of the ground.

12. Perennials with the generalized type of root-system have the widest local distribution, and those with a pronounced development of the tap root have the most limited distribution. Plants with laterals well developed, the cacti especially, are most abundant on the bajada and on Tumamoc Hill, where the soil is shallow, and seldom occur on the flood-plains.

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