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Desert plants, including *Carnegiea gigantea*, *Echinocactus wislizeni*, and *Opuntia versicolor*, which accumulate a large water balance.

THE WATER-BALANCE OF SUCCULENT PLANTS

BY

D. T. MACDOUGAL AND E. S. SPALDING

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THE WATER-BALANCE OF SUCCULENT PLANTS.

BY D. T. MACDOUGAL AND E. S. SPALDING.

INTRODUCTION.

GENERAL ASPECT OF THE PROBLEM.

The activities of the seed-plant make necessary a movement of solutions from the surface intakes of roots or other absorbing organs in contact with the medium or substratum to various tissues, the residue of liquid and content finally reaching the excretory or transpiratory membranes of the leaves, stems, or other aerial members. This water-service involves a supply of available moisture in the substratum or medium, absorbing organs, whose tissues sustain a higher osmotic activity than the substratum, conducting tracts of adequate capacity, and transpiratory organs, which in response to the evaporating action of the air throw off the water of the solutions entering the roots, in the form of vapor, at a rate variously modified by the purely physiological activity of the protoplasts.

The individual and contributory action of all of these factors is greatly influenced by many internal and external conditions, physiologic, morphogenic, and physical. The relation of the plant to the moisture-supply and to the evaporating capacity of the air constitutes a limiting factor of great importance in determining distribution and habitat selection.

It is evident that the moisture relation is one of the most intricate of those entering into the environmental complex, and that it is correspondingly difficult of analysis. Partly as a result of this complication, the mechanism of the ascent of sap in the trees and the value of transpiration as a function have been singled out for an amount of attention far beyond their relative importance. Both questions have now come to be discussed in a purely academic manner, and with but little actual progress. Meanwhile, actual experimentation continues to yield profitable results in the hands of the few workers taking up the subject by the proper methods. The present paper is chiefly concerned with the results of observations upon plants characteristic of arid regions, and which consequently take up solutions from the substratum under well-defined conditions widely different from those to which the plant in moist temperate regions is subject.

The soil undergoes daily variations in temperature of wide range, and the percentage of soil-moisture sufficient to yield a supply to the plant is afforded only during very limited periods. The plant may carry on the

absorbent functions during the season of vegetative and reproductive activity or at some other time of the year. A large number of the species existing under such conditions have a capacity for absorption and conduction of water far in excess of the rate of loss from the transpiratory surfaces. Such forms accumulate a large balance which may be contained in swollen roots; in stems, as in the cacti and euphorbias; in leaves, as in the yuccas and agaves; or in all of these organs, as in the Crassulaceæ.

The habit of accumulating a large water-balance is not a property of any morphological type, nor is it confined to any group of forms capable of being phylogenetically related. Succulents are prominent constituents of the floras of salt springs and of the beaches of saline lakes and seas, as well as of arid areas in which the scanty rainfall comes within a restricted, regularly recurring seasonal period. Some are also found in tropical rain-forests and in humid situations in temperate zones. Few occur in high latitudes in which the effect of low temperatures on dilute solutions would tend to be injurious to tissues.

The Sonoran desert, inclusive of southern Nevada, Arizona, and Sonora, with the coastal belt to the southward, is especially rich in forms which habitually carry a large water-balance, and a number of these are abundant in the vicinity of the Desert Laboratory, offering opportunities for a study which has been prosecuted with some diligence since 1906, attention being chiefly directed to the great tree-cactus (*Carnegiea gigantea*), the bisnaga (*Echinocactus wislizeni*), and some common prickly pears (*Opuntia blakeana* and *O. discata*).

It may be safely assumed that practically all perennials carry an appreciable balance, as the flow of solutions from absorbing surfaces to the various tissues is by no means direct or by way of conduits that allow a clearing stream. This balance may be large in trees and other woody plants, but in none of these forms does it play such an important part in the cyclic activity of the plant or constitute such an important feature in survival and endurance as in the succulents of the arid regions. The condition of this balance may be the determining factor which may inhibit or promote seasonal activity, including growth, and variations in the balance are accompanied by reversible changes in form and size unknown in other types of plants.

The long series of measurements recorded in the present paper have been made for the purpose of determining the amount of the balance, its variations, the factors influencing its volume, and the relation of the various proportions of the balance to growth and the reversible changes to which such plants are subject. Some attention has also been given to analyses of the sap for the purpose of ascertaining the concentration of the solutions held by the plant and the implied osmotic activity.

The data derived by these methods have permitted some conclusions as to the action of selective agencies and survival in desert plants, and also have justified some speculation as to the origination of succulent forms of

the desert and sea-shore. The desired information could only be obtained by observations extending over a number of years, a fact that accounts for the dearth of evidence upon the general subject.

PHYSIOGRAPHIC, CLIMATIC, AND FLORISTIC FEATURES OF THE SONORAN DESERT.

The region in which are found the plants that were made the subject of the observations detailed in this paper consists of a series of mountain ranges with a general trend northwardly and southwardly, the intervals between neighboring ridges having the aspect of being broad plains or valleys, and being in reality troughs filled with material worn down from the mountains and spread out in such a manner as to make a series of layers, hundreds or even thousands of feet deep. The gentle slopes, or *bajadas*, leading away from the mountains, are generally devoid of water, and it is only in the lower parts of the valleys, along the streamways, that water is to be found within such distance from the surface as to be available for even deeply-rooting plants. In such places the vegetation may include forms characteristic of humid regions. The spinose and succulent xerophytes with which this paper is especially concerned inhabit the *bajadas* and the rocky slopes of the mountain.

The total annual precipitation amounts to about 30 cm. at elevations below 1,250 meters altitude, and more than one-half of this amount is received in the violent torrential rains of July and August, each downpour causing the channels of the steeply-graded streamways to run with a torrent which quickly subsides as the rain ceases. The remainder of the precipitation is more evenly distributed throughout December, January, and February, with some in March and April and perhaps in November. The general effect of the precipitation is to increase the soil-moisture of the surface-layer of the *bajadas* to a depth of a meter or less, and the greater number of native species occupy more than half this depth with their roots. (Fig. 1.)

The *sahuaro* (*Carnegiea gigantea*) forms a tall, columnar trunk with thick branches, which may reach a height of 25 meters or more, and it develops a short tap-root and many horizontal branches which lie from 20 to 50 cm. below the surface. The *bisnaga* (*Echinocactus*) has a thickened cylindrical trunk rarely attaining a length of more than a meter, with a diameter half as great. Many roots issue from the base of the stem and ramify in a superficial layer of the soil, not penetrating more than 12 to 18 cm. deep, thus lying above those of the *sahuaro* when the two are found in contiguity. The irregularly branching stems of the prickly pears (*Opuntia*) consist of many flattened joints and a very short basal trunk from which the roots issue to spread horizontally through the upper layers of the soil. (Plate 1.)

The temperature of the soil at 12 to 15 cm. shows a daily variation between 45° and 57° F. in February, near the end of the winter wet season, which gradually rises until at the end of the arid foresummer, late in June, the daily range is from 87° to 104° F. At a depth of 25 cm. the temperature is more equable, ranging from 55° to 60° F. in February and between 86° and 88° F. late in June. The equable-temperature room of the Desert Laboratory varies between 56° and 58° F. in February and 74° F. in June and July, representing the conditions at a depth of about 2.5 and 3 meters in the open.

Air-temperatures vary from between 28° and 75° F. in February to between 57° and 114° F. late in June. The integration of the temperature record shows that the total number of hour-degrees heat-units (Fahrenheit) amounts to 326,385.

The relative humidity ranges from saturation in July and August, to as low as 10 and 12 per cent in May and June, falls again in September and October, and rises with the winter rains.

The succulents described in this paper absorb some solution from the soil during the winter wet season despite the low temperatures and the fact that the greater part of the root-system is decorticated and brownish. This will be evident upon an examination of the measurements recorded. The temperature exposures of March induce root-development in the sahuaro, and flower-buds begin to swell on the terminal portions of the trunks and branches formed during the previous season of growth. Fruits are matured and ripened about the time of the beginning of the summer rains, and another addition to the water-balance takes place which is accompanied by a growth-extension of the trunks and branches. These become distended to the utmost, and as the rains cease a gradual loss begins which is only checked by the beginning of the moist season of the winter.

Both growth and flower-formation occur in the prickly pears chiefly during the dry foresummer, the flattish joints becoming much shrunken during the latter part of June and late in November. Growth and reproduction take place in the bisnaga during the summer rainy season, and the shrinkage of the short, thick trunks is not so noticeable to the eye as in the other types mentioned. (MacDougal, D. T., *The Course of the Vegetation in Southern Arizona*, *Plant World*, xi, pp. 189, 217, 261 (1908); *Across Papagueria*, *Plant World*, xi, pp. 93, 123 (1908); *Botanical Features of North American Deserts*, Publication 99, Carnegie Institution of Washington (1908).)

FORM-ALTERATIONS AND GROWTH OF CACTI.

By E. S. SPALDING.

SAHUARO (CARNEGIEA GIGANTEA).

CONDITIONS AND METHODS OF MEASUREMENT.

In a former article* it was shown that the giant cactus not only possesses a structure remarkably fitted for the storage of a large quantity of water, but also, without the slightest interference with the efficiency of its mechanical system, promptly adjusts itself by a change of form to the increased supply taken up from the soil after a rain, and to its diminution during subsequent periods of drought. The interest attaching to this plant, presenting as it does the most conspicuous and perhaps the most perfect arrangement for water-storage yet developed in any of the plants of the region to which it belongs (plate 1), together with its fine mechanical adjustment, the peculiarities of its root-system, and the correlation of its structure and habits with what has been observed of its local and general distribution, appeared to justify the continuance of the work previously undertaken, with the hope that a longer series of measurements might contribute something more definite regarding certain questions that were not satisfactorily settled. Accordingly the study has been continued at intervals, the whole period covered being nearly five years, in the course of which the influence of certain external and modifying factors has been more exactly determined, rate and mode of growth have been ascertained, and comparative studies of some other species of cacti have been made.

As regards the sahuaro, the methods already described have been employed without essential change. Points were located in pairs on opposite sides of a furrow or rib and marked with India-ink. Distances between the points were measured at stated intervals with a pair of dividers provided with a micrometer screw, so that slight movements might be accurately noted (plate 2). In this way changes in width of furrows or thickness of ribs on different sides of the trunk and at different heights were observed and correlated with records of rainfall at the Desert Laboratory, all the plants under observation being located within a few rods of the

*Spalding, E. S. Mechanical Adjustment of the Sahuaro (*Cereus giganteus*) to Varying Quantities of Stored Water. Bull. Tor. Bot. Club, 32, 57-68, 1905.

laboratory building. The results of some series of measurements are expressed in the diagrams (figs. 2 to 15) in which the movements of the ribs were calibrated to one sixty-fourth of an inch, the amount of the rainfall being expressed in vertical heavy lines.

FIG. 1.—Curve of precipitation at Desert Laboratory, 1908-09.

The flat opuntias, to which reference will be made later, were measured with calipers; and although it was found to be impossible by this means to obtain a high degree of accuracy, it was nevertheless possible to secure data of value for comparison.

Method of measuring intervals between ridges of sahuaro (*Carnegiea gigantea*).

REVERSIBLE ALTERATIONS.

DIRECT ADJUSTMENT TO VARYING AMOUNT OF SOIL-WATER.

If, after the earlier work to which reference has been made, any doubt remained as to the direct relation of the contraction and expansion of the trunk of the sahuaro to the amount of available water in the soil, it would be removed at once by comparing the measurements of a single furrow extending over a period of nearly five years with the rain record for that time. On no occasion had this relation been more apparent than in the winter and spring of 1903-04 (fig. 2) and the fall of 1906 (fig. 3). The former period was a time of extreme drought, and out of 56 intervals*

FIG. 2.—Three curves from measurements of three intervals on the north side of sahuaro No. 1, December 10, 1903, to May 12, 1904.

measured, 19 reached the very lowest measure in that period. The rapid response to a half inch of rain, February 6, 1904, is plainly seen in the curves (fig. 2). In the fall of 1906 there had been but 0.29 inch of rain from August 20 to November 18, and out of 84 intervals measured within this period, 48 reached the lowest measurement for four years between October 31 and November 19. On the night of November 17-18 there

*The term "interval" is adopted for convenience to indicate the measured distance between two points on opposite sides of a furrow or rib. In some cases several intervals were located in the same furrow.

was a rain of less than half an inch, and by November 19 some of the furrows showed a marked expansion. This was followed by other rains, and afterwards most of the sahuaros expanded steadily for over a month (fig. 3).

FIG. 3.—Eight curves from measurements of four intervals in a north and four in a south furrow of sahuaro No. 13, at corresponding heights on the two sides as follows: Intervals II and IX, 12 inches; IV and XI, 3 feet; V and XII, 3 feet 11 inches; VI and XIII, 5 feet 3 inches. October 31, 1906, to June 6, 1907.

But it is not only these marked responses with great expansion that are significant. The slight increase, determined only by exact measurements, which follows light showers, and the barely perceptible contraction which occurs when the earth has just begun to dry, afford fully as conclusive criteria. As little as 0.25 inch of rain is sufficient to produce a distinct expansion, as is shown by the measurements following the rain of March 5, 1907 (fig. 4). Before this there had been a slight contraction, there having been only 0.1 inch of rain since January 30, but after the fall of 0.25 inch on March 5, measurements of many intervals showed a distinct expansion which could hardly be due to any other cause.

INDIVIDUAL AND LOCAL PECULIARITIES.

Long-continued measurements have brought to light several minor facts which, while they do not affect the main question, are of sufficient importance to record. As might be expected, each plant has a marked individuality, and it was possible before the measurements were made to predict with considerable accuracy what their deportment with regard to present conditions would be. One plant responded to rain more quickly than another, or in a more marked degree, and some expanded for a longer period and were slower to contract when the weather became dry. The latter class usually included the more vigorous individuals, with larger trunks and wider furrows. There was no external indication of a cause for this condition of affairs, but it seems likely that in such cases the water was in some way held longer in the soil or pockets of rock to which their roots had access.

As already noted elsewhere, not only the individual plant, but parts of the same plant, respond differently to variations in amount of water in the soil, according to their location as to height and to points of the compass. But aside from this there are sometimes marked differences in the action of two intervals so close together that neither height nor exposure to the sun could account for the difference. Perhaps the most marked case of this kind is that of intervals Nos. I and VI on sahuaro No. 4 (fig. 5). Both are on the southwest side of the stem, little more than 10° apart, and No. I is but 3 inches higher than No. VI, the latter being located just below the insertion of a rib where the furrow forks. As would be expected from their proximity and general similarity of position, both exhibit the same general response to changes of water-supply, the curves rising and falling together with much regularity; but VI plainly shows more sensitiveness and mobility, and its changes of width are much greater than those recorded by No. I. Thus on May 20, 1905, No. I measured 118.5 units* and VI 163.5 units; but between May 20 and May 30 No. I contracted 1.5 and VI 15.5 units; and by June 27, No. I had contracted 7 and VI 42 units more. By August 21 No. I was actually wider than VI, but conditions were reversed again as soon as the rain came.

FIG. 4.—Curves from four intervals on sahuaro No. 4, and one from No. 7, showing response to one-fourth inch of rain on March 5, 1907. (See also fig. 3.)

*A unit equals one sixty-fourth of an inch.

This is but an extreme case of variations which are frequently noticeable. In this instance VI is probably in a position where there is great flexibility of the parts, and it appears possible, from the fact that No. I showed even less contraction than the other intervals on the plant, that the strong contraction at VI might have exerted a pull to keep the next furrow spread open. At all events it is evident that in the movements attending absorption and transpiration the plant does not act merely as a

FIG. 5.—Curves from two intervals on sahuaro No. 4. These represent an extreme case of variation between two intervals located very close together. May 20 to October 23, 1905.

mass of homogeneous tissue, but expands and contracts differently in very localized regions, and that while these regions may, to some extent, be classified according to their general position in the plant, this by no means accounts for all the variations. When the furrows seem to have reached the limits of their expansion during the rainy season the movement of selected points was quite irregular and highly localized, as was illustrated by the action of sahuaros Nos. 12 and 13, upon which intervals were taken

at several places along the same furrow. Here, if at all, uniformity might have been expected; but much variation was found, as may be seen by inspection of curves VI to IX, fig. 6.

Probably these variations are the result of a combination of factors not easily differentiated. The following simple experiment at least reveals a mechanical condition which makes such changes possible:

A section 35 cm. long, with a diameter of 25 cm., weighing 30 pounds 6 ounces, was cut from a sahuaro trunk and brought into the laboratory.

FIG. 6.—Curves from four intervals in the same furrow of sahuaro No. 12, showing local variation. January 24 to June 1, 1906.

About 3 hours after cutting it was set up on the lower cut end and a bell-jar, which covered the surface to the inner edges of the furrows, was placed on the upper end to prevent evaporation. A circle of spines was removed and the circumference, measured by a metal tape-line, was 77.1 cm. On the following day the circumference had decreased 3 mm. and the ends had shrunk in, forming cavities holding 400 c.c. The shrinkage

in volume may be estimated at about 744 c.c.; but when weighed its loss was only 70 grams. This discrepancy can only mean that in the part remaining 674 c.c. must be accounted for as air-space, and that the soft tissues are in a state of tension or negative pressure, making them very responsive to any external or internal change of condition; and a response to such change might easily be expressed by a local shifting of pressure, the outer shell of the sahuaro being sufficiently flexible to permit this to show itself to a measurable degree.

DIFFERENCES IN AMPLITUDE OF VARIATION FROM BASE TO APEX OF TRUNK.

But, aside from these irregular variations, the measurements have made it possible to establish certain facts in regard to the difference of response of different parts of the same sahuaro to changes of condition, thus confirming what was inferred from the work of the first year, though not fully established at that time.

It is hardly necessary to repeat that both contraction and expansion are less in the lower, woody parts of the plant, but it is of interest to compare a series of curves made from measurements at different heights along the same furrow, as in Nos. 12 and 13. On the latter the lowest point was 5 inches and the highest 6 feet from the ground, the plant itself being 12 feet or more in height, the variations of the intervals increasing upward (fig. 7). On No. 12, however, a plant about 6 feet high, the variations were less at the top and bottom and greatest in the middle. In table 1 the numbers grouped are for the same furrow and show that in this case the greatest variation occurs in each furrow about halfway from the base to the apex of the trunk. The variation is ascertained by subtracting the width of the furrow at its time of greatest contraction from that of its greatest expansion for the entire period during which records have been kept. The variation for any one year would be somewhat less than this.

TABLE 1.—*Variations at different heights in three furrows of one plant (No. 12).*

No. of interval.	Units of variation.	Height of interval measured.	No. of interval.	Units of variation.	Height of interval measured.	No. of interval.	Units of variation.	Height of interval measured.
		ft. in.			ft. in.			ft. in.
VI	20.5	5 10	X	32	5 6	XIV	25	5 10
VII	24	5 3	XI	41	4 9	XV	30.5	5 5
VIII	43	3 4	XII	49	3 3	XVI	36.5	4 2
IX	32.5	1 1	XIII	16.5	2 1	XVII	41	3 3

In such a case as the one just described the solidity of the tissues at the base of the trunk prevents wide variation, while in the upper part of the plant the tissues are still growing, and the turgidity of growth necessarily interferes with the processes of contraction and expansion; the furrows are

narrower, so that the arc of contraction and expansion is shorter; and furthermore the ribs arch and close together at the apex of the stem, thus offering a mechanical obstruction to free movement.

FIG. 7.—Curves constructed from measurements of six intervals, three in a northern and three in a southern furrow of sahuaro No. 13, at the following heights: II and IX, 11 inches; IV and XI, 3 feet; V and XII, 3 feet 11 inches. June 27 to October 30, 1905. (For rainfall data see fig. 5.)

EFFECTS OF INSOLATION.

After the first winter's measurements it was stated that "a comparison of measurements from the north and south sides of the same plants shows that the contraction is greater on the south than on the north side and that, while the southern furrows may begin to expand earlier, the northern ones expand longer." Further measurements have confirmed this statement for the winter, the only part of the year during which, at that time, observations had been made; but the summer records subsequently taken, though less complete, indicate that for a period during which there is greater insolation of the north side the reverse holds true.

Sahuaro No. 13 was chosen for observation with direct reference to ascertaining the differences in behavior of the north and south sides of the same plant. On each of these sides a furrow was selected in which seven intervals were marked at corresponding heights, and measurements of these gave the data for comparison. The curves for this plant show little difference as to promptness of response to change in amount of soil-water, except that in March, 1907, some of those on the south side began to fall earlier than the others (fig. 3); but there is a marked difference in the amount of contraction and expansion on the two sides and a plain reversal in the summer of what had been observed in the winter. This is shown most plainly in the descending curves indicating contraction, which will be considered first.

In the fall of 1906, between September 7 and November 19, the intervals on the north side contracted severally from 2 to 18 units, while those on the south side contracted from 8 to 31 units in the same period. But in the summer of 1905 the measurements taken June 27 showed that since May 30 the intervals on the south had contracted from 1 to 8.5 units, while those on the north had contracted from 3 to 18 units in the same time. The same condition of affairs was shown, though in a less marked degree, in the summer of 1906, when, between May 19 and June 25, the intervals on the south side contracted from 2 to 13 units, and those on the north from 2.5 to 21 units.

Without attempting an exact statement as to the modifying nature of insolation on expansion and contraction, the results of the observations may be summed up in the following:

The precipitation records in connection with the curves of expansion and contraction show very clearly that there are two principal seasons of contraction, *i. e.*, the dry times succeeding the summer and winter rains, and that the maximum contraction is reached at the end of these periods.

April, May, and June are usually months in which slight precipitation occurs, and the rapid drying of the soil is followed by contraction of the intervals. After the summer rains are over there is another long, dry season lasting until the winter rains begin, which may be in November, or, in some years, not until January, and contraction of the intervals again takes place. It is, as a rule, the early summer and the late fall in which the sahuaros reach their maximum contraction, and this is manifestly due primarily to the drying of the soil.

It is equally plain, however, that insolation is a potent auxiliary factor. To demonstrate this, an equal number of intervals on the north and the south sides of different sahuaros, 52 intervals in all, were located within 50 degrees or less of the meridian, and the times of their maximum contraction noted. It is impossible to give a complete tabulated statement of the times when the point of maximum contraction is reached, since the

intervals on only a few of the sahuaros under observation were measured in the summer, and for two years the first measurements were not made until after they had begun to expand subsequently to the first winter rain; but from the observations that were made it is clearly seen that the majority of the intervals reaching their maximum contraction from June to September were on the north, and of those which did not do so until just before the winter rains the majority were on the south side.

An accumulation of data of this sort, for the most part omitted here, makes it certain that insolation exerts a marked influence on the expansion and contraction of the trunk of the sahuaro and that, as regards contraction, the prolonged insolation of the north side for a period which includes or is near the summer solstice results in reversing the relations observed in the winter. The inference seems plain that strong insolation is followed by a high rate of transpiration on the side presented to the sun, and this is followed by more rapid contraction of the tissues on that side of the plant. It is obvious that this fact must be borne in mind in any attempt to express quantitatively the extent of mechanical adjustment to varying quantities of stored water of which the sahuaro is capable.

As regards expansion, the most important facts thus far established may be seen at a glance by a reference to the records, or simply by an inspection of the corresponding curves. Referring again to sahuaro No. 13, it is noted that the first measurement after the rains of September 24 and 28, 1905, was made October 2 (fig. 7). All the intervals showed expansion, those on the south side from 1 to 17 and those on the north from 3 to 18 units. On the date of the next measurement, October 10, only 3 intervals on the south had continued to expand, while on the north 6 out of 7 showed further expansion, which in one case was continued to October 16. Between June 27 and July 19, 1905, 4 intervals on the south side expanded and 3 contracted, while on the north side all expanded, one as much as 12 units. A year later, between June 25 and July 30, 1906, the intervals on the south side expanded variously from 1 to 12.5 units, and those on the north side from 2 to 19 units. After the rain of November 18, 1906, the intervals on the south side of this plant expanded more than those on the north, but they also began to contract sooner, so that the northern furrows remained at the maximum of expansion nearly two weeks longer than the southern.

The curves for intervals I (south) and II (north) (fig. 8) for sahuaro No. 6 show that the interval on the south side responded more quickly to the rain of February 6, 1904, but that on the north continued to expand longer and was still expanding March 11, when the interval on the south side had contracted to the same dimensions it had before the rain. From a comparison of these two curves it would seem that the tissues where interval II was measured are more elastic than those at I, and since it is

some 25 units wider it would naturally show more pronounced expansion and contraction, but even with this advantage, in the summer of 1905, between June 27 and July 19, the interval marked in the southern furrow showed more expansion. This, however, for whatever reason, was not the case the following summer. In the fall of 1906 (fig. 9), after the rain of November 18, the southern interval responded more decidedly at first, but the northern one again outstripped it and remained longer at or near its maximum.

Similar data may be derived from other individuals, and some are given in the form of curves in the paper already referred to, but it hardly seems necessary to review a greater number. In general, it may be said that in the fall and winter the intervals on the south side respond more quickly after a rain than do those on the north side, sometimes showing expansion several days before the latter; in the summer the observations on this point were too few to admit of a positive statement. As to amount of expansion, however, it is plain that in the winter the intervals on the south expand more than those on the north side, but that the latter remain expanded longer, and there is some evidence that in midsummer the reverse is true.

While the summer records are incomplete, a tabulated statement (table 2) of the months in which the northern and southern intervals attained their maximum expansion confirms what has been stated as to the more rapid response of the southern furrows in the winter. The same intervals were chosen as for the observation on contraction, and since the most favorable season for expansion is in the winter, when most of the measurements were made, the results are more conclusive. It is evident that the southern intervals expanded more quickly, the majority attaining their maximum in January

FIG. 8.—Curves from measurements of two intervals, one in a south and the other in a north furrow of sahuaro No. 6. Jan. 29 to Apr. 20, 1904.

and February, while most of the more slowly expanding northern intervals did not reach their maximum until March and April.

FIG. 9.—Curves from measurements of two intervals, one in a north and the other in a south furrow of sahuaro No. 6. Oct. 31, 1906, to May 25, 1907.

TABLE 2.—Periods in which the intervals attained their maximum expansion, by months.

Month.	North.	South.	Month.	North.	South.
January	8	23	May	15	13
February	9	20	August	1	1
March	17	6	November	4	1
April	19	9	December	4	6

From the data here presented, and from measurements of other individuals which point in the same direction, it is evident that the simple bellows-like movements of the ribs and furrows of the sahuaro, executed in response to the absorption and loss of water, are appreciably modified by the effect of insolation. There is no other apparent cause for the fact that after a winter rain the ascending curve of absorption of an interval on the south side rises more promptly than does the corresponding curve of an interval on the north side, and reaches a greater height, but falls more quickly and to a lower point; while in summer, with more of northerly insolation, the reverse proves to be true. It is equally clear that, so far as mechanical adjustment is concerned, insolation acts as a secondary factor, and that the curves of expansion and contraction, though distinctly modified, are not radically changed by its influence. But the effect of insola-

tion, though limited, is definite, and it is a matter of much interest that the results of its action are seen not only in accelerating and otherwise modifying the mechanical adjustment of the sahuaro trunk, but are also plainly reflected in its structure.

As shown by plate 3, the furrows of the younger parts of the sahuaro stem are of approximately the same width on all sides, while those of older parts, including especially all the middle portion of the trunk, are distinctly wider on the north than on the south side. Now, as we have seen, insolation, of whatever side of the trunk, results finally in marked contraction, but in this latitude, where the south side receives, for a longer period of time and at a less angle of incidence, the direct rays of the sun, the furrows become permanently narrower than on the north side. That there is here a causal relation can hardly be doubted. The temporary change which has been described, and which is only temporary as far as the younger tissues are concerned, becomes permanent in the older parts of the stem.

Additional evidence of the direct effect of insolation was secured by shading one of two plants growing under similar conditions. On January 20, 1909, a shelter was constructed for No. 10. At first this was composed of a single thickness of burlap, but it did not prove a complete shade either in size or thickness. On February 3 it was enlarged and an additional layer of burlap placed over it.

Another plant (No. 21), about the same size as No. 10 and growing within a few rods of it, was selected for comparison. No. 21 grew on the same slope, was a little smaller, and not in quite as good a condition as No. 10, but an inspection of the two at the beginning of the experiment left the impression that a comparison between them would be a fair one.

The photographs taken in February, 1910 (plate 4), show the very evident difference at that time, and a comparison of the curves of the intervals on the two plants show it even more plainly (fig. 10). The amount of contraction of 8 intervals on No. 10 was 35 units and on No. 21 for the same period 104.5 units. Moreover, the contraction began over a month earlier on No. 21 than on No. 10; the contraction beginning March 5 on No. 21 and April 14 on No. 10.

Temperature records taken for a few days in November, 1909, showed that the temperature through the middle of the day averaged 6° F. lower inside the shelter than outside in the sun.

Before leaving this division of the subject, reference may be made to an interesting phenomenon apparently connected with the effects of insolation. As is well known, the sahuaro produces, in early summer, a large number of conspicuous white flowers very near the apex of the stem. The first flower-buds, though exceptionally formed as early as March, are usually seen in the latter part of April, and the plant is in full flower in May. A regular order in the formation of flowers and opening of buds is observa-

A

B

Two cross sections of a sahuaro trunk, nine feet high.
 A, one foot from top. B, fifteen inches from base.
 The widest ridges mark the north side of the trunk.

Effect of insolation on Carnegiea. The thinner plant had received full exposure to sunlight while the more turgid individual standing near it had been enclosed in a shelter of loosely woven cloth for a year.

ble, the process beginning on the southeast and advancing on either side to the northwest, so that finally the apex of the stem is encircled, wholly or in part, by a crown of flowers.

TABLE 3.—*Difference of internal temperature on north and south sides of the same plant.*

Date and time.	North.	South.	Date and time.	North.	South.
	° F.	° F.		° F.	° F.
Apr. 12—12 ^h 45 ^m p. m.	81.5	86.9	Apr. 15—12 ^h 15 ^m p. m.	77.0	80.6
1 35 p. m.	83.3	89.6	2 25 p. m.	78.8	82.4
3 00 p. m.	86.9	95.0	Apr. 19—1 00 p. m.	72.5	74.3
6 50 p. m.	98.8	101.0	3 10 p. m.	80.6	87.8
Apr. 13—6 40 a. m.	79.3	77.9	Apr. 20—2 50 p. m.	74.3	80.6
1 40 p. m.	86.0	92.3	Apr. 22—10 00 a. m.	51.8	52.7
5 55 p. m.	95.0	98.6	11 00 a. m.	56.6	58.4
Apr. 14—7 35 a. m.	77.0	76.1	12 00 noon	64.4	68.0
5 55 p. m.	88.7	91.4	1 00 p. m.	66.2	71.6
Apr. 15—7 40 a. m.	74.6	74.0	3 00 p. m.	71.6	78.8
10 40 a. m.	75.2	78.8	May 6—1 00 p. m.	70.6	76.1

FIG. 10.—Two curves representing the sums of variations of eight intervals on sahuaro No. 10 (shaded) and No. 21 (unshaded). Jan. 22 to May 21, 1909.

Observations of the internal temperature of a sahuaro trunk were made during the period April 12 to May 6, 1907, by means of bent thermometers, the bulbs of which were inserted about 3 inches below the surface, one on the north and the other on the south side. As shown by table 3, the average temperature indicated by the latter was 1.1° higher in the morning and 4.6° in the afternoon than that shown by the former.

Observations on diurnal change of internal temperature were not made during the time the sahuaro was in flower; but in June and again in November observations were carried through 24 hours. In each case a bent thermometer was inserted directly below the point where the first buds appeared (southeast) and another directly opposite to it (northwest). Table 4 and curves (fig. 11) show the results.

The average temperature was in both cases higher on the southeast and the period of greatest difference in June lay between 5 a. m. and 2 p. m. It seems fair to infer that had the observations been made in April and May, when the sun was farther to the south, the difference between the two sides would have been still more marked. Naturally in November the plants were less warmed by the sun's rays, and consequently internal temperature showed less variation.

While these observations are too limited to admit of further discussion, it is evident that the tissues on the south and southeast sides show a greater number of heat-units than those on the north and northwest, and since the sum of heat-units is a factor of the first importance in determining the date of flowering, it may well be in this case that the regular order in which the buds appear and the flowers open is determined by the same factor.

INFLUENCE OF CHANGES OF AIR-TEMPERATURE.

Of necessity insolation can hardly be considered apart from temperature changes induced by it in the tissues of the sahuaro, but in the discussion thus far it has been connected chiefly with transpiration, since it is probably the increased transpiration of that part of the trunk subjected to the strongest insolation that causes the greater contraction of that part. The effect of seasonal changes of air-temperature would be quite different, and whatever contraction or expansion might arise from this cause would naturally be very difficult to differentiate from that caused by variations in amount of available soil-water; but under certain conditions this can be done to some extent.

An example of expansion following rise of temperature is presented by the records from November 2 to 16, 1906. During this period there was continued high temperature, but no rain had fallen since August 20, and the intervals had been contracting pretty steadily; but the measurements of November 3, 7, and 14 showed distinct expansion of 22 intervals. This is perhaps the most conclusive case of the kind, but the following furnishes additional evidence of the same sort: Between March 16 and 22, 1907, a

TABLE 4.—*Difference of internal temperature on the southeast and northwest sides of same plant for 24 hours in June and November.*

Date and time.	South-east.	North-west.	Date and time.	South-east.	North-west.
	° F.	° F.		° F.	° F.
June 5—11 ^h 00 ^m a. m.	35.0	29.0	June 6—9 ^h 00 ^m a. m.	31.75	24.0
12 10 p. m.	34.0	30.0	10 00 a. m.	33.0	25.25
1 00 p. m.	34.0	32.0	Nov. 17—10 35 a. m.	26.5	18.0
2 00 p. m.	34.0	34.0	11 30 a. m.	21.0	18.5
3 00 p. m.	33.75	35.5	12 30 p. m.	21.0	19.5
4 00 p. m.	33.0	36.5	1 30 p. m.	21.5	20.5
5 00 p. m.	32.25	36.5	2 30 p. m.	21.5	22.0
6 00 p. m.	31.5	34.5	3 30 p. m.	22.0	23.0
7 00 p. m.	30.0	32.0	4 30 p. m.	22.0	23.5
8 00 p. m.	28.5	30.0	6 30 p. m.	21.5	23.0
8 50 p. m.	27.75	29.0	7 30 p. m.	21.5	22.4
June 6—4 40 a. m.	21.5	21.25	8 30 p. m.	21.4	22.0
5 00 a. m.	22.0	21.0	Nov. 18—6 00 a. m.	18.0	18.5
6 00 a. m.	25.5	21.0	6 30 a. m.	17.8	18.1
7 00 a. m.	28.5	21.5	8 30 a. m.	17.8	17.8
8 00 a. m.	30.75	23.0

FIG. 11.—Curves showing differences of internal temperature on opposite sides of sahuaro trunk, constructed from data in table 4. Each vertical space represents 10° F. and each horizontal space 1 hour. The two upper curves should be crossed somewhere between 8^h30^m p. m. and 4^h40^m a. m.

period of high temperature occurred, the thermometer indicating as high as 96° F. The last rain before this was on March 5, and amounted to only 0.25 inch, so that all conditions were favorable for contraction; but during this time of high temperature the measurements made March 20 showed expansion of 13 intervals. Similarly, the measurements of April 10, 1907, showed that 8 intervals were expanding. As already stated, no rain had fallen since March 5, but between April 8 and 15 high temperatures prevailed, the thermometer reaching 97° F. Again, from May 15 to 28 of the same year, no rain having yet fallen and the thermometer reaching as high as 99° F., 5 intervals on sahuaro No. 13 were found to have expanded when the measurements of May 25 were made.

These data appear to furnish sufficient evidence of a slight expansion of parts of the sahuaro trunk in response to rise of temperature. It must be remembered, however, that these changes are local, and in no case do they represent more than a small percentage of all the intervals measured, the larger number acting in such a way as to afford no indication of the influence of temperature. But when all has been said, the consistency observable in the cases reported leaves no room for doubt that there has been a reaction to a definite stimulus, and no other cause than rise of temperature is suggested by the observed facts.

Cases in which contraction is observed to follow lowering of temperature are less numerous and the evidence is less conclusive, but this would naturally follow from the fact that cold periods in the winter usually come just after a rain, so that whatever effect the fall of temperature might have would be offset, wholly or in part, by increased absorption. There is, however, at least one place in the records where there are indications that a fall of temperature induces contraction. From February 3 to 13, 1905, was a period of continued cold weather, the mercury falling to 34° and 35° F. There was rain on February 4, 6, and 7, over 1.5 inches falling on February 6. The intervals had not yet reached the limit of their expansion for the year, and under the conditions we should expect them to expand. As a matter of fact, the larger number did so, but at least 14 intervals on different individuals were found to have contracted.

Further evidence of the influence of temperature is obtained from the data regarding the time and conditions under which the intervals reach their greatest expansion. In the main this is controlled by the time of greatest precipitation, but study of the records makes it plain that this is not the only factor involved. The intervals expand rapidly after the first winter rains, reach their maximum, and remain there, with slight variations, until the ground begins to dry. If the rains mostly come in the fall and stop early, the period of greatest expansion is in the winter, but if they continue even as light rains in the late winter and spring, intervals that have remained almost stationary for two months during the heavy rains will expand a little more.

The following may be cited as examples: In the year 1904-05 there were heavy and frequent rains all winter, and in the latter part of April two rains of over 0.5 inch. In April and May, mostly the latter, 76 intervals reached their greatest expansion, while but 14 did so in December, January, and February. In 1905-06 the heavy rains all occurred in November, and by December all rapid expansion had ceased. There were, however, rains which kept the ground moist through the first part of February. In the latter part of March about 0.5 inch fell, and 0.6 inch on the 8th of April. Under these circumstances, while 50 intervals attained their maximum before the first of March, there were 11 to do so in March and 26 between April 10 and 20. The fact that 37 intervals did not attain their maximum until spring was plainly not due to the lack of soil-water. In 1906-07 the heaviest rains were in December and January, and after a rain of 0.6 inch January 30 no more of any consequence fell until March 5, when there was 0.25 inch precipitation, after which there was but 0.15 inch until June. This year 40 intervals attained their maximum before the first of March, 20 in March, and 29 in the late spring and summer.

It is impossible to study these plants through the spring, when the conditions are so favorable to rapid shrinkage, without being convinced that they do not contract as readily at that time as at other periods of the year. As an example, three furrows on sahuaro No. 1 reached their maximum expansion from May 3 to 5, 1905, and in spite of the fact that there was but 0.03 inch rain in May, only one of them contracted more than 1 unit until after May 12, and they were all broader at that time than in February and March, when the ground was soaked with water, while in May not only was there practically no rain, but the ground was drying with the increased heat. Thus, while the evidence is not absolutely conclusive, it certainly points toward the conclusion that it requires a less amount of soil-water to produce the same degree of expansion in warm than in cold weather.

Reviewing all the available evidence, there seems to be no doubt that both contraction and expansion as the result of changes of air-temperature have been detected by the measurements of intervals on the sahuaro trunk. In the majority of cases, however, this action of temperature is completely masked by the greater movements which are connected with variations in amount of soil-water.

LIMITS OF EXPANSION.

Theoretically the limit of expansion for the trunk of a sahuaro would be determined by the elasticity of the outer shell after the furrows had disappeared; and in some cases in the foothills, where the supply of water is comparatively constant, the ridges are little more than rows of spines and the outline of the circumference would show only slight irregularities. In general, however, this is not true, except on the lignified bases of the trunks. Where the tissues remain green the surface is always in ridges and furrows of varying height, and this is true even where the ground

remains soaked for weeks. Moreover, each plant seems to have a very definite limit beyond which it will not expand, no matter how much water it can get.

FIG. 12.—Curves from measurements of three intervals on sahuaro No. 1 and one curve (a) showing combined variation of the three others. Effects of watering. November 28, 1908, to May 14, 1909.

During the winter of 1904–05 the ground was wet much of the time from January 1 to April 15. If at any time between these dates a sahuaro which had been deprived of water for some time had been transferred into this soil, it probably would have absorbed water and expanded rapidly. But the sahuaros which were already in the ground, while they responded promptly to the first rains, showed little or no expansion thereafter until the warm weather in May. In the following winters, 1905–06 and 1906–07, though less rain fell, the intervals reached practically the same size. But in the winters of 1903–04 and 1908–09 there was so little rain that the ground was not saturated long enough at any time for the intervals to reach their maximum expansion. These statements will be evident from table 5, which shows the greatest expansion attained by the three marked furrows of No. 1 for several years.

On March 2, 1909, after the winter rains were over, the three intervals together measured 45 units, or about five-eighths of an inch less than on March 4 of the preceding year, and this in spite of the fact that some water had reached the roots of the plant by artificial means. After this, at several times, the plant was watered (fig. 12), but not enough to take the place of the thorough wetting of the ground from a rain. The plant responded by an expansion of the furrows, but the increase only amounted to 12 units, leaving them considerably smaller than in previous years.

TABLE 5.—*Greatest expansions reached by the intervals of sahuaro No. 1 for 5 years.*

Date.	No. of interval.		
	I.	II.	III.
	<i>units.</i>	<i>units.</i>	<i>units.</i>
Mar. 2, 1904	108	121	129
Feb. 22, 1905	116	126	137
Mar. 22, 1905	117	128	137
May 3, 1905	119	131	140
Nov. 20, 1905	119	128	139
Mar. 31, 1906	118	130	138
Apr. 10, 1906	119	131	139
Mar. 20, 1907	114	126	138
Mar. 2, 1909	104	110	115

It therefore seems plain that (1) the sahuaro has a limit of expansion, and when it is reached the water taken up by the roots is limited by the amount of transpiration; (2) that the maximum expansion is reached only when the soil is saturated with water for some time.

VARIATION IN WATER-CONTENT.

For the determination of the water-content of the sahuaro trunk two individuals were selected, one of which measured 211.5 cm. and the other 176 cm. in height. These were cut down May 22, 1907, after a long, dry period, there having been only 0.5 inch of rain since February 1, and this so scattering that relatively small amounts could have been available for the plant. Under these circumstances the percentage of water would be less than if the determination had been made after a rainy period. On the other hand, the individuals were young and in normal condition, so the presumption is that the results are as nearly representative as could well be obtained.

Three sections, each measuring 3 cm. in thickness, were taken from each individual, one 6 cm. above the ground, one just below the apex of the trunk (just below where the marked curvature begins), and the third halfway between these two. A quarter of each section was placed in a can immediately after cutting, and the can then tightly closed to prevent loss of water. In each case weighings were made of the can and its contents, after which the piece of sahuaro was removed and thoroughly dried in a

ventilated attic. As this was done in summer, when there was a very low percentage of atmospheric humidity, it is safe to assume that very little more loss of weight would have resulted from any other method of artificial drying. Accordingly the weights before and after drying and the water-content in per cent of the original fresh weight, as given in table 6, may be taken as correct within a narrow limit of error.

TABLE 6.—*Amount of water in sahuaro trunk obtained by air-drying at ordinary temperatures.*

Section.	Plant 1; height 211.5 cm.				Plant 2; height 176 cm.			
	Fresh weight.	Dry weight.	Loss.	Loss per ct. of fresh weight.	Fresh weight.	Dry weight.	Loss.	Loss per ct. of fresh weight.
	<i>gms.</i>	<i>gms.</i>	<i>gms.</i>		<i>gms.</i>	<i>gms.</i>	<i>gms.</i>	
1	400.7	82.5	318.2	79.41	288.2	64.487	223.718	77.62
2	576.57	60.852	515.718	89.45	421.135	73.03	348.105	82.65
3	475.00	47.02	427.98	90.1	283.61	29.855	253.755	89.12

From the data thus obtained it is seen that for the sahuaro 211.5 cm. high the total amount of water in an average section 9 cm. thick is 5.048 liters, and the amount in the whole plant (not allowing for narrowing at the apex) 118.618 liters. For the sahuaro 176 cm. high the total amount in an average section 9 cm. thick is 3.302 liters, and in the whole plant (not allowing for narrowing at the apex) 64.576 liters.

A more accurate and complete analysis was made of one plant growing on the slopes west of Tumamoc Hill on October 17, 1909. This plant consisted of a single cylindrical trunk 5.6 meters high, with a maximum diameter at the largest part of 60 cm. The total weight was found to be 767.8 kg. A sample including the normal proportion of spines, epidermis, cortex, wood, and medulla, weighing 3.024 kg., was taken for water determinations, being dried in an oven. From the data thus obtained it was found that the body of the plant contained 91 per cent of water, which may be taken as being near the maximum, since the plant was very turgid. The highest water-content is found near the apex of the trunk and the lowest near the base, in which the woody cylinder occupies a large part of the cross-section.

By quite a different method the attempt was made to calculate the amount of water which might accumulate in a trunk within a stated period. Sahuaro No. 11, a plant some 6 meters in height, had the spines removed in two circles about the trunk, one about 2 meters, the other about 0.65 meter from the ground. The circumference was accurately measured at these places by a metal tape. By this means the extent of shrinkage during drought and of expansion after rain was determined for the entire circumference.

The extreme differences in the circumference at the upper place of measurement between the time of the greatest contraction (November 14,

1906) and that of the greatest expansion (March 9, 1907) amounted to 27.3 cm. and at the lower to 8.1 cm., showing a difference of 19.2 cm. in the expansion at these two points, the upper part expanding nearly three times as much as the lower one. As stated, the plant in question was 6 meters high, and as the variation increases instead of decreasing toward the top, it will be well within the limits of safety if we assume the variation at 2 meters as the average.

At this height, at the time of greatest expansion, it measured 1.713 meters in circumference. This gives a diameter of 54.532 cm. At its minimum the circumference was 1.44 meters, giving a diameter of 45.8 cm.; that is, there is a difference of 8.732 cm. in the diameter at maximum and minimum. This represents the gain of a hollow cylinder of water measuring 1.713 meters on its outer and 1.44 meters on its inner circumference, with a thickness of 4.362 cm. and a height of approximately 6 meters, or a volume of 412.393 liters of water, which were absorbed and stored between November 14, 1906, and March 9, 1907. In addition to the amount lost by transpiration, which would not be inconsiderable, this calculation does not take the branches into consideration, so that the total amount taken up must have been much more than the amount given.

A general review of the observations shows that the water-balance is depleted very slowly by transpiration, and that the loss is quickly regained in the rainy season. Thus the circumference of sahuaro No. 11 decreased at the rate of 4.3 mm. per day from March 6 to June 1, the dry foresummer, but increased at the rate of 6 mm. per day from November 17 to December 15, 1906. After the last date the rate fell to zero in March, 1907, when a shrinkage set in, which reached a rate of 2.3 mm. per day on May 25, 1907.

The rate of water-loss from the flowers by transpiration, however, has been found to be very rapid. The flowers are produced in large numbers immediately below the apex of the trunk, where they form a conspicuous crown, including several hundred in favorable seasons. Relatively few are open at any one time. The production of buds and opening of flowers begin on the southeast side, and from there advance to the northwest, until the top is nearly or quite encircled, the process requiring several weeks for its completion. It has been observed that the number of flowers is much greater in wet than in dry years, and that they are especially numerous on individuals of the giant cactus growing where there is a constant and abundant water-supply.

It is evident that during the period of flowering an additional demand is made upon the water that the plant has stored during the winter rainy season. In order to form some estimate as to the extent of this, some determinations were made of the actual transpiration of the sahuaro flowers and buds in the summer of 1907. These were cut from the plant and the cut end at once covered with vaseline to prevent evaporation; they were

then weighed, and weighed again at the end of an hour, during which they were left in the open air in full sunlight. Table 7 shows the amount of water lost.

TABLE 7.—*Loss of water by transpiration in flowers of sahuaro.*

Original weight of flower.	Loss.	Time of exposure.	
<i>gms.</i>	<i>mg.</i>		
39.390	848	11 ^h 45 ^m a. m. to 12 ^h 45 ^m p. m.	
34.145	805	11 15 a. m.	12 20 p. m.
40.027	885	2 05 p. m.	3 05 p. m.
37.337	925	1 50 p. m.	3 00 p. m.

The average transpiration of a fully opened flower, as shown by these weights, is 851 mg. for an hour of full sunlight. Each flower lasts but one day, but a single plant may bear hundreds, and the transpiration of the bud must go on for many days; so it is clear that the water lost by the plant during the flowering season is no small amount, and, moreover, in estimating the amount of water used by the inflorescence we must add that used in the tissues of the flowers themselves.

The dry weight of one flower was found to be 13.2 per cent of its weight, leaving 86.8 per cent as the water-content. Estimating from the average of the flowers weighed, about 3.27 liters of water are stored in the tissues of every 100 flowers.

Notwithstanding these amounts, which in themselves seem very considerable, they form such a small portion of the entire amount stored in the plant that no difference has ever been detected by the measurements in the contraction of flowering and non-flowering plants, though the flowers are mostly formed after the end of the winter rains, when there is comparatively little water in the soil. It is worth noting, however, that the plant does not flower until it has attained considerable size, and that, as has already been pointed out, the abundance of flowers is directly correlated with the amount of available water in the soil.

GROWTH.

But little evidence has been obtained as to the relation between the growth of the sahuaro and rainfall. Growth in length occurs during the time of the summer rains, and these have not failed for a single season since the observations were begun. There is, however, a single instance where a plant under observation was deprived of a part of its water-supply. Sahuaro No. 9 (plate 5) grew close to the laboratory and at times received some water from artificial sources. Between April, 1905, and January, 1906, it increased 19 cm. in height. This was the greatest growth which any measured plant attained during that summer. The following summer

Three stages in the growth of a small sahuaro. No. 9. A, May, 1904.

B, Dec., 1906. C, Feb., 1909. The three pictures are not exactly on the same scale. For comparative lengths, see table 8.

an addition was made to the laboratory; a stone wall and cement gutter were built over the roots of the plant, and one large root was cut off. For a time it was very much shriveled up, but it soon put out new roots and recovered; yet the following year it grew but 5.5 cm., while in the next two years it gained 22 cm., or an average of 11 cm. each year. So far as this evidence is of value it indicates that growth in height may be checked by a lack of water. The enormous development of the storage system of the sahuaro might, however, render the plant in good measure independent of ordinary seasonal vicissitudes in the matter of growth.

GROWTH IN CIRCUMFERENCE.

From simple inspection of young and old sahuaros it is evident that the trunk grows in thickness for a period of years, after which it maintains a very nearly exact columnar form. The base of a sahuaro trunk, for a foot more or less from the ground, is usually distinctly smaller than any other part, and its diameter may steadily increase from below upward (plate 5) until the plant attains a height of 6 feet or more. This is because growth in this species is apical, and the increments of each succeeding year increase in diameter until the trunk attains its full thickness, after which it maintains through its life a substantially uniform size.

At the base of all but the very young plants there is always a brown portion of the trunk which extends upward as the age of the plant increases. Here the ribs and furrows are sometimes hardly discernible, and the surface is rough and suberized. The tissues, too, from circumference to center are thoroughly hardened. Along the irregular boundary between this and the green part of the trunk longitudinal cracks often appear in the green shell of epidermis and mechanical tissue; the edges of the crack draw apart for some time, perceptibly widening the furrow in which they occur, and finally the whole is overlaid by suberized tissue. The repetition of this process has its share in causing the brown appearance of the base of the trunk. This phenomenon of cracking and the fact that in the older plants the furrows for the first few feet are often almost flattened out are indications of a slight growth in circumference at the base of the trunk.

If the green trunk of the sahuaro increases in circumference after it attains its columnar form it should be evident by an increase in the size of the intervals from year to year; but of 84 intervals measured for four successive years, from 1903 to 1907, only 10 attained a greater width in 1907 than at any other time; 8 of these 10 were on a small cactus, measuring a little more than 3 feet high; 4 were so close to the top that the furrows in which they were located would expand with the elongation of the trunk; 2 were close to the base, and but 1 in the middle of the trunk. It is plain that if growth occurs in the diameter of the main body of the sahuaro it is exceedingly slow, especially after the plant has attained 4 or 5 feet in height.

GROWTH IN HEIGHT.

Over a dozen sahuaros were measured from time to time during a period of from 2 to 4 years for the purpose of ascertaining the essential facts of their longitudinal growth. A sharp-pointed style, made to slide along an upright standard, on which was a metric scale, indicated the distance from a fixed point at the base to the topmost point of the converging ribs, so that the vertical growth during a given period was determined by subtracting the measurement at the beginning from that made at the close of the period; besides this, points were located at equal distances along some of the furrows, and these distances were carefully measured from time to time. Except at the apex, no lengthening of the stem was ever detected, and the necessary conclusion follows that the longitudinal growth of the sahuaro is strictly apical.

TABLE 8.—*Growth in height of Carnegiea gigantea.*

Date.	No. 4.	No. 9.	No. 10.	No. 12.	No. 19.	No. 21.	No. 22.	No. 24.	No. 25.
1905.	<i>meters.</i>	<i>meters.</i>	<i>meters.</i>	<i>meters.</i>	<i>meters.</i>	<i>meter.</i>	<i>meters.</i>	<i>meter.</i>	<i>meter.</i>
Apr. 26	1.621	1.418	0.868						
May 3				1.638					
May 12					2.236	0.704	2.302		
1906.									
Jan. 23	1.695	1.613	.922	1.724	2.392	.839	2.411		
Mar. 8								0.045	0.374
May 10		1.622						.059	.384
May 18			.931		.851				
1907.									
Jan. 23	1.832	1.679	.993	1.744	2.444	.898	2.547	.074	.435
Mar. 27	1.826	1.706	.997			.902		.076	.430
May 17	1.838	1.711	.993	1.749	2.461	.909	2.545	.080	.438
1908.									
Mar. 23			1.062			.969		.096	.518
Oct. 22	2.049	1.899		2.068	3.016		2.832		.668

The longitudinal growth of nine individuals, measured as indicated, is given in table 8. The period of measurement extended over nearly 5 years, but only Nos. 4 and 9 were measured for the full length of this time. It will be seen that in most of these cases the growth is slow and also irregular. The average growth for sahuaros over a meter in height is about 12 cm. per year, but the very small ones grow very slowly; for example, No. 24 grew only 4 cm. in 2 years.

If we assume 10 cm. as the average rate of yearly growth, it follows that the sahuaros on the laboratory domain which have attained a height of from 1 to 10 meters (a large proportion of them fall within these limits) have been growing where they now stand for periods ranging from 10 to

100 years. As already stated, the observations leave no room for doubt that the period of active growth is in summer. Though not clearly indicated in the table, the fact may be accepted without question.

Plate 5 shows the characteristic change in the contour of the younger plants. The earliest photograph exhibits the stage in which the circumference increases up to within a few inches of the apex, while the later pictures of the same plant show it after it has assumed its columnar form. Table 8, No. 9, shows the rate of growth for the period during which the photographs were taken. The pictures are not all made to the same scale, as the table will show.

BISNAGA (*ECHINOCACTUS WISLIZENI*).

The measurements of *Echinocactus* were not so extensive as those on the sahuaro, but when taken in connection with the work already done on the sahuaro they serve to establish certain important facts. It is plain from the beginning that the bisnaga, like the sahuaro, adjusts itself to varying quantities of stored water by a bellows-like action of its ribs. In the winter of 1903-04 two plants were marked in the same manner as the sahuaros, one with three intervals on the north and the other with three intervals on the south side of the plant, and in 1909 another plant (No. 11) was marked all around the circumference, each interval including two furrows measured from the edges of the ribs. Each of the three plants responded in the same manner as the sahuaro to the presence or absence of water in the soil, and in one case where a little water accidentally reached the roots the effects were plainly evident (fig. 13), expansion replacing contraction in a very dry time and continuing nearly a month from the time the plant was watered. The only difference which was apparent between the responses of the sahuaro and the bisnaga to soil-water seems to be that contraction and expansion are somewhat less pronounced in the latter.

In the winter of 1903-04 the greatest expansion of any interval in a bisnaga was 13 units, while one interval on a sahuaro expanded 38 units, and many from 15 to 20. The greatest contraction of any interval on a bisnaga was 16 units, and on the sahuaro the contraction reached as high as 30 units. It might seem that the small number of bisnagas under observation scarcely warrants this conclusion, but the same difference is also shown in the single plant marked in 1909. This may be partly due to the fact that in many cases a furrow of the *Echinocactus* represents a smaller fraction of the circumference than does a furrow of the sahuaro.

EFFECTS OF INSOLATION.

The same phenomenon as in the sahuaro (though again in a less marked degree), of broader furrows and thicker ribs on the north than on the south side, is evident in the bisnaga; but in the bisnaga there is another morphological character which is also related to insolation. The ridges are not only thicker, but longer, on the north side. This causes the plant to bend slightly to the south, so that the growing apex, except in the very young plants, is never straight on the top, but faces the south.

FIG. 13.—Curve representing the sum of the variations of the intervals comprising the entire circumference of a bisnaga (No. 11). Sudden rise in curve shows the combined effect of a light watering and a very light shower. January 2 to May 21, 1909.

The comparative amount of response to insolation has not thus far been definitely determined. On the two plants under observation in 1904 the furrows on the south began to contract from one to three weeks earlier than those on the north, but the fact that only two plants were being considered, and that one was marked only on the north and the other only on the south, gives us the element of individuality to which the variations might be due instead of insolation. The plant marked in 1909 showed no perceptible differences in the contraction or expansion of the two sides,

but two plants which had been uprooted and exposed to the sun at the same time and were drying up did exhibit a very marked response to insolation. These were Nos. 9 and 10, described on pages 61 and 63.

Bisnaga No. 9.—On January 6 the plant was taken from the porch where it had been standing and placed on a stone wall near the south side of the laboratory, in the full sun. Intervals were marked all the way around. At first some of those on the north increased slightly, but after January 19 every interval contracted. Fig. 14 shows two curves constructed from the data furnished by this plant, *N* showing the contraction of an interval on the north and *S* on the south side of the plant. The interval most directly north contracted 20 and that most directly south 48 units, while the sum of the contraction of the intervals on the north was 145 and on the south 213 units.

FIG. 14.—Two curves, *N* from measurements of a northern, and *S* from a southern interval on bisnaga No. 9. January 6 to May 21, 1909.

Bisnaga No. 10.—This plant stood within 6 inches of the south wall of the laboratory. On November 17, 1908, three intervals were marked, No. I on the side away from the wall, No. II on the side next the wall, and No. III between them on the east. It was left in this position until January 2. During this time No. I lost 22 units, No. II lost 10 units, and No. III lost 17 units. On January 2 the plant was turned around so that No. I faced the wall, II away from the wall, and III the west. As would be expected, II began to contract much more rapidly than before. The rate of contraction also increased in III, though to a lesser degree, but No. I actually expanded until January 22, gaining 8 units, and at the end of the experi-

ment, May 21, was only 2 units smaller than on January 2, when it was turned toward the wall. Moreover, between March 30 and April 10 it expanded 6 units after having been contracting for nearly two months. The rapid contraction in other parts of the plant must have caused a mechanical pull which held the ribs on the opposite side apart while they were drying up, though less rapidly, than the other parts exposed to the sun (fig. 15).

FIG. 15.—Three curves from measurements of intervals on bisnaga No. 10.
November 17, 1908, to May 21, 1909.

This evidence is from plants which were not under normal conditions, but taken in connection with the morphology of the bisnaga it confirms the conclusion that the effects of insolation in the bisnaga are practically the same as in the sahuaro.

COMPARISON OF WEIGHTS AND MEASUREMENTS.

In addition to the observations on normal growing plants, some of the bisnagas described on pages 54 and 58 which had been uprooted and brought to the laboratory were marked and measurements made in order to correlate, if possible, the loss by weight with that by volume, as indicated by the measurement of parts of the circumference. At the same

time one plant growing in the ground was marked and records kept for comparison with those that had been taken up. The numbers used in referring to these plants are the same as those used on pages 54, 58, and 61, and indicate the same individuals.

Bisnaga No. 3 (see page 54).—On February 2 each rib was measured at its base in approximately the same plane. In two cases the ribs were so shrunk together that one measurement had to include two ribs. At first the circumference continued to shrink slightly, losing 7 mm. by February 12; after that it gained about 3 mm., and then remained practically stationary until May 21, when measurements were discontinued. On October 11 it was again measured and found to have gained 21.2 cm. in circumference. On account of the plant being in the earth it was not practicable to ascertain its weight at this time, but this increment in circumference represents an increase of 6 cm. in diameter, and since the bisnagas shrink in all directions there was probably a similar gain in height.

Bisnaga No. 6.—On December 12, 1908, the whole circumference of about 132 cm. was marked off into intervals of two furrows each, measured from the edges of the ridges, and measurements of these were taken at intervals until May 21. During that time the circumference had lost 2 cm. Judging from the measurements, the circumference at times seemed to increase slightly. This could hardly have been the case, for the plant was at this time under the same conditions as the others which showed a constant loss of weight. It might possibly be explained as due to a shifting of the internal pressure, so that the part of the circumference measured was actually increased at the expense of some other part. When the plant was measured again, October 28, 1909, the circumference had farther shrunk 2.3 cm., making a total loss since December 12 of 4.3 cm.; and besides this it had lost 4.1 cm. in height. This is offset by a loss in weight of 2,235 grams.

The irregular outline of this plant makes any computation as to the comparison of loss by weight and measure impracticable, but comparative measurements and weights of Nos. 6 and 9 show that the loss in circumference does bear a fairly direct proportion to loss in weight. From January 25 to May 21 No. 6 lost 2 cm. in circumference, while No. 9 lost 13 cm., or 6.5 times as much. During the same period No. 9 lost 6.33 times as much weight as No. 6. On the other hand, an effort was made with two plants to estimate loss in circumference by the measurement of a small portion of the same. This method was found to be totally unreliable, as the proportions of loss in weight and circumference, during the time of measurement, were completely reversed (p. 58).

Bisnaga No. 9, which served in the experiment for effect of insolation, was placed in the ground after losing 4.840 kg. Up to May 21 it had lost approximately 5.238 kg. in weight and 13 cm. in circumference. On

October 20 it had gained 10.685 kg. in weight and 29.5 cm. in circumference. The proportion of loss in weight and circumference to the gain in the same do not agree very well, the loss in weight being 403 grams per centimeter of circumference and the gain 368 grams per centimeter. It must be remembered, however, that the loss was not exactly known, but was estimated for 29 days since the last weighing (p. 61).

The measurements of *Echinocactus*, so far as they have been carried, show: (1) the same principles in general govern its expansion and contraction as in the case of the sahuaro; (2) measurements of a part of the circumference are not necessarily proportional to the whole; (3) measurements of the entire circumference may agree almost exactly with changes in weight, but the changes in any one dimension, in a plant where the changes of form are more or less local, can not be relied upon to bear exact proportion to changes in weight. The only safe method of drawing conclusions from such data is in the comparison of a large number of measurements carried through a considerable period of time.

GROWTH.

From the great difference in the morphology of *Carnegiea* and *Echinocactus* it is plain that their growth must be very unlike. Both start in much the same form, but one may become a branched column 15 meters in height, while the other never branches and rarely attains the height of over a meter.

TABLE 9.—Rate of vertical growth of *Echinocactus wislizeni*.

Date.	No. 1.	No. 2.	No. 3.	No. 4.	No. 5.	No. 11.
	<i>meter.</i>	<i>meter.</i>	<i>meter.</i>	<i>meter.</i>	<i>meter.</i>	<i>meter.</i>
May 10, 1905	0.603	0.655				
Jan. 23, 1906		.658				
Mar. 8, 1906			0.070	0.064	0.122	
May 10, 1906			.083	.071		0.116
Feb. 18, 1907			.106	.078	.201	
Mar. 27, 1907		.700	.110	.084	.216	.146
June 6, 1907			.102	.087	.208	.140
Mar. 23, 1908	.709			.108	.237	.164
Oct. 22, 1909	*.770	.758		.125	.248	.245

*This was only approximate, as the original mark near the base could not be found. It is probably within 2 cm. of the correct measurement.

The younger plants seem to grow almost equally in all directions, as they assume an almost globular form, which continues until they are about 30 cm. high. Occasionally a plant is found which seems to have grown faster laterally than vertically, since its diameter exceeds its height; but plants over about 30 cm. high begin to assume a cylindrical form with the apex facing the south. The growth in length is apical, and the increase in circumference is provided for by the insertion of new ribs from time to time.

While the furrows do become much flattened at the base, this is not such a prominent feature as in the sahuaro. They are often partially spiral near the top and in the older plants.

The rate of growth in height is much slower than in the sahuaro, as is shown by table 9. The records were obtained in the same manner as the similar ones of the sahuaro.

Plant No. 11, which was described on page 31, after growing 5 cm. in 2 years, suddenly increased 8 cm. between March, 1908, and October, 1909. This is the only instance observed of such rapid growth. No. 2 increased only 10 cm. in 4 years; No. 3 nearly 5 cm. in 2 years; and Nos. 4 and 5, 6 cm. or more in 3 years. Judging from the plants measured, the average growth is a little more than 2 cm. per year. At this rate it would require over 40 years for a plant to attain the height of a meter.

PRICKLY PEAR (*OPUNTIA* SP.).

While work on the *Opuntia* was carried on during several seasons, the measurements of any one plant extended only through a single season, and consequently the results, like those of the bisnaga, are of a fragmentary nature. Naturally, too, the problems presented by the *Opuntia* are of a very different nature from those of the sahuaro. It can not, in the nature of the case, store such quantities of water, and its mechanical system is developed in an entirely different manner; but it is apparent that the joints do have the capacity to store some surplus water and that the segments vary in thickness under varying external conditions.

In order to determine the relation of these conditions to the changing thickness of the *Opuntia* joints, four plants were selected in the fall of 1906 and the thickness of the joints measured at marked places by means of micrometric calipers from November 3, 1906, to May 25, 1907. Owing to difficulties in always placing the instrument at the same angle, and to the nature of the instrument itself, these measurements were not as accurate as those made by dividers upon the sahuaro, but in using the figures obtained anything less than a hundredth of an inch was discarded, and in making the curves of expansion and contraction it is evident from their similarity that their general trend can be relied upon and certain facts established.

Prickly pear No. 1 (*Opuntia discata*) was measured four times on the same joint. As might have been expected, the four series of measurements were very similar throughout. On April 10 two small buds were seen on the segment under measurement, and on May 15 they were within a few days of flowering. On May 25 they had been picked off.

On No. 2 (*Opuntia toumeyii*) six terminal joints were measured, each in one place. Three joints were on the north and three on the south side of the plant, but no difference was evident between the two sets. Budding

was first seen on March 11 and by March 29 twenty-three buds were developed on five of the six joints measured, two of which formed joints and four remained undeveloped. By April 29 six had flowered and the rest were nearly ready to do so (fig. 16).

On No. 3 (*Opuntia discata*) eight terminal joints on different parts of the plant were measured, each in one place. Budding was first seen on March 18, and by March 29 each of the eight joints was bearing from 1 to 13 buds, 55 in all, 3 of which failed to develop.

On No. 4 (*Opuntia* sp.) six joints were measured, each in one place. These six joints formed a series, of which 1 was the oldest and lowest and 6 the terminal joint. On March 11 a bud was seen on the second joint, followed on March 18 by one each on the fourth and sixth. By April 29 the three were nearly full-grown.

FIG. 16.—Curves from measurements of six *Opuntia* segments of plant No. 2, three on north and three on south. X shows date when buds were first seen. November 3, 1906, to May 25, 1907.

In constructing the curves from the measurements of *Opuntia* each vertical space represents 0.01 inch and each horizontal space 1 day.

It was perfectly plain that the joints increased in thickness under the influence of added water in the soil. In fact, this needed no demonstration, for the contrast between the thin, wrinkled segments at the end of a long dry period and the same parts, smooth and well filled out after a rain,

is a striking phenomenon, familiar to even a casual observer. But a careful study of the measurements revealed some other facts and some points of difference between the response of the *Opuntia* joints and that of the sahuaro trunk.

When the measurements were first made it was at the end of a long dry period, no rain sufficient to wet the ground having fallen for over two months. A few drops did fall on October 29, five days before the first measurement, but it lasted only a few minutes and cleared, leaving the ground dry. But in the following two weeks, before any rain came, the segments, already much shrunken, showed in many cases a gain in thickness (fig. 16).

After the rains came the plants responded by a considerable increase in thickness, but, like the sahuaros, they seemed to reach a limit of expansion soon after the ground was thoroughly soaked, and then not to increase to any marked degree. But the *Opuntias* (with the possible exception of No. 4) showed a second period of expansion which began early in February and continued a month or more, although there had been very little rain. The joints reached their fullest expansion when the buds of the flowers and new joints began to develop. The beginning of the dry period in the season during which the measurements were made was almost coincident with the beginning of the contraction of the *Opuntia* segments, and this corresponded very closely with the time of contraction of the sahuaro trunk. The fact that at this time buds were developing most rapidly might of course be a factor in the ensuing shrinkage, but there was no evidence to support this inference, for the measurements showed no difference between the segments that bore buds and those that did not.

There was no apparent difference between the expansion of the joints on different sides of a plant, but in case of a series of joints the older (lower) ones expanded more than the younger ones. The three lower segments became too thick for measurement with the instrument, the limits of which were 1 inch, so that the exact amount of expansion is uncertain; but ignoring all beyond an inch (which is considerable), the lower three joints expanded 30 units more than the upper three. (In speaking of the *Opuntias* a unit represents 0.01 inch.)

The manner of growth of the *Opuntia* segment is told in plate 6, which shows the joints in different stages of development. Their period of growth is in March and April. The new joints are, for the most part, borne on the terminal ones of the plant, but they may also be produced on the older joints. Table 10 shows the growth in length and width of four segments from March 27 to April 10. It is evident that the growth is soon completed, as segments 1 to 3 grew 3.35, 3.97, and 4.92 cm. in length in 13 days, while No. 4 increased 6.8 cm. in 19 days.

When the young joint has become fully expanded its growth in length and breadth practically ceases and these dimensions do not share in the

changes which occur when water is absorbed or given up. Some measurements made from November 3, 1906, to January 29, 1907, during a period of expansion showed absolutely no changes except in the one dimension—thickness. In this dimension, however, the joint not only changes with the water-content, but also from year to year, gaining in thickness especially as it bears other joints. It has seemed possible that the second period of expansion, which occurred at a time when the sahuaros were contracting, might be due to growth preparatory to the formation of flower-buds and new segments (fig. 16).

TABLE 10.—Rate of growth of *Opuntia* segments.

Date.	No. 1.		No. 2.		No. 3.		No. 4.	
	Length.	Width.	Length.	Width.	Length.	Width.	Length.	Width.
	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.
Mar. 27	2.93	2.47	1.95	1.55	2.23	2.09		
29	3.53	2.90	2.12	1.93	2.32	2.26	1.60	1.72
30	3.90	3.50	2.23	2.20	2.63	2.53	1.88	1.92
31	4.10	3.85	2.43	2.32	3.13	2.83	2.00	2.00
Apr. 2	4.55	4.10	2.95	2.80	3.64	3.28	2.30	2.25
3	4.70	4.10	3.10	2.80	3.70	3.30	2.50	2.35
7	6.10	5.20	4.10	3.65	4.70	4.05	3.20	2.80
9	7.10	6.20	4.70	3.90	5.50	4.60	4.20	3.50
10	7.85	6.60	5.30	4.50	6.20	5.00	4.75	3.65
17							8.40	6.80

The number of buds borne by an *Opuntia* is sometimes very great, but this varies with the species. One medium-sized plant of *Opuntia* bore 247 flowers in a good year. They were borne on 56 joints. Table 11 gives some data as to the relative number of flowers and joints. Since these data were collected before the species to which the plants belonged had been identified, the name of the species is not given.

TABLE 11.—Relative number of buds and segments on *Opuntia* sp.

No. of speci- men.	No. of full- grown joints.	Flow- ers and flower- buds.	New joints.	No. of speci- men.	No. of full- grown joints.	Flow- ers and flower buds.	New joints.	No. of speci- men.	No. of full- grown joints.	Flow- ers and flower- buds.	New joints.
1	80	88	1	8	22	4	2	15	46	30	3
2	95	103	2	9	34	60	0	16	46	10	1
3	56	30	10	10	119	144	12	17	53	30	2
4	137	113	7	11	37	50	3	18	31	9	0
5	100	247	...	12	37	5	2	19	67	58	10
6	23	0	9	13	34	33	3	20	38	14	6
7	13	0	2	14	146	77	2	21	59	43	7

Six stages in the development of an *Opuntia* segment. In the oldest, 6, the leaves are beginning to drop off and the spines are appearing.

The proportion of the number of flowers and young joints to the entire number of segments in the plant indicates that there must be a considerable drain upon the water stored in their tissues to support transpiration and to form the new tissues. To gain a more exact knowledge of the amount of water required for these purposes, weighings of flowers and buds were made, as in the case of the sahuaro. Table 12 shows the amounts transpired in an hour by the different parts of the *Opuntia*, together with the dry weight and percentage of water in two flowers and joints.

TABLE 12.—*Loss of weight by transpiration, and water-content of flowers, buds, and segments of Opuntia.*

	Original weight.	Loss.	Time.	Dry weight.	Percent- age of water in original weight.
	<i>gms.</i>	<i>mg.</i>		<i>gms.</i>	
Flower.....	23.570	260	12 ^h 15 ^m to 1 ^h 15 ^m p. m.	3.281	86
Do	23.677	262	1 45 2 45 p. m.	3.222	86
Do.....	23.949	279	3 10 4 05 p. m.		
Bud.....	17.542	187	2 45 3 45 p. m.		
*Joint of present season	111.655	205	1 20 2 20 p. m.	22.690	89
Joint 1 year old at least.....	118.790	233	2 00 3 00 p. m.	37.095	82

*Approximate surface 306.15 sq. cm.

It will be seen from table 12 that the proportion of water in the flowers, buds, and plant itself are not far from that in the sahuaro. The average transpiration of a flower in an hour of full sunlight, as shown by these weighings, is 267 mg., and that of a joint seems to be nearly as much. The transpiration of No. 10, table 11, would be 67 c.c. per hour of full sunlight if all the flowers were open at once. But according to the percentage of water in the plant itself, one of the joints would contain about 100 c.c. of water, and the plant in question only had 119 joints previous to the flowering season. It is likely that this estimate of the water in the joints is low, for it was made in May, after they had been contracting for some time, but at the best it is evident that the roots of the *Opuntia* must, in such cases as the foregoing, be able to draw some water from the soil, even in a dry time, to make good the loss from transpiration.

SUMMARY.

The data presented in the preceding pages, together with the conclusions to which they lead, may be summarized as follows:

(1) Observations on the mechanical adjustment of the sahuaro trunk have been greatly extended and the conclusions drawn from previous studies have been confirmed. This has been especially emphasized in what has been established regarding the direct adjustment of the plant to amounts of available water in the soil.

(2) In the course of measurements continued for a term of years it has become apparent that each plant has a marked individuality as regards promptness, extent, and duration of response to external stimuli, so that it is even possible to predict its behavior with a considerable degree of accuracy. Parts of the same plant also show certain peculiarities of response. These are referable to internal changes, and especially to shifting of pressure in the tissues. The causes of the former are not yet clearly determined.

(3) Insolation is a potent secondary factor operating in conjunction with water-supply and modifying its effects, though not to such an extent as radically to change the curves by which these effects are expressed. Under the influence of insolation, expansion after rain is more prompt, but contraction during long periods of drought is also more marked on the side most strongly insolated. Such contraction is greater in the winter on the south side of the trunk, while in summer, for the period during which there is greater insolation of the north side, the reverse holds true. For the year taken as a whole it results that the furrows on the south side of the sahuaro are considerably narrower than those of the north side. Thus it is seen that what might be taken as a definite morphological character is, in reality, a response to the action of an external stimulus, but it nevertheless becomes, in the course of ontological development, a distinctive structural feature.

(4) Apart from direct insolation, evidence has accumulated going to show that slight expansion and contraction of the sahuaro trunk follow changes of air-temperature, but in most cases these minor changes are masked by those occasioned by variations in amount of soil-water.

(5) After the first few years, growth in the sahuaro is apical, the increments of succeeding years increasing in diameter until the trunk attains the full thickness, which it afterwards maintains through life. The average yearly growth in height of individuals was between 10 and 12 cm. From these data, which are all thus far available, it appears that a giant cactus requires on an average approximately 100 years to attain a height of 10 meters. Observations thus far do not establish any definite relation between growth and rainfall, though it is hardly conceivable that such a relation does not exist. On the other hand, the fact that growth takes place chiefly in the summer time is unquestioned.

(6) The percentage of water in an ordinary healthy sahuaro in a dry time ranges approximately from 75 per cent of the fresh weight in its lower part to more than 90 per cent in its upper part. An individual 6 meters in height absorbed and stored approximately 412 liters of water between November, 1906, and March, 1907, besides the amount transpired. Transpiration from the trunk is necessarily slow, but is rapid from flowers and flower-buds. The average transpiration of a fully-opened flower is at least 850 mg. for an hour of full sunlight. About 3.27 liters of water are stored in the tissues of every 100 flowers, but even when this is added to the amount transpired it is an inconsiderable quantity in comparison with the entire amount stored in the trunk. None the less, the abundance of flowers has been observed to be directly correlated with the amount of available water in the soil.

(7) Comparative observations show that the bisnaga approaches the sahuaro closely in its structural features and presents essentially the same form of mechanical adjustment. Its habits as regards water-storage and its relations to external factors, particularly to insolation, present some modifications, but do not differ widely from those of the sahuaro. In mode of growth, however, there are important differences, and the apical growth of the bisnaga, as compared with the sahuaro, is exceedingly slow. In like manner, observation of different species of flat opuntia go to show that the proportions of water in the body of the plant and in flower-buds are not far from those of the sahuaro, and that in general the behavior of plants of this genus, as regards absorption, water-storage, and loss, is very similar to what has been observed in the giant cactus, while in the mode of growth altogether different relations prevail. None of the opuntias approach the sahuaro in perfection of mechanical adjustment, in development of the water-storage system, or in growth in dimension, yet they are extremely well adapted to the conditions under which they are now living over a far wider area than that inhabited by the sahuaro.

Comparison of the several genera thus far studied goes to show that the end attained by the highly perfected mechanical adjustment of the sahuaro may be realized apparently quite as efficiently in a much simpler way. An *Opuntia* joint may be roughly compared to a flat rubber bottle which swells or shrinks according to the quantity of water which it has received or lost. There is no complicated device whatever in its construction, and yet with its exceedingly simple structure the *Opuntia*, as already stated, has spread far more widely than the sahuaro and is now adapted to a far wider range of external conditions. Thus it appears that, among the cacti at least, the lines of descent in which simpler rather than more highly perfected adjustments in relation to water-storage have been developed are at present the most successful as regards survival in a great variety of external conditions and extension over a wide range of territory.

As regards mode of growth, the case of the bisnaga is instructive. Its form, at first nearly spherical, becomes, later, irregularly columnar, and it then simulates the habits of the sahuaro, but its root, apparently quite insufficient for the support and anchorage of a heavy column, is often torn from its place as the unwieldy trunk is prostrated by desert winds or overturned by its own weight. The apical growth of this plant, however, is unsymmetrical and extremely slow; facts that, coupled with the frequent destruction of the bisnaga in the manner indicated, suggest a relatively ill-adapted form, a view which receives confirmation from the sparse occurrence of this plant in regions where it is now found. These, however, are speculative considerations which may well be deferred to a period of greater knowledge.

In general, it may be said that whatever may be the theoretical interest established by the series of observations and measurements now brought to a close, it is quite possible that their chief value lies in the close approach to a quantitative expression of certain biological relations, carried out through a period of years. The determination of such relations by weighing and measuring, though possible at present only in a relatively limited field, is to be regarded as a step towards the exactness of conception and expression which should be realized in the further development of biological science.

VARIATIONS OF THE WATER-BALANCE.

By D. T. MACDOUGAL.

PURPOSE AND SCOPE OF THE EXPERIMENTS.

As soon as the measurements described in the previous section of this paper were well under way, it became evident that some determinations of the amount of the water-balance and its variations would be necessary for the interpretation of the changes of form and volume revealed by these measurements.

A second lot of the plants was therefore selected in which the amount of water present and its seasonal variations were determined by weighing. Attention was directed chiefly to obtaining data from succulents detached from the substratum under conditions of natural exposure in the open air and under the modified conditions furnished by the Desert Laboratory. Some measurements were made of these detached specimens in order to correlate changes in volume and form with variations in weight in the same individual.

The observations upon loss of water by plants separated from the substratum for extended periods secured facts bearing upon the effects of the climatic factors of the various seasons, the relation of the water-balance to growth and reproduction, and also justified some generalizations as to the relation of these succulents to their habitats, especially concerning the constructive efficiency of the water-balance as a factor in endurance and survival.

Chemical analyses of the sap of the plants used were made, and some of the information secured has already been of great value in a consideration of the conditions leading to parasitism, discussed in a previous paper (MacDougal and Cannon, Conditions of Parasitism, Publication No. 129, Carnegie Institution of Washington, 1910). The fuller citation of the facts in question has been made to demonstrate the relation between the state of the water-balance and the varying composition of the juices.

CARNEGIEA GIGANTEA.

A sahuaro about 2 meters in length was taken from the bajada west of Tumamoc Hill on May 8, 1908, the root-system was trimmed back to the central cylinder of the stem, and set up on a base of loosely-piled stones, being held in position by a rope girdle and guy-wires. On July 8 the body was seen to be noticeably shrunken, the ridges being drawn together, thus interlacing the spines, giving the plant a grayer aspect, by reason of the covering of the green surfaces by them. The 61 days during which the

plant had received no water included the most rigorous part of the dry fore-summer, with a relative humidity rarely exceeding 25 per cent, and standing at 7 to 10 per cent during the greater part of many days. Maximum temperature of 112° occurred and the tissues exposed to the sun doubtless reached 140° F. or even higher on some days.

The summer rainy season now came on and the air was relatively moist at times, but no water-vapor was taken in, since it has been shown by Prof. V. M. Spalding that desert plants in general do not absorb water in measurable quantity from the air. On November 4 the plant was examined and found to have developed three small roots which depended downward among the large, loose stones of the support, but did not reach the soil. All the cut surfaces had become calloused and the plant appeared to be in a healthful condition, although subjected to the severest rigors of the desert for six months.

The difference between conditions in the open air and in an inclosed room, not heated, being but little, except as to wind effects at this time of the year, the plant was now removed to the laboratory. Its length was found to be 148 cm. and the maximum distance between the center of any ridge and the nearest one to it was 10 cm. It now weighed 32.518 kg. and was set in a mounting, for convenience in handling, that brought the total weight to 32.933 kg. December 8, 1908, 33 days later, the preparation weighed 30.783 kg., showing a loss of 2.050 kg., or a rate of 62 grams daily. On May 15, 1909, a year from the beginning of the experiment, an examination was again made. The length had shrunk from 148 to 140 cm., the ridges now showing a maximum separation of but a trifle over 4 cm. and the weight having fallen to 28.750 kg., giving a rate of loss for the period of 23 grams daily.

This plant had lost over 4 kg. of water in an inclosed room at comparatively low temperature during the six months ending in May, 1909, this being accompanied by shrinkage in both length and diameter.

The apical portion of the stem, 20 cm. long, was removed, and a complete section 33 cm. long was then taken for examination in the chemical laboratory. The sap expressed from the tissues gave the following data:

Specific gravity of sap as extracted	1.0355
Acidity calculated as H ₂ SO ₄grams per 100 c.c..	.163
Total solids in sap	Do..... 9.622
Ash-content of sap	Do..... 2.754

The tissues were distinctly moist to the touch, and the stump of the plant, about a meter in length, was set in the soil under a lath shelter and seemed normal in March, 1910. As may be seen, the proportion of inorganic material was about 2.76 times as great as the normal (see data of normal plant, page 47), indicating that the plant had lost over 57 per cent of its original weight, which may be estimated at 50.44 kg., and had given off about 63 per cent of the water originally held in its tissues.

A second young plant, specimen No. 1a, was taken from the soil near the Desert Laboratory on October 22, 1909, and the root-system neatly cut away, after which it was fitted to a metal stand weighing 7.315 kg., the whole preparation giving a draft of 52.640 kg., which would make a net weight of 45.325 kg. for the plant. It was then put in a laboratory room. The data obtained are shown in table 13.

TABLE 13.

Date.	Gross weight.	Loss.
	kg.	kg.
Nov. 22, 1909	49.110	3.530
Jan. 8, 1910	48.760	.350
Feb. 9, 1910	48.265	.495
Feb. 19, 1910	48.320	.055

The plant with its mounting was now removed to the open, where it was exposed to the full action of wind and sun. The conditions of exposure were such as to be fairly equivalent to those of a plant on a rocky slope during the same period. .

On May 13, 1910, the gross weight of this plant had fallen to 42.675 kg. by a loss of 5.535 kg. The rate of depletion was 117 grams daily in November, immediately after it had been taken from the soil; 7 grams daily during December; 15.5 grams daily during January; 5.5 grams daily during the early part of February indoors; and 66.5 grams daily in the open during a period of 83 days from February 19 to May 13, 1910. A comparison with the results previously described shows that the rate of loss in the open was between two and three times as great from plants in the open as from others in shaded rooms. It is of interest to note that the rate of depletion from the sahuaro in the open was less than that of an *Echinocactus* taken up at the same time.

TABLE 14.—Analyses of sahuaro trunks at different dates.

Specimen.	Specific gravity of sap.	Acidity as H ₂ SO ₄ per 100 c.c.	Total solids per 100 c.c.	Ash-content per 100 c.c.
		gm.	gms.	gms.
No. 1.	1.023	0.187	5.924	1.556
No. 2 (2.5 meters high)	1.022	.150	5.352	1.740
No. 3 (3 meters high)	1.020	.181	4.512	1.724
No. 4	1.0145	.1619	3.434	1.002

A terminal section of a trunk of a plant which was growing in the open was obtained late in the foresummer, June 15, and the analysis yielded the data shown in table 14, opposite the line No. 1.

A heavy rain on June 26, 1909, ended the dry foresummer and two small sahuaros were taken, two days later, to the chemical laboratory for

an analysis of the portion of the trunk corresponding to the samples previously treated. The data obtained are given opposite No. 2 and No. 3 in table 14.

Another specimen taken on August 10 yielded the data shown opposite No. 4 in table 14.

In order to obtain data upon which to base an estimate of the amount of water in the bodies of sahuaros an individual consisting of a single columnar trunk growing near the southwestern corner of the domain of the Desert Laboratory was cut down on October 17, 1909. It was found to be in a condition of extreme turgidity and measured 5.6 meters in length, representing the height above the surface of the soil, while the diameter at the swollen middle portion was 60 cm. The trunk was cut into sections of about 60 kg., which were weighed on a balance having a draft of 100 kg., the whole plant having a draft of 767.8 kg. A sample, including one ridge with spines and a section of the cortex and wood extending to the center of the medulla, was taken for a water determination. Its weight was 3.024 kg., and the residue after drying was 276 grams, indicative of an original water-content of 2.748 kg., or 91 per cent of the sample. The entire plant therefore held 698 liters of water. The age of this plant may be estimated as about 60 years.

Plants of maximum size, 12 to 20 meters in height, would contain from 2,000 to 3,000 liters of water. Such individuals might lose from 1,000 to 1,600 liters of water during a protracted arid period and still survive. The results of the observations described on page 54 suggest that the total loss might be regained within a few days if the drought were followed by sufficient precipitation. No noticeable growth would ensue, however, in the desiccated condition, and the lessened rigidity of the trunks and the branches would render them especially liable to be broken by the action of the wind.

The acidity of the sap seemed to bear no direct relation to its concentration, the lowest being found in a plant growing in the open at the end of the dry foresummer, while it was slightly greater in a plant that had lost 63 per cent of its water-balance and was highest in a plant examined at the end of the dry foresummer. The proportion of total solids carried in solution by the sap increases with desiccation, but not at the same rate as the dissolved salts. The latter may increase from 1 to 3 per cent, while the total solids vary between 3.4 per cent in the most turgid condition to 5.9 per cent in the most desiccated state, which indicates an organic content of 2.34 per cent in a plant containing a maximum amount of water, 2.8 and 3.6 per cent in the sap of plants at the end of the dry foresummer, and 3.4 per cent in the plant which had lost 63 per cent of its water-balance.

The water-balance of the sahuaro doubtless constitutes a very important factor of safety, since the vicissitudes of the climate of a large part of its

Dead trunks of *Carnegiea gigantea* bearing living branches. The larger individual on the right bore flowers one year after the death of the trunk.

habitat are such that a whole year might pass without sufficient precipitation to yield a supply which would be equal to the transpiration loss. The strata in which the anchorage of this plant is made are loosely placed and the shiftings which would disconnect the absorbing organs are frequent. The large balance would allow the extension of the root-system in a way that would remedy the defect, although during the interval in which the plant was drawing upon its accumulated balance but little growth would ensue.

Another form of survival is to be seen when the trunk dies and large branches remain alive. The death of the trunk often results from infection of wounds in the trunk, however slight, in the rainy season, and the soft outer tissues decay quickly, leaving the bare woody skeleton, upon which two or more branches are often held in place, apparently untouched by the disintegration of the remainder of the living tissues. Many examples of this have been observed.

One illustration occurred on Tumamoc Hill, near the Desert Laboratory, and was photographed on March 4, 1908. In this instance one large branch and one small secondary branch remained alive. The large branch was carefully freed from the dead skeleton and its woody base set in a box of soil in the greenhouse on July 8, 1908, but its tissues soon began to turn yellow and decay began by July 30, partly as a result of the heightened temperatures.

A second example in the same locality, bearing two large branches, was followed through the autumn and winter wet season of 1909-10. (See MacDougal, *Across Papagueria*, *Plant World*, xi, page 93, 1908.)

The most notable demonstrations of this kind, however, are to be seen at a point 22 km. east of Tucson, on the bajadas that come down from the southern base of the Santa Catalina Mountains. A dead skeleton was seen on May 25, 1909, bearing three living branches, the trunk having decayed during the previous year. Despite this fact, the living branches bore a profusion of flowers. On September 21, 1909, one large branch remained alive and a small globular secondary branch which had arisen on an isolated green branch was alive, but would probably soon undergo desiccation. The large water-balance seems to have a highly localized value and the woody bases of the branches offer some resistance to the spreading of infection and decay processes. Isolated members of many of the cacti are capable of regeneration and thus effect vegetative propagation, but in no instance has this been observed in the sahuaro, nor has it been accomplished experimentally. It does not seem probable that it occurs in any part of the range of the plant, since no root-formation seems to ensue, except about the bases of the trunks. (Plate 7.)

The bases of the trunks of the sahuaro, especially in small trees, are girdled, probably by rabbits and mountain sheep, leaving the central cylinder intact, in which condition they survive for extended periods and may attain great age.

ECHINOCACTUS.

The short stems and relatively enormous thickness of the echinocacti, together with the curved or hooked spines and amount of accumulated water which they contain, has caused them to be designated by a number of local names, such as "barrel cactus," "bisnaga," "desert fountain," etc. One or more of the South American species, together with *E. emoryi* and *E. wislizeni*, hold so much water, which is readily yielded upon crushing, that the sap is used as an emergency drink by the aboriginal tribes of both North and South America. The great body of the Sonoran species named has a very thin central woody cylinder, occupying but little of the space within the plant, which is chiefly composed of a soft parenchymatous tissue with fragile strands of fibrovascular tissue running out to the nodal points. (See Coville and MacDougal, Desert Botanical Laboratory, Carnegie Institution of Washington Publication No. 6, 1903; also MacDougal, Carnegie Institution of Washington Publication No. 99, (1908.)) The expressed juice is found to contain less dissolved material than that of any other plant examined.

The contents of these watery cylinders are easily available to the thirsty traveler. A large knife is convenient for decapitating the plant, but when this is lacking the large curved spines may be burned away by a lighted match or wand, and then the top crushed with a stone. Singularly enough, the apical newer tissues do not yield their juices as readily as the older parts, being leathery and retentive of the sap. After this is removed the underlying parenchyma may be crushed by pounding with a stake or stone and the juice squeezed into the cavity from which the tissues were removed. A liter of refreshing fluid may be obtained by a skillful operator in a few minutes, and the rigors of thirst on many desert journeys have been mitigated by its means. (Coville, F. V., Desert Plants as a Source of Drinking-Water, Smithsonian Report for 1903, p. 499, 1904.)

A large number of specimens of *Echinocactus* have been seen in a prostrate position on various explorations within the last five years. The root-system, while very extensive, lies within 15 cm. of the surface of the soil, and a slight dislocation due to the action of a torrential rain may loosen the anchorage of a large individual in a few minutes. Here, again, no exact observation may be reported, but many have given evidence of survival for long periods after being freed from absorbent contact with the soil. No instances have been reported in which new roots were seen to arise from the lateral points of a prostrate trunk, although when the apical portion is destroyed regeneration may occur by which several heads or branches are formed, while fasciations or "cristations," probably due to injury, are by no means uncommon in the two species specially studied. Widely varying experimental observations were designed to test the water-relations of these forms, and the results are described below.

ECHINOCACTUS No. 1.

On March 4, 1908, a large plant in good condition growing among volcanic rocks near the stone reservoir of the Desert Laboratory on Tumamoc Hill, at an altitude of about 800 meters, was taken up without injury, the roots cut away cleanly, and the base seated on a wooden ring padded with excelsior. This preparation was now placed on a platform scale in a ventilated room in the laboratory. The gross weight was found to be 42.743 kg., or about 42 kg. net. A continuous record of the weight was kept for 16 months, and as it is the most complete of any series, the data are given in full in table 15. The close observation to which this individual was subjected made it evident that weights taken at longer intervals would meet the requirements of the present investigation. It is to be noted that a change of the preparation was made at the beginning of 1909, for which a correction is necessary to show the difference between the earliest and final weights.

TABLE 15.—Record of weight of *Echinocactus* No. 1 for 16 months.

Date.	Weight.	Daily rate of loss.	Date.	Weight.	Daily rate of loss.	Date.	Weight.	Daily rate of loss.
	kg.	gms.		kg.	gms.		kg.	gms.
Mar. 4	42.743		June 11	41.324		Jan. 2	39.529	2.7
9	42.656	17	24	41.092		6	39.509	7
11	42.627		July 4	40.889	20	9	39.490	1
12	42.598		6	40.860	29	13	39.480	2.5
13	42.512		7	40.831	7	19	39.450	5
20	42.454		11	40.802		22	39.437	4
31	42.338	10	14	40.773		26	†39.432	1
Apr. 1	*42.280		16	40.744	14	29	39.382	16
3	42.251		25	40.657	10	Feb. 5	39.378	1
4	42.193	14	29	40.528	7	12	39.367	2
13	42.106		Aug. 2	40.470	14	23	39.332	3
17	42.048		6	40.440	8	Mar. 16	39.260	3.4
20	41.090		14	40.318	15	23	39.225	5
25	41.961	8	Sept. 2	40.108	11	30	39.210	2
28	41.876	29	12	39.088	12	May 12	38.900	7
May 2	41.848	8	17	39.900	18	June 5	38.755	6
8	41.819	5	20	39.870	10	12	38.645	15.6
12	41.790	7	Oct. 3	39.622		15	38.625	6.9
13	41.761	29	8	39.596	5	Aug. 1	38.160	10.9
16	41.703	19	10	39.570	13			
18	41.674	14	12	39.544				
20	41.643	10	21	39.520	3			
23	41.614		29	39.470	6			
29	41.530	14	Nov. 4	39.448	4			
June 2	41.470	15	Dec. 7	39.416	1			
5	41.440	10		†39.599				
9	41.382	19						

*By adjustment of mounting.

†By adjustment of scale and mounting.

‡Room heated.

The specimen was dead when examined on September 20, 1909.

The daily rate of loss has been given in the nearest integer, except in instances where the smaller differences were of critical value, as in calcu-

lations of the rate for extended periods. Furthermore, the rate is not given except when changes ensued. It is to be noted that this plant was kept in a room devoted to other uses and that the opening of doors and windows and the occasional heating would account for some of the erratic features of the curve of water-loss. Allowing for these, however, it is to be seen that the rate of transpiration was much higher during March-June of the first year than the corresponding period in the second. The maximum (29 grams daily) was reached early in July, 1908, at the close of the dry foreshummer, the rate for the previous month being between 19 and 20 grams daily. The average high rate of 14.4 grams daily persisted until July 6, 1908, and it then fell to 11.6 grams daily for the period of 31 days ending September 2, rising to 15.7 grams during September, and averaging 5.5 grams for the month ending November 4. The rate was 1 gram during November, 2.7 grams during December, 4.4 grams during January, and about 3 grams daily during February and the first half of March. During the last 14 days of March the rate was 3.5 grams daily. This is to be compared with a rate of 14 grams daily during the corresponding period of the previous year. During 42 days ending May 12, 1908, the rate was 11 grams daily, and during 43 days ending May 12, 1909, the loss was but 7 grams daily. The loss was 12.2 grams daily during the 31 days ending June 11, 1908, while it fell to 8.2 grams daily during the 31 days ending June 12, 1909.

This plant weighed approximately 42 kg. when the experiment was begun in March, 1908, and about 38 kg. of this amount may be estimated as water; 3.666 kg. was lost during the first year.

Some slight manifestations of growth were seen at the apex of the trunk in August of 1908, during the first season of deprivation of a water-supply, but none ensued in the following year. The rate of transpiration during the second year was found to vary between one-fourth and two-thirds of that of the previous year, although scarcely more than a tenth of the total water-balance originally present had been lost. A comparison with the data obtained from other specimens shows that the loss from this plant was much less than would have occurred had the plant been exposed to the evaporating action of sunlight and air-currents. (See plate 8.)

ECHINOCACTUS No. 2.

On November 5, 1908, a small individual growing near the Desert Laboratory was taken up and the roots cut away cleanly, after which it was found to weigh 5.136 kg. A mounting of wire netting was provided and the plant was set up in the same room with No. 1.

On December 8, 1908, the weight was found to be 5.065 kg., indicating a loss of 71 grams in 33 days, a rate much in excess of No. 1 for the same period when comparison of weights or surfaces is made. The actual loss from No. 1 during the corresponding period was 32 grams, although its

The water-balance of *Echinocactus* and *Ibervillea*. The larger *echinocacti* have received no water for over a year; the smaller one, not for 30 months. The tubers of *Ibervillea* live for years in the condition shown. Picture of Papago Indian drinking juice of *Echinocactus* in back-ground.

weight was seven times that of No. 2. Some of the excessive loss of No. 2 may be attributed to the fact that freshly-cut and hitherto unexposed surfaces were exposed to the action of dry air.

On February 13, 1909, the weight was found to be 4.966 kg., indicating a loss of 99 grams in 66 days, which is to be compared with a transpiration of 232 grams by No. 1, which was now showing a decrease, presumably owing to its long exposure to the evaporating action of the air.

The preparation was now removed to the constant-temperature dark-room, which stood at a temperature of 56° F. at this time.

On August 1, 1909, the temperature had risen to 75° F., the maximum of the year. The weight was found to be 4.872 kg., indicating a loss of 94 grams in 138 days in a chamber with no air-currents and a comparatively high relative humidity (80 to 90 per cent). This would give a rate of 0.7 gram daily.

On October 16, 1909, the weight was found to be 4.77 kg., indicating a loss of 102 grams in 76 days. The temperature had now fallen to 71° F. No new spines, as a result of growth, were to be seen in the apical region. A registering hygrograph placed in the room for 48 hours gave a relative humidity of 88 and 89 per cent.

The actual amount of water-vapor in the air of the chamber probably does not vary much during the year, and the relatively slight variation in the temperature would make fairly constant conditions. The rate of loss was therefore practically constant during a period of 8 months, showing that transpiration in this case is a very direct reaction to external conditions.

On February 19, 1910, the weight was 4.736 kg. and the thermometer reading was 56° and 57° F., with humidity unchanged.

The total loss of this plant during a year (371 days) amounted to 220 grams, or about 4.4 per cent of the original weight, when placed in the constant-temperature chamber.

On February 21, 1910, the weight was found to be 4.728 kg., after which the preparation was set out in the open.

On February 23, 1910, the weight was 4.716 kg., a loss of 12 grams in 2 days, which is not an excessive increase over the rate displayed in the moist atmosphere of the equable dark-room. The exposure had resulted in the blanching of the surfaces on the southern side of the plant.

On March 23, 1910, the weight was 4.292 kg., a loss of 424 grams in 28 days, a rate of 15 grams daily. The blanched surfaces were now tinged with red and the general condition of the plant was good, despite the great length of time it had been deprived of water and the abrupt change from equable conditions to the desiccating effects of the wind and sun.

On April 21, 1910, the weight was 3.865 kg., a loss of 427 grams in 29 days, a rate of 15.7 grams daily.

On May 13, 1910, the weight was 3.412 kg., a loss of 453 grams in 22 days, a daily rate of 20.6 grams.

The plant had partly recovered from the blanching effects, but was much shrunken, having lost over 54 per cent of its original weight in the 18 months during which it had been cut off from a supply of water. It was taken to be still capable of growth and of accumulating a water-balance if a supply were furnished.

ECHINOCACTUS No. 3.

On March 6, 1908, a small *Echinocactus* from the bajada west of Tumamoc Hill was taken up, the smaller roots cut off, and it was set up on a small pile of rocks on a stone platform. Exposure to the sun and evaporating action of the air combined to dry out the plant to such an extent that the ridges were undulating, thin, and drawn closely together, and the plant had taken on a reddish tinge on November 5. The weight at this time was found to be 3.893 kg., which was probably about six or seven tenths of the original weight.

The plant was now placed under the same conditions as No. 1.

On December 7, 1908, 32 days later, a gain of 14 grams in weight had been made. Every precaution was taken to eliminate error, and the only explanation available is that the increase represented water-vapor taken up hygroscopically by the spines and other dead tissues (see page 56). An adjustment of the preparation was now made, by which it weighed 3.921 kg.

On January 30, 1909, a loss of 43 grams had ensued in the preceding 54 days, the weight now being 3.878 kg. Although the stage of desiccation of this plant was far in advance of that of No. 1, it showed a relatively high daily rate of loss, which might be attributable either to its immaturity or to loss of water from the spines.

A number of young flower-buds were beginning to push out, but these did not develop beyond the form of small buttons, when they dried out. The plant was now set in a dish of water, from which about 100 c.c. was absorbed in two days, with an apparent increase of 14 mm. in circumference, as estimated from the measurements between two ribs. The total increase of weight on February 5 had been but 14 grams and on the 12th this had been reduced to 6.5 grams.

A box of loam was now prepared, the roots set in this, and water furnished in the ordinary manner. On May 21 the measurements showed that no further decrease appreciable by measurement had taken place, the transpiration being balanced by absorption. Upon lifting from the soil a number of roots 8 to 10 cm. long, amply furnished with root-hairs, were found. The plant was replaced in the soil and set in a shaded room.

On August 1, 1909, the plant had apparently regained its original volume, being turgid, with the ribs separated and of a healthy color. This specimen had been separated from a water-supply for 11 months, exposed to great evaporating action, and when set in a moist soil had developed a

root-system and regained its original volume in a period under 100 days in length. How much less than this can not be told, since no examination was made in the interval.

On October 16, 1909, the plant had been duly watered and cared for in the glass-house, so that growth ensued much as in plants under the usual habitat conditions. The apex had expanded, showing a clear central area surrounded by the reddish, newly-formed spines, which however, had hardly reached their full length. The whole preparation was now brought into the shaded laboratory, and the spaces between the body of the plant so wedged with cotton wool that the evaporation from the soil would be reduced to a negligible quantity and the roots left undisturbed in the soil, from which they might continue to draw water for some time. The total weight was now found to be exactly 26 kg. The vessel containing the soil was of tin and no water could be lost through its walls.

On October 21, 1909, the weight was 25.895 kg. The entire preparation was now set out on the stone wall in the courtyard of the laboratory with No. 9. Both were covered by a sash of glass to shield them from the direct action of the rain.

The records on various dates from November 8, 1909, to May 13, 1910, are given in table 16.

TABLE 16.

Date.	Weight.	Loss.	Time.	Daily rate of loss.
	<i>kg.</i>	<i>gms.</i>	<i>days.</i>	<i>gms.</i>
Nov. 8, 1909	23.390	840	...	60
Jan. 8, 1910	21.130	1,420	47	30.5
Jan. 28, 1910	20.840	650	20	32.5
Feb. 26, 1910	19.305	1,175	...	40.5
Mar. 22, 1910	18.155	750	...	30.3
Apr. 21, 1910	17.870	685	30	23
May 13, 1910	17.435	435	22	19.9

It is to be seen that this preparation displayed a rate of loss of 60 grams daily in October and November, 30.5 grams daily during November, December, and early January, 32.5 grams daily during the greater part of January, which increased to 40.5 grams daily during February; then, with conditions of the arid foresummer becoming increasingly favorable for transpiration, the rate fell to 30.3 grams daily during March, 23 grams daily during April, and 19.9 grams daily during May. The lessened rate may be attributed to the increasing concentration of the sap, as the plant had now apparently been depleted of over half of its original store.

ECHINOCACTUS No. 4.

On March 6, 1908, a small plant near the Desert Laboratory was taken up and placed on a rock pedestal, as in the case of No. 3.

On November 5, 1908, shrinkage had occurred as in No. 3, and the weight was found to be 795 grams.

On December 8, 1908, the weight had increased to 838 grams, showing an increase of 43 grams in 33 days. The tentative suggestions applied to No. 3 are the only explanations that may be offered for this very noticeable change.

On May 21, 1909, the weight was found to be 752 grams, indicative of a loss of 82 grams in 182 days.

On June 15, 1909, the weight appeared to be 756 grams, an apparent gain of 4 grams in 24 days, although the entire amount might be due to error and the use of a different scale in making the determination.

On August 1, 1909, the weight was found to be 728 grams, showing a loss of 28 grams in 47 days, at a rate of nearly 0.6 gram daily, which is not far below that of No. 3 during the same period in the constant-temperature room, although the latter had a weight over six times as great.

On October 16, 1909, the weight was 700 grams, showing a loss of 28 grams in 76 days.

The rate was now scarcely half that shown in the early summer.

Several records taken between November 8, 1909, and February 25, 1910, are given in table 17.

TABLE 17.

Date.	Weight.	Loss.	Time elapsed.
	<i>gms.</i>	<i>gms.</i>	<i>days.</i>
Nov. 8, 1909	692	8	22
Nov. 18, 1909	690	2	10
Jan. 8, 1910	684	6	51
Jan. 27, 1910	680	4	19
Feb. 25, 1910	676	4	31

The preparation was now removed to the dark-room, with the temperature at 58° F., and the relative humidity 62 per cent.

On February 27, 1910, no change of weight could be detected.

On March 3, 1910, the weight had increased to 678 grams, denoting an increase of 2 grams in the 6 days in the dark-chamber. The preparation was now brought into a well-lighted and ventilated room.

On March 22, 1910, the weight was 670 grams, a loss of 8 grams in 19 days. The rate was greater than before being taken into the dark-room, by reason of the advance of seasonal conditions.

On April 21, 1910, the weight was 664 grams, a loss of 6 grams in 30 days, a daily rate of 0.2 gram.

On May 13, 1910, the weight was 650 grams, a loss of 14 grams in 22 days, a rate of 0.6 gram daily.

The lessened supply present may be taken to account for the fact that during the 182 days ending May 21, 1909, the loss was 82 grams, at the rate of 0.4 gram daily, while during the 125 days ending May 13, 1910, the rate was less than 0.3 gram daily. Even in this desiccated condition, after having been deprived of water for 26 months, the rate of relative loss was greater than that of the tubers of *Ibervillea* which had been recently taken from the soil.

ECHINOCACTUS No. 5.

On March 6, 1908, a large plant was found on Tumamoc Hill which had fallen prostrate, but which retained absorbent connection with the soil by one large root. It had lain in this position for nearly a year and was apparently sound and normal. The roots were cut away and the plant was placed in an upright position on a pedestal of loosely piled rocks, being fully exposed to the sun and to the evaporating action of the air.

On November 5, 1908, the plant was removed to the room with No. 1, and found to weigh 19.99 kg. It was mounted so that the preparation weighed 20.937 kg.

On December 8, 1908, the weight was found to be 20.850 kg., indicating that the net loss during the previous 33 days had been 87 grams. No. 1, which had twice its weight, lost but 32 grams during the same period.

The facts suggest that the plants brought in from the open air continued to lose water at a rate only slightly decreased and much greater than that of a plant which had been indoors for several months.

On February 13, 1909, the root-system was taken away by a clean transverse cut, and a cylindrical cavity bored directly upward in the central woody cylinder. A clay bougie of the form used in the Livingston atmometer was fitted into this tightly, the seal being made with plaster of Paris, waterproofed on the outside with grafting-wax. A rubber stopper through a 40 cm. glass tube was fitted to the clay cylinder and the whole system was filled with water and the preparation was set upright, with the lower end of the tube immersed in a dish of water. The preparation was completed at 2 p. m.

The amount of water taken up between February 16 and March 5, 1909, is shown in table 18.

The rate now began to fall more or less steadily until April 10, when it varied from 7 to 10 c.c. per day. The exposed tissues had begun to decay and gave off a fetid odor, as if from proteinaceous decomposition. The weight of the preparation, allowing for the mounting, was about 19.840 kg., showing a total net loss of about 990 grams in 153 days, with an absorption of nearly the same amount. The total transpiration had therefore been at about three times the rate of No. 1, which showed a weight about double that of this plant.

The average estimated loss of No. 5 during this winter period was nearly 13 grams daily.

The preparation was dismantled and the tissues around the more external part of the clay cylinder were found to be blackened and decayed. Doubtless this disintegration of the tissues had acted to decrease absorption, which, in the beginning of the experiment, was carried on at a rate that would soon have replaced the loss of the previous summer.

TABLE 18.

Date.	Time.	Amount of water taken up.	Time elapsed.
1909.		<i>gms.</i>	<i>hours.</i>
Feb. 14	11 a. m.	45	20
Feb. 15	11 a. m.	53	24
Feb. 16	12 noon	57	25
Feb. 17	12 noon	45	24
Feb. 18	11 a. m.	50	23
Feb. 19	2 p. m.	40	27
Feb. 23	3 p. m.	85	97
Feb. 26	3 p. m.	62	72
Mar. 2	2 p. m.	50	95
Mar. 5	12 noon	65	70

ECHINOCACTUS No. 6.

On November 7, 1908, a large *Echinocactus* was taken from the bajada west of Tumamoc Hill, the roots trimmed neatly, and the plant was found to weigh 28.573 kg. It was put on a mounting weighing 1.149 kg., the preparation thus amounting to 29.722 kg. The crown bore 17 ripening fruits, which were carefully noted at each observation, as given below. The preparation was placed in the room with No. 1.

On December 8, 1909, the weight was found to be 29.310 kg., indicative of a loss of 412 grams in 31 days, or a rate of 13 grams daily. The daily rate of No. 1 for the same period was but 1 gram daily. Doubtless some of the excessive rate of No. 6 during this period may be ascribed to loss from the freshly wounded surfaces from which the roots were cut. Other and unknown causes must have contributed to a total action by which the rate of transpiration in the open was thus maintained after being brought under shelter, as was noted in No. 5.

On May 12, 1909, one fruit had been lost and the weight was now 28.360 kg., which indicated an estimated water-loss of about 935 grams in 155 days, an average rate of 6 grams daily.

On June 12, 1909, the weight was 28.055 kg., indicative of a loss of 305 grams in 31 days, at a rate of nearly 10 grams daily.

On August 1, 1909, the weight was 27.585 kg., indicating a loss of 470 grams in 47 days, maintaining the rate set up in the arid foresummer of the previous period; 16 fruits were still present.

The excessive rate of loss exhibited when the preparation was first made continued with some diminution through the 155 days of the second period of measurement, and not until after nearly 6 months of confinement did the transpiration fall to a rate comparable with that of No. 1.

On October 16, 1909, the weight was found to be 26.895 kg., indicative of a loss of 590 grams in 76 days, at the rate of nearly 8 grams daily.

The singular action of this individual with regard to loss of water was coupled with some remarkable variations in form or volume. On November 13, 1908, a space including two furrows and a rib was measured and marked. On December 12 one furrow had narrowed and the other had remained stationary. The whole circumference was measured and interval marks established upon this circle. By May 12 a loss of 20 mm. was shown on the circle, but this had not been steady in every portion of the periphery. Each measurement included only a part of the line, from which it is safe to infer that any given furrow or space between two ridges might be contracted or widened by stresses set up in the plant from transpiration or other causes. Variations in diameter or circumference might thus ensue which would be difficult of analysis unless a comprehensive series of calibrations were made. The soft cylindrical trunk being not homogeneous in its mechanical structure, the varying turgidity might be expected to cause such irregular changes in form.

On January 27, 1910, the weight was 26.795 kg., a loss of 100 grams in 103 days. Various tests applied during this long period indicated slight gains in weight in some periods a few days in length, but the critical amounts to be tested were below the coefficient of error of the scales used.

On February 25, 1910, the weight was 26.725 kg.; loss, 70 grams in 31 days.

On March 22, 1910, the weight was 26.625 kg.; loss, 100 grams in 25 days. The increase in the rate of transpiration was commensurate with the heightened temperatures and lowered relative humidity.

On April 21, 1910, the weight was 26.485 kg.; loss, 140 grams in 30 days, a rate of 4.6 grams daily.

On May 13, 1910, the weight was 26.350 kg.; loss, 135 grams in 22 days, a rate of 6 grams daily.

ECHINOCACTUS No. 7.

On November 7, 1908, a large turgid plant was taken from the bajada west of Tumamoc Hill and brought into the laboratory after the roots had been neatly trimmed; 20 ripening fruits were included. The weight was found to be 35.818 kg., and with mounting 37.595 kg.

On December 8, 1908, the weight was found to be 37.040 kg., indicative of a loss of 555 grams in 31 days, or a rate of nearly 18 grams daily, which was something higher than No. 6, which was of the same origin and received the same treatment. It is to be pointed out that the rate was much higher than that of No. 1.

A number of records on various dates from January 6 to August 1, 1909, are given in table 19.

TABLE 19.

Date.	Weight.	Loss.	Time elapsed.	Daily rate of loss.
	kg.	gms.	days.	gms.
1909.				
Jan. 6	36.795	45	4	10.5
Jan. 9	36.751	44	..	14
Jan. 13	36.722	29	..	7
Jan. 19	36.630	92	..	15
Jan. 22	36.607	23	..	7.6
Jan. 26	36.598	9	..	2.25
Jan. 29	36.552	46	..	15
Feb. 2	36.528	24	..	6
Feb. 5	36.480	48	..	16
Feb. 12	36.400	80	..	11
Feb. 23	36.222	178	..	16
Mar. 16	36.170	52	..	2.5
Mar. 23	36.120	50	..	7
May 12	35.615	505	..	10
June 12	35.320	295	..	9.5
June 15	35.295	25	..	8
Aug. 1*	34.750	445	..	9

*20 fruits still present.

It is to be noted that this plant followed the behavior of No. 6 in its excessive rate of transpiration during the first six months after being brought in. The data for several periods appear in table 20. The rate during March was almost double that of February.

TABLE 20.

Date.	Weight.	Loss.	Time elapsed.	Daily rate of loss.
	kg.	gms.	days.	gms.
Nov. 8, 1909	33.885	125	35	4
Nov. 18, 1909	33.850	35	10	
Jan. 8, 1910	33.765	85	51	
Jan. 27, 1910	33.695	70	19	
Feb. 25, 1910	33.615	80	31	
Mar. 22, 1910	33.480	135	25	
Apr. 21, 1910	33.345	135	30	4.5
May 13, 1910	33.150	195	22	9

On October 16, 1909, the weight was 34.040 kg., indicative of a loss of 710 grams in 76 days, at a daily rate slightly greater than 9 grams; 20 fruits were present, but 2 were dried out and were removed after weighing. The two dried fruits weighed 12 grams, which would make the total weight of the preparation for further observations 34.028 kg.

Great numbers of greenish adventitious roots had risen around the base of the old dried roots. These were so thickly placed in areas of several square centimeters as to cover the surface completely.

The above results are notable by reason of the fact that this plant displayed approximately the same rate of loss during corresponding periods ending in May, 1909 and 1910. This may be attributable to the comparatively small depletion which it had suffered, since less than 13 per cent of the original balance had been lost.

ECHINOCACTUS No. 8.

On November 7, 1908, a healthy *Echinocactus* was taken up, the roots trimmed away neatly, and found to weigh 28.811 kg. It was now put on a mounting, the total preparation weighing 29.976 kg., 19 ripening fruits being included. The entire preparation was placed in room with No. 1.

On December 8, 1908, the weight was found to be 29.780 kg., indicative of a loss of 196 grams in the 31 days ending with this date, or at a rate of 6 grams per day. This plant was found to display a transpiratory activity fairly parallel to No. 1.

Table 21 shows a number of records taken between January 2 and August 1, 1909.

TABLE 21.

Date.	Weight.	Loss.	Daily rate of loss.	Date.	Weight.	Loss.	Daily rate of loss.
1909.	kg.	gms.	gms.	1909.	kg.	gms.	gms.
Jan. 2	28.659	121	*5	Feb. 12	29.490	47	*7
Jan. 6	29.635	24	6	Feb. 23	29.430	60	5.5
Jan. 9	29.608	27	9	Mar. 16	29.312	43	6
Jan. 13	29.605	3	1—	Mar. 30	29.300	12	*2
Jan. 19	†29.610			May 12	28.605	595	14
Jan. 22	29.587	23	7.6	June 12	†28.730		
Jan. 26	29.568	21	5	June 15	28.710	20	7
Feb. 2	29.551	17	2.5	Aug. 1	28.270	440	9
Feb. 5	29.537	14	4.6				

*Nearly.

†By adjustment of scale.

‡Adjustment of scale made.

ECHINOCACTUS No. 9.

On November 7, 1908, a sound *Echinocactus* growing near the Desert Laboratory was taken up, the root-system trimmed, and the plant placed on a base of wire-netting, the entire preparation weighing 17.339 kg., of which the mounting was 261 grams. The crown bore 22 ripening fruits. This plant and No. 10 were comparable with Nos. 7 and 8, the latter being placed in the room with No. 1. Nos. 9 and 10 were placed on an open porch on the south side of the laboratory, where the full effect of the sun and of the evaporating action of the air would be received. It is noted elsewhere that the ridges on the side of these plants exposed to the sun are generally closer than those on the northern side, and these preparations were oriented with respect to this feature.

On December 8, 1908, the weight of the preparation was found to be 15.940 kg., indicative of a loss of 1.130 kg. in 31 days, or a rate of 36.4 grams daily.

On May 12, 1909, two fruits had been lost and a new base provided which weighed 1.640 kg. The total weight was now 11.370 kg., with a total actual loss of 4.840 kg., at the rate of 38 grams daily for the entire period of six months.

The excessive rates displayed by this plant in comparison with Nos. 7 and 8 in the inclosed room are doubtless due to exposure to the evaporating effects of sunlight and wind, and are, of course, much greater than that of No. 1.

The plant was now set in the soil near the east end of the parapet of the laboratory, and on August 1, 1909, had regained all of its original plumpness. It is to be noted that before being put in the soil it had lost about 35 per cent of its original weight, or about 40 per cent of its entire supply of water.

Intervals were marked around the circumference on January 6, 1909, and these were measured frequently until May. At first some of those on the northern side, where the ridges were most widely separated, began to increase their separation, but a total contraction ensued by which the circumference had diminished 13 cm. by May 21, 1909, an amount six times as great as that of No. 6, in the inclosed room, which had undergone previous desiccation. The data also show that a loss in weight over six times as great had also ensued. The total contraction on the north side of the plant among the more widely separated ridges was 145, as compared with 213 on the southern exposed surface.

On October 17, 1909, the apical spines had not been pushed apart, and 8 greenish fruits were still retained. The plant was now taken up and it was found to have developed a great number of small roots, which spread out in all horizontal directions from the base in a dense tangle. All were broken off except a mass that might have been inclosed in a space of 100 cm. These roots and the soil particles that could not be shaken off might fairly be taken to be equal in weight to the fruits that had been lost since the plant was set out, so that the weight now, 20.370 kg., represents a draft comparable to that obtained on the last weighing. It weighed 17.010 kg. when taken from the soil, November 5, 1908, and this had decreased to 11.370 kg. in May, 1909, by deprivation of water-supply, and after it had been replaced in the soil it had developed a root-system and made a gain of 9.600 kg., which was a net gain of 3.360 kg. over its original weight. Measurements by Mrs. E. S. Spalding showed that the circumference of the upper part of the trunk had increased 33 cm. since May, 1909.

On October 20, 1909, the weight, after 3 days in the laboratory, was 21.155 kg. gross, 20.285 kg. net. The preparation was now placed on the stone wall with No. 3.

Records taken at several dates between November 8, 1909, and May 13, 1910, are given in table 22.

TABLE 22.

Date	Weight.	Loss.	Time elapsed.	Daily rate of loss.
	kg.	gms.	days.	gms.
Nov. 8, 1909	19.855	1,300	19	68.5
Nov. 22, 1909	19.070	(*)	..	
Jan. 8, 1910	17.485	1,585	..	34
Jan. 28, 1910	16.750	735	..	37
Feb. 26, 1910	15.425	1,325	29	45.6
Mar. 22, 1910	14.740	685	24	28.5
Apr. 21, 1910	13.700	970	30	32.3
May 13, 1910	13.335	335	22	15

*Loss of weight by fruits, 200 gms.; loss of weight by transpiration 585 gms., at the rate of 42 gms. daily.

During the six months ending May 12, 1909, the average rate of loss was found to be 38 grams daily, and must have been much higher than this during the later part of the period. From the results of the last observation it is to be seen that the rate fell to 15 grams daily during May, 1910, by reason of the depletion of the water-supply.

The amplitude of fluctuation of which such plants are capable is well illustrated by the summarized observations made on this individual. The original weight, with mounting, 17.339 kg., when taken from the soil November 7, 1908, was decreased by 4.840 kg. by May 12, 1909. After being set out in the soil until October 12, 1909, it absorbed water and made growth, bringing the weight up to 20.370 kg., which is to be contrasted with the minimum weight of 11.370 kg. The final minimum, as shown in the last observation, was 13.335 kg. at a corresponding season and after equivalent desiccation, so that an actual gain by growth of about 1.965 kg. of material between May, 1909, and May, 1910, may be assumed. The condition of the plant at the last observation indicated that a much greater amount of water might be lost without serious injury.

ECHINOCACTUS No. 10.

On November 7, 1908, a healthy *Echinocactus* growing near the Desert Laboratory was taken up, the roots trimmed, and placed on the base of an upturned tin box. The total weight was 15.040 kg., and the net weight, including 13 ripening fruits, 14.588 kg. The preparation was placed near No. 9, and under practically the same conditions of exposure.

On December 8, 1908, the weight was found to be 13.130 kg., indicative of a loss of 1.910 kg. during 31 days, or at the rate of 61.6 grams daily. Although much the smallest of the quartet of Nos. 7 to 10, the loss was at a rate 10 times as great as that of No. 8, nearly 4 times as great as that of No. 7, and nearly 5 times as great as that of No. 6. But the most startling comparison is that with No. 1, it having lost water at a rate 60 times as great

as that plant, although No. 1 has nearly 3 times the size of No. 10. It is to be noted that the smaller specimens previously exposed, when taken indoors at this time, gained by the supposed absorption of the spines. Some of the increased weight of loss of this plant may be attributed to the fact that its base was a brownish tin box and that it stood nearer a blackish stone wall than No. 9. The reflected heat from both surfaces would doubtless exercise a marked effect. Similar arrangements of rock faces and exposures in a natural condition must constitute an important selective factor among these plants.

On May 12, 1909, the weight was found to be 8.080 kg., including but 2 remaining fruits. The total estimated loss was about 4.680 kg., a rate of 30 grams daily, which was slightly less than that of No. 9, but much greater than the loss of plants in an inclosed room.

The following comment upon changes in form of this plant has been furnished by Mrs. E. S. Spalding:

On November 17 three intervals of two furrows each were marked—I on the side away from the wall, II on the side next the wall, and III between the two on the east. The plant was left in this position until January 2. During this time No. I lost 22 units, II 10 units, and III 17 units. On January 2 the plant was turned around so that II faced the wall and III to the west. After this II began to contract much more rapidly than before. The rate of contraction for III also increased, but No. I expanded until January 22, gaining 8 units, and at the end of the experiment, May 21, was only 2 units smaller than when it was turned around. Moreover, between March 30 and April 10 it expanded 6 units after having been contracting for nearly 2 months. It can not be supposed that the plant was not losing weight all this time, and the local expansion can only be accounted for by a mechanical pull due to the fact that other parts of the plant were drying out more rapidly.

The total loss of water during its exposure may be estimated at about 36 per cent of its total weight, or about at 40 to 45 per cent of the water present at the beginning of the observation.

The plant was now taken to the chemical laboratory and an analysis made of the sap from the white inner pulp, which gave the following data:

Specific gravity of sap.....	1.035
Acidity, calculated as H_2SO_4 per 100 c.c.....	gram .. .1064
Total solids per 100 c.c. of juice.....	grams.. 7.060
Ash-content per 100 c.c. of sap.....	grams.. 3.000

A small plant growing undisturbed in its habitat on the bajada west of the laboratory was taken up on September 9 and sent to the chemical laboratory to obtain data for comparison. Occasional rains had fallen in the few weeks immediately previous to this date and the water-balance of the specimen may be taken to have been in the neighborhood of the maximum. 1.355 kg. of the white pulp was taken, from which 1,125 c.c. of liquid were obtained by a Büchner press, indicating that this tissue contained nearly nine-tenths of its weight of water, and that of the whole plant about 85 per cent was water. The analysis gave the following data:

Specific gravity of juice.....	1.0095
Acidity, calculated as H_2SO_4 per 100 c.c. of sap.....	gram .. .0887
Total solids contained in 100 c.c. of sap.....	grams.. 2.092
Ash-content, per 100 c.c. of sap.....	gram .. .772

It is thus seen that the desiccation or reduction of the water-balance in the *Echinocactus* may continue to such an extent that the specific gravity and acidity of the sap is notably increased and the concentration of the sap raised from 2 parts in 100 to 7 parts in 100, while the dissolved salts are increased from less than 0.8 part to 3 parts in 100. The increase of concentration due to dissolved salts is therefore greater than that of other dissolved material. The total concentration undoubtedly increases the osmotic activity of the sap enormously. (See MacDougal and Cannon, Conditions of Parasitism in Plants, Carnegie Institution of Washington, Publication No. 129, p. 35, 1910)

ECHINOCACTUS (INVERTED).

On January 28, 1909, an *Echinocactus* which was used for some experiments in xeno-parasitism furnished data of interest in the present connection. This plant had been freed from the soil a week previously, and it was now brought in, set in a reversed position, with the apical end downward, and the root-system removed by a cut which was made squarely across the tapering base of the stem from which the roots arise. A cylindrical cavity was bored into the central cylinder of the stem, and into this a clay bougie from a Livingston atmometer was fitted into the cavity tightly with a thin solution of plaster of paris, the outer surfaces being sealed with a thin coating of grafting-wax. A U-tube, of glass, with rubber connections, was fitted to the cylinder, the whole system filled with water, and the free arm of the U set in a glass dish containing a layer of mercury, above which the water stood to a depth of several centimeters.

The whole preparation gave opportunity for the absorption of water by the tissues of the plant through the walls of the clay cylinder which would draw a supply from the glass dish. The preparation being complete at 2 p. m., the free arm of the U-tube was thrust into the mercury, with the result that at 3 p. m. a column 145 mm. had been raised in an hour. Although the plaster had been allowed to set some few hours before, its action was not entirely excluded. The column of mercury was allowed to escape by raising the free arm above its surface to permit of absorption and replacement of water.

On January 29, 2 p. m., 50 c.c. of water had been taken up in 22 hours. The free arm of the U-tube was lowered into the mercury for 3 hours, during which time a column of the metal 120 mm. was raised. The arm was again raised to allow absorption of water and various parasitic insertions were made into the body of the plant, but these may be disregarded in the present connection. The data given in table 23, on the following page, were obtained from the preparation, corrections being made for possible evaporation from the dish of water from which the plant drew its supply.

TABLE 23.

Date.	Time	Amount of water taken up.	Time. elapsed.	Date.	Time.	Amount of water taken up.	Time elapsed.
1909.		c.c.	hours.	1909.		c.c.	hours.
Jan. 30	2 ^h 00 ^m p.m.	25	24	Feb. 19	2 ^h 00 ^m p.m.	18	27
Feb. 2	11 00 a.m.	18	45	Feb. 23	3 00 p.m.	44	25
Feb. 3	Noon.	35	25	Feb. 26	3 00 p.m.	12	72
Feb. 4	Noon.	25	24	Mar. 2	2 00 p.m.	200	95
Feb. 5	Noon.	25	24	Mar. 5	Noon.	14	70
Feb. 8	3 ^h 00 ^m p.m.	70	27	Mar. 9	Noon.	6	72
Feb. 11	11 30 a.m.	72	68.5	Mar. 16	Noon.	5	168
Feb. 13	11 30 a.m.	35	*48	Mar. 19	Noon.	2	72
Feb. 15	12 30 p.m.	40	49	Mar. 23	Noon.	3	96
Feb. 16	1 30 p.m.	30	25	Mar. 26	Noon.	3	72
Feb. 17	Noon.	20	22.5	Mar. 30	Noon.	No absorption	
Feb. 18	11 ^h 00 ^m a.m.	16	23	Apr. 10		Do.	

*Cloudy, cool.

Hitherto the preparation had stood in a glass-house at a temperature practically the same as in the open air, but without as much exposure to air-currents. It was now removed to an inclosed room, and, the fitting seeming to be in good condition, it was not disturbed. The tubing was refitted and a receiver for water arranged to exclude evaporation from the surface of the water in it. The entire preparation was placed on a balance and found to weigh 26.110 kg. on May 13.

On May 17, 18 c.c. of water had been taken up, but the whole preparation now weighed but 26.065 kg., giving a transpiratory loss of 47 c.c. in 4 days.

On May 21, 15 c.c. of water had been taken up, the preparation weighing 26.025 kg., indicative of a transpiration amounting to 40 c.c. of water in 4 days.

On June 5, 1909, the amount of water was not noted, but when the receiver was filled to zero the preparation weighed 25.935 kg., indicative of a transpiratory loss (net) of 90 c.c. in 15 days, which was slightly less than the estimated rate for the previous period.

On June 15, 1909, 22 c.c. of water was necessary to replace loss from receiver, and the whole preparation, after this was done, weighed 25.800 kg., indicative of a total loss of 160 c.c. of water in 10 days.

The transpiration at this time was greater than the amount taken up by the artificial absorptive apparatus, although not as great as the capacity of this device when it was first arranged. The contact with the fluid by this apparatus when freshly put in place might well furnish better facilities for taking in water than the root-system itself. But little doubt exists that in the natural condition in the open air the echinocacti in the Tucson region lose more water than they take from the soil during May and June, this period being the arid foreshummer, with its high temperatures, low relative humidity, and great wind-flow.

On August 1, 1909, 85 c.c. of water were necessary to replace loss from water-system, after which the weight of the entire preparation was found to be 25.445 kg., indicative of a loss of 355 grams in 47 days, at a rate of nearly 7.5 grams daily.

On October 1, 1909, 135 c.c. of water were necessary to replace loss in water-system, after which the preparation weighed 25.215 kg., showing a loss of 720 grams in 88 days, at a rate of over 8 grams daily. The column of water in the inverted U-tube was broken.

On October 5, 1909, the U connection with a vessel of water was removed to the top of the bougie, cleaned and fitted with soft wax, filled with water, and a glass cover put on, which was sealed by the wax. The preparation now weighed 23.410 kg.

On October 16, 1909, 35 c.c. of water were needed to refill the bougie to zero. After this was done the weight of the preparation was 23.410 kg., or exactly the same as 11 days earlier. The loss from the outer surfaces of the plant had therefore been balanced by the amount withdrawn from the clay cylinder.

In order to test the behavior of an *Echinocactus* freshly taken from the soil, a specimen with the main root bent at right angles was taken up on February 18, 1910, and it was found to weigh 49.390 kg. After trimming, the greatest diameter, measured in the plane of the bent root, was 41.3 cm. and the greatest length 58.5 cm. The plant was now supported in its original position on a base of loosely piled rocks, where it would be exposed to the full effects of the sun and wind.

On May 12, 1910, the weight had decreased to 36.900 kg., showing a loss of 12.490 kg., or nearly 25 per cent of the total in 84 days, at a daily rate of 148.7 grams. This was the most rapid depletion noted during the entire investigation. The length had decreased from 58.5 cm. to 56 cm., and the thickness from 41.3 cm. to 37 cm. The shrinkage therefore was equivalent to a hollow cylinder with closed ends, the walls of which were 22 mm. in thickness, the ends 33 mm. in thickness, with a length of 58.5 cm. and a diameter of 41.3 cm.

OPUNTIA SP.

The flattened joints of *Opuntia* are known to carry a water-balance and to exhibit such slow transpiration that joints have survived in dry rooms for many months, or even as long as 2 or 3 years, and it was deemed important to ascertain the rate of loss of water for brief periods. This was done with great care by Mrs. E. S. Spalding. Terminal joints of plants growing near the Desert Laboratory were taken, being cut off at the narrowest part of the constriction by which they were joined to the part below. The cut surfaces were sealed with grafting-wax and exposures arranged as below. Table 24, on the following page, is a record of the losses in No. 1.

TABLE 24.

From—	To—	Loss.	Rate of loss per day.
		<i>gms.</i>	<i>mg.</i>
Mar. 2, 11 ⁰⁰ ⁰⁰ a. m.	Mar. 5, 12 ⁰⁰ ⁰⁰ noon.	2.205	725
5, 12 00 noon	9, 12 00 noon.	3.445	861
9, 12 00 noon	16, 12 00 noon.	3.055	436
16, 12 00 noon	19, 2 30 p. m.	2.195	716
Total		10.900	*641

*For 17 days.

No. 1 was weighed first on February 23, 1909, and suspended from a palo verde tree in nearly full sunlight and wind. Some mistake was made in the first weighing, so that the rate of loss for the first week can not be recorded and the first interval to be estimated is from March 2 to 5. Weight on March 2 was 172.650 grams (table 24).

TABLE 25.

From—	To—	Loss.	Daily rate of loss.
		<i>gms.</i>	<i>mg.</i>
Mar. 5, 3 p. m.	Mar. 9, 1 p. m.	4.157	1061
9, 1 p. m.	16, 12 noon.	.975	139
16, 12 noon	19, 3 p. m.	.773	248
19, 3 p. m.	23, 3 p. m.	.805	201
23, 3 p. m.	30, 2 p. m.	1.073	154
30, 2 p. m.	Apr. 10, 1 p. m.	2.272	207
Apr. 10, 1 p. m.	14, 1 p. m.	.765	191
14, 1 p. m.	17, 2 p. m.	.765	252
17, 2 p. m.	23, 3 p. m.	1.002	166
23, 3 p. m.	May 4, 3 p. m.	2.025	175
May 4, 3 p. m.	7, 2 p. m.	.595	201
7, 2 p. m.	14, 2 p. m.	1.090	155
14	21	.997	142
21	Oct. 16	15.553	105

No. 2 was suspended in a closed room in the laboratory. The weighings showed the losses given in table 25; original weight was 175.357 grams. The total loss in 77 days was 17.294 grams, or a little less than a tenth of its entire weight.

Nos. 3 and 4 were left in the open air, but were soon injured, so that the results were vitiated. The weighings made showed the following:

No. 3: Original weight 173.655 grams. Loss from March 8 to March 16, 6.74 grams, or 1.833 grams per day.

No. 4: Original weight, 151.479 grams. Loss from April 10 to April 14, 6.107 grams, or 1.529 grams per day.

Nos. 5 and 6 were exposed in the open air, and while the period of weighing was shorter than that of No. 2, they afford a fair comparison,

except that the time was a month later than that when the weighings of No. 2 were made, so that the temperature was higher and the air probably drier. Table 26 gives the rates of transpiration of the two.

TABLE 26.

From—	To—	Loss per day.	
		No. 5.*	No. 6.†
		mg.	mg.
Apr. 14	Apr. 17	310	615
Apr. 17	Apr. 23	662	677
Apr. 23	May 4	446	549
May 4	May 7	298	577
May 7	May 14	394	584
May 14	May 21	459	497
May 21	Oct. 16	202	331

*Original weight of No. 5, 140.385 gms.

†Original weight of No. 6, 206.970 gms.

In the 37 days during which the weighings were being made, No. 5 lost one-ninth and No. 6 one-tenth of its entire weight, while it required No. 2, which was left indoors, 77 days to lose one-tenth of its weight.

MICRAMPELIS FABACEA.

On November 10, 1908, a large tuber of *Micrampelis fabacea* which had been taken from the ground at Carmel, California, packed in straw, and shipped to Tucson, was weighed after lying in a shaded room for a month, and found to give 28.834 kg., and with a suspension harness 28.950 kg. This was now placed in a room with a sahuaro and several echinocacti, being subjected to the same conditions.

On December 8, 1908, the weight was found to be 26.208 kg., showing a loss of 2.742 kg., at a rate of 94 grams daily.

On May 15, 1909, the weight was only 18.570 kg., indicative of a loss of 7.630 kg., at a rate of 48 grams daily. Although the tuber had lost 35 per cent of its weight, or nearly 45 per cent of its total water-balance, its tissues were still moist, cool to the touch, and alive. The growing-points were capable of sending up vines. This plant would, however, rarely be subjected to the temperatures and evaporating action of the Arizona desert in its native habitat. When exposed to conditions of this character the rate of water-loss was such that its desiccation would have ensued much more quickly than in the cacti on which the observations were made.

On October 19, 1909, the tuber having been allowed to dry out during the summer, it became very hard and showed huge cracks. The weight was now found to be 7.625 kg., showing a loss in weight of about 73.4 per cent, which would probably be increased to 75 per cent by the ordinary methods of analysis in the laboratory.

IBERVILLEA SONORÆ.

One of the authors has already published a note upon the great value of the balance of water and food-material accumulated in the tubers of *Ibervillea sonora*. These tubers are enlargements of the basal part of the stem, and a system of thin roots springs from the tubers and penetrates the soil during the brief midsummer rainy season of Sonora. The long, thin, tendril-climbing stems are sent up during the same period, but the amount of material used by them is evidently much less than that taken up by the roots, for each season results in an accretion to the size and weight of the tuber, although some of this is lost by decay and abscission in an irregular manner. Only a few of these plants have been brought under observation, but the observations upon one of them have given such remarkable results that they are worth recording here, although published previously in part. (Carnegie Institution of Washington Publication No. 99, page 20, 1908.)

A tuber weighing not more than 7 or 8 kg. was taken from the sandy soil near Torres, Sonora, in February, 1902, and shipped to New York, where it was soon afterwards placed on a wooden shelf of a closed museum-case, exposed to diffuse light and temperatures above freezing-point in winter and to 80° or 90° F. in midsummer at extreme ranges of the thermometer. The case was quite tight, and hence the plant was not subjected to the evaporating action of air-currents.

The accumulated balance of food-material and water was sufficient to allow the formation of short green stems every year in summer, for eight successive years, from 1902 to 1909, inclusive, and the tuber weighed 4.205 kg. on January 14, 1910, and 3.551 kg. on July 21, 1910. The tuber now appeared distinctly wrinkled and shrunken, but was still alive. About half of its original weight had been lost in 8 years, indicating that the rate of loss from *Ibervillea* must be very low, and a test was made with a small specimen which had been established in a terrace near the Desert Laboratory for three years. The tuber was taken up, the vine cut off above, and the sparse roots taken cleanly away from the lower surface. The surface was cleaned with a stiff brush and the wounds sealed with grafting-wax, so that any decrease in weight might be fairly attributed to transpiration. Immediately after this preparation, on October 22, 1909, the weight was found to be 530 grams, which was confirmed on a precision-balance to within a small fraction of a gram. The tuber was now placed on a wire stand, allowing free circulation of air, but in a closed and shaded room.

Table 27 gives the records for various intervals between November 6, 1909, and May 12, 1910. The rate of transpiration in March was nearly double that of February, an increase fairly parallel to that of the echinocacti, although much less in absolute quantity.

TABLE 27.

Date.	Weight.	Loss.	Time elapsed.
1909.	gms.	gms.	days.
Nov. 6	524	6	15
Nov. 18	522	2	12
1910.			
Jan. 8	518	4	51
Jan. 29	518	1—	19
Feb. 25	516	2	27
Mar. 22	512	4	25
Apr. 21	510	2	30
May 13	506	4	22

A number of other tubers were brought in and set up in the laboratory during April, 1910, for the continuation of the endurance tests, and the results of the observations justify the assumption that the record of the plant given above represents the average behavior of the species. A comparison with *Echinocactus* shows that a small plant of the latter reduced to a weight of 530 grams by desiccation for 26 months lost 6 grams of water during the 30 days ending April 21, while an *Ibervillea* weighing 510 grams freshly taken from the soil was depleted of only 2 grams in this period. The *Echinocactus* lost 14 grams during the next 22 days, while the *Ibervillea* decreased but 4 grams.

This comparison illustrates the obvious conclusion that indurated tubers and woody stems are much more efficient as storage organs than the green, soft bodies of the cacti and other succulents.

GENERAL CONCLUSIONS.

The results of observations upon the general climatic conditions prevalent in the Tucson region and the facts brought to light by an inspection of the data obtained by weighing and measurement of native succulents present some features of unusual interest. These are briefly set forth in the following paragraphs.

The annual cycle includes two seasons in which the soil-moisture content is high and the relative humidity is at its maximum. During the summer rainy season the temperature may reach 115° F., while in the winter wet season the temperatures are low, but rarely remain below the freezing-point for more than a few hours. Alternating with these seasons in which moisture is more abundant is the dry foresummer of April, May, and June and the arid aftersummer of August, September, and October, in which the temperatures are high and the relative humidity very low, sometimes falling to 8 and 10 per cent in June.

The rate of the transpiration is largely determined by the evaporating capacity of the air and operates to make a notable depletion of the water-balance in the plants under natural conditions during the dry foresummer and aftersummer. The influence of other conditions and of separate agencies may be detected, however. First is to be noted the individuality of the reactions found in the alternations in form and volume, which is well illustrated by a comparison of the loss of weight shown by echinocacti Nos. 7 and 8. The former, weighing 36 kg., lost weight at a rate of 10 to 14 grams daily in the month preceding January 9, 1909, while No. 8, under the same conditions of illumination, temperature, relative humidity, and wind action, showed a rate of 5 to 27 grams daily, although its weight was but 29 kg.

Both plants were in an inclosed room. Nos. 9 and 10 (echinocacti) were exposed to open-air conditions and the first weighing, 17 kg., showed a rate of loss of 36 grams daily for the month ending December 8, 1908, and No. 10, weighing 15 kg., showed a rate of 61 grams during the same period; No. 9 lost at the rate of 38 grams daily during the six months ending May 12, 1909, and No. 10 at the rate of 30 grams in the same period. The conditions were more favorable for rapid transpiration in this plant than in No. 9. The disparity would doubtless have been even greater under equivalent conditions.

Of the pair in the inclosed room, the larger lost most water during December, but the smaller showed a rate, low at first, but which increased until it was nearly double that of the plant which had a total weight one-fourth greater. The pair of plants in the open displayed a reverse rela-

tion. The smaller plant at first lost weight at the rate of 61 grams, while the larger gave but 36 grams. Later the larger plant gave off more water than the smaller. Numerous other comparisons might be formulated by reference to the results of weighings, and similar individuality of behavior was found by the long-extended series of measurements. It is evident, therefore, that no equation expressive of relation of volume, water-balance, and loss in weight may be formulated for the massive cacti described in the present paper.

The depletion of the water-balance is of course less rapid during the second and succeeding years of exposure of detached plants than during the first year. The data obtained from observations on echinocacti Nos. 1, 3, 6, and 7 serve as an example of this fact. The rate during the second year under equivalent conditions in corresponding seasons is not more than 66 or even 55 per cent of that of the first year. In the absence of any information as to structural changes which might serve as a regulatory factor, the decrease of the rate may well be attributed primarily to the increased concentration of the sap and its consequent greater osmotic activity. Thus in *Carnegiea* the proportion of mineral salts in the sap was seen to increase from 1 to 3 per cent, while in *Echinocactus* an increase from less than 0.8 to 3 per cent of dissolved salts ensued.

The rate of loss of plants exposed in the open may be as much as 4 to 8 times that of plants in inclosed but well-ventilated rooms, in which the direct action of the wind and sun are eliminated. This is apparent even when the plants tested in the shade were much larger than those in the open.

Observations on a number of specimens show that some gain in weight may be expected in small specimens of *Echinocactus* detached and kept in well-ventilated rooms during January and December. This gain may be attributed to hygroscopic absorption. A small plant which had been desiccated for two years, when put in a dark-room with equable temperature at about 60° F., with the relative humidity 80 to 90 per cent during February and March, 1910, was found to gain 2 grams in six days.

Carnegiea was seen to lose 63 per cent of its maximum water-balance without disorganization. *Echinocactus* showed a loss, calculated at about 69 per cent of the total balance, without losing the power of growth and repletion of its water-supply.

An inspection of the proportions of organic material and ash shows no relative variation in the sap of plants in which the supply of water had been partially depleted by desiccation. The total solids in the juice of a turgid *Echinocactus* amount to 2.692 grams per 100 c.c., of which the organic matter is 1.320 and the ash 0.772. The total solids in a desiccated specimen amounted to 7.060 grams, of which 4.060 was organic and 3 ash. The general concentration had been increased in the ratio of 2 to 7, the concentration of organic matter from 1.3 to 4, and the concentration of

the ash as 1 to 3. The total solids dissolved in the sap of a turgid *Carnegiea* amounts to 3.4 parts in 100, of which 2.4 is organic material and 1 ash. In the desiccated plant the dissolved solids amount to 9.6 parts in 100, of which 6.8 are organic and 2.8 ash. The general concentration was as 3.4 to 9.6, the concentration of organic material as 2.4 to 6.8, and of the ash as 1 to 2.8.

The extremely great individual variability with regard to the rate of loss of water makes it impossible to institute any comparison between the two massive cacti employed, except to say that the water-balance was depleted in very much the same general way in both forms. It is to be readily seen, however, that the rate of loss is very much greater in these green plants with their chlorophyllose stems than in the indurated tubers of *Ibervillea*, which is in effect in a resting condition except during the brief periods during which the thin vines are being developed.

The depletion of the water-balance in the cacti is accompanied by reversible changes in form and size, which may change the volume and appearance of the trunks or stems very markedly. The repletion of the water-balance necessitates reversible changes in form and volume, which may or may not be accompanied by irreversible additions, due to growth or morphogenetic changes. Some measurements of the bodies of massive cacti are seen to be influenced by insolation and by temperature.

Practically all of the species examined would be capable of endurance for an entire year in the open, although the water-supply were cut off. Not all of the individuals might survive, but some would. Slight growth of the trunk was seen in desiccated individuals of the bisnaga, but none in the sahuaro. Many individuals may be encountered in the open which show no indications of growth during the previous year, suggesting a lack of moisture. It is notable that even very much desiccated cacti which do not display growth of the succulent stems by reason of the depleted water-supply may still send out roots. The capacity of root-formation seems to be retained so long as the plant lives. During the second year of deprivation of water the rate of loss is very much lessened, and if a large number of individuals of *Echinocactus* and *Carnegiea* under the diversified conditions offered by their habitats be taken into account it would seem justifiable to assume that a second season of desiccation in the open might be endured by these plants. Individuals in shaded rooms were in good condition at the close of three seasons' deprivation of water. These limits apply especially to the green bodies, or stems, of succulents, the superficial layers of which are chlorophyll-bearing, and in which the major part of the photosynthetic work is carried out.

The short tuberous stems of *Ibervillea* upon which the observations were made sustain an entirely different morphological and physiological relation to the life of the plant. These bodies represent the bases of stems the apical portion of which is ephemeral. While the upper portions of the

tubers have a green layer, it is covered by a heavy corky layer, and but little photosynthesis may result from the action of its chlorophyll. The sap of these tubers carries a large proportion of dissolved material. The concentration of the sap and the induration of the surface prevent anything except a very low rate of depletion, a rate which is only a fraction of that of the green stems of *Echinocactus* of similar mass. Detached plants of *Ibervillea* may make a growth of stems year after year, and carry a water-balance that might suffice for such diminished activity for a quarter of a century. One specimen has been kept under observation for eight years, lost half of its water-balance during that time, and still displays seasonal activity.

It has been amply demonstrated that the shoots and seedlings of plants grown in darkness do not accumulate a water-balance beyond that carried by ordinary herbaceous plants. Etiolated stems contain a larger proportion of water than others of the same species normally formed in light, but the total bulk of such stems is very small.

The floras of arid regions are so rich in specialized forms that the conclusions seem justifiable that these types bear some sort of adaptation or fitness by which they have survived under the conditions presented. They may be readily grouped into (1) the spinose trees, shrubs, and herbs; (2) the succulents. The spinose forms are those in which the shoot shows the effects of an inherited atrophy of its members and a reduction of its surfaces. The result of such reduction shows narrow leaves, short, pointed branches, and short axes, these changes also being accompanied by an induration of the epidermal surfaces. Many of these changes are of the same character as those produced when a plant from a moist region is grown under arid conditions, and the inference that these plants have come about by such an inherited variation is generally allowed to pass in botanical writings. The fact that many of the features of desert plants could not be brought about by such direct causal action, however, suggests caution in the matter, and that the origination of these forms is not capable of any simple explanation or interpretation, the chief difficulty being experienced in the explanation of the fact that a high evaporating action of the air of a habitat acts directly upon organs and also upon the organisms as a whole in a manner which may be directly antagonistic as far as morphogenic action is concerned.

The reduction of the members of the shoot and the induration of the surfaces may be regarded as the more primitive or initial modification in connection with desert conditions, and the enlargement or increase of tissues accommodating a large water-balance as a secondary or consequent change of a more highly specialized character. Morphological alterations of the first-named kind are discernible in plants inhabiting not only arid regions, but all localities in which the evaporating action of the air over-balances the available absorptive capacity of the vegetation.

The habit of accumulation of a large water-balance affects some forms in which the reduction of the shoot has been carried to its greatest extent, and the forms displaying both modifications, such as the massive euphorbias and cacti, constitute the most pronounced types of desert vegetation. It is to be seen, however, that succulency is manifested by many plants, in which the primitive xerophytic modifications have not been extensive, and a water-balance is carried in roots, stems, leaves, and special organs. The inference seems a fair one, therefore, that succulency is not the result of the simple causes leading to xerophytism.

A review of the conditions connected with the existence and distribution of succulents shows that they are abundant in northern and southern Africa, certain deserts in South America, and especially numerous in the arid regions of western and southern North America, reaching a maximum development as to size and number of species in the elevated basins and bolsons of southern Mexico, where several species of great tree-cacti are prominent in the landscape. The regions characterized by succulents have a soil often rich in lime, in which the precipitation is received in regularly recurring seasons. Cactaceæ and Crassulaceæ may thus be found down to the limit of the spring tides in the North Temperate Zone, while a few of these and other succulents occur far north in rain-forests and very cold regions. An analysis of the conditions mentioned is not to be allowed to account for succulency, however, since one group of plants showing the capacity for accumulation of water, the halophytes, inhabit saline shores and soils around the world and through a wide range of latitude. The only invariable conditions attendant upon the development of succulents seem to be the existence of an abundant supply of moisture in the soil or substratum during certain seasons and the presence of solutions of high osmotic activity in contact with the absorbent organs. Some halophytes occur in localities in which the soil-solutions are continuously of high concentration, while in other cases they may be subject to a wide range of variation by floods and tides.

An examination of the chemistry of these forms might probably lead to results of value in the interpretation of their development. The cacti of the Tucson region, and probably all of these forms, are rich in calcium carried in solution in the sap as an accident of its occurrence in abundance in the soil. The sap shows a high degree of osmotic activity, ranging from 5 to 12 atmospheres in various species in a state of maximum turgidity, to perhaps twice this pressure when the water-balance is depleted. Furthermore, these plants, especially the halophytes, are known to be capable of an accommodative reaction by which the osmotic pressure may be automatically increased in response to the increased concentration of the soil-solutions.

The sap of succulents is characterized by a high degree of acidity, which seems to be least in *Echinocactus* and greatest in *Opuntia versicolor*

in the forms examined. This acidity results from a modification of the photosynthetic processes and hence is not directly connected with the state of the water-balance, although it is probable that some slight concentration or heightening of the acidity might ensue with desiccation. Thus an *Echinocactus* after the summer rains showed an acidity equivalent to 0.090 grams H_2SO_4 per 100 c.c., while another that had lost nearly seven-tenths of its water showed 0.106 gram. A *Carnegiea* in a condition of maximum turgidity showed an acidity equivalent to 0.161 gram H_2SO_4 , and one in a state of nearly maximum desiccation near the close of the arid foresummer gave 0.187 gram, but a specimen desiccated for six months in the open and then a similar period in a shaded room yielded but 0.161 gram. Two plants growing within a few meters of each other taken two days after the beginning of the summer rains gave 0.150 gram and 0.181 gram, respectively.

A careful control of the water-supply and the illumination might reveal some heightening of the acidity with the depletion of the water-balance, although the data given above do not demonstrate such a relation. The two recognized characteristics of succulents—the high osmotic activity and the modified photosynthesis resulting in great acidity—are not sufficient to explain their occurrence and development in deserts and saline situations, and it is evident that a more extensive investigation of their chemistry must be made before an adequate interpretation can be offered for the origination of the capacity for accumulation and retention of great water-balances such as are carried by the succulents of the desert and the seashore.